DIPTEROCARPACEAE:

TREE-MYCORRHIZAE-SEEDLING CONNECTIONS

Irsyal Yasman

Promotoren	:	Dr.Ir. R.A.A. Oldeman, professor of Silviculture and Forest Ecology, Landbouwuniversitet Wageningen. Dr.Ir. Ishemat Soerianegara, professor of Silviculture and Tropical Forest Management, IPB Bogor.

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Abstract

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Research on natural regeneration of Dipterocarpaceae is described. Work in greenhouse experiments, in planting experiments in natural forests and from monitoring of natural regeneration in undisturbed natural forest are discussed. In addition work on photosynthesis measurements is discussed. The findings show that survival of dipterocarp seedlings under closed forest canopies is not related to any chemical soil properties or to light intensities. Best growth takes place nearest to the fine roots of the mother tree. The photosynthesis measurements show that 89% of the time light intensity is not high enough for photosynthesis in the dipterocarp seedlings and that these seedlings survive despite a negative carbon balance from photosynthesis. Sugar analyses of roots and stems show that available carbohydrate is relatively higher in the roots and also higher during the night time than in daytime, while also being higher closest to the roots of the mother tree, indicating a transport of sugars from the mother tree to the seedlings through the ectomycorrhizal connections. It is concluded that in practical forest management this nursing role should be taken in consideration when formulating silvicultural management options, particularly in forest regeneration.

CIP-DATA KONINKLIJKE BIBLIOTHEEK, DEN HAAG.

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PROPOSITIONS

1. Light is one of the most important factors in the formation of ectomycorrhizae on dipterocarp seedlings, either very low or, although indirectly, very high light intensities hampering ectomycorrhizal formation. (this thesis).

2. Co-selection of fungi and dipterocarps in natural forest results in a limited number of plant-fungus associations in Dipterocarpoidea.

3. The appearance of sporocarps in natural forest shows masting season alternating with period of reduced sporocarp numbers. (this thesis).

4. The availability of mycorrhizal propagules is an important factor for seedling survival, facilitating beneficial mycorrhizal interconnections between mother tree and seedlings. (this thesis).

5. Crooked trees also nurse seedlings via mycorrhizal interconnections, as well as straight trees do.

6. The tropical rain forests still exist because of their high economical value.

7. Deforestation is no synonym of logging.

8. There is no single indigenous human group which has a monopoly as native Indonesian and the more than two hundred known tribes have the same right to live, to proper education and prosperity in Indonesia.

9. Most statesmen consider the feasible thing to do, idealists regard what they feel is the good thing to do, whereas government people will preferably execute the safe thing to do.

10. God would not make something without meaning.

11. Religion starts by believing, science starts by hypothesizing

Dipterocarpaceae: Tree-Mycorrhizae-Seedling Connections.
June 13, 1995 Wageningen, The Netherlands.

Irsyal Yasman
The International MOF-Tropenbos Kalimantan Project
c/o PT. INHUTANI I Unit Balikpapan
Jalan Jend. Soedirman 30
Balikpapan 76103 - INDONESIA

TABLE OF CONTENTS

LIST OF APPENDICES

LIST OF BOXES

LIST OF FIGURES

LIST OF TABLES

FOREWORD

The research presented in this book was initiated with my first involvement at the Wanariset forestry research station in Samboja, East-Kalimantan, Indonesia, where I was appointed as a counterpart of the cooperative project between the Agricultural University Wageningen and the Indonesian Ministry of Forestry, representing the state forestry enterprise PT. INHUTANI I in this project. In the first weeks at this project I was asked to do an inoculation experiment in which to compare the effect of fertilization to the effects of ectomycorrhizal inoculation upon the growth of some stunted dipterocarp seedlings in the greenhouse. Yielding the opposite effect of what I expected, that the plants receiving fertilization were not reacting while those given a single centimetre of ectomycorrhizal root started vigorous growth, I was convinced of the importance of ectomycorrhizae for Dipterocarpaceae. Since this memorable moment in early 1986 I have devoted my time to the study of Dipterocarpaceae with the main focus on regeneration aspects and mycorrhizae.

It was most fortunate that through my position with PT. INHUTANI I many of the research results could be tested at a large scale immediately. This large scale testing of research results has undoubtedly assisted in distributing the research results to most of the Indonesian forestry practice.

The research result of which are presented in this book are based upon data collection which was started in 1988. During that year I was given the opportunity to visit The Netherlands for a training course on plant physiology. During this visit I contacted Prof.Dr.Ir. R.A.A. Oldeman to discuss some aspects of dipterocarp mycorrhizae. He was very supportive and stimulated me to write a proposal for my doctorate research and to start preparations for a qualifying examination, and find an Indonesian professor to act as another promotor namely Prof.Dr.Ir. Ishemat Soerianegara from the Bogor Agricultural University (IPB Bogor). I am very happy that I was able to follow up his recommendations and pursue my research resulting in the present publication.

During my research the type of work necessitated the acquisition of very expensive equipment especially for photosynthesis measurement, which cost more than the total budget needed to let our team, of at that time 25 people, work in Indonesia. I am very grateful for the enormous effort by the Tropenbos Foundation and the Institute for Forestry and Nature Conservation (IBN) from Wageningen, The Netherlands, in acquiring this equipment under harsh financial conditions.

My years at the Wanariset station with many foreign and national scientists have been decisive for the direction of my career. I hope that also in the future I will be able to continue to work in such stimulating teams and working environment, and to contribute to sustaiable natural forest management in in Indonesia.

Balikpapan, February 1995

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I gratefully thank the people of IBN-DLO Wageningen for their hospitality during my stay in the Netherlands, especially to Henk Lijftogt, Ans Lijftogt, Ella Vermeer, Nathalie Tahapary, Joke Mahulete, Junus Tahitu, Arie Stolk, Jan van de Scheur, Sjoerd van Eeden, Marjolijn Bolderman and Dorien

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction

The Tropical Rain Forests in South East Asia covers an extensive area from Burma (Myanmar), peninsular Thailand, passing through peninsular Malaysia to the Indonesian archipelago and Papua New Guinea. Members of the family of Dipterocarpaceae represent the predominant tree species in this type of forest. The family consists of about 500 species, 267 of which are found on the island of Borneo and among these 155 are endemic (Ashton, 1982; Figure 1). Dipterocarpaceae also occurs in India and Sri Lanka, while the subfamily Monotoidea occurs in Africa and South America. The family may make up about 80% of the forest canopy in South-East Asian rain forests, which is why this type of forest is often called dipterocarp rain forest or mixed dipterocarp forest.

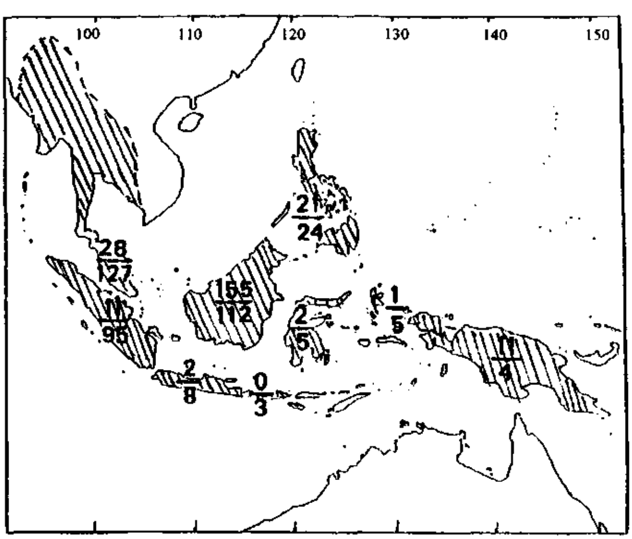


Figure 1. Distribution of the family Dipterocarpaceae in South-East Asia.

The dipterocarp lowland forests of Indonesia (especially those in Sumatra and Kalimantan), have been exploited for timber production since the early nineteenth century, though it was initially limited to only the most commercial species from the families of *Dipterocarpaceae* and *Sapotaceae* (Van de Koppel, 1945). The first trial of mechanized logging was undertaken in 1957 in the Mentawir area, East Kalimantan (Soepono and Ardiwinata, 1957). Since then conventional logging by the "panglong" or "banjir kap" system has been gradually replaced by mechanical logging using heavy machinery. The extraction of timber was limited to a small number of species until the 1960s when the introduction of mechanized logging coincided with a marked worldwide increase in wood demand, particularly in processed wood products, which resulted in the use of more species. Consequently, the dipterocarp forest rapidly became more intensively utilized. In Indonesia this was accelerated by the enactment of the foreign investment law in 1967 and the domestic investment law in 1968, which opened up the possibility for much investment in the forestry sector that led to a large scale exploitation of the natural forest (Armitage and Kuswanda, 1989). World-wide concern is now focused on the exploitation of rainforests, and sustainable forest management has become an issue of great importance.

Regeneration of mixed dipterocarp forest after logging is still problematic. Plantation trials of many dipterocarp species have been reported with greatly differing success rates. This is one reason why many exotic species like pines were introduced all over Indonesia in reforestation efforts in the early 1970's. These attempts, however, are generally considered to have failed and only very few plantations are reported as being successful. In the early 1980's and within the framework of Indonesian forestry programs industrial plantation of mostly exotic species were established on the unproductive forest lands. Many locally exotic species such as *Acacia mangium*, *Eucalyptus* spp. and other fast growing species were introduced, while a few indigenous dipterocarp species represented only a small proportion of the total program.

In the past some of the problems with establishing plantations of dipterocarp species on a large scale were related to the poor and uncertain supply of planting stock of Dipterocarpaceae because of the irregular flowering behaviour of many members of this family in the non-seasonal zone (Yasman and Smits, 1987), and because the seeds of this family cannot be stored longer than a few weeks (Tamari, 1976), except for some species growing in deciduous forest and possessing special seed characteristics such as the occurrance of ridges (Tompsett, 1987). Nowadays these problems have been solved by producing dipterocarp planting stock through vegetative propagation which is applied in large-scale nurseries. Another problem faced in the past was the frequent failure of seedlings to establish in the field, notably in open areas, such as former skid roads. It was only realized recently that dipterocarp species need an ectomycorrhizal symbiont which is mostly absent in these places (Smits, 1983). Some studies showed that this seedling failure was due to poor development of the ectomycorrhizae of the seedlings growing in open areas due to high soil temperature (Smits *et al.*, 1987; Noor and Smits, 1988). Development of mycorrhizae in the soil may also be hampered by soil compaction (Bowen, 1980) as often occurs on former skid roads after logging with heavy machinery

Research activities involving dipterocarp mycorrhizae are still very scattered and scarce. The dayak people in West Kalimantan have practiced a correct method of planting dipterocarp trees using mycorrhizae, along time before mycorrhizae on roots of Dipterocarps were first described by Van Roosendael and

Thorenaar (1924, p. 507). They observed mycorrhizae associated with the roots of *Hopea mengarawan* Miq. growing in South Sumatra. This was about 39 years after Frank (1885) coined the term 'mycorrhiza' for his description of fungal-root associations in plants, which he believed correctly to be beneficial for nutrient provision. Fruiting bodies of mycorrhizal fungi in dipterocarp forest, however, were observed by Beccari (1904) in a Sabah forest before Van Roosendael and Thorenaar's observation, though he did not mention clearly that the mushrooms were in some way connected with dipterocarp trees. After these first observations, no results were reported concerning dipterocarp mycorrhizae until Singh (1966) noted ectomycorrhizae on some dipterocarp seedlings. Singh's report is considered to be an important step in initiating more recent mycorrhizal research on Dipterocarpaceae.

The importance of mycorrhizae for the dipterocarp forest ecosystem and its management has only recently been realized. After Smits (1983) suggested that ectomycorrhizae might play an important role for successful regeneration after logging in lowland dipterocarp forests, much more attention was paid to the ecological aspects of dipterocarp ectomycorrhizae. Only a few studies concerning ecological aspects of mycorrhizae in dipterocarp forest ecosystems have been undertaken so far (Becker, 1983; Smits, 1983; 1994; Yasman, 1993).

Dipterocarps are among the few species in tropical forests of which the seedlings can survive and grow under very low light intensities on the forest floor. Several possible factors that have been mentioned in the literature to explain this phenomenon. Photosynthesis in dipterocarps seedlings may be highly efficient like many better known understorey species and they may have a very low compensation point. This allows them to use the very low intensity of light which penetrates through the canopy gaps. Another possibility is that they may make a better use of short burst of sunflecks that have been thought to be of importance for carbon gain of understorey plants (Chazdon and Pearcy, 1986; Pearcy, 1988; 1989). Another possibility is that dipterocarp seedlings growing on the forest floor may benefit from interconnection of their root system with a mature tree through ectomycorrhizal connections as described for other plants by Read (1994). Light is the most important environmental factor involved in the production of carbohydrates required by ectomycorrhizal fungi through photosynthesis either from adult trees which are fully illuminated or from seedlings growing in the shade. Therefore light and ectomycorrhizae are the two main factors examined in the present study, while other factors that may influence these two factors are also examined such as soil temperature and soil fertility.

1.2 The significance of this study

Since mycorrhizae are important in the complex ecosystem of a dipterocarp forest (Smits, 1994), their role in forest regeneration may be much more important than was previously realized. Only a few studies have reported on the role and function of ectomycorrhizae in a dipterocarp forest (Smits, 1983; Lee, 1988; Omon 1994). The present study therefore has the following aims:

1. To examine dipterocarp ectomycorrhizal functions and to reconnoitre their role in the energy flow of a dipterocarp forest ecosystem especially the relation between regeneration, light and ectomycorrhizae.

2. To contribute to a better understanding of complex dipterocarp forest ecosystems that will in turn lead to recommendation for better management of these forests through the application of correct silvicultural measures in the future.

1.3 Dipterocarpaceae and Mycorrhizae

The term mycorrhiza was originally spelled as "mycorhiza". The spelling accepted in the present publication (see Smits, 1994) was first applied by Frank (1885) and is derived from Greek, literally meaning 'fungus root'. It is used to indicate a mutualistic symbiosis between a plant root and a fungus. The early classification of mycorrhizae distinguished two main types of mycorrhizae based upon the structure of the root-fungus association namely *endomycorrhizae* and *ectomycorrhizae*. These terms were proposed by Peyronel *et al*. (1969), but later on other terms were used namely *endotrophic* for endomycorrhizae and *ectotrophic* for ectomycorrhizae (Harley, 1971). The latest classification of mycorrhizae as proposed by Harley and Smith (1983) devides them into seven group namely *Vesicular-arbuscular Mycorrhizae (VAM), Ectomycorrhizae, Ectendomycorrhizae, Arbutoid mycorrhizae, Monotropoid mycorrhizae, Ericoid mycorrhizae* and *Orchid mycorrhizae*. Nearly the same classification was proposed by Moser and Haselwandter (1983). In the first group (VAM) the endophyte is a fungus with aseptate hyphae belonging to the order Endogonales of the Zygomycetes, in the other six groups the endophytes are fungi with septate hyphae belonging the Ascomycetes or Basidiomycetes. The first two groups of the latest classification will be often referred to in this thesis namely Vesicular Arbuscular Mycorrhizae (abbreviated as VA-mycorrhizae or VAM) and Ectomycorrhizae (abbreviated as ECM)

VA-mycorrhizae are mycorrhizae characterized by the formation of vesicles and arbuscules in the root cortex which also contains inter- and intracellular aseptate hyphae connected with an external mycelium (Moser and Haselwandter, 1983). Ectomycorrhizae are mycorrhizae characterized by the possession of an external fungal sheath or mantle around the plant root, where the hyphal growth between the epidermal and often the cortical cells forms the so called Hartig net. The mycorrhizae that possess both characteristics of both VA- and ectomycorrhizae are called *ectendomycorrhizae*.

Worldwide, most plant families can form VA-mycorrhizae with only about 70 to 80 species of fungi (Jülich, 1989), while more than 1000 fungi can form ectomycorrhizal associations with a small number of plant families such as Betulaceae, Fagaceae, Pinaceae, Myrtaceae, Leguminosae and Dipterocarpaceae.

Based on the degree of dependency of plant species on mycorrhizae, plants can be grouped into three categories namely non-mycorrhizal, facultatively mycorrhizal and obligatory mycorrhizal (Bagyaraj, 1989). Non-mycorrhizal plants are those which grow normally without forming mycorrhizae. Facultative mycorrhizal plant are those which are able to grow with or without mycorrhizae. Obligate mycorrhizal plants are those plants which under natural conditions can neither grow nor survive without mycorrhizae.

A number of studies confirm that dipterocarp species are obligatory ectomycorrhizal (Noor and Smits, 1988; Omon, 1994; Smits, 1994). Endomycorrhizae so far were noticed by Shamsuddin (1979) on *Hopea odorata* Roxb. and by Chalermpongse (1987) on *Dipterocarpus macrocarpus*. Ectendomycorrhizae were noticed by Chalermpongse (1987) on *Anisoptera costata* Korth. in Thailand, and in vitro by Louis and Scott (1987) on *Shorea roxburghii*. Smits (1994) has also observed a new type of dipterocarp root-fungus association which differs from the known types of symbiosis, for which he has coined the name *amphimycorrhizae* (see Glossary).

Most reports on dipterocarp mycorrhizae deal with the symbiosis rather than the function of mycorrhizae in the forest ecosystem. After Singh (1966) reported ectomycorrhizae on some dipterocarp seedlings, Hong (1979) and Shamshuddin (1979) also reported the observation of ectomycorrhizae on dipterocarp seedlings. Becker (1983) was the first to try to determine environmental requirements for ectomycorrhizae. He found that seedlings growing under different light conditions showed different degrees of ectomycorrhizal colonization. He also distinguished some types of ectomycorrhizae associated with seedlings growing in natural forests in Malaysia. Other researchers investigating this subject are Smits (1983), Hadi (1987), Noor and Smits (1987), Lee (1988) and others.

The poor development of ectomycorrhizae on roots of dipterocarps explains the poor regeneration of dipterocarp trees on former skid roads and open areas (Smits 1983; cf. Jülich 1989; Smits, 1994). Research on the influence of environmental factors on the physiological responses of mycorrhizae made the role and function of mycorrhizae in the forest ecosystem better understood. Janos (1985) for instance, suggested that low availability of phosphorus in the soil and lack of seasons in a tropical soil may cause tropical species to depend upon mycorrhizal activities for survival and growth. Furthermore, he also noted that the species composition of tropical forests may differ between sites due to the availability of propagules of (VA-) mycorrhizal fungi. The important role of ectomycorrhizae in survival and growth of trees in boreal and temperate forests is also well known (Amaranthus and Perry, 1987, 1989). The presence of ectomycorrhizae in Dipterocarpaceae may explain the predominance of dipterocarps in the tropical forests in South-east Asia (Smits, 1994).

The family Dipterocarpaceae in the mixed dipterocarp forest is characteristized by irregular flowering behaviour, having a mass flowering season once every four to five years (Burgess, 1972; Janzen, 1974; Ng, 1977). However, about ten percent of the trees in the lowland dipterocarp forests do not follow the mass flowering season and may flower in the intervening years (Smits, 1986). When mass flowering occurs, a very dense carpet of seedlings of many different species is established on the forest floor (Ashton, 1964). Although most dipterocarp species possess wings on their fruits, most of the fruits fall not far from their mother trees (Beccari, 1904; Burgess, 1972). This mechanism facilitates the integration of seedlings with the root system of their mother trees where they may become infected by hyphae from established mother tree mycorrhizal soon after germination.

Experiments under controlled conditions have shown that inter-plant transfer of nutrients may occur through the mycelia of ectomycorrhizae (Brownlee *et al*., 1983; Read and Francis, 1985; Read and Finlay, 1985). They found that interconnections provide channels through which carbon, phosphorus and water can be transferred between linked individual plants. Read and Francis (1985) showed that similar patterns of transfer of nutrients occur in both endomycorrhizal and ectomycorrhizal fungi. These experimental results suggest that the same processes might occur under natural conditions in temperate as well as in tropical forests. In natural forests this transfer may have ecological importance with respect to the regeneration of seedlings whereby seedlings may get nutrition from big trees (Harley and Smith, 1983).

Logging operations by mechanical systems using heavy machinery may cause ecological damage to forests through soil compaction of the skid roads. Alteration of the microclimate after the removal of the big trees may occur due to an increase in light intensity in the gaps (ter Steege, 1993). Increasing soil compaction from bulk density 1.2 to 1.6 g/cm^3, reduced mycelial growth by 90% which would be expected to reduce nutrient uptake by mycorrhizal roots (Bowen, 1980). Another aspect of the change in microclimate is that light penetrating throught the canopy and reaching the forest floor may increase the soil temperature up to 45°C which is extremely high for the development of dipterocarp ectomycorrhizae. High soil temperature reduces the number of mycorrhizal infections in dipterocarp seedlings (Noor and Smits, 1988). It was shown in greenhouse experiments that the critical soil temperature for ectomycorrhizal development is about 32°C (Smits *et al*., 1987). Another effect of the open areas created by removing big trees and by skid roads may be the dense growth of pioneer species which under tropical conditions will compete successfully with old growth species in open areas. This could create problems for the successful natural regeneration of dipterocarps after forest exploitation.

Natural regeneration always depends on the availability of seedlings in the forest. In Indonesia, the selective felling system regulations (known as Tebang Pilih dan Tanaman Indonesia or TPTI, formerly TPI) state that whenever natural regeneration is insufficient after logging, enrichment planting by means of line planting has to be done in order to obtain enough regeneration of the commercial species for the next rotation (Soerianegara, 1972). Experience shows that this line planting is not very successful due to the lack of maintenance after planting (personal observation; Oldeman 1990), especially giving more light to the seedlings after their root systems have been established, which has been proven to be a very important factor in seedling establishment in plantations (Lamprecht, 1989). It has also been suggested that unsuitable ectomycorrhizal species used for inoculation in the nursery may lead to the failure of dipterocarp seedlings to establish in the field (Smits, 1992). Of these environmental factors, light intensity is particularly important (Mori, 1980). It should be moderately available for dipterocarp species so that they can photosynthesize actively and facilitate the development of ectomycorrhizae underground by providing enough carbohydrates under conditions of good aeration and a favourable soil temperature.

Smits (1983) has come with a preliminary evidence that there is some degree of specificity of dipterocarp ectomycorrhizae. This was considered as a controversial idea by Alexander (1988) and Jülich (1988). Differences in the interpretation of the concept of mycorrhizal specificity (see Harley and Smith, 1983; Molina *et al.*, 1992) seem to be the cause of differences of opinion as to whether or not specificity of dipterocarp mycorrhizal fungi does occur. Therefore, Smits (1994) has now defined specificity in dipterocarp mycorrhizae in terms of ecological specificity to limit the concept to the degree of specificity found under a certain set of environmental conditions. Moreover, he limits it to the degree of interdependency in undisturbed primary mixed dipterocarp rain forest. In such a sense it seems that specificity of dipterocarp ectomycorrhizae might occur, although it needs to be confirmed further by more research. With regard to higher levels of specificity, there are now a few reports which seem to indicate that inoculation with certain fungi yield better growth of some dipterocarp tree species than inoculation with other fungi (e.g. Omon, 1994)

1.4 Light, Soil Temperature and Mycorrhizae

There are several environmental factors which may influence the development of mycorrhizal fungi, namely light intensity, soil temperature, soil fertility (such as the availability of nitrogen and phosphorus), soil moisture, aeration, soil pH etc. Considering the nature of ectomycorrhizae in dipterocarp forests, light seems to be the most important factor since carbohydrates which plants build up by photosynthetic processes, play a key role in the symbiosis. This is one of the reasons for investigating the relationship between mycorrhizae and light.

All energy in a tropical forest, in fact in any type of forest, originates from solar radiation through photosynthesis by green plants which can be converted into readily used compounds for others organisms below or above the ground. The solar radiation which is important for photosynthesis of green plants occurs especially in the region from 400 to 700 nm known as Photosynthetically Active Radiation (PAR). This fraction of radiation may contribute to about 50% of the total solar radiation received by the earth (Monteith, 1972).

Light is the main environmental factor to be considered in any type of forest research because it influences all aspects of the ecosystem. In forests which consist of many step and layers of canopy (Oldeman, 1990), the determination of the total amount of light reaching the forest floor becomes more complicated because light reaching the forest canopy will be partly reflected, transmitted or absorbed by irregularly distributed green plants. Due to this phenomenon much research concerning light in the forest is mainly on how to measure the light penetrating the canopy or gaps in the forest stand, in order to better understand its influence on ecological processes. Two techniques have been developed that involve computer simulation to estimate the amount of light reaching the forest floor. These are the SILVISTAR model, which has been developed for temperate forests (Koop, 1989), and the PPFDCALC model for tropical forests (ter Steege, 1992).

In general, light on the forest floor consists of diffuse light and sunflecks. The diffuse light is composed of light reflected by the leaves as well as light transmitted through leaves. Therefore, the diffuse light represents the light in the shade at low light intensity. On the other hand, sunflecks consist of short burst of direct sunlight penetrating canopy gaps. The total amount of light, either sunflecks or diffuse light, reaching the forest floor depends upon the canopy structure of the forest (Pearcy, 1983). The light quality of sunflecks is quite different from that of the diffuse light (Sasaki and Mori, 1981). The sunflecks contain much of the red light of the spectrum, but the spectral energy distribution is different from that of the global solar radiation. The most distinct difference between sunflecks and global solar radiation (sunlight radiating through a cloudless sky) relates to the spectral energy distribution of red light. The sun flecks are composed of uniform spectral energy between 400 and 800 nm, whereas the open sunlight has a peak at 450 nm with a gradual decline toward the red light spectral region. As the seedlings utilize the red light for photosynthesis more effectively than the blue light, the sun flecks may be the most effective light for seedling growth (Bazzaz, 1989). How much light from solar radiation can reach the forest floor after being filtered by the canopy layers in the forest, is also dependent on the development phases of the forest structure (see Oldeman, 1990). It has been reported that in the mature phase of natural forests the average amount of light reaching the forest floor varies from 0.5 to 15 percent (Richards, 1952; Sasaki and Mori, 1981). Daily illumination also varies as Richards (1952) observed that sunflecks are present only during a period of 4 or 5 hours in the middle of the day. In lowland dipterocarp forest only 2% of the incoming light reaches the forest floor under sunny conditions, while 50% of the total annual light received by understorey plants in that forest consists of sunflecks (Whitmore and Wong, 1959). Moving sunflecks evidently play an important ecological role, because more than forty percent (vs 50% estimated by Whitmore and Wong, 1959) of total light on the forest floor of the rain forest is due to sunflecks (Pearcy, 1983). These sunflecks bring almost full, unfiltered daylight into stand interiors, sometimes penetrating down to the forest floor through a gap.

In the forest only the highest canopy layers receive full light. The average light intensity gradually decreases to the lower part of the canopy and it falls down so swiftly that it can reach less than one percent near the ground. The differences in light intensities with different height in the forest may cause different reactions of the plant leaves. On the other hand, plants growing under these different light conditions will also adapt their physiological processes, for instance by reducing transpiration rates or increasing efficiency of photosynthetic processes under low light intensity (Fitter and Hay, 1981), or by having low light compensation points (Bazzaz, 1989).

The growth of the seedlings in the understorey is highly correlated with duration of sunflecks. Pearcy (1983) tried to measure the duration of sunflecks on the forest floor and found that about two third of the sunflecks last half a minute or less. Despite only short term local illumination, these sunflecks seem to provide an essential impulse, stimulating photosynthesis (Lamprecht, 1989). The annual total light for photosynthesis is derived half from sunflecks, 6% from canopy gaps and 44% is reflected from, or passes through leaves (Mabberley, 1992). These sunflecks, however, may contribute to about 60% of the daily carbon gain by understorey plants in tropical forests (Pearcy and Calkin, 1983).

Björkman and Ludlow (1972) (cited by Etherington, 1982) measured average irradiance on the forest floor of the rainforest and found it to be only 2.5% of that in the clear sky above the canopy, but the PAR quantum flux was only 0.41 %, thus indicating the large change of spectral quality which makes the understorey light photosynthetically less useful. On the forest floor, it has been suggested that the intensity of fluctuating sunflecks under the canopy affects the plants more favourably than the same intensity of light beneath a continuous opening (Watson, 1932).

Responses of seedlings to light can be very different between tree species. Different species may require different light conditions during establishment of seedlings in the forest. Dipterocarpaceae which are morphologically rather constant within species (Ashton, 1969), as well as being genetically uniform among genera (Somego, 1978), on the contrary still showed different light preferences for their optimal growth. The pioneer experiments by Voogd (1932) showed that too much light and too little light both are harmful for the growth of *Shorea platyclados* seedlings, so he suggested that a high and interrupted canopy without intermediate layers constitutes the best condition for growth of dipterocarp seedlings. Experiments by Tomboc and Basada (1978), however, showed that the growth of *Shorea contorta* is much faster in an open area than in a secondary forest. Seibert (1990) summarized some experiments on light requirements of seedlings of Dipterocarpaceae and reported great differences in the results for different species of seedlings in response to the light environment. Brown (1990) also found significant differences in growth in reaction to light by *Shorea macroptera* and *Dryobalanops lanceolata*. These examples demonstrate the differences between species of Dipterocarpaceae.

Considering the photosynthetic capacity of plants in the understorey, Fitter and Hay (1981) state that if a plant is shade-resistant and makes no attempt either to place its leaves in unshaded spots, or to restrict their activity to periods of high illumination, selection pressure will act rather on the photosynthetic process itself. The problem faced by understorey plants is how to maintain a positive carbon balance in such a low light intensity, that for most of them it lies below the compensation point. Otherwise, seedlings in the understorey remain stunted unless they gain carbon from the carbon pool in the rhizosphere. This latter mechanism, however, was not yet fully understood.

Under the stress of low light conditions, the plants have three possible options: 1) to reduce their respiratory rate, to lower the compensation point; or 2) to increase their leaf area relative to total plant biomass, to provide a greater surface for light absorption; or 3) to increase their photosynthetic rate per unit of light energy and unit of leaf area. The first possibility is more likely for the plants because the second and the third need extra energy from the plants under stress. Therefore it is very important to know the compensation point and dark respiration of plants growing in the understorey in order to calculate the carbon economy of the plants. Björkman (1968) found that shade leaves respired five times slower per unit area than sun leaves. The light compensation point of shade plants is consequently much lower than that of sun plants, as Boardman (1977) found in a rainforest, where understorey species in the forest have a compensation point of 50 times lower than that of full sunlight species.

In relation to mycorrhizae, there is little information available that proves a direct relationship between light intensity and mycorrhizae especially for tropical tree species. In the temperate region, mycorrhizae research by Björkman (1942) on *Pinus* and *Picea* has proven a positive relationship between mycorrhizal formation and light intensity. He found that the number of ectomycorrhizal formations increased with light intensity (Björkman, 1942). Hacskaylo, (1985) reported the result from several experiments on nutrition, light intensity, and photoperiod and their effect on ectomycorrhizal formation. He came to the conclusion that high levels of nitrogen and phosphorus as well as low light intensity accompanied by a short photoperiod, all tend to reduce photosynthesis and diminish ectomycorrhizal formation. Generally, trees growing under high light intensity have more abundant mycorrhizae than those growing in the shade. Observations in natural forests of the Wanariset show that roots of some dipterocarp species form fewer mycorrhizal roots than the same species of the same age grown in the greenhouse (personal observation). Under natural conditions the number of mycorrhizal infections on dipterocarp seedlings is higher in open areas (gaps) than for seedlings growing under closed canopies (Becker, 1983). From all this it seems that carbohydrates which plants build up by photosynthesis are the important factor involved in the symbiosis. Hormones may also be involved in the symbiosis (Slankis, 1971; Melin and Nilsson, 1957).

In mycorrhizal symbiosis, the larger part of the carbohydrate required by the mycorrhizal fungi is derived from photosynthesis of the host plants (Harley and Smith, 1983). Host plants with hyphae of mycorrhizal fungi on their roots may be able to absorb water and nutrients from a considerable distance from their root system through these hyphae, which is an active process. Therefore a sufficient carbon flow from the host plant must occur to maintain the symbiosis (Nylund, 1988). Detailed experiments by Lewis and Harley (1965) on beech indicated that the conversion of glucose and fructose to trehalose and mannitol in the fungus established a concentration gradient; hence transport of carbohydrate occurred in the direction of the fungus. They concluded that translocation of sugars into the fungal sheath tends to convert a supply of carbohydrates for metabolic processes by the associated fungi. Melin and Nilsson (1957) traced ^{14}C applied as CO_2 to the needles of *Pinus sylvestris* down through the shoot and root into the mycelium. A similar method was applied by Reid and Woods (1969) and they found movement of ^{14}C reciprocally between *Thelephora terrestris* mycelium and the root of *Pinus taeda* through connecting mycelial strands. This and other experiments demonstrate that formation and reproduction of ectomycorrhizae is directly linked to the photosynthetic activity of the host plant.

The possibility of carbohydrate being shared by neighbouring plants through mycelial interconnection has been proven for temperate tree species by controlled experiments (Read and Finlay, 1985; Read and Francis, 1985; Read, 1991). However, it has been tested under field conditions neither for tropical species nor for temperate species. Several authors speculated this mechanism does occur under natural conditions in which understorey seedlings are integrated in the mycelial network of the root systems of big trees which have a better position for receiving light from solar radiation (Harley and Smith, 1983; Marx, 1991; Read 1994).

Different types of mycorrhizal symbiosis may have a different threshold of carbohydrate level. Ectomycorrhizal fungi may require more photosynthetic products (carbohydrates) from their host than VA-mycorrhizal fungi from similarly dependent hosts for one of the following reasons: first, because of a greater biomass of fruiting bodies, hyphae and rhizomorphs in ectomycorrhizae than in VA-mycorrhizae, hence a higher carbon cost if equal hyphal respiration rates of ectomycorrhizal and VA-mycorrhizal fungi are assumed; second, ectomycorrhizal fungi are a stronger sink for photosynthetic products than VA-mycorrhizal fungi, because ectomycorrhizal fungi produce plant hormones that influence carbon compound translocation, and they convert the host's sugars into storage sugars. Therefore in the forest ecosystem where the ectomycorrhizal species predominate as in dipterocarp forest, the role of ectomycorrhizae in the carbon allocation of the ecosystem is expected to be of primary importance.

Concerning the influence of light upon mycorrhizal development, two different influences must be distinguished. First, the direct influence of the light through carbohydrate production of the host plant, and secondly, the influence of radiation affecting other factors such as soil temperature. The first one is strongly related to physiological processes such as infection processes in the symbiosis (Björkman, 1942; Handley and Sanders, 1962; Harley, 1969; Harley and Smith, 1983; Hacskaylo, 1985; Walander, 1992). High soil temperature has been proven to be a limiting factor for development of ectomycorrhizae in dipterocarp species (Smits, 1983; Noor and Smits, 1987), but this could not be confirmed in a greenhouse experiment using other dipterocarp species (Brown, 1990). Brown's experiment, however, probably failed to confirm the previous results because he neglected the gradient of soil temperature at different depths in his experiment. Another experiment showed that high soil temperature due to an increase in light intensity coupled with low soil moisture becomes limiting for the growth of dipterocarps (Nicholson 1964 ex Whitmore 1984). The relationship between light and mycorrhizae in dipterocarp species is furthermore complicated by the fact that different mycorrhizal associations may show different reactions to the light intensity or to the soil temperature.

There are only a few other publications available concerning the effect of soil temperature on ectomycorrhizal development, besides those which have already been mentioned above. More research on the effect of temperature on mycorrhizae has been undertaken in temperate than in tropical forests because of the great variation of temperature due to seasonal change. The influence of very low temperature on the survival and recovery time of mycorrhizal fungi after a period of freezing is particularly important (Moser and Haselwandter, 1983), but the highest critical temperature that may hamper the development of mycorrhizal roots is very seldomly reached in the temperate zone. Different ectomycorrhizal fungi have different resistance to high temperature (Marx and Bryan, 1971).

One study which examined the effect of temperature and desiccation on *Suillus granulatus, Rhizopogon roseolus, Pisolithus tinctorius*, a symbiont of *Pinus elliottii* and of *P. radiata* showed that the hyphae of these fungi were killed by 48 hours exposure to temperature between 28 and 38 °C and that of *P.arrhizus* at 45 °C (Bowen and Theodorou, 1973). Another study demonstrated that hyphal growth of *Pisolithus tinctorius* were stopped at a temperature above 40 °C (Marx *et al.*, 1970). In tropical tree species, Smits (1983; Smits *et al.*, 1987) found that hyphae of symbionts associated with *Anisoptera marginata* seedlings were killed at temperatures of 32 °C, and most mycorrhizal growth stopped at this temperature with other species, where as such fungi are usually killed at temperatures above 50°C. He found that the optimal soil temperature for ectomycorrhizae was between 23 to 25 °C and that the mantles of ectomycorrhizae were killed at 32 °C. The effect of heat on the growth of ectomycorrhizal fungi shows much variation between species or even between the strands of a single species, but most of them have an optimum temperature for growth somewhere between 8 and 27 °C (Harley and Smith, 1983).

For the formation of ectomycorrhizae, different tree species and associated fungal species show different optimum temperatures. An optimum temperature for infection of *Pinus taeda* by *Thelephora terrestris* was found to be 24 °C, and by *Pisolithus tinctorius* 34 °C (Marx and Ross, 1970). Infection of *Pinus radiata*, however, had an optimum temperature between 23 and 25 °C, differences occurring between fungal species or even strains of one species (Theodorou and Bowen, 1971).

In a tropical climate where humidity is very high, the negative effect of heat is likely to be more important than that of cold for growth of mycorrhizae because the lowest temperature that may inhibit mycorrhizal development is never reached. In an open area the temperature at the surface of forest soil could rise up to 50 °C, whereas there are no fluctuations of the soil temperature at 75 cm depth (Mabberley, 1992). In a greenhouse experiment, the maximum soil temperature may exceed 42 °C based on measurement in the upper layer of 10 mm depth (Brown, 1990). At the Wanariset station (East Kalimantan), the maximum soil temperatures measured in the pot range from 36 to 45 °C, depending on the composition of the soil media (Yasman, unpublished data). Under natural conditions the maximum soil temperature is slightly higher than in the greenhouse experiments. In former skid roads the maximum soil temperature can reach up to 50 °C at 5 cm depth (Yasman, personal observation).

Under natural conditions the critical soil temperature may be quite different. Seedlings growing in natural forest normally have poor, superficial roots. Smits, (1994) has classified three different zones in soil depth that determine the presence of ectomycorrhizal roots, namely 1; the zone of top soil temperature influence, 2; the zone of optimal performance of ECM and 3; the zone of lack of oxygen. Superficial roots of the seedlings growing under natural condition are mostly present in the zone of top soil influence. The long stable microclimate common in the understorey of natural forest may be very vulnerable to interference. Sudden exposure (for instance caused by logging activity) may cause an increase of the temperature of the top soil zone that may lead to physical or physiological damage to ectomycorrhizae on the roots of the seedlings. Therefore poor regeneration of dipterocarps is often encountered on former skid roads in logged-over forest.

1.5 Hypothesis

Several studies have proven that several dipterocarp species are obligately ectomycorrhizal in their lifetime (Smits, 1994; Omon, 1994). Directly following seed germination, seedlings still have reserves from their normally large cotyledons. In this stage ectomycorrhizal infection should take place after depletion of these reserves. The lack of carbohydrate exudate from the roots may cause an absence of mycorrhizal infection.

Normally the seedlings of dipterocarp species on the forest floor are very abundant after a mass flowering season. Natural selection diminishes the number of seedlings considerably. This selection process is affected by complex environmental and physiological factors, such as light and ectomycorrhizal potential.

The light intensity at the forest floor is very low, except in sunflecks and presumably it is below the compensation point, which is insufficient for seedlings to maintain their carbon balance following their independence from their cotyledon food source. Although there is high mortality amongst the seedlings, nevertheless, quite a number of dipterocarp seedlings can establish in this environment in natural lowland dipterocarp forest.

Considering the obligatory symbiotic relationship of the fungus and seedlings as well as adult trees of Dipterocarpaceae, it is hypothesized that mycorrhizal fungi connect through their hyphae the seedling to the root system of the mother trees, thereby providing the nutrition needed for the seedlings to survive under unfavourable environmental conditions such as very low light intensity. A major component of this exchange via the hyphae in the soil are carbohydrates, which plants normally build up through photosynthetic activity. The question to be answered is whether or not the surviving seedlings need the carbohydrates nutrition because they do not receive enough light intensity for a sufficient level of carbon assimilation. This question can only be answered by measurement of the light level in the forest and carbon assimilation in the leaves of the seedlings by means of photosynthesis measurement. The aims of this study is to experimentally examine the relationships between light, carbon assimilation and ectomycorrhizae, so as to check in how far the carbohydrates provided through interplant mycelial connections influence the survival and growth of the seedlings.

CHAPTER 2

INFLUENCE OF LIGHT INTENSITY ON THE FORMATION OF ECTOMYCORRHIZAE IN DIPTEROCARP SEEDLINGS

2.1 Introduction

It has been proven by many researchers working with temperate tree species that light intensity is one of the most important environmental factors in the formation of ectomycorrhizal symbiosis (Björkman, 1942; Hacskaylo, 1973; Nylund and Unestam, 1982; Harley and Smith, 1983) since the symbiosis of a fungus with a green plant concerns the exchange of carbon (carbohydrate) and nutrients. In general, an increase in light intensity will increase transport of assimilates to the root and thereby increase the carbohydrate level in the root of the host plant. Other environmental factors that may be important for the formation of ectomycorrhizae are soil temperature, soil fertility (especially availability of nitrogen and phosphorus), soil compaction (aeration) and soil pH. Physiological factors of the fungus and of the host plant may also influence the formation of ectomycorrhizae. The process of infection and the factors involved in the process are not yet fully understood.

Species of Dipterocarpaceae are among the few tropical tree species which have been shown to be obligately ectomycorrhizal. In natural forests, light requirements for optimal growth of dipterocarp tree species range from shade tolerant to light demanding. Light intensity at the forest floor is very low except when sunflecks occur. Under natural conditions, very low light intensity on the forest floor tends to delay and stunt the growth of most dipterocarp seedlings. In a dipterocarp plantation experiment, seedlings with poorly developed ectomycorrhizae exhibited yellowish leaves and stunted growth (Noor and Smits, 1988). Seedlings which survived in the forest, however, have never shown such symptoms except on open places like skidroads. Although the light intensity on the forest floor is very low, dipterocarp seedlings which survive in the understorey always possess ectomycorrhizal roots. They might become infected soon by hyphae derived from the mycorrhizae of the mother tree (Read, 1994). It is not yet fully understood how such factors may influence the formation of ectomycorrhizae under natural conditions. As far as carbohydrate is concerned, however, light is the most important factor involved in this process.

The aim of the experiment described in this chapter was to determine the influence of light intensity on the formation of ectomycorrhizae in dipterocarp seedlings. It was intended to use the results as an indicator for the degree of ectomycorrhizal formation occurring in seedlings in the natural forest where the light intensity is very low.

2.2 Materials and Methods

2.2.1 Species selected for the study

The species used in this experiment were *Dipterocarpus confertus* Sloot. and *Shorea leprosula* Miq. The criteria for species selection were based upon the temperament (see Oldeman and Van Dijk, 1991) of the species under natural conditions. *Dipterocarpus confertus* is a relatively shade tolerant species of moderate growth, while *Shorea leprosula* is a light demanding species (widely distributed in Kalimantan and Sumatra), and is one of the fastest growing species of dipterocarps (Meijer and Wood, 1964). In the natural forest of the Wanariset research station both of these species are very common. They are both economically very important in the wood market. These two species show the same flowering patterns in the Wanariset region. The two species produced fruits at the same time just before this experiment was started.

2.2.2 Location and time of experiment

The experiment was carried out in a greenhouse at the Wanariset research station located 38 km north-east of Balikpapan in East Kalimantan (Fig. 2). The experiment started in January 1991 with planting the seedlings originating from seeds germinated in a greenhouse, and ended in June 1992 by harvesting the seedlings to get quantitative data on mycorrhizae and biomass. Root sampling and mycorrhizal root analysis were done in the laboratory.

2.2.3 Preparation and design of experiment

The seeds for the experiment were collected from the Wanariset Forest during the mass flowering season of November till December 1990. The seeds were germinated in sand that had been pasteurized before use by means of solarization (see Box 1: Solarization). One to two weeks after sowing, all of the seeds had germinated and produced two leaves (a pair) while the cotyledons were still attached. During germination contamination by unknown fungi was prevented by covering the sowing bed with carefully cleaned plastic sheet. Also the surface of the concrete germination beds was pasteurized before sowing of the seeds. Then seedlings of about the same size (height and leaf area) were selected from the germinated specimens to be included in the experiment. One week after germination when the leaves were strong enough,

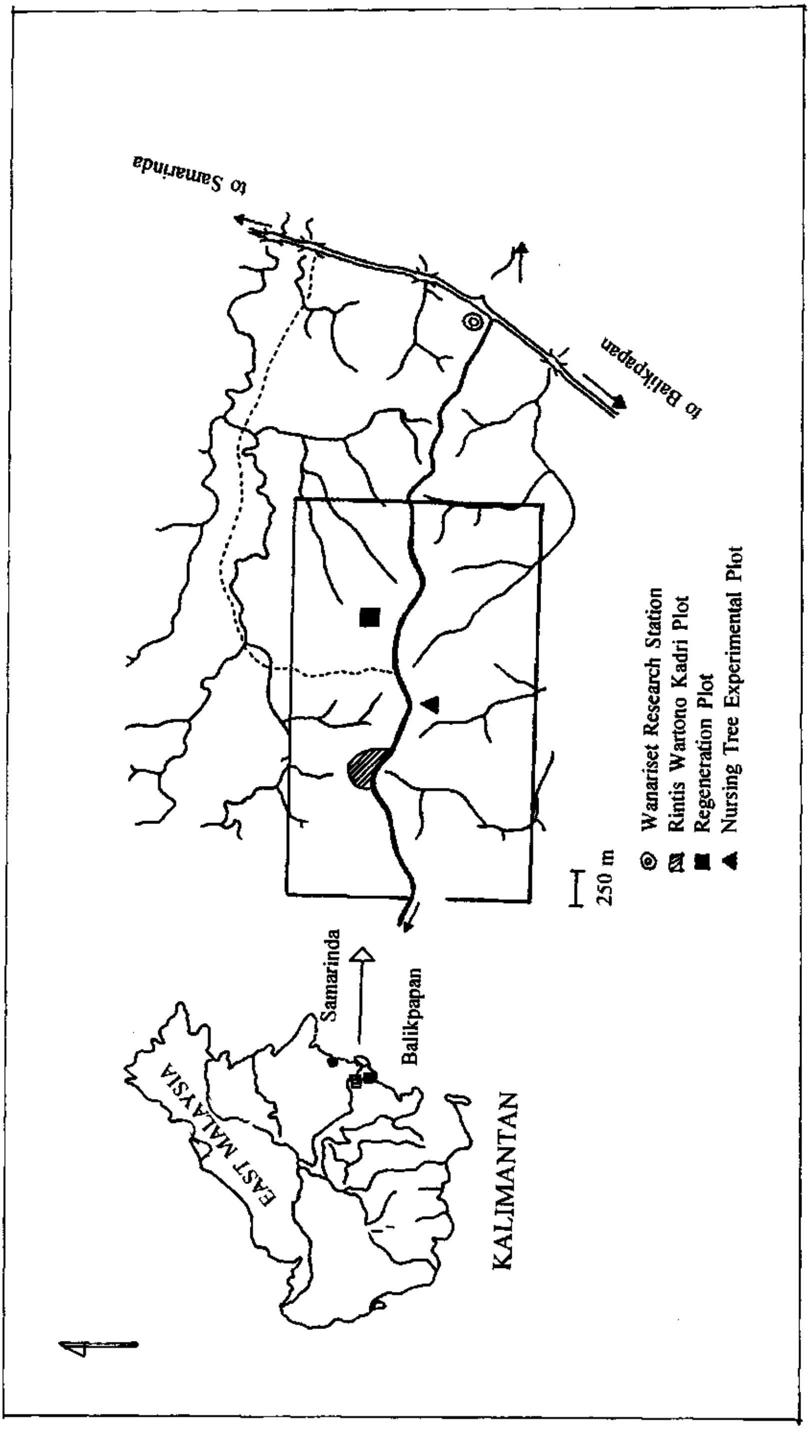


Figure 2. Map of the Wanariset Research Forest, East Kalimantan

the seedlings were transplanted to pots made from concrete (22 cm high, 10 cm diameter at the base and 15 cm diameter at the top). These kind of pots were found to be good containers for the development of mycorrhizal roots in previous experiment (unpublished results). The media used in the containers consisted of 1 part of top soil, 2 parts of subsoil, 1 part of peat and 1 part of sand. All media had been pasteurized by means of solarization for three to four days before use.

The easiest and simplest method for preventing ectomycorrhizal fungus deficiencies on seedlings in nurseries is to apply soil, humus, or litter containing mycorrhizae and associated mycelia. It is the most commonly used method to ensure consistent development of mycorrhizae (Mikola, 1973; Smits *et al.*, 1988), therefore this experiment used inocula from soil collected from the trunk base of 'mother trees' (term used for adult dipterocarp trees from which the seed/seedlings originated).

Inocula for the experiment were taken from two different mother trees namely a *Dipterocarpus confertus* tree and a *Shorea leprosula* tree growing in the same location (a 200 meters apart from each other) of the Wanariset forest. The collection of the inocula was done on the same day as the inoculation to ensure that the mycorrhizal inocula were still fresh. The inocula were collected from a maximum of 50 cm distance from the buttresses of the mother trees from a top soil and litter layer of 10 cm thickness to increase the probality that the inocula came from the selected mother trees.

Four different classes of light intensities were tested using green polyvinyl mesh to shade the seedlings. The first class of light environment was created by shading the seedlings with three layers of the polyvinyl mesh resulting in a measured light intensity of approximately 25% of full sunlight, the second class used two layers of mesh resulting in about 40% of full sunlight, the third class used one layer resulting in 60% of full sunlight, and the fourth class had no net but seedlings were placed in the greenhouse. The light intensity of this class was 90% of full sunlight. Light intensities were measured with a Photosynthetic Radiometer with Quantum Response type RA 200 Q (PAR meter with spectral band 400 to 700 nm) made by Bottemanne Weather Instruments (The Netherlands). The values obtained were converted to percentage of full sunlight by using of the as a standard value measured in an open area at the same time.

Seedlings were inoculated at the time that they were transplanted to the containers (pots). Ten inoculated seedlings of each of the two species were placed randomly in the block. Each block received one of the four classes of light intensity and one of the two different inocula (Table 1).

Box 1 : Solarization

Indonesia is situated in the tropics and the duration of solar radiation in a day remains about the same during whole year viz. about 12 hours per day, from 6.00 - 18.00 hours. This solar radiation received by the earth as well as by the plant serves an energy source for metabolism. When it is received by the earth the energy will be converted into heat. Under normal conditions, the highest temperature in a day occurs between 11.00 till 14.00 hours. Solar radiation at this time can rise soil temperature in open areas up to 45 °C. This heat has been proven to kill dipterocarp ectomycorrhizal fungi (Smits, 1994). This is the reason to use solar radiation for pasteurization of media used in the ectomycorrhizae experiment. Although not all microorganisms would be killed at this temperature, most of the ectomycorrhizal fungi will not survive under this conditions. One added advantage of this method is that the medium does not become completely sterile. This may assist in preventing easy development of common detrimental nursery fungi such as *Fusarium* and *Pythium*.

The working principle of this system is that heat comes from two sides, i.e. direct solar heating and absorbed heat of the compact media such as concrete cement (Fig. 3)

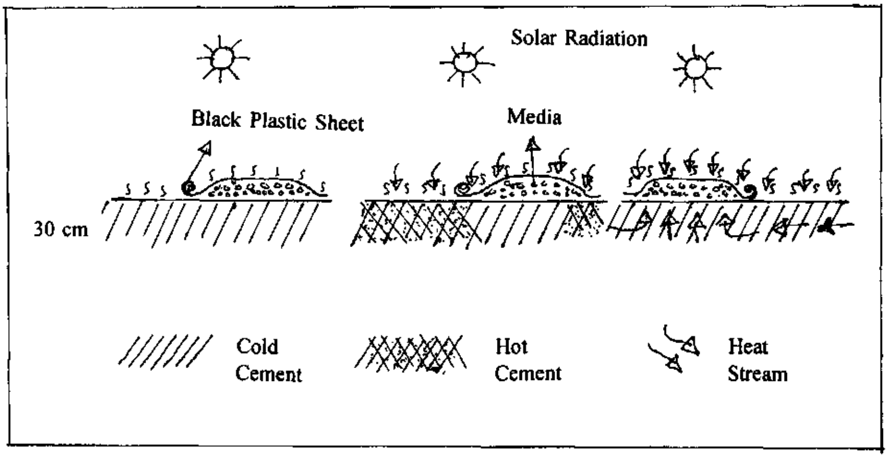


Figure 3. Solarization of the growing media used in th ectomycorrhizal experiment.

The temperature of the media after exposure to solar radiation with the simplest method for about 3 to 4 hours can reach 40 to 46 °C, depending on the composition of the media and the amount of sunlight. For example, media consisting mainly of sand would reach a temperature up till 46 °C, whilst media of lam top soil would reach temperatrues of about 43 °C. Heating of the mdia for 3 to 4 days was found to be enough to kill all ectomycorrhizal fungal hyphae. The spores of some species , however, would probably remain alive at this temperature as described by several authors to be the case for *Pisolithus tinctorius.* Ashton (1989; p. 230) assumes that fungal spores lack dormancy in the humid and warm environment of the tropical forest understorey. In our work, the media are normally collected several weeks before use in any experiment. This further reduces the risk of surviving spores still being present in the inoculum. Our experience in using solarized soil inoculum for non-mycorrhizal cuttings of Dipterocarps showed that formation of ectomycorrhizae was very rare in such instances and that when ectomycorrhizae developed, they normally belonged to common nursery fungi like *Thelephora terrestris* or *Scleroderma* spp. (Smits, 1991). The first one we never found in natural forest, whereas the second ones are generally limited to secondary forest types. This therefore supports the assumption that late stage fungi (Last *et al.*, 1984) do not form ectomycorrhizae after solarization. The common nursery fungi very probably originated from airborne spores.

Table 1. Summary of experimental design for testing the influence of light intensity on the formation of ectomycorrhizae.

Attribute	No. of treatments	Detail
Species	2	*Shorea leprosula* *Dipterocarpus confertus*
Light Intensity Inocula Replications: Seedlings/replicate	4 2 10	25% of full sunlight 40% of full sunlight 60% of full sunlight 90% of full sunlight soil from *S. leprosula* tree soil from *D. confertus* tree
Total seedlings	120	there was no *D. confertus* inoculated with soil from *S. leprosula* tree

2.2.4 Measurements and data collection

The parameters measured were the height of the seedlings and the number of leaves. The first measurement was done one month after transplantation to ensure that the seedlings had become less dependent upon the food sources in the cotyledons. During the first month two seedlings died and were replaced. Measurement of the height and counting of the number of leaves were repeated every month. Observations on flushing were done weekly by observing the new leaves produced during the previous week. All of the seedlings were harvested at the end of the experiment for a quantification of ectomycorrhizae following the method described by Schenk (1982) and Giovannetti and Mosse (1980). The following data were recorded: number of infected and non infected roots, type of ectomycorrhizae (ECM) formed, the number of each type of ECM, and dry weight of shoots and roots of seedlings. Each type of ECM was distinguished on the basis of colour, type of ramification, macroscopic structure of ECM, and hyphal structure (as described by Zak 1971 for identification of ectomycorrhizae of Douglas-fir). In case infected and non-infected roots were difficult to distinguish, colouring with Ponceau S (described by Daughtridge *et al.*, 1986) was used to contrast the difference between them.

2.2.5 Data analysis

Growth data of seedlings were first analyzed by regression of the logarithm ($\log_n$) of height (cm) against time (month). From this analysis the regression coefficients and the intercepts of the regression lines for each seedling were obtained. These regression coefficients were used to estimate the growth rate of seedlings and to enable statistical comparisons between the treatments. Second, factors such as the influence of light, inocula, and species on the formation of mycorrhizae, and biomass data were analyzed by regression and analysis of variance (ANOVA) to test the influence of each factor and the interaction between those factors on ectomycorrhizae formation. Data were analyzed using the Genstat statistical package (Lane *et al.*, 1985).

2.3 Results

The summary of the statistical analysis of the effect of light intensity, species and inocula on the growth of the seedlings is presented in Table 2. Because there was no inoculation of *Dipterocarpus confertus* seedlings with soil of the *S. leprosula* tree, the analysis of the effect of different light intensity and type of mycorrhizae was made separately. The summary of results of the ANOVA test of the effect of light intensity and types of mycorrhizae formed is presented in Table 3.

Table 2. Summary of Analysis of Variance (ANOVA) of the effect of light intensity, species, and inocula on seedling growth parameters of two species at an age of 18 months.

Factors	df	rc	log_n-shoot	log_n-s/r	s/r ratio	number of type	non-infected root
light intensity	3	0.98^{+++}	8.60^{+++}	0.94	6.47^{+++}	2.29^{+}	3.97^{+}
species	1	0.20^{+++}	114.54^{+++}	205.88^{+++}	136.16^{+++}	78.89^{+++}	34.54^{+++}
inocula	1	1.00	0.09	1.25	4.91^{+}	2.11	
light x species	3	1.00	1.79	9.21^{+++}	7.16^{+++}	1.83	
light x inocula	3	0.99	1.90	2.11	3.66	2.01	

Note: $^{+++}$ Significant at $P < 0.001$

$^{++}$ Significant at $P < 0.005$

$^{+}$ Significant at $P < 0.010$

rc Regression coefficient of the growth curve

s/r Dry weight shoot-root ratio

df Degree of freedom

Table 3. Summary of ANOVA of the effect of light intensity and type of mycorrhizae of *Dipterocarpus confertus* and *Shorea leprosula* seedlings.

Factors	*Dipterocarpus confertus*		*Shorea leprosula*	
	df	number of infected root	df	number of infected root
light intensity	3	5.72^{+++}	3	10.98^{+++}
type of mycorrhizae formed	2	3.33	4	55.42^{+++}
light x type	6	2.88	12	2.59^{++}

Note: see Table 2 for description.

2.3.1 Correlation between light intensity, seedling growth and biomass

The analysis of variance of the regression coefficients of seedling growth after 18 months observation shows significant differences in seedling growth under different light intensities ($F=0.98$; $P<0.001$; Table 2). The growth of seedlings under light intensities of 40% and 60% was faster than the growth of seedlings under light intensities of 25% and 90% respectively.

The analysis of regression coefficients against other factors such as light intensity, species and inocula with covariance of intercept of the regression line shows that, although there was a significant influence of different light intensities and different species on growth (the regression coefficient) ($F=114.54$; $P<0.001$), there was no significant influence of different inocula ($F=1.00$). This means that different inocula sources and the type of ectomycorrhizae did not appear to affect the growth of seedlings (at least during the first 18 months).

There were different growth responses to light exhibited by *Dipterocarpus confertus* and *Shorea leprosula* (see Figure 4).

Both species had an optimal light intensity range from 40 to 60%. But under a light intensity of 90% the growth of *D. confertus* differs from that of *S. leprosula.* The growth of *D. confertus* was slowest under a light intensity of 25%, while growth of *S. leprosula* was slowest under a light intensity of 90%. Under the sam light condition the result indicated that the growth of *S. leprosula* seedlings was faster than that of *D. confertus* seedlings (Figure 5). These results show that seedlings of different temperament (shade or light demanding species) indeed react differently to the same light conditions. The difference may also be due to the radiation-dependent effect of different daily soil temperatures. *Dipterocarpus confertus* seedlings have larger-sized leaves that may capture much more light than seedlings of *Shorea leprosula.*

Measurements of soil temperature in the pots of *S. leprosula* and *D. confertus* showed a difference in the average daily temperature measured on sunny days. Table 4 shows the average soil temperature for both species.

Compared to soil temperatures under natural conditions, these values are slightly higher. The average soil temperatures measured between 11.00 am and 12.00 noon at different depths and site conditions in the plantation experiment are given in Table 5.

Regarding the biomass of the seedlings in terms of dry weights of the shoots

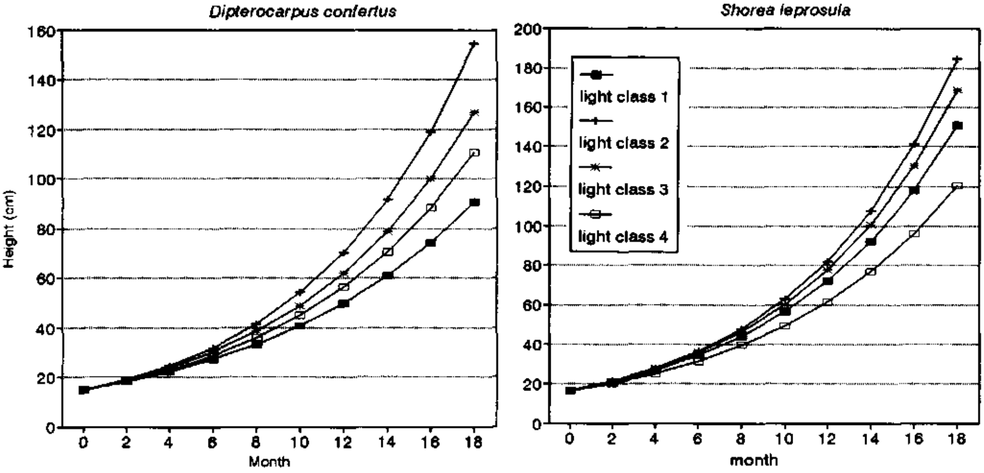


Figure 4. Growth response of *Dipterocarpus confertus* and *Shorea leprosula* seedlings growing at different light intensities.

and roots, the results show that there is a significant influence of different light intensities and of species ($F = 8.60$; $P<0.001$ for light intensity; $F=114.54$; $P<0.001$ for species; Table 2). For shoot-root ratio the significant influence resulted at $F=6.47$; $P<0.001$ (for light intensity) and $F=136.16$ $P<0.001$ (for species).

The influence of inoculum sources on the shoot-root ratio is significant ($F=4.91$; $P<0.05$), but it is less clear than other factors, particularly light intensity and species. These have been shown to be the most important factors affecting the early growth stages of dipterocarp seedlings in this experiment. This effect might be different under natural conditions where competition among species in the 'rhizosphere' (the environment below ground under the influence of the roots of the plants) makes the importance of ectomycorrhizae much more significant for the seedlings of dipterocarps to survive under competition.

When the dry weight of the shoot is analysed separately, the result is similar to the analysis of the shoot-root (s/r) ratio showing higher dry weight of the shoot for seedlings growing under 60% light intensity, then followed by seedlings growing at light intensities of 40%, 90% and 25%. The highest s/r ratio is also obtained for seedlings of both species growing under 60% light intensity, then followed by seedlings under light intensities 40%, 90% and 25%. This result suggests that the growth of shoots is followed by the growth of roots underground and that the effect of light is similar to its effect on shoot growth.

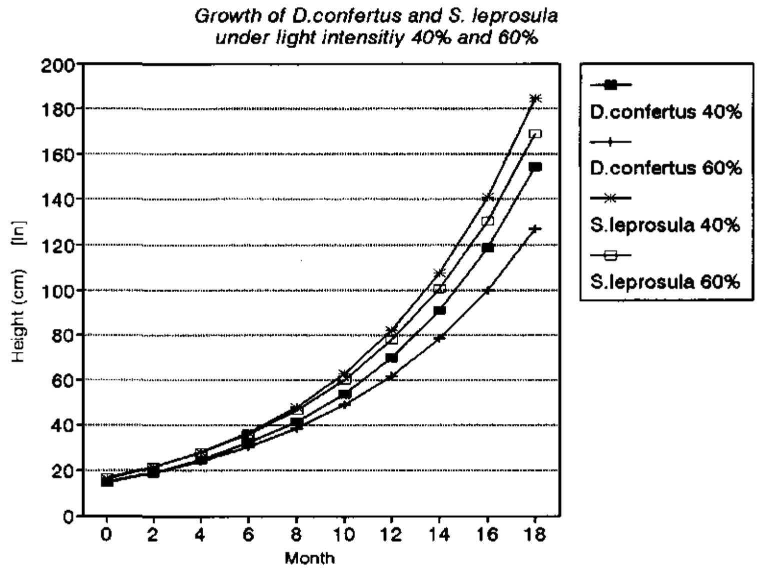


Figure 5. Growth of *Dipterocarpus confertus* and *Shorea leprosula* seedlings under light intensities 40% and 60%.

Table 4. Soil temperature (°C) in the upper layer (10 mm depth) of the pots containing seedlings of *Dipterocarpus confertus* and *Shorea leprosula*.

Time of Measurement	Light intensity 25%	Light intensity 40%	Light intensity 60%	Light intensity 90%
09.00 am	24*) 23**)	25 24	28 28	28 28
10.00 am	28 26	29 28	32 30	32 31
11.00 am	30 28	31 30	32 30	35 33
12.00 am	30 28	32 30	32 30	36 34
01.30 pm	30 30	32 30	32 31	41 34
02.00 pm	30 29	32 30	33 30	40 35
03.00 pm	30 29	32 31	32 31	40 35
04.00 pm	30 28	32 30	31 30	38 33
07.30 pm	28 25	27 27	27 25	28 27

Note : *) Measurements were done in the pots of *S. leprosula*
**)Measurements were done in the pots of *D. confertus*

Table 5. Average soil temperature measured from 11.00 to 12.00 a.m. at different soil depths in different site conditions. (After Noor and Smits, 1988).

Depth (cm)	Primary Forest (3.1 to 4.2%)* (°C)	Secondary Forest (13 to 18%) (°C)	Strip (32 to 56%) (°C)	Open Area (100%) (°C)
0	26.8	29.0	29.0	34.8
5	26.0	28.0	28.2	32.8
10	26.0	27.3	27.5	31.3
15	26.0	26.9	27.0	29.7

* % light intensity measured

Table 6. Average shoot-root ratio of *Dipterocarpus confertus* and *Shorea leprosula* under different light intensities and with different inocula.

Light Intensity	*Dipterocarpus confertus*	*Shorea leprosula*
25%	1.24	6.44*)
		5.15**)
40%	2.00	5.22
		3.49
60%	1.94	2.93
		3.86
90%	1.54	4.61
		3.84

*) inoculum source at the foot of *D. confertus* **) inoculum source at the foot of *S. leprosula*

2.3.2 Correlation between light intensity and ectomycorrhizae formation

Seven types of ectomycorrhizae were distinguished in this experiment. The criteria used to distinguish each type are described by Zak (1971). Most of the distinguishing features are based on macromorphological differences.

The types of each type of ectomycorrhizae found in the experiment are described as follows (Table 7) :

Table 7. Description of ectomycorrhizal types encountered in the experiment on the influence of light intensity on the formation of ectomycorrhizae.

ECM type	Description
Type 1	Dark brown mycorrhizae, short with brown hyphae, infrequently branched, relatively thick diameter. (Figure 8 A)
Type 2	Light brown mycorrhizae sometimes whitish, pyramidal form with whitish brown hyphae, mycorrhizae often only present at the end of root tip, surface often silvery. It looks similar to ectomycorrhizae formed by *Inocybe petiginosa* (Ingleby *et al.*, 1990). (Figure 8 B)
Type 3	Similar to Type 1, but it has relatively long mycorrhizae, sometime pyramidal, often waving, thinner than Type 1, hyphae rare, if present dark brown in colour. (Figure 8 C)
Type 4	Light brown mycorrhizae, pyramidal form, branched at rather irregular distances, mantle surface shiny, rhizomorph whitish. (Figure 7 D)
Type 5	Similar to Type 1, but is thicker, mycorrhizae often waving, brown straight hyphae very abundant, sometimes pyramidal. (Figure 8 E)
Type 6	Dark brown mycorrhizae, sometimes brown, almost without hyphae, long, mantle surface sometimes shiny. Similar to Type I found in *Dipterocarpus alatus* from Thailand (Sangwanit and Sangtian, 1991). (Figure 8 F)
Type 7	Light brown mycorrhizae, relatively thin, sometimes branched, rhizomorph brown and rare, mantle surface smooth sometime with silvery surface. (Figure 8 G)

The number of types of ectomycorrhizae formed for both species are highly significantly influenced by the host plant species ($F = 78.89$; $P<0.001$; Table 2). The influence of light intensity on the number of types is also highly significant ($F=2.29$;

P<0.010; Table 2). This means that increasing light intensity causes an increase in the number of types which can be formed. This relationship will differ between dipterocarp species. There was no significant influence of different inocula on the number of types encountered (F=2.11; Table 2). The results suggest increasing the rate of photosynthesis by increasing light intensity to be favourable for mycorrhizal infection due to the high level of carbohydrates in the roots of host plants.

The types of ectomycorrhizae associated with roots of both species did not differ with the different inoculum sources (F=2.11; Table 2). This means that type 3 for example is very common in association with either *D. confertus* or *S. leprosula*. This is an indication that specificity in dipterocarp mycorrhizae, although often considered to occur, was not demonstrated in early growth stages in this experiment. However, the experiment were executed in artificial condition.

Statistical analysis shows a very highly significant relation between light intensity and the formation of ectomycorrhizae for both *D. confertus* and *S. leprosula*. For *D. confertus* the result was F= 5.72, P<0.001 and for *S. leprosula* F=10.98, P<0.001 (Table 3). The result indicated that the number of infected roots as well as the number of mycorrhizal types formed in the roots increase in the high light intensity. Table 8 and Table 9 show the number of ectomycorrhizae of different types associated with roots of *D. confertus* and *S.leprosula*. There was no inoculation from the soil of *S. leprosula* to *D. confertus* seedlings because there were not enough *D. confertus* seedlings available for the experiment. Therefore the tables are presented separately.

Table 8. Total number of roots infected by each type of ectomycorrhizae on *Shorea leprosula* under different light intensities and from different sources of inocula.

Light intensity	Inoculum sources	Number of infected root by each type						
		Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7
25%	1*)	124	4	8	0	158	62	7
	2**)	82	40	175	15	64	219	5
40%	1	50	23	260	3	303	76	0
	2	206	6	169	1	133	435	5
60%	1	90	26	281	8	235	428	27
	2	45	10	325	3	244	104	13
90%	1	330	17	87	0	148	209	19
	2	295	3	362	2	43	138	48

*) Inoculum source from topsoil of *Dipterocarpus confertus* tree

**) Inoculum source from topsoil of *Shorea leprosula* tree

Table 9. Total number of roots infected by each type of ectomycorrhizae on *Dipterocarpus confertus* seedlings under different light intensities.

Light Intensity	Total number of infected root for each type			
	Type 1	Type 2	Type 3	Type 4
25%	36	61	4	0
40%	139	81	117	13
60%	218	69	37	42
90%	42	53	80	7

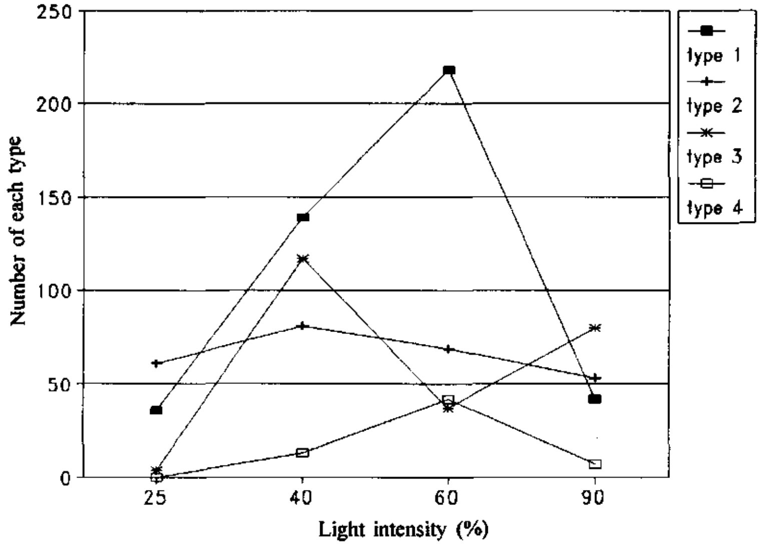


Figure 6. Relation between light intensity and total number of each ectomycorrhizal type encountered on the roots of *Dipterocarpus confertus* seedlings.

No mycorrhizal Types 5, 6 and 7 were encountered in *D. confertus* seedlings.

The results presented in Table 10 show that the percentage of non-infected roots of *S. leprosula* is less than that of *D. confertus*. For both species the results show that the number of uninfected roots is lowest at light intensities of 40% and 60% of full sunlight. No nutrients such as nitrogen or phosphorus were added as the results from previous experiments show that conifer ectomycorrhizae are influenced by these elements (Björkman, 1942; Handley and Sanders, 1971; Walander, 1992). In the present experiment, as the growth media consisted of subsoil, sand and peat with low nutrient content, it was assumed that the seedlings did not become less dependent on mycorrhizae. The chemical soil data of this experiment are presented in Table 11. The soil analysis shows that available phosphate, which is very important for mycorrhizae, is present in very high concentrations in the media for both species.

Table 10. Percentage of non-infected roots of *Dipterocarpus confertus* and *Shorea leprosula* seedlings under different light intensities.

Light Intensity	*Dipterocarpus confertus*	*Shorea leprosula*
25%	75.87	54.98
40%	62.62	39.42
60%	62.64	39.44
90%	66.23	43.25

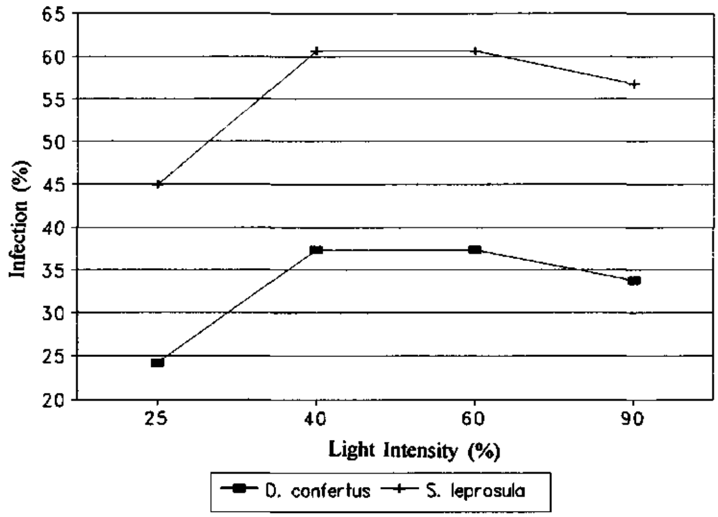


Figure 7. Relation between light intensity received by seedlings and percentage of ectomycorrhizal infection

Figure 7 shows that for both species the infection percentage is higher for the seedlings growing at light intensities 40% and 60% than for seedlings growing at light intensities 25% and 90%.

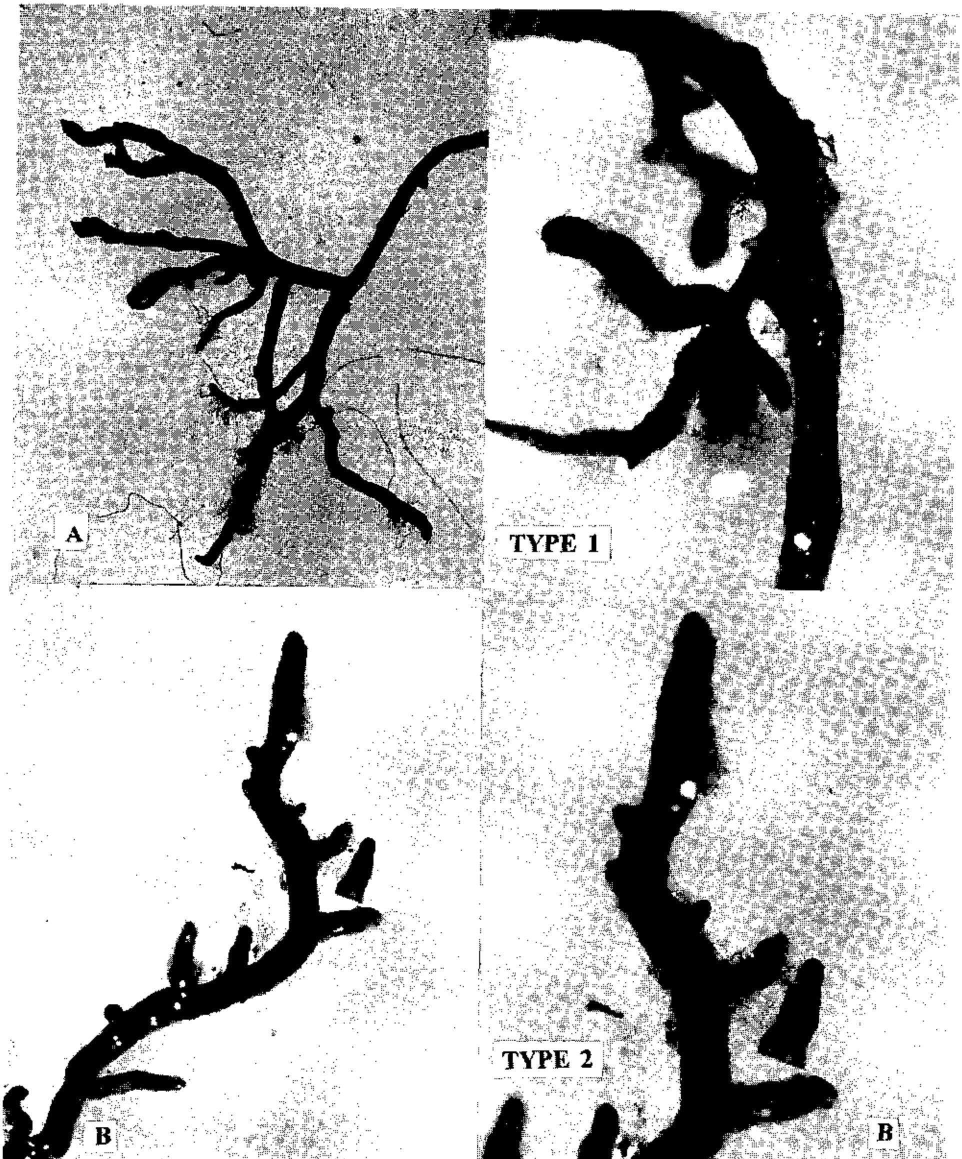


Figure 8. Ectomycorrhizal types found in *Dipterocarpus confertus* and *Shorea leprosula* seedlings.

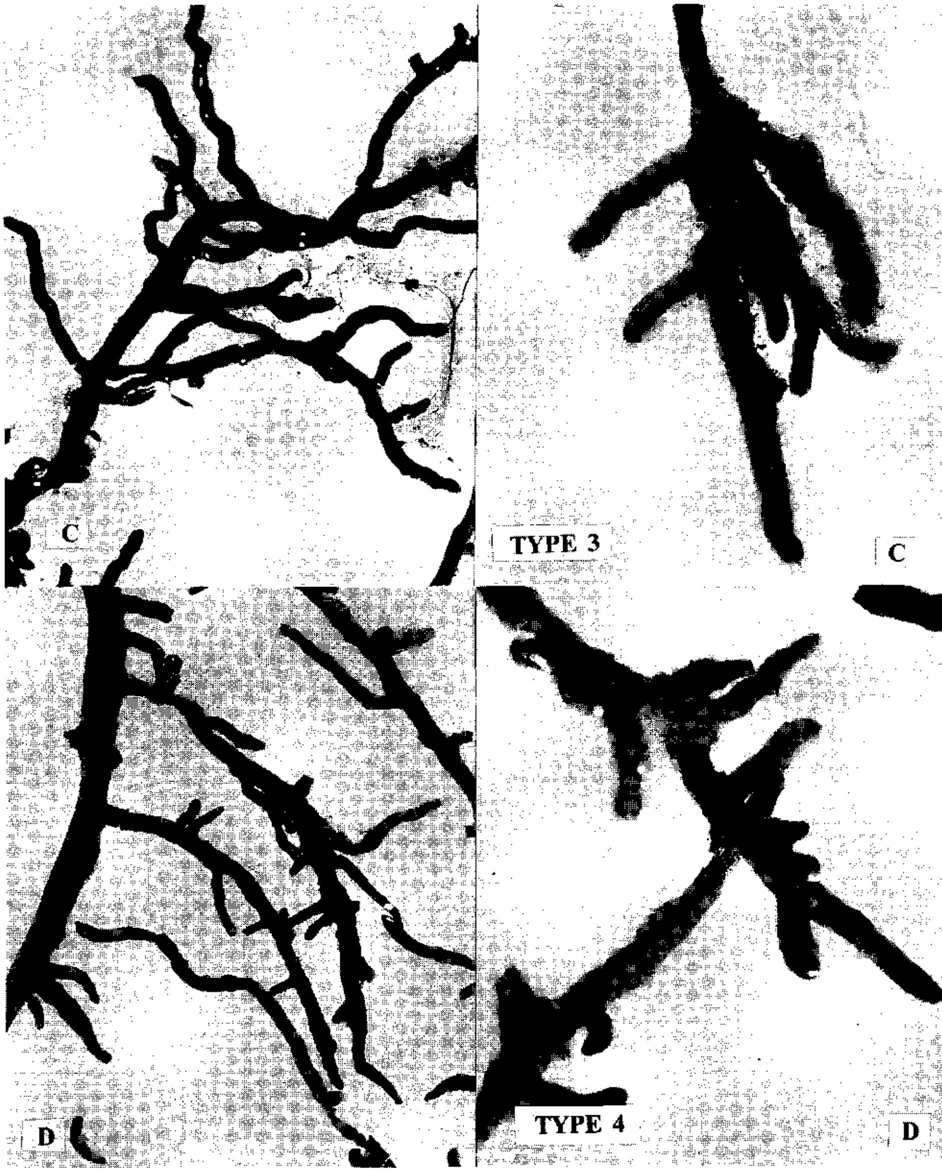
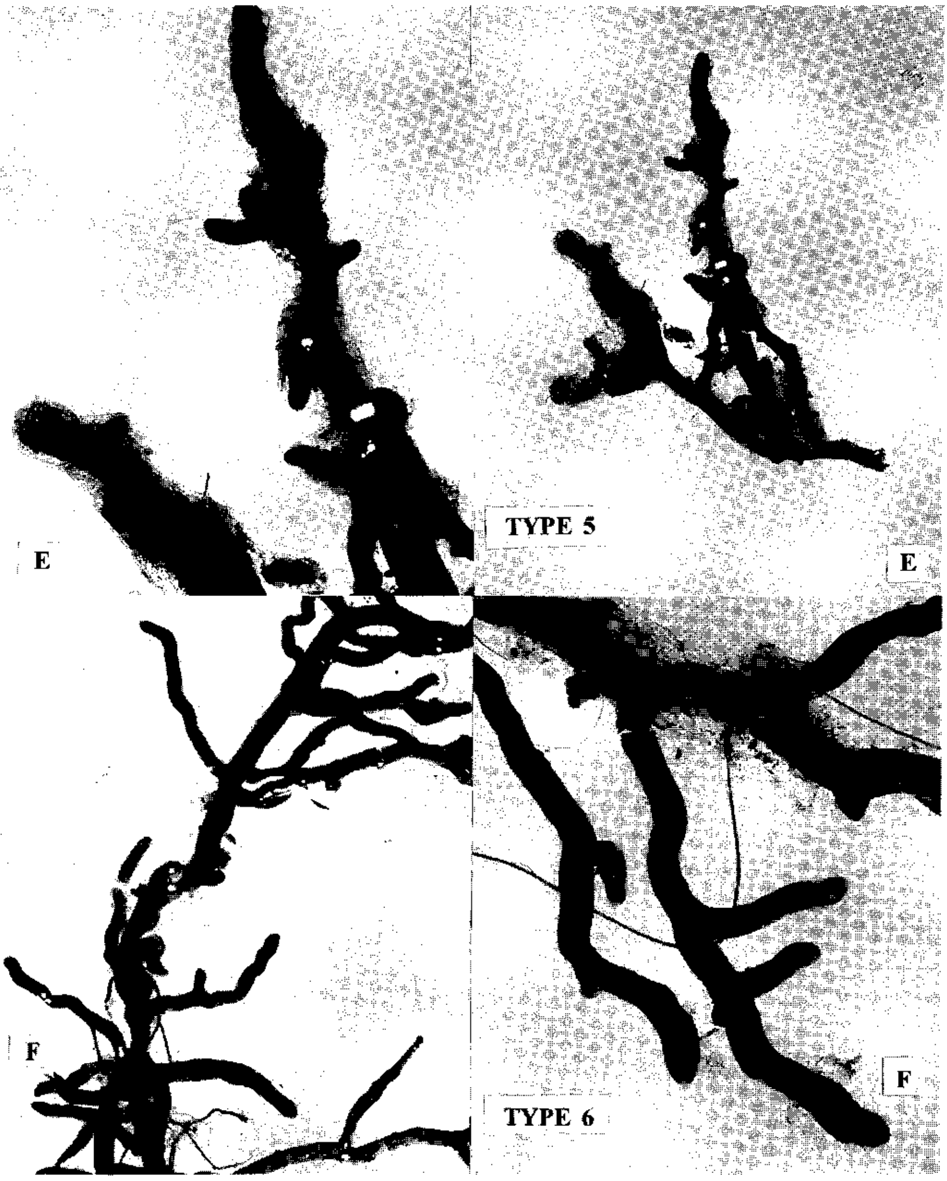


Figure 8. (Continued)



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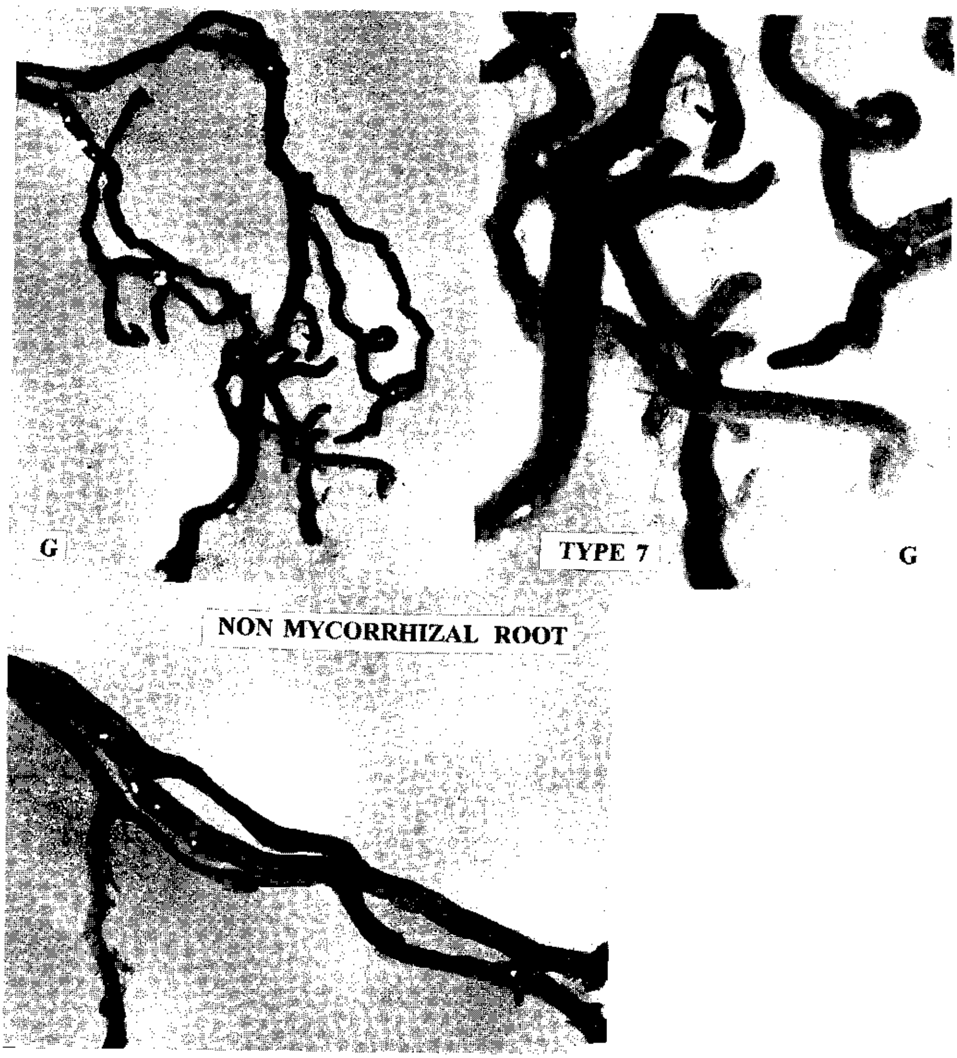


Figure 8. (Continued)

Table 11. Soil nutrient status of the media used for the experiment on the influence of light intensity on the formation of ectomycorrhizae. Soil samples taken at the end of the experiment; biomass nutrient content was not determined.

Soil from pots of	Texture (%)			Organic Matter Content			HCl 25 %		Bray	Exchangeable Cations (m.e/100g)				pH
	Sand	Silt	Clay	C	N	C/N	P_2O_5 (mg/100g)	K_2O (mg/100g)	P_2O_5 (ppm)	Ca	Mg	K	Na	
D. confertus	71	19	10	1.18	0.08	15	45	31	159.6	5.04	0.45	0.37	0.25	5.9
S. leprosula	70	19	11	2.23	0.14	16	51	32	183.8	8.35	1.17	0.35	0.17	6.1

The average number of mycorrhizae types are also different between *D. confertus* seedlings and *S. leprosula* seedlings inoculated with different inocula. *Shorea leprosula* seedling formed more types than *D. confertus* seedlings. Table 12 shows the average number of types associated with roots of seedlings at different light intensities and different inocula sources.

Table 12 shows that the average number of types of ectomycorrhizae is greater in *Shorea leprosula* than in *D. confertus*. This indicates again that light demanding species form more types of ectomycorrhizae than shade tolerant species. If we look at the same light intensity for both species, *D. confertus* growing under high light intensity (90%) has a low average number of types. This is an indication that this tree species probably only selects mycorrhizae which are well adapted to its temperament while *S. leprosula* could select many different types.

Table 12. Average number of types encountered in association with the roots of *D. confertus* and *S. leprosula* seedlings at different light intensities and sources of inocula.

Light intensity	Inocula sources	*Dipterocarpus confertus*		*Shorea leprosula*	
		Average number	(%)	Average number	(%)
25%	D.confertus	2.2	31	3.2	46
	S.leprosula			4.4	63
40%	D.confertus	2.8	40	4.1	60
	S.leprosula			4.2	61
60%	D.confertus	2.8	42	4.3	61
	S.leprosula			4.7	67
90%	D.confertus	2.1	30	4.9	70
	S.leprosula			4.5	64

Note : - % is the relative value of the average number of types divided by the total number of types encountered in the experiment (7 types), e.g. 2.2/7 = 31%

2.4 Discussion

The growth of seedlings under light intensities of 40 and 60% is faster than under light intensities of 25 and 90%. Similar results were found by

Nicholson (1960) who noted that the growth of *Dryobalanops aromatica* seedlings was faster under light intensity of 50% than under of 75%, was faster under 75% than under 87.5% and was faster under 87.5% than under 100%. Faster growth of *Parashorea malaanonan,* however, was obtained under light intensities of 75% than under of 50%, was faster under 50% than under 87.5% and was faster under 87.5% than under 100%. Mori (1980) found that fastest growth of *Hopea helferi* was obtained under a light intensity of 33% and observed a decrease in growth above and below this light intensity. Sasaki and Mori (1981) also demonstrated faster growth of some dipterocarp seedlings at 30 to 50% light intensity for shoot growth and 50 to 60% light intensity for root growth. Results of the present study as well as results from previous studies by other researchers on dipterocarp seedlings as reported by Seibert (1990) show great differences in growth responses to different light intensities. Almost all results, however, show that dipterocarp seedlings need a light intensity level between 30 and 70% of full sunlight for optimum growth (cf. Whitmore 1984). This optimal light requirement changes when seedlings reach the sapling or tree stage.

The analysis of factors such as the influence of light intensity, species, and inoculum indicate that there was no significant influence of different inocula on the growth of seedlings prior to the age of 18 months. The effect of different fungi used as inoculum in the Wanariset nursery was revealed after 3.5 years for *Shorea leprosula* (Yasman *et al.* in prep.). The significantly fastest growth of *Shorea leprosula* was obtained after inoculation with *Amanita* sp indet 19 (cf. Smits, 1994), while inoculation with other fungi such as genera *Russula* and *Lactarius* did not show a significant difference in growth (unpublished data). In the early growth stages of the seedlings, there may still be enough carbohydrate resources so that the effect of different mycorrhizae could not as yet be seen. As often occurs in a dipterocarp nursery, aggressive fungi like *Thelephora terrestris* (Smits, 1992) and *Scleroderma* sp. (personal observation) may infect different species of dipterocarp seedlings if there is no inoculum introduced. In the early stages of the growth the different effects of these fungi could not be seen in the nursery. In temperate regions, infection by common nursery mycorrhizal fungi such as *Cenococcum geophilum* and *Thelephora terrestris* is particularly frequent.

At a light intensity of 90% the responses of the two species were also different (Figure 4). These differences can be explained by the fact that *D. confertus* seedlings have larger leaves than *S. leprosula.* Thus *D.confertus* can intercept a larger proportion of light before it can reach the soil than can *S. leprosula.* This difference in soil shading can explain the variation exhibited by the two species with respect to the daily soil temperature in the pots. At a light intensity of 90% in an open area, soil temperature can reach 39 °C, thereby exceeding the critical soil temperature for growth of ectomycorrhizae in Dipterocarpaceae, which is normally about 32 °C (Smits, 1983; Smits *et al.*, 1987). A similar result was found by Noor and Smits (1988) who described high mortality of *Shorea assamica* seedlings planted in open areas. They suggested that there is a correlation between different site conditions (such as primary forest, secondary forest, strip planting and open places) and the mortality of the planted seedlings which is due to the high soil temperature. They measured soil temperature at the sites (Table 5) and found that in an open place soil temperature could reach 34.8 °C at the surface and caused 67% mortality of ectomycorrhizal roots.

Nicholson (1960) also indicated the effect of high soil temperature on the different growth responses of seedlings to high light intensity. Early experiments on the influence of light intensity on the growth of dipterocarp seedlings by Mori (1980) did not take into account the effect of soil temperature. However, Sasaki and Mori (1981) state that the reduction of growth at higher than optimum levels of light appears to be caused by the strong irradiation of the direct sunlight which may negatively alter growth condition and make them unsuitable for seedling growth by the detrimental effect of ultraviolet light. This also may include the effect of a rise in soil temperature up to the critical temperature for the growth of mycorrhizal roots. It is suggested that in experiments with the effect of light intensity on Dipterocarpaceae it is very important to take into account that high light intensities may increase soil temperature and this will affect the parameters to be measured. The effect of high light intensity is not only due to the direct effect of on photosynthesis but may include physiological effects upon the symbiosis below ground.

However, dipterocarp seedlings can also grow in full sunlight if soil temperatures do not exceed the critical temperature for the growth of mycorrhizal fungi. Plantation experiments under alang-alang (*Imperata cylindrica*, Gramineae) in the PT Inhutani I nursery (East Kalimantan) with *Shorea leprosula* and *S. assamica*, and at the Wanariset station with *Dryobalanops aromatica* show vigorous growth of the seedlings up to five years old under full sunlight with treatment of mulching (Smits, 1994). Another reason for the fact that the growth of seedlings may not be optimal is that very high light intensity coupled with high humidity in the tropics may cause a photoinhibition (cf. Brown, 1990) or a depression of photosynthesis at midday when the leaf temperature is high as found by Roy and Salanger (1989) in the rain forest of French Guyana.

There is a positive correlation between light intensity and the ability of seedlings to form ectomycorrhizae. In general, an increase in light intensity will result in an increase in mycorrhizal formation (Harley and Waid, 1955; Reid *et al.*, 1983). The results of the present experiment revealed that light intensity does not show a linear relation with the amount of root infection. There is an optimum light intensity (in my experiment 40 to 60% of full sunlight) which is associated with soil temperatures below the threshold for the survival and growth of ectomycorrhizae. Under this light intensity, the optimum temperature for mycorrhizal infection can be reached which for temperate mycorrhizal fungi is about 23 to 25 °C (Theodorou and Bowen, 1971). In tropical mycorrhizae the optimum temperature for the development of ectomycorrhizae is likely to be higher than for temperate mycorrhizae.

In temperate zones the effect of light on mycorrhizal formation was first studied by Björkman (1942) in pine and spruce. His findings suggested that light is of paramount importance in the formation of ectomycorrhizae. According to him, mycorrhizal fungi generally can utilize soluble carbohydrates from the host plant only. Increasing the rate of photosynthesis by increasing light intensity is directly related to available carbohydrates that might attract fungi to the roots of host plants. This indicates that carbohydrates from host plants play an important role in the formation of mycorrhizae. Their absence or presence in only very small quantities in roots could be directly related to the factors that limit mycorrhizal formation. The physiological mechanism, however, was not examined in the current study because there was no further analysis of the carbohydrate content of the mycorrhizal roots of the seedlings growing at different light intensities.

The soil analysis of the media used in the experiment show a similar nutrient status for both species, except for Phosphate, Ca and Mg (Table 11). The latter element is the important element for dipterocarp mycorrhizae which may improve absorbtion of phosphate by ectomycorrhizal roots (Ashton, 1989). Phosphate and Mg are slightly higher in the soil of *S. leprosula* than in *D. confertus* soil. This may also explain why the number of ectomycorrhizae type formed is higher in *S. leprosula* than in *D. confertus* seedlings.

An increase in light intensity above a certain level (in this experiment above 60% of full sunlight) causes a decline in the number of infected roots. It is suggested that the high soil temperature resulting from to the high light intensity affects the physiology of the fungus as well as the roots of the host seedlings.
At lower light intensity, below 25% of full sunlight, a decline of the number of infected roots was also observed. This result indicates that a condition of low light intensity and high phosphate may be inhibitive for the formation and development of ectomycorrhizae. Björkman (1942) used several levels of soil fertility. The light intensities used in Björkman's experiment were 6, 12, 17, 23 and 49% of full sunlight. He found that mycorrhizal development was good in all plants growing under 49% and 23% light intensities. It seems that at these levels of light intensity most of the tree seedlings maintain a positive photosynthetic rate, whereas the soil temperatures do not reach the levels that may influence the physiology of mycorrhizal fungi. Unfortunately there is no information about this in Björkman's experiment. It is unlikely that in Björkman's experiments heat became a limiting factor, as under the conditions of his experiment soil heating was unlikely to occur. Under natural conditions where light intensity is very low, it is unlikely that the seedlings growing on the forest floor reach their maximum photosynthetic rate. At 25% light intensity (the lowest light intensity in this experiment) equal to

approximately 400 mmol/m^2/s in PAR while no value available for Björkman's experiment), seedlings could only reach less than 70% of maximum photosynthetic rate. It is not clear from this experiment whether seedlings need a maximum photosynthetic rate for the optimal formation of ectomycorrhizae. This experiment, however, was done in the greenhouse using inoculated seedlings that may give quite different responses to light in comparison to seedlings growing under natural conditions which have little root development and only superficial roots. Under natural conditions, poor development of mycorrhizal roots might not always be the effect of insufficient supply of carbohydrates, but might also be a strategy of the seedlings to diminish their metabolism to maintain the carbon balance for the symbiosis in this way.

The effects of light and mycorrhizal formation are so closely related that it is impossible to consider the problem of mycorrhizal formation without taking into account the effect of light on root development. Reduction in illuminance to 20% of full daylight greatly reduces the number of new roots produced (Hoffmann, 1967 cited by Marks and Foster, 1973). Another experiment showed that the reduction of illuminance to 15 to 20% intensities virtually stops root growth (Richardson, 1953 cited by Marks and Foster, 1973). Some effect of soil heat balance on the root and mycorrhizal fungi might occur. However, little is known about these mechanisms at work in ectomycorrhizal roots, whether the effect of light as well as of hot soil on root and ectomycorrhizae development is a physical or a physiological effect. These complexities cannot be explained by the present experiment.

Considering the sensitivity of ectomycorrhizal roots to soil heating, it seems that certain types of ectomycorrhizal fungi can adapt to high soil temperatures. Ectomycorrhizal roots of *Shorea balangeran* growing near the coast in Samboja (East Kalimantan) can grow under high soil temperatures (in open areas) and on an extremely infertile sandy soil (the same as *Pisolithus tinctorius* mycorrhizal fungi in pine plantations in Suriname, Dr. T. Limonard, (1994), personal communication). However, deeper sand layers tend to have good aeration, lower soil temperature and may provide survival opportunities for ectomycorrhizal roots. Only one type of light brown mycorrhizae with cottony brown rhizomorph and associated with *Shorea balangeran* was observed (personal observation). This type is similar to the one associated with *Shorea* sp. growing in heath forest (Kerangas) in Longnah (East Kalimantan) on similar soils in the area which was heavily damaged by the great forest fires in 1982/1983.

Another observation in a 12 year old *Shorea polyandra* plantation in Pulau Laut (South Kalimantan) shows chlorotic symptoms after thinning in a part of the crowns where neighbouring trees were removed. Smits (1994) expected a problem due to change of the microclimate for mycorrhizae as an effect of the canopy opening. It is not clear whether the effect of thinning causes either water stress or physiological or physical damage to the mycorrhizal root. This would indicate that mycorrhizal roots which are well adapted to a certain microclimate will suffer when the microclimate is suddenly changed. It is also not clear whether this effect is due to temporary or permanent damage of the mycorrhizae leading to the death of the trees. It was observed that some of these trees were dying while most of them survived and then grew well.

Results presented in Table 9 show that only ectomycorhizal types 1, 2, 3 and 4 were encountered in *Dipterocarpus confertus* seedlings. There are two possible explanations for this. First, only types 1, 2, 3 and 4 are suitable for shade tolerant species while types 5, 6 and 7 specialize on light-demanding species. Specificity of mycorrhizae in relation to light demanding species is found in beech mycorrhizae (Harley and Waid, 1955). Secondly, types 5, 6 and 7 were not available in the inocula from soil taken underneath a *Dipterocarpus confertus* tree. In the seedlings of *Shorea leprosula*, however, all of ectomycorrhizal types could be formed. Little is known about whether one species of mycorrhizal fungus could form different morphological types of mycorrhizal root in different species of plants. Therefore the result of this experiment could not explain the degree of specificity because classification of types was based on morphological types of ectomycorrhizae encountered in the experiment. According to Dr. T. Limonard (1992, personal communication) different types of ectomycorrhizae can be formed by one species of fungus depending on the environmental conditions of the symbiosis such as soil conditions and roots of the host plants. If the second possibility occurred, the result of this experiment may suggest that shade tolerant species will select the most suitable fungus which also needs a low threshold of carbohydrates due to the low carbon gain (photosynthesis) of their host plant. Light demanding species on the other hand could associate with any type of fungus because exchanges between host plant and fungus are not limited by such factors as in the shade tolerant species. Little is known about the selection process in mycorrhizal symbiosis. Some species of ectomycorrhizal fungi, however, show different abilities to use carbohydrates and to accumulate nutrients (Hadi and Santoso, 1988; Omon, 1994).

2.5 Conclusion

The conclusion from this experiment is that light intensity influences the formation of ectomycorrhizae in dipterocarp seedlings. The influence of the light varies between different species. There is no specific difference in the types of mycorrhizae formed in seedlings inoculated with different sources of inocula taken from the same region. The number of ectomycorrhizal infections increases with increasing light intensity as long as soil temperature does not go above a critical threshold for the growth of dipterocarp ectomycorrhizae. The results reported in this chapter confirm that light which is required by the plant to produce carbohydrates is essential to maintain the symbiosis between fungi and plants.

CHAPTER 3

NURSING OF *Shorea lamellata* Foxw. SEEDLINGS

3.1 Introduction

The transfer of carbohydrates from a host plant to the root systems of other receiver plants through mycelial connections has been tested in laboratories under environmentally controlled conditions (Brownlee *et al.*, 1983; Read and Finlay, 1985; Read and Francis, 1985; Söderstrom *et al.*, 1986; Finlay *et al.*, 1985). The results suggest that such transfer might also occur under natural conditions where mycelia from a mycorrhizal root network in the rhizosphere, may play an important role in the energy flow of the forest ecosystem (Amaranthus and Perry, 1989). The consequence of such interconnections is the possibility that seedlings or understorey plants under severe competition for light and nutrients may have access to carbon from neighbouring plants that are in a better positions to exploit light or nutrients (Whittingham and Read, 1982).

This has been confirmed in temperate forests where approximately 60 to 80% of carbohydrates produced through photosynthesis is transported to the root system (see Stenström, 1990). Harley and Smith (1983) also report on the high carbon cost and large sink for carbohydrate in the ectomycorrhizae and roots. There are two possible ways in which mycorrhizal fungi and roots may utilize these carbohydrates. First, mycorrhizal roots may directly utilize carbohydrates readily available in soluble form in the root environment or second, the carbohydrate must be synthesized by the plants and transported to the roots before it can be taken up by the fungi. Since most mycorrhizal fungi show limited or no ability to use cellulose and hemicellulose in pure culture (Smith and Douglas, 1987; Richards, 1987), they probably obtain little of their carbohydrate requirements from the soil. Therefore the host plant is likely to be the main, or possibly the only carbohydrate source for the fungi. The latter possibility is more likely than the first, because if most mycorrhizal fungi could use carbohydrates directly they would be independent of the host plant, which is not the general condition. Only certain species like *Paxillus* spp. and *Thelephora terrestris* seem to be facultative ectomycorrhizae.

The transport pathway of carbohydrates within large trees and surrounding plants has never been demonstrated under field conditions due to technical difficulties. Tracing the transport of assimilation products from the crown to the root system of a tree, as well as to the external environment (such as seedlings growing around the tree) is considered technically very difficult to accomplish in the forest due to: a) the complexities and the extent of the root system, b) difficulties in handling the material such as radioactive substances in the forest because of regulations, and c) the large size of the trees especially in a dipterocarp species where it would be extremely difficult, for example to apply ^{14}C tracer in the forest canopy.

One of the methods often thought suitable for this kind of investigation is the use of radioactive ^{14}C for tracing its transport. Unfortunately this method could not be applied in the present study because of difficulties in obtaining permission as well as lack of expertise, funds and technicians to execute the experiment in the field in East Kalimantan (Indonesia). This method has been used to prove the transport of assimilation products to the mycelium of mycorrhizal fungi in laboratory experiments by several researchers but has never been applied in the field. It was therefore decided to apply another approach in the present study i.e., investigating interconnections of mycelia arising after planting of uninoculated seedlings surrounding a large tree (such trees from now on will be indicated as "mother trees").

The objective of this experiment was to determine whether or not the ectomycorrhizae of the mother tree influence the growth and survival of seedlings planted at various distances from the primary root system as an indication for mycorrhizal connection.

3.2 Materials and Methods

3.2.1 Location and execution of the experiment

The study was undertaken at Kilometre 3, south of the main road, in the Wanariset research forest (Fig. 2). For this experiment, a tree that was relatively isolated from other trees of the same species, genus and family was selected as a mother tree. This was done in order to enhance the probability that the mycorrhizal fungi infecting the seedlings after planting originated from that mother tree only. A suitable site was found where a *Shorea lamellata* tree grew relatively far from other potential dipterocarp mother trees. The dipterocarp species taxonomically closest was *Shorea johorensis* growing 80 metres away from the chosen *S. lamellata* mother tree. This site was affected by light burning during the extensive forest fires of 1982/1983 and the overall regeneration of dipterocarp species was sparse.

The seeds used in the experiment were collected from the Wanariset research forest in October 1990, at which time most *Shorea lamellata* trees flowered earlier than the other Dipterocarps trees, during a mass flowering season in this region. The seeds were sown in clean subsoil believed to be not containing any ectomycorrhizal inoculum and were transplanted about one week after germination to plastic containers without inoculation with ectomycorrhizal fungi. All possible contamination during germination was avoided during germination by means of covering the sowing bed with plastic sheets. The media for transplanting consisted of one part of sand and three parts of subsoil. All of these media were pasteurized by means of solarization for four days before transplantation. To avoid infection by undesirable mycorrhizal fungi from the air or by human activity in the greenhouse, all seedlings were isolated (covered) with plastic sheets prior to planting. In November 1990, one week after transplantation, the seedlings were planted in the experimental plot. Before planting, planting holes of 15 x 15 x 15 cm, each 1 metre apart, were prepared in the field. Seedlings were planted in a square plot of 30 x 30 metres in the centre of which the big *Shorea lamellata* (mother tree) was situated (Fig. 9). All planted seedlings were labeled with numbers. There were 899 seedlings planted in this plot.

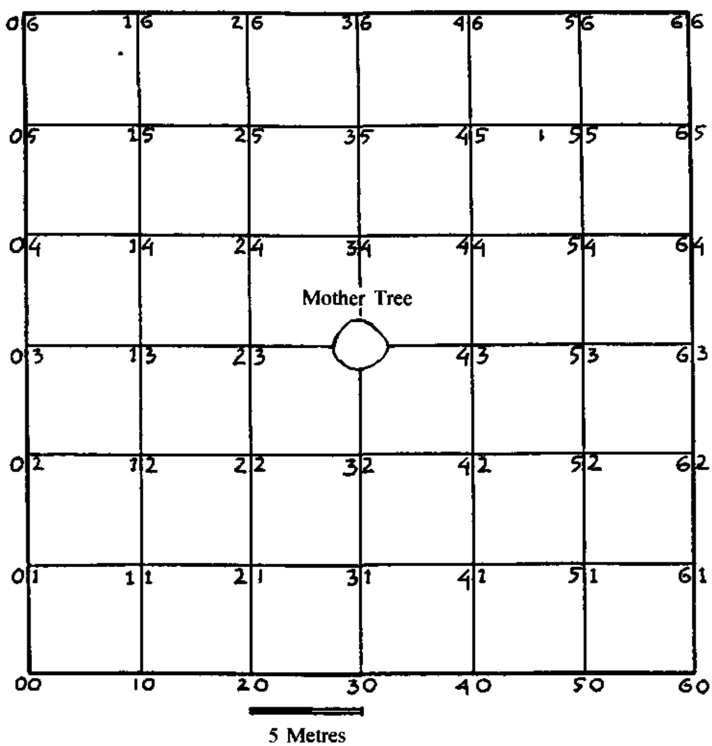


Figure 9. Layout of the nursing tree experimental plot.

The plot was divided into subplots of 5 x 5 metres in order to facilitate data recording. Subplots were numbered according to the coordinate system such as 0.0, 0.1, 0.2,..,6.6. All seedlings planted in the subplots were numbered from 1 to 30. Some plots contain less than 30 seedlings, due to the presence of dead trees and or the presence of the selected mother tree. The coordinate position of the seedlings were determined in order to facilitate data recording and processing in a Geographical Information System (GIS) with the ARC/INFO method.

The parameters measured were the number of leaves and the height of the seedlings. Some of the surviving seedlings were sampled for counting of mycorrhizae. The amount of light that each seedling received was also recorded. The thickness of litter, fermentation and humus layers was measured every 2.5 metres (i.e. two spots per subplot). In June 1993, the soil of the plot was sampled and sent to the Centre for Soil and Agroclimatic Research in Bogor for chemical analysis. The results of soil chemical analysis of these samples are shown in Table 14.

In the first month all seedlings were monitored one to two times a week to determine whether seedling mortality was caused by normal fallout taking place after planting. Dead seedlings were replaced only during the first month after planting. This was done to ensure that seedling mortality after one month was caused by physiological or environmental factors only. The first growth measurements in the plot were made one month after planting. Measurements were repeated every six months. Until June 1992, the growth measurements were carried out four times. Unfortunately measurements in 1993 could not be recorded because many seedlings proved to have been affected by *Agrobacterium tumefaciens*, which causes 'crown gall' disease.

In order to assess the distribution of the roots and thus the potential presence of ectomycorrhizae of the mother tree in the plot, the main root systems of the mother tree was traced during the experiment. There are several methods that can be used to trace the root system of a living tree. One of these methods is a destructive one in which the soil in which the tree is situated is washed out. This method requires a lot of water at very high pressure in order to loosen all of the soil surrounding the tree. This method was used successfully by Kahn (1982), Smits (1994) and Atger (1992) to investigate the root systems of tropical forest trees. In 1987, Smits tried to wash out the root system of *Hopea rudiformis* in the Wanariset forest with a diameter of about 50 cm. To do this, more than 50 m^3 of water were needed to wash only two of the main root courses. This method, however, destroys all vegetation beneath the tree. No such method has been proven to work successfully without any negative impact to either the tree itself or to its direct environment.

The method used in this experiment was the use of a sharp iron pin of 15 mm diameter (see Fig.10). The main root course was traced from above by means of pushing the pin in the ground and the course of the root system is followed as far as possible. Stabbing is done every five to ten centimetres away from the stem base along the big roots. Each stabbing is recorded on a scaled millimetre paper. The results of this method are shown in Figure 11. This method inflicts relatively little damage.

Light reaching each seedling was measured on cloudy days to get a value of the diffuse light each seedlings received in the plot. Light was measured with the Photosynthetic Radiometer with Quantum-Response (PAR meter) type RA 200 Q built by the Bottemanne Weather Instruments Holland. The unit of measurement is a Photosynthetic Active Radiation (PAR) in *micromol/second/meter*^{2}. Because measurements were taken on cloudy days only, conversion was necessary to calculate the actual light value of the clear sky. The conversion factor was obtained by measuring the light under clear and cloudy weather at the same time of the day. The value of this conversion factor was calculated as factor 2.98.

Mycorrhizal infection of the seedling was also recorded. Systematic sampling was done by sampling two vigourous seedlings out of the surviving seedlings in every 5 by 5 metres subplot and observing whether or not the bore mycorrhizae on their roots. The types of ectomycorrhizae were recorded for each seedling by using the method described in Chapter 2.

To count the number of fine roots in relation to the distance from the stem base of the mother tree, root samples were taken every metre up to a distance of 15 metres. Soil core samples of 15 x 15 x 15 cm were taken. Soil cores were washed out carefully following the standard procedures for separating roots from the soil (Schenk, 1982). Root pieces from the mother tree were used as a reference for the recognition of the same roots in the soil cores. The total root length in the samples was estimated by the use of the line transect method described by Giovannetti and Mosse (1980) for mycorrhizal roots.

3.2.2 Data collection and data processing

All the data were stored in a spreadsheet on the basis of the coordinate system and the number of the seedlings in the field. The data were transferred to the ARC/INFO system to be able to sort out them for further analysis of survival and growth of the seedlings at various distance classes from the main root of the mother tree. Regression coefficients of the growth of surviving seedlings at different distances from the mother tree were used to analyze seedling growth. The distances from the root system of the mother tree were classified into classes 0 to 2, 2 to 4, 4 to 6, 6 to 8 and greater than 8 metres. All of the data analysis was done with the Genstat statistical package at the IBN-DLO (Institute for Forestry and Nature Conservation) Wageningen, The Netherlands.

3.3 Results

3.3.1 Growth of the seedlings in relation to distance from the 'mother tree'

There were 899 seedlings planted in the plot. A total of 489 seedlings (54%) survived until the third measurement. Survival after the second and the third

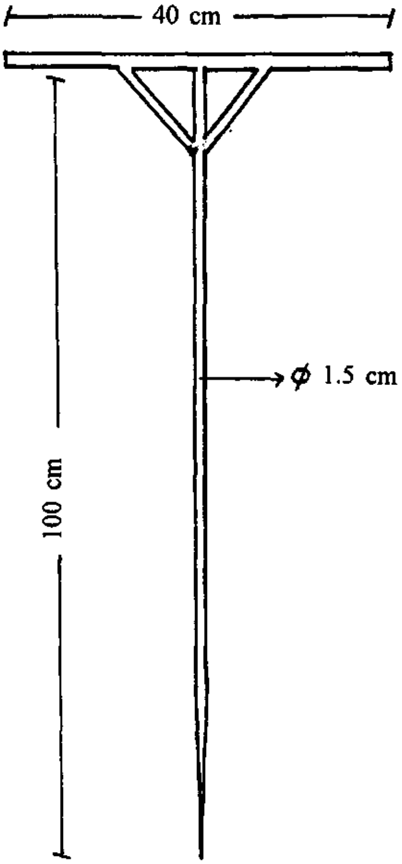


Figure 10. Metal sounding pin used for tracing the extent of roots in the nursing tree experiment

measurement series was not very different from that after the first measurement. This means that a lot of seedlings died during the first 6 months after planting. Visual interpretation of the distribution of the dead seedlings showed that the seedlings planted far away from the root system of the mother tree tended to be clumped while the dead seedlings close to the root system were scattered (Figure 12).

The number of seedlings still growing until the third measurement were 58, 124, 88, 73 and 155 for the five classes respectively. The data analysis shows that there is no significant difference in survival at different distances from the mother tree. The survival of seedlings at each distance was 52 % (0 to 2 m), 54 % (2 to 4 m), 56 % (4 to 6 m), 54 % (6 to 8 m) and 54 % (>8 m).

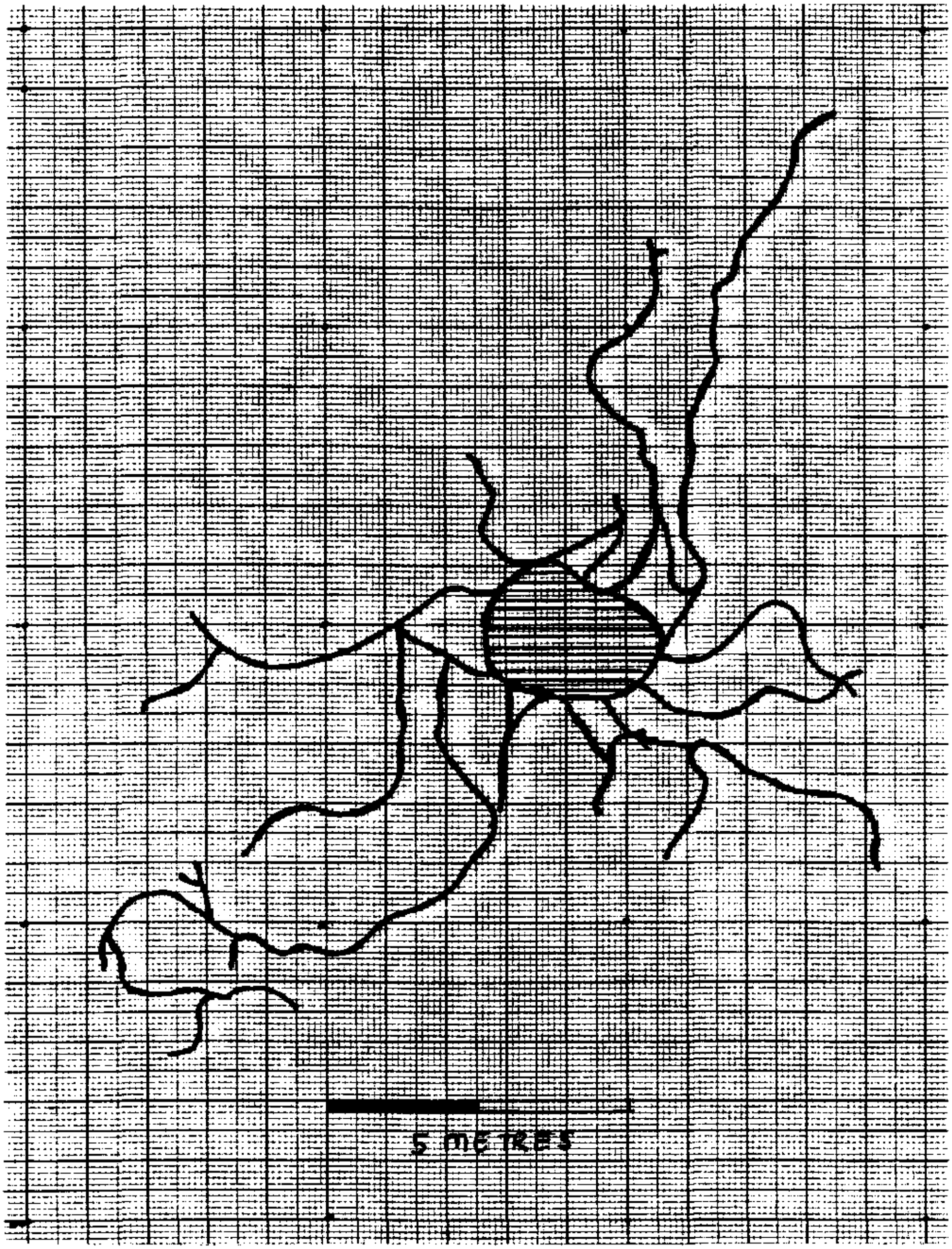


Figure 11. Drawing from the fieldbook, showing bthe main roots to scale their course having been traced by means of stabbing (cf. Fig. 10).

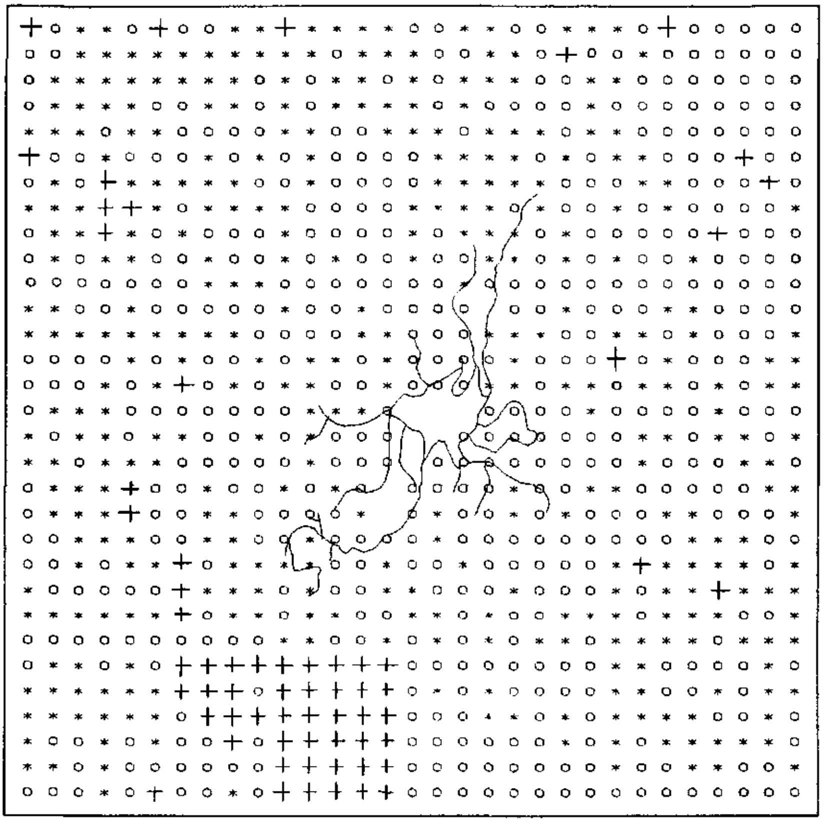


Figure 12. Distribution of dead seedlings in the nursing tree experimental plot(○ = dead seedlings; * = survived seedlings; + = not planted; line = main root system).

The mean thickness of the organic layers in the plot is presented in Table 13.

The regression analysis of organic layer data against the growth of the seedlings showed there was no significant influence of the thickness of the organic layer upon the growth of the seedlings.

Neither light data nor from organic matter data could explain seedling mortality. The light intensity reaching the forest floor in the plot was thought to be too low to raise soil heat to a critical level impeding the growth of dipterocarp ectomycorrhizae.

Table 13. Mean thickness of the organic layer measured at various distances from the main root system of the *Shorea lamellata* mother tree.

Location of measurement (metres from the main root system)	Litter thickness (mm)	Fermentation thickness (mm)	Humus thickness (mm)
<2	(6.7±1.4)	(7.9±1.2)	(8.1±1.4)
2 to 4	(8.5±1.4)	(8.8±2.2)	(9.8±2.1)
4 to 6	(9.3±1.8)	(9.4±1.4)	(10.0±2.0)
6 to 8	(8.6±1.4)	(9.5±2.3)	(8.3±1.4)
>8	(9.9±1.3)	(9.5±2.6)	(1.02±0.3)

The growth curves of seedlings at different distances from the main roots of the mother tree are shown in Figure 13.

Large trees with their crowns exposed to full light in the upper canopy of the forest have greater potential for nursing ability than suppressed trees. Consequently in this experiment it is assumed that mycorrhizal infections come only from the *Shorea lamellata* tree. Fortunately, there was no other dipterocarp species growing neither in the upper canopy nor in the lower layers. Some planted seedlings of 3 years old *Hopea rudiformis* outside the plot could not be expected to be sources of mycorrhizal infection. Ectomycorrhizae from *Hopea rudiformis* seedlings are quite typical (see Smits, 1994), so that they can be identified if present on *Shorea lamellata* seedlings

As presented in Figure 13, seedlings at distances of 4 to 6 and 2 to 4 metres from the main roots of the mother tree grew faster than seedlings at distances of <2, 6 to 8, and >8 metres. An interesting aspect is that the growth of seedlings which are very close to the mother tree (< 2 metres) was slower than those at a distance of 2 to 4 and 4 to 6 metres.

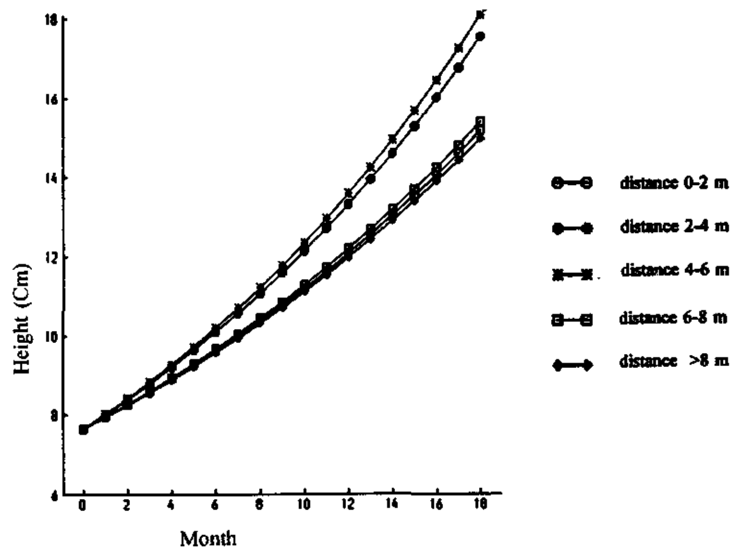


Figure 13. Growth response of *Shorea lamellata* seedlings at various distances from the main root system of the mother tree.

3.3.2 Relation between root distribution and tree crown projection

Figure 11 shows the distribution of the main roots as traced by the stabbing method. The smaller roots which could not be observed by this technique, are assumed to extend further but not very far from the main roots. Root sampling showed that there were no fine roots at a distance greater than 10 metres from the main roots. The hyphae of mycorrhizae may extend still further to take up nutrients further away from the roots. The main roots, however, normally do not extend far beyond the crown projection area. Observation of root extension of some tree species in Malaysia showed that there is a relation between tree diameter and the extension of the root system (Baillie and Mamit, 1983). The relationship between crown diameter and root extension is shown in Figure 15 for several dipterocarp species (after Baillie and Mamit, 1983).

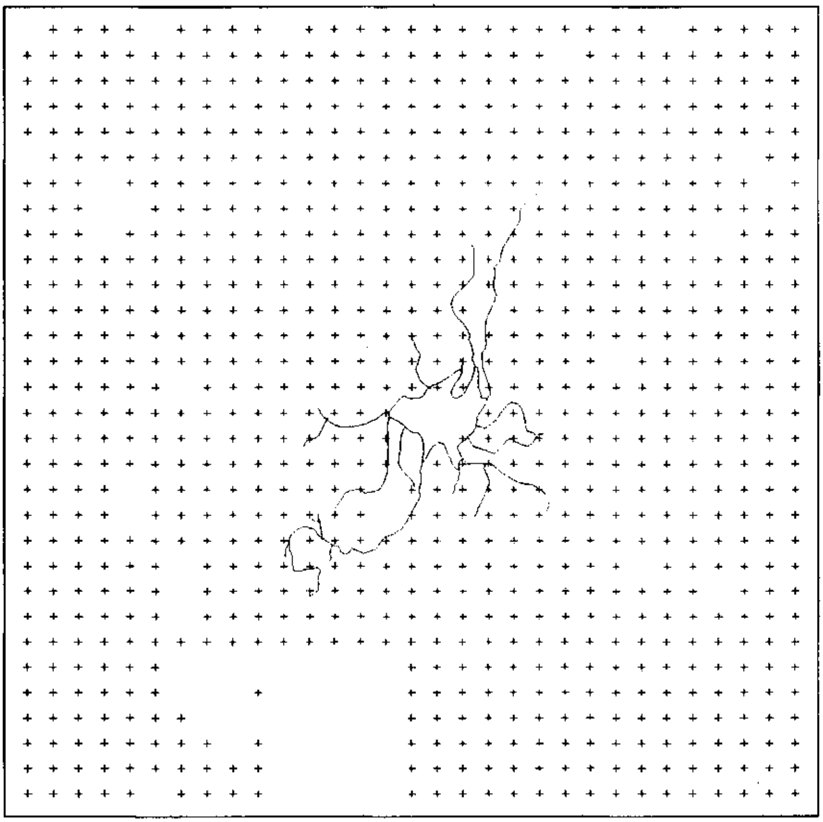


Figure 14. Distribution of the main root system (line) and the position of planted seedlings (+) in the nursing tree experimental plot.

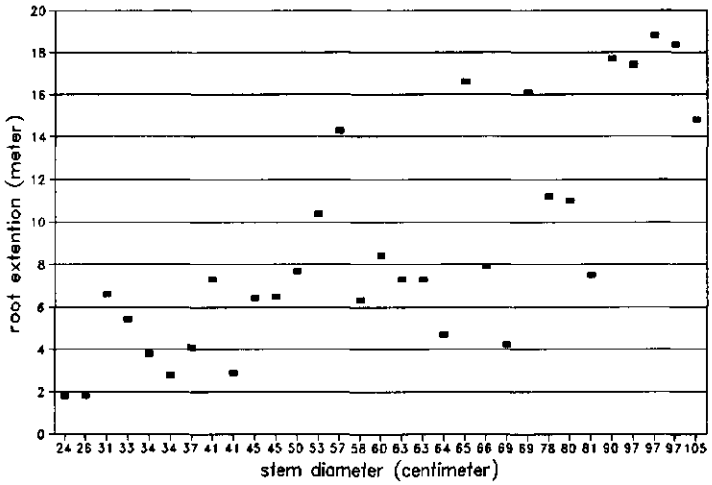


Figure 15. Correlation between stem diameter and root extension of some dipterocarp species (using data from Baillie and Mamit, 1983).

Table 14. Soil nutrients status of the nursing tree experimental plot at Kilometre 3 of the Wanariset Research Forest, East Kalimantan.

Location of the sampling (subplot)	Depth (cm)	Texture (%)			pH		Organic Matter Content (%)			P_2O_5	K_2O	P-Bray (ppm)	Exchangeable Cations (meq/100g)					CEC (meq/ 100g)	Base sat. %	Extractable Al.	
		Sand	Silt	Clay	pH H_2O	KCl	C	N	C/N ratio				Ca	Mg	K	Na	Sum			Al (meq/ 100g)	H) (meq/ 100g)
1.1	10	25	43	31	4.2	3.4	4.16	0.19	22	12	16	10.2	0.81	0.59	0.17	0.13	4.43	9.92	15	4.41	0.56
1.3	10	24	46	30	4.3	3.5	2.74	0.19	15	15	17	14.5	2.04	0.79	0.22	0.08	3.06	8.21	37	2.92	0.32
1.5	10	23	44	33	4.3	3.7	2.39	0.15	18	17	22	13.4	2.04	1.12	0.22	1.76	4.14	9.90	65	1.77	0.19
4.5	10	19	52	29	3.9	3.3	4.2	0.24	18	18	22	9.4	1.25	0.88	0.23	0.62	4.82	12.32	23	4.22	0.43
5.3	10	22	55	23	4.9	3.8	1.98	0.14	14	13	25	8.8	2.04	1.26	0.22	1.59	5.11	7.03	73	1.20	0.15
4.1	10	22	55	23	4.5	3.6	2.32	0.14	17	12	14	13.8	0.77	0.93	0.13	0.03	2.88	7.25	26	3.01	0.35

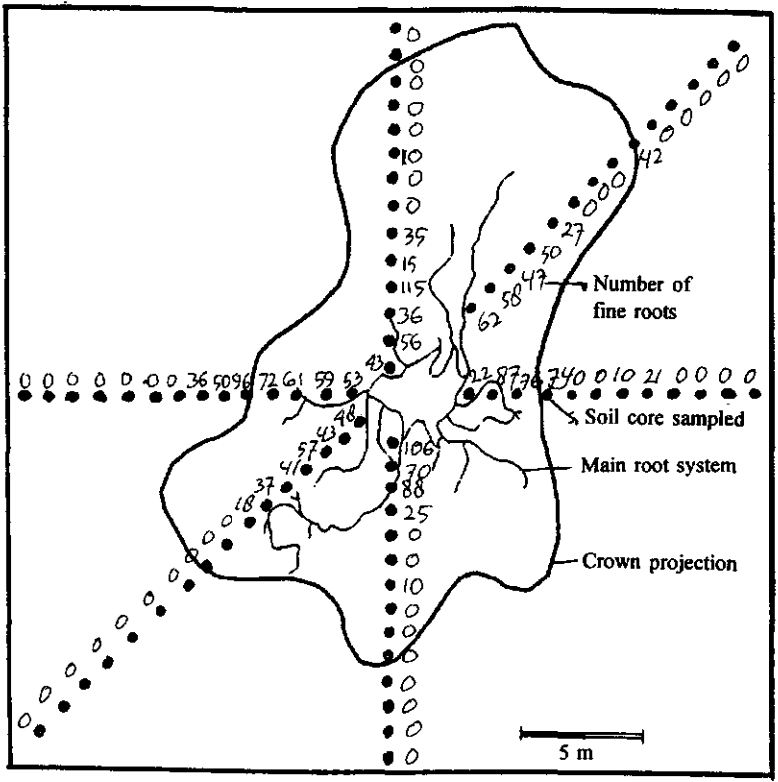


Figure 16. Number of fine roots and their distribution within the crown projection area.

The length of roots encountered at various distances from the tree foot is presented in Table 15.

Table 15. Average length of roots of various diameters in samples at various distances from the tree foot base of the mother tree.

Distance	Fine root (diam. <0.5mm) (cm)	Root diameter 0.5-1.00 mm (cm)	Root diameter 1.00-3.00 mm (cm)	Root diameter >3.00 mm (cm)	Total root length (cm)
<2 m	41	26.5	19.5	21	108
2 to 4 m	41.5	29.5	15.5	11	97.5
4 to 6 m	43.5	32.5	10.5	3.5	90
6 to 8 m	33	15.5	11.5	3	63
>8 m	3	0	21	0	24

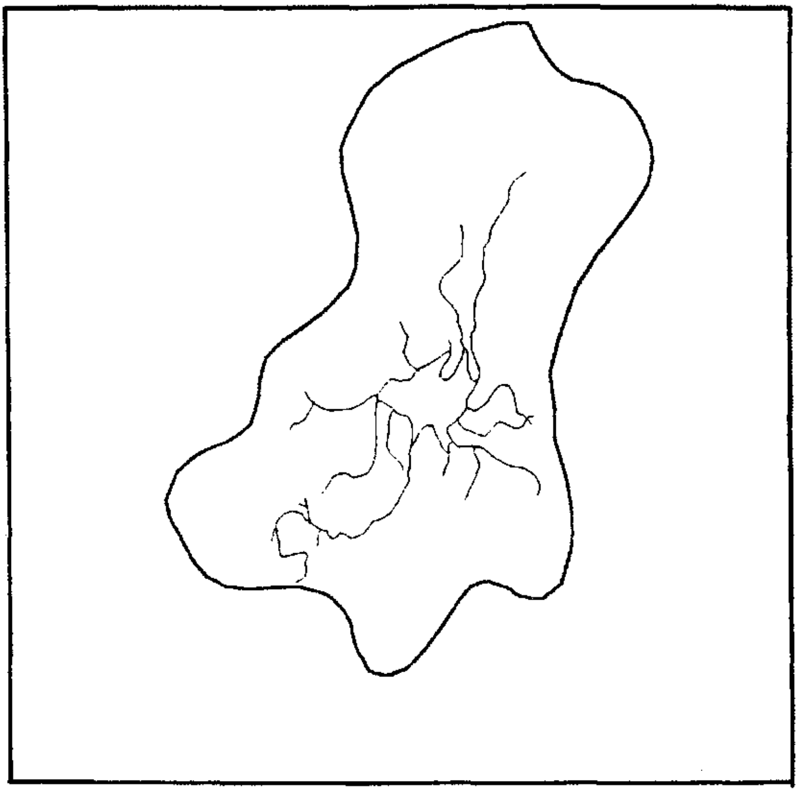


Figure 17. Map of the main root system and the crown projection of the *Shorea lamellata* mother tree.

The average number of roots encountered decreased with increasing distance from the foot tree. The greatest number of roots (particularly roots with diameter of <0.5 mm and 0.5 to 1.0 mm) were found at a distance of 2 to 6 meters from the stem base. The distribution of the fine roots are restricted within the area of the crown projection of the mother tree (Figure 16).

There were no fine roots found further than 10 metres from the stem base.

When the main root system and the crown projection are plotted together (Fig. 17), it can be seen that the projection of the crown is approximately congruent with the map of the distribution of the large root system.

3.3.3 Horizontal root distribution and presence of different types of ectomycorrhizae

The different mycorrhizal types found in the root systems of seedlings are presented in Table 16. All sampled seedlings had mycorrhizal roots. There was no relation between the location of the seedlings in the experimental plot and the type of mycorrhiza. Regarding the number of types encountered in the sampled seedlings in relation to the distance from the mother tree, regression analysis showed that the number of types decreases with decreasing distance ($R^2 = 0.64$). This means that fewer types were found in seedlings growing closer to the trunk of the mother tree.

Table 16. Types of ectomycorrhizae on the roots of *Shorea lamellata* seedlings growing in the plot of the nursing tree experiment.

Subplot	Average distance from the stem (m)	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Number of Types
0.0	---							
0.1	---							
0.2	16.6	+	+	+	+	+	-	5
0.3	14.3	+	+	+	+	+	-	5
0.4	14.3	+	+	+	+	+	-	5
0.5	16.6	-	+	-	+	+	+	4
1.5	13.6	-	+	-	-	-	+	2
1.4	7.6	-	+	-	-	-	+	2
1.3	7.8	-	+	+	-	+	+	4
1.2	10.6	-	+	+	+	+	-	4
1.1	14.6	+	+	+	+	-	-	4
2.5	7.9	-	+	+	+	-	+	4
2.2	4.1	-	+	-	-	-	-	1
2.3	3.2	-	-	-	+	-	-	1
2.1	13	-	+	+	+	-	+	4
2.0	13	-	+	+	-	-	+	3
2.6	14.6	+	+	-	+	-	+	4
3.3	3.5	-	+	-	-	-	-	1
2.4	3.6	-	+	-	-	-	+	2
3.0	13	-	+	+	-	+	+	2
3.1	8	-	+	-	-	-	+	2
3.2	3	-	+	-	-	-	+	2
3.4	7.8	-	+	-	-	-	+	2
3.5	14.6	-	+	-	+	+	+	4
4.0	16.6	+	+	-	-	+	+	4

Table 16 (Continued)

4.1	10.6	+	-	-	-	-	+	2
4.2	8	+	+	-	-	-	+	3
4.3	8	-	+	-	-	+	+	3
4.4	10.6	-	+	+	+	-	-	3
4.5	14.6	+	-	+	+	+	+	5
5.0	17.6	-	+	+	+	+	+	5
5.1	14.2	-	+	+	+	-	+	4
5.2	12.7	+	+	-	-	+	+	4
5.3	12.7	-	+	-	+	+	+	4
5.4	14.6	+	+	+	+	-	+	5
5.5	17.6	+	+	+	-	+	-	4

Note :

+ :	Type present in the sampled seedlings
- :	Type absent from the sampled seedlings
Type 1 :	Dark coloured mycorrhizae, short with few hyphae,
Type 2 :	Dark brown mycorrhizae, pyramidal
Type 3 :	Yellowish mycorrhizae, white rhizomorph sometimes yellowish
Type 4 :	Dark brown mycorrhizae, rhizomorph brown and straight, similar to Type 5 in the experiment of Chapter 2.
Type 5 :	White shiny colour,sometimes pyramidal with white hyphae.
Type 6 :	Yellow mycorrhizae with yellow hyphae, hyphae rare

Comparison with the mycorrhizal types in natural regeneration of *Dipterocarpus confertus* seedlings based on macroscopic observations (especially with regard to colour and type of ramification) showed that the number of mycorrhizal types in seedlings growing close to the stem of the mother tree (inside the crown projection area) is larger than the number of types on seedling growing further away from the mother tree (Table 17). Moreover, the types from the roots of the mother tree are less numerous than on the roots of seedlings close to the mother tree.

3.4 Discussion

The low impact investigation of the root system used in this experiment gave the same results as obtained by observation of roots using more destructive methods such as those of Kahn (1979) and Atger (1992). Since destructive methods, such as the application of radioactive elements or digging and washing out of the roots are not suitable for continuous observations, the method used in this experiment is a good alternative. However, this method can only locate the main roots of a certain size (approx. diameter > 3 cm), and fine roots can not be recognized by stabbing from above the ground. The experiments by Kahn (1979) and Atger (1992) showed that the fine roots always close to the main roots of the tree. The root system normally does not extent very far away from the trunk because its function is to take up nutrients that are transferred to the above-ground parts of the tree.

Table 17. Number of ectomycorrhizal types found on the seedlings and the mother tree of *Dipterocarpus confertus* under natural conditions.

	Location	Types observed	Remark
Seedlings of *D. confertus*	Underneath the mother tree	1 2 3 4	Sampling from each 5 seedlings
	ca. 20 m from stem of mother tree.	1 3 4 5 6	3 types are similar to the above.
mother tree of *D. confertus*	In crown projection	1 2 *)	Colour is similar to types encountered in seedlings.

*) Soil core samples were taken from three places in the root system area of the mother tree, following the buttresses of the tree. Types of ramification could not be seen completely, but from the broken mycorrhizal roots the types of ramification could still be distinguished.

As shown in Figure 13 the growth of seedlings is fastest at a distance of 2 to 4 metres from the main root, while the slowest growth of seedlings occurred at a distance less than 2 and more than 8 metres. These results may be due to the fact that most of the fine root systems are present at 2 to 6 metres from the main root system. The slower growth of seedlings closer than 2 metres to main roots, might be explained by the results described by Kahn (1982, 1983) and Atger (1992) concerning the development of root systems of tropical trees. They found that development of the tree crown is followed by an equal development of the root system underground.

On the root system of the mature tree, the primary root system which originated from seedlings have grown out from the tree at a considerable distance distally (see Oldeman, 1990). In the mean time an empty space between trunk and the distal roots is filled by the development of a secondary root system. According to Oldeman (1990) the development of the secondary root system begins when the tree crown starts to develop its architectural metamorphosis. Crown architectural metamorphosis is a programmed period of tree development to form subcrowns which repeat an architectural pattern displayed in early branching in each subcrown. Architectural metamorphosis in dipterocarps commences when the trees have reached the mature phase (Edelin, 1984; Halle and Ng, 1979) in which empty space in the crown (between subcrowns) is filled by reiteration. Results from the present study indicate that the primary root system of the trees, after extending distally, seems to be more beneficial for the seedlings than secondary root systems because distal roots can exploit much more nutrients at a considerable distance whereas the secondary root system often forms sinker roots.

When new root tips of the secondary root system develop, the carbohydrate pool is rapidly utilized for the formation of new ectomycorrhizal roots and this will cause rapid depletion of soil nutrients near the base of the mother tree which leads to competition with the seedlings underneath, either for water or for nutrients. Another possible explanation for the slower growth of the seedlings near the stem is that the stem flow of the dipterocarp tree (which is usually high in resin content) may negatively influence the growth of mycorrhizal seedlings underneath.

Results from the present experiment confirmed that root infection by ectomycorrhizal fungi through root to root contact is the main source of mycorrhizal infection for seedlings in the forest. The clumping of the dead seedlings indicated that the area far away from the root system might not contain mycorrhizal fungal propagules that facilitate infection of the seedlings. Although some of the dead seedlings were present within the area of the root system, it is not yet clear why such seedlings failed to form mycorrhizae. One possible reason is that seedlings died due to having difficulties recovering from the transplanting stress (Al-Abras *et al.*, 1989). Under natural conditions, seedlings may become infected soon after germination by propagules originating from the mycorrhizal hyphae on the adult tree (Read, 1991). The clumping habit of dipterocarp species in the natural forest may be due to the primary mycorrhizal infection originating from their mother trees of seeds after germination. The ecological significance of this mechanism is the inefficiency of seed dispersal by wind in dipterocarp species (Beccari, 1904; Burgess, 1972; John, 1987). It will be an advantage for seedlings to be infected by ectomycorrhizal mycelia of their mother trees. If specificity of dipterocarp mycorrhizae does occur, this mechanism will facilitate the seedlings obtaining the appropriate fungi from their mother tree.

When seeds fall and germinate within the area of the root system of the mother tree, they become infected by mycorrhizae through direct contact with the mycelium of ectomycorrhizal roots of the mother tree. This way, there always is a direct connection between the roots of the mother tree and the seedling. This has been confirmed experimentally in *Betula* ectomycorrhizae (Fleming, 1983), when high concentrations of carbon are derived from the crown by the root system of the tree. Since there is interconnecting mycelium between plants, they may have a flow of carbon from high concentration (sources) to low concentration (sink). The seedlings of dipterocarps growing on the forest floor never reach the maximum photosynthetic rate. This supports the view that the carbohydrate content of the root systems of seedlings usually lies below the carbohydrate content of the mother trees. This fits with a direction of energy transfer between plants in a forest ecosystem going from the big trees which have a better position in the sun to the seedlings. However, it has never been proven directly as yet by tracing the transfer under field conditions since it is technically very difficult to apply methods such as the application of radioactive elements in the forest. Although a number of laboratory experiments have shown that labelled assimilation can be distributed from the donor plant to the young seedlings (Brownlee *et al.*, 1983; Read, 1971), this mechanism still might be different under natural conditions.

The number of ectomycorrhizal types of seedlings was found to be greater than the number of types of their mother tree, indicating that the seedlings may be infected by early stage fungi that still exist in the roots of the mother tree without able to express themselves as one type, because they dominated by late stage fungi. This would explain why still new types were formed in the seedlings, which were not found in their mother tree. It is also possible that the different types of ectomycorrhizae found on the seedling and its mother tree could be due to the morphological change of some ectomycorrhizal types under the influence of the supply of carbon assimilated from the mother tree canopy (Arnebrant and Söderstrom, 1989).

3.5 Conclusions

The method for investigating the root system of the adult tree described in this experiment is one of the few low impact methods which allows continuous study of the root system. Although only the main root system of the tree can be determined by it, the fine root system can be calculated by sampling procedure.

Mycorrhizal infection by hyphae from ectomycorrhizae of the adult tree is possible. Most of the potential for infection lies within the range of the crown projection of the tree. It was found in this experiment that the growth of the seedlings far away from the main root system of the mother tree (more than 8 metres) was slower than that of seedlings growing close to their mother tree (2 to 6 metres distant). Slow growth of the seedlings was also found for the seedlings growing very close to their mother tree (less than 2 metres), due to the effect of the development of the root system of the adult tree whereby the primary root system functions are transferred to the distal roots when the tree reaches its crown metamorphosis.

Box 2 : Brief description of the species included in the research.

Dipterocarpus confertus Sloot. (Apitong or Keruing tempudau)

Trees can reach up to 45 metres in height with a diameter up to 1.2 metres. Bole cylindrical, buttresses low. Bark grey to pale, scaling with vertically elongated, outer bark thin with many lenticel, inner bark brownish. According to Kessler and Sidiyasa (1994), the anatomical characteristics of adult trees are as follows: Twigs 0.8 to 1 cm in diameter, somewhat flatted, stipule up to 5 cm long and broad, obtuse, soon falling. Petioles 5 to 6 cm long, persistently tufted hairy. Leaves broadly obovate to circular, parchment-like, concave, base usually almost peltate, apex obtuse or shortly acuminate. Fruit almost sessile, calyx densely pale rusty brown hairy, 2 longer calyx lobes up to 14 cm long, 3 shorter lobes up to 1.7 cm long, c. 0.7 cm wide, oblong, recurved to apex.

D. confertus is one of a very few *Dipterocarpus* species that is suitable for plywood because of its low resin content. This species is endemic in Borneo (Ashton, 1982). Trees are less resinous compare with other *Dipterocarpus* species. Wood can be used for roof shingles instead of Ulin (*Eusideroxylon zwageri*) due to the very long straight bole.

The seedlings are easy to recognize in the field, the leaf base always being peltate and hairy; petiole hairy; stipule red, turning brown when falling.

Shorea leprosula Miq. (Red meranti or Meranti tembaga)

Trees can reach up to 60 metres in height, with a diameter of up to 1 metre. Buttresses are small. Crown wide, umbrella-shaped. Resin yellow. Bark greyish brown, V-shape, shallow fissured. Inner bark fibrous, yellowish brown (Kessler and Sidiyasa, 1994).

The seedlings are very easy to recognize in the field because they have domatia at the back side of the leaf along the main nerve. Domatia will become less abundant when seedling reach pole size. Leaves oblong. Domatia continuously along both main and secondary nerve when young. Stipule reddish green, not persistent (Yasman, 1994).

S. leprosula is one of the fastest growing species among the dipterocarp species of which the growth can be more than two cm diameter increment per year. The species is widely distributed in South East Asian rain forests, but is most abundant on the islands of Sumatra and Borneo. This species was the first to have been reported being successfully to be propagated by means of stem cutting (Ardikoesoema and Noerkamal, 1957). In the timber trade this species is known as light meranti. Timber commonly used for construction and plywood.

Box 2 (Continued)

Trees with diameter more than one metre often have brittle heart.

According to Kessler and Sidiyasa (1994) taxonomical characteristic of adult trees are as follows : Twig slender, terete, smooth. Stipule c. 10 cm long, c 3.5 cm wide, oblong, fugacious, falling off early. Petiole 1 to 1.5 cm long. Leaves elliptic to ovate, 8 to 14 cm long, 3.5 to 5.5 cm wide, cream scaly, base obtuse, apex acuminate, secondary vein 12 to 15 pairs, tertiary veins densely ladder-like (scalariform), domatia confluent.

Shorea lamellata Foxw. (White meranti or Meranti putih/Melapi))

Trees can reach the height up to 45 metres with diameter up to 1.8 metres (Kessler and Sidiyasa, 1994). Trees are relatively slow growing. A big trees are characterised by short buttress, fissured grey bark and damar is clear when present. Inner bark is lamellate in which the name of 'lamelata' originated (Figure 18). Trees growing commonly on deep fertile lay-rich soil, preferably growing on the saddle of the hill.

According to Kessler and Sidiyasa (1994) the taxonomical characteristic of adult trees as follows: Twigs slender, rugulose. Stipule c. 3 cm long, c. 1 mm wide, narrowly elliptic falling off early. Petiole 0.8 to 1.5 cm long. Leaves ovate to lanceolate, 5 to 13 cm long, 2 to 6 cm wide, margin wavy, glabrous, parchment-like, base almost equal, wedge shaped, secondary veins 7 to 9 pairs, tertiary veins more or less net-like. Fruit pedical to 2 mm long, 3 longer lobes up to 9 cm long,c. 2 cm wide, 3 shorter lobe up to 6 cm long, c. 0.5 cm wide.

The seedlings are susceptible to *Agrobacterium tumefaciens* which causes the common crown gall disease (Smits *et al.*, 1990). Characteristic of the seedlings : Leaves dark green, secondary veins 7 to 10 pairs, descendent to the back side. Petiole up 2 cm long with pulvinus. Stipule lanceolate sharp up to 3 mm wide.

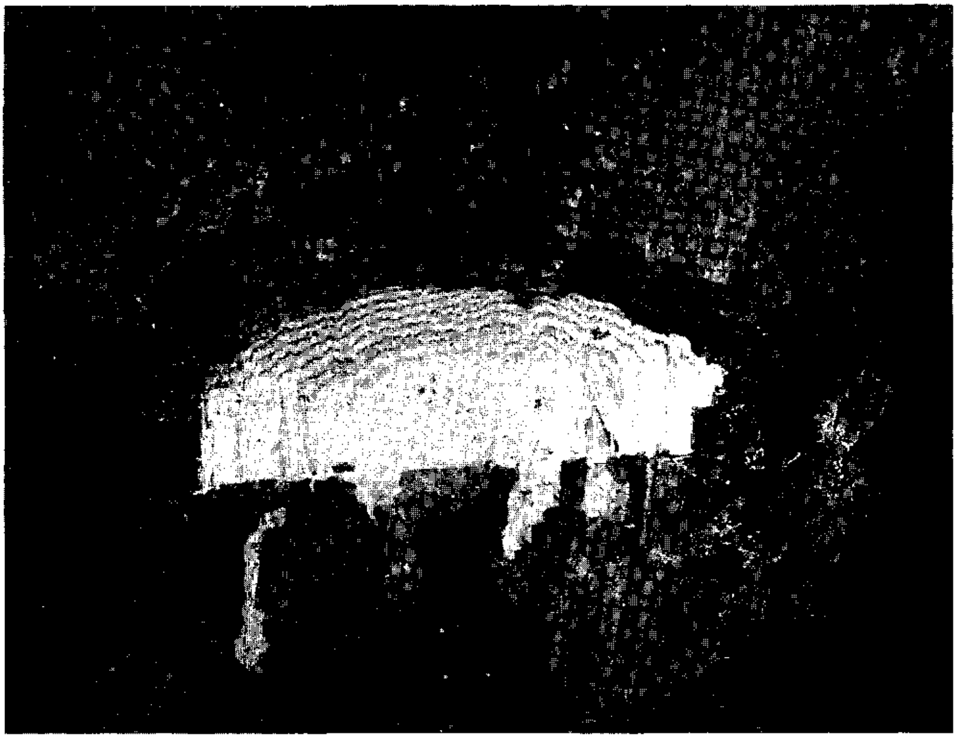


Figure 18. Characteristic view of inner bark of *Shorea lamellata* Foxw., showing of many layers.

CHAPTER 4

RELATION BETWEEN NATURAL REGENERATION, ECTOMYCORRHIZAE, LIGHT, SOIL AND OTHER PHYSICAL FACTORS IN A DIPTEROCARP FOREST

4.1 Introduction

In dipterocarp rain forests, up to 80% of the upper crown canopy is occupied by emergent trees belonging to the family Dipterocarpaceae (Ashton, 1982). These trees play a preponderant role in the primary production and energy flow in this forest. It has never been discussed thoroughly why a single family predominates in this type of forest which is particularly found on poor soils. One of the reasons which may partly explain is that dipterocarp species are obligatorily ectomycorrhizal and so they may use soil nutrients more efficiently than non-mycorrhizal tree species.

Natural regeneration of dipterocarp rain forests is determined by a complex constellation of factors that may differ from other tropical forests. Ectomycorrhizae of Dipterocarpaceae may be the key to the differences between regeneration patterns in Southeast Asian and South American rain forests. Dipterocarp tree species predominate Southeast Asian rain forests and it has been claimed that their ectomycorrhizae enhance the regeneration of understorey seedlings whereas South American rain forests lack this advantage (Oldeman and Fundter, 1986). For the natural regeneration of dipterocarps, it is hypothesized that if the 'mother tree' and the seedlings are interconnected by mycorrhizal mycelia, this may provide additional nutrition to the seedlings and allow them to grow faster than seedlings without contact with the root system of their mother tree.

The importance of ectomycorrhizae in the regeneration of dipterocarp forests is particularly brought to mind after logging operations, due to the fact that the increase in light intensity reaching the soil after the removal of big trees drastically change the microclimate in the forest. This alteration in turn affects the development of mycorrhizae, particularly because of an increase in soil temperature (Smits, 1985). Failure of dipterocarp seedlings to establish on former skid roads is also due to soil compaction which is unfavourable for the development of mycorrhizal roots. Further, a change in the microclimate after wood extraction leads to water stress due to high evaporation rates from the soil, something to which Dipterocarpaceae are sensitive (Ashton, 1982).

In mature forests, light is the most important environmental factor that influences the growth of understorey trees. Under natural conditions the average light intensity on the forest floor is very low, between 0.5 and 2% of full light (Richards, 1952; Whitmore, 1984). This light intensity is considered to be very low for the growth of Dipterocarpaceae and most shade-tolerant species. On the other hand, some of the dipterocarp seedlings show that they can either prolong their growth or exhibit stunted growth under low light intensity. This is due to the presence of dipterocarp ectomycorrhizae, by which seedlings may benefit from adult trees through mycorrhizal interconnections (Chapter 3).

Since carbohydrates built up by photosynthesis are the main factor involved in the exchange between plant and fungus in mycorrhizal symbiosis, light is an important factor. There is an apparent correlation between the presence of ectomycorrhizae in the roots of dipterocarp seedlings and the light intensity that seedlings received (Chapter 2). Light is also one of the important factors which determines the formation of ectomycorrhizae in temperate trees (Björkman, 1942, Hacskaylo, 1973).

The growth of seedlings in natural forests is influenced by water, soil nutrient status, light, and microorganisms (for example mycorrhizal fungi) associated with their root systems. These factors may influence seedling growth either directly or through interactions with other factors. It is thought that ectomycorrhizae play an important role in the forest ecosystem (Allen and Allen, 1992), especially in lowland dipterocarp forests where they determine successful regeneration (Smits, 1983; Janos, 1985). Becker (1983) was the first to investigate the effect of environmental factors such as light on the frequency of mycorrhizal associations in natural dipterocarp forests (especially on *Shorea leprosula* and *S. maxwelliana).* He found that the percentage of infection of *Shorea* seedlings by mycorrhizal fungi depends on the amount of light that seedlings receive. There is very little information regarding the influence of the soil and nutrient status upon mycorrhizal growth in natural dipterocarp forests. Phosphorus and magnesium are the main soil nutrients in dipterocarp forests that may be important for ectomycorrhizae (Baille and Ashton, 1983; Ashton, 1989) because of the ability of mycorrhizae to mobilize these mostly limiting elements from the soil to the plant roots.

The objective of this experiment is to investigate the influence of different factors (light, ectomycorrhizae and soil nutrient complex) that may be involved in the natural regeneration of Dipterocarpaceae.

4.2 Materials and Methods

4.2.1 Description of study area

The plot is situated in the Wanariset research forest, 2 km from the research station at an elevation of about 100 metres above sea level (see Fig. 2). The forest is representative of lowland dipterocarp forest. The study site is one of the few areas that was not affected by the great fires of 1982/1983. The study site is species-rich. About 400 m from the study area, 207 tree species with a diameter above 10 cm were recorded (Sidiyasa and Smits, in prep) in a one-hectare plot of forest, while Kartawinata *et al.*, (1982) recorded 269 species in a 1.8 ha plot at another site approximately 400 m from the study site.

The species of dipterocarp which was investigated in this research plot was *Dipterocarpus confertus.* Natural regeneration of the species for this experiment had become established in April 1989, after the mass fruiting season in this region in 1988. The seeds of the selected species were estimated to have fallen and germinated in December 1988 and January 1989.

The climate is classified as rainfall type A or B according to the Schmidt and Ferguson (1951) classification. The rainfall of the study area during the study period is shown in Table 18. The air temperature was 23 to 24 °C at night and 30 to 33 °C during the day.

4.2.2 Sporocarp inventory

In order to study the dynamics and the degree of specificity of dipterocarp mycorrhizal fungi, two permanent plots were established where the appearance of sporocarps could be monitored regularly. One plot was established in 1986 located at Kilometre 4 (Rintis Wartono) and another was established in 1989 at Kilometre 2 (see Fig. 2). Data presented here were obtained from observations of the latter plot, called 'regeneration plot'.

The plot size was 100 m x 100 m (one hectare). This plot was divided into subplots of 5 m x 5 m. All of the subplots were numbered according to a coordinate system from 0.0 to 20.20. The number of each subplot was marked on an ironwood painted red at the top. All of the observations and measurements were referred to following the stick number in the plot. Figure 20 shows the grid and its squares.

Table 18. Monthly rainfall (in mm) at the Wanariset forest over the years 1988 till 1993.

Month	1988 (mm)	1989 (mm)	1990 (mm)	1991 (mm)	1992 (mm)	1993 (mm)
January	203	127.5	625	223	132	201
February	154	272.5	174	301	6	0
March	164	170	520	233	301	0
April	168	71	533	118	238	251
May	106	16	131	43	249	363
June	119	125.5	219	39	257	183
July	164	108	263	3	274	133
August	78	32	110	0	137	14
September	48	106	107	45	25	170
October	101	88	92	128	247	207
November	166	531.5	126	109	464	435
December	161	496	416	293	304	534
Total	1632	2144	3316	1535	2630	2491

Sources : Wanariset and Bukit Soeharto Weather Stations, East Kalimantan

Observation of sporocarp appearance commenced in November 1989 and was carried out every three days when there was no peak appearance of sporocarps. Whenever many sporocarps appeared, observations were made every 2 days. Observations in the plot were made using the system described in Figure 20 to avoid double recording of the newly appeared sporocarp. Every time a new mushroom was found in the field, a description of that mushroom was made according to the standard format of Largent (1986) and Smits (1994). The date of observation and morphological and other features of the mushrooms were recorded such as smell and taste. The mushroom was then stored in a herbarium (both wet and dry material) and a photograph was taken if not present in the photographic file of mushroom collection at the station. This material was used as a reference for the next observations to determine whether or not a particular mushroom encountered was new for that plot or had already been observed before in the plot or in another plot in the Wanariset forest.

4.2.3 Soil data collection

The inventory of soil and site characteristics in the plot was done according to methods described by Van Bremen and Iriansyah (1989). This method was used as a standard method by the Soil and Site Classification group in the MOF-Tropenbos Kalimantan project, East-Kalimantan.

In a one-hectare plot, starting from the coordinates 0.0 the soil was sampled with an auger to a depth of 120 cm every 10 m in order to characterize the soil with regard to colour, texture, coarse fragments, consistence, mottling, drainage and effective soil depth. Two soil profile pits, 120 cm deep, were made being representative, one for well-draining sites and the other for imperfectly draining sites. The profile pits were described according to the FAO Guidelines for Soil Profile Description (FAO, 1977). The colour notation was according to the Munsell Soil Colour Charts (Munsell, 1975). Descriptions of these two pits are given in Appendix 4.

Five different soil map units were distinguished in the map, on the basis of the soil auguring data. The soil map units of the plot are shown in Figure 19. A description of the map unit codes is given in Table 19.

Table 19. Code used in describing soil map units of the regeneration plot.

Mapping Unit	Geomorphic Component	Slope Gradient	Slope Shape	Drainage Class
u.m.1.3	upper slope	moderately steep	convex	well drained
s.st.3.3	saddle slope	steep	convex	well drained
u.m.5.3	upper slope	moderately steep	complex	well drained
u.st.5.3	upper slope	steep	complex	well drained
c.f.5.3	crest	flat	convex	well drained

Chemical soil data were collected for each map unit by sampling 15 random places with 3 repetitions each. Two different depth intervals were distinguished namely <10 cm and 10 to 20 cm in the upper layer. The soil chemical analysis was done by the Centre for Soil Research in Bogor.

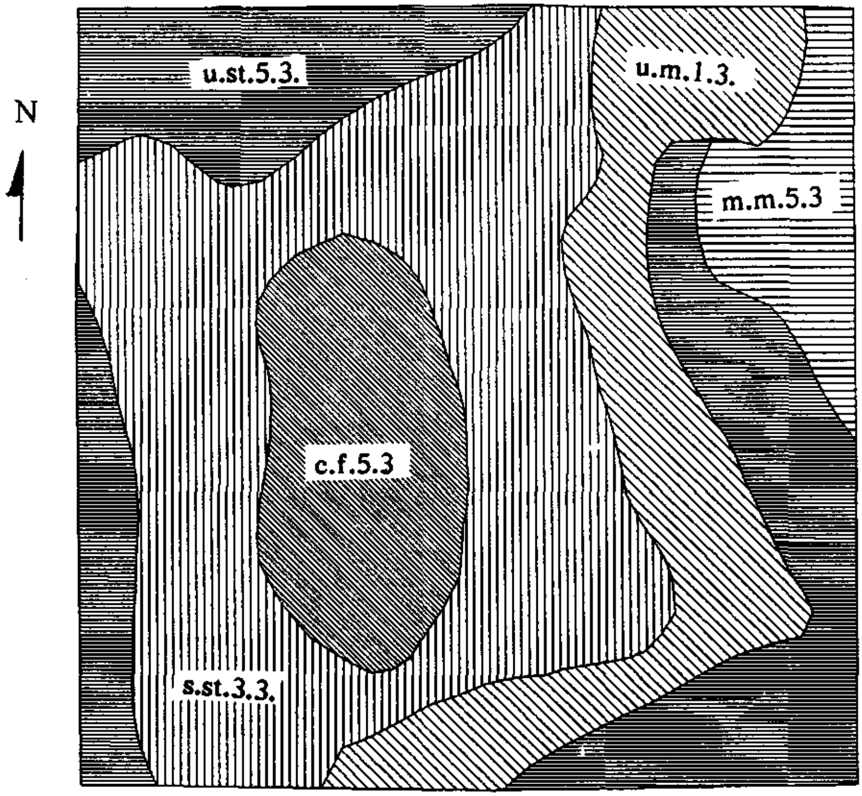


Figure 19. Soil map units of the regeneration plot at Kilometre 2 of the Wanariset forest

The physical soil data were collected for each map unit by sampling 5 random places without repetition. Two different depth intervals were distinguished, namely <5 and 5 to 10 cm in the upper layer. These intervals are considered representative of the depth at which the seedlings mycorrhizal roots are found (Smits, 1994). The procedure for sampling the physical soil data corresponds to the method described by Van Bremen *et al.* (1990). The soil sample analysis for physical data was done by the Soil Laboratory of Mulawarman University in Samarinda (East Kalimantan).

The thickness of litter, fermentation and humus layers were measured in the plot. Measurements were done systematically in every 2.5 x 2.5 m square. The criteria for the designation of these organic horizons are given in Table 20. (Oldeman and Iriansyah, 1993).

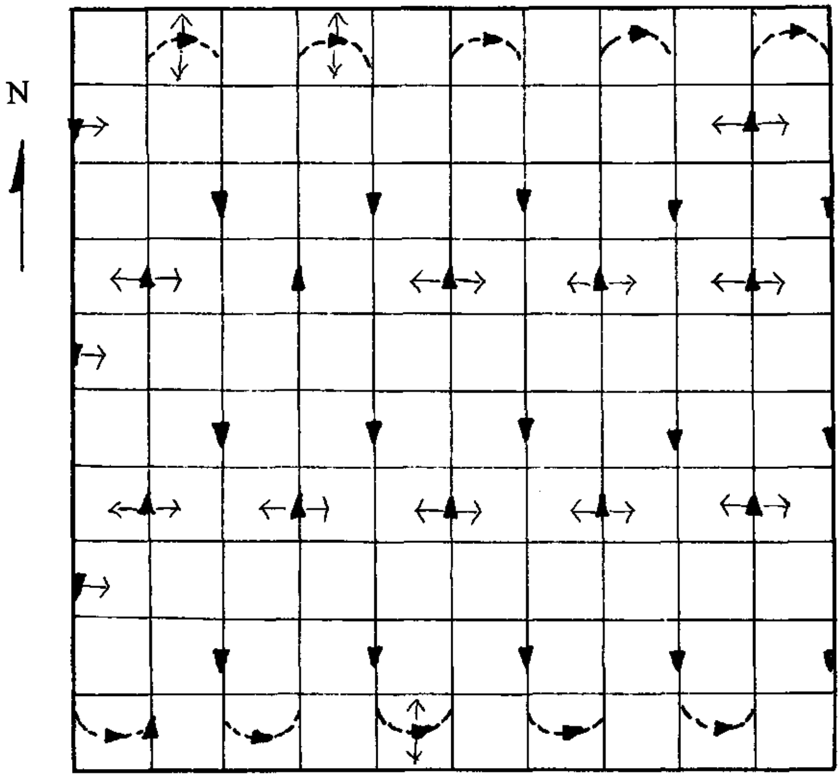


Figure 20. Inspection trail in the plot for observation of sporocarp appearance. Triangular arrowheads: walking direction; thin arrow: looking direction.

4.2.4 Light data measurement

The equipment used for light measurements was a Photosynthetic Radiometer with Quantum-Response (PAR meter) type RA 200 Q built by Bottemanne Weather Instruments Holland. The unit of measurement of Photosynthetic Active Radiation (PAR) is micromol/second/m^2. Measurements were only taken during cloudy days when the light penetrating the canopy and reaching the forest floor was considered to be diffuse. This was done to avoid great fluctuations due to the effect of sunflecks. Measurements were taken in order to be able to calculate the relative value of the

Table 20. Criteria for the designation of organic layers in the soil.

Layer	Non to slightly fragmented litter	Fine organic material	Mineral material
Litter (A_l) Fermentation (A_f) Humus (A_h)	x x	<10% 10 to 70% >70%	 none to some

percentage of light reaching the forest floor. Measurements were done at every 1 x 1 m square resulting in ca. 9975 light measurements over the whole grid (25 squares were not recorded due to a technical omission). It was not possible to collect all the data in a single day so one fixed point was used as the reference for the next day's measurements. The next day's measurements were only continued whenever the light measured at the fixed reference point equalled the reference measurement of the previous day. Measurements were taken between 11.00 am and 2.00 pm. In order to obtain the percentage of the light penetrating through the canopy, the light outside the plot was also measured at the same time. During clear weather, the light at those same points was also measured. These data were used to calculate the value of light reaching the forest floor. The conversion factor between equalled light on cloudy day and on a clear day is 2.07.

4.2.5 Tree measurements and herbarium collection

All trees with a diameter of over 5 cm were measured with respect to height, diameter, crown projection and inner crown cover (Koop, 1989) as well as the height of the first branch, periphery and top of the tree. These measurements were intended to be applicable according to a method such as the SILVISTAR simulation model. Because of time constraints, these results could not be presented in this report. Herbarium samples of the trees in the plot were collected and identified were by taxonomist from Rijkherbarium Leiden and Wanariset Herbarium. Some species could only be identified to the genus instead of species, because of a lack of fertile material, particularly flowers and fruit.

4.2.6 Data processing

All data were stored in a spreadsheet of the computer program "Quattro Pro". Recording systems of the data set were prepared using a Geographical Information System method of analysis (GIS) i.c. the ARC/INFO method. In order to get data sets for statistical analysis from this geographical survey of the data, the ARC/INFO program was used to sort, relate and calculate the data. The data were then transferred to an ASCII file for further regression analysis of the data set using the Genstat 5 statistical package (Payne *et al.*, 1987).

The plot was established four months after the seeds were estimated to have fallen down according to the phenological records of Noor and Smits (in preparation) of the same species in nearby locations. Because of this time lag the number of seedlings germinating could not be counted accurately. The standing dead seedlings, however, still were present in the plot and therefore it was possible to estimate the number of germinated seedlings approximately.

The survival rate of the seedlings was calculated by determining the percentage of surviving seedlings from the estimated number of initially germinated seedlings in the plot 4 months, 17 months and 35 months after germination.

Using the ARC/INFO program, all of the different data sets were put in 'coverage'. The coverages of the plot consisted of seedlings which survived at the first count, second count and third count; the appearance of ectomycorrhizal sporocarps during four years observation; soil data and soil map units; light measurements at every 1 x 1 m square; and litter, fermentation and humus thickness data. All of these data sets were overlaid to examine the influence and the inter-relationships between the parameters measured. A geographical distribution map of each data set was produced from these coverages.

Relationships between the appearance of sporocarps and seedling survival were determined by means of sorting (overlay between two coverages) the number of surviving seedlings at the third count which were closest to where a mushroom appeared within a 10 m radius.

Growth of the seedlings was indicated by regression curves of growth against the time of measurement. These regression coefficients were correlated with the light data, appearance of sporocarps and soil chemical and physical properties, litter, fermentation and humus data.

4.3 Results

4.3.1 Correlation between seedling survival and presence of ectomycorrhizae

Surviving seedlings encountered at the first count were plotted as shown in Figure 21. The first of seedling count was done in June 1989, approximately 6 months after seed germination. Systematic sampling of the 5 x 5 m square was done to calculate the number of dead seedlings after six months. On the average, there were 17 seedlings per square on average with a maximum of 25 and a minimum of 11 seedlings, including dead seedlings. The total number in 400 squares is 400 x 17 seedlings = 6800 seedlings evenlydistributed in the one-hectare plot. These seedlings originated from four mother trees in the plot. In this sampling, dead seedlings were counted from the number of standing dead stems which were still present at the time of the first measurement.

The first measurement of the surviving seedlings resulted in 3471 live seedlings. This means that the percentage of seedlings surviving 4 months after germination was 3741/6800 x 100% = 51.04%. This high mortality is strong correlated with an extremely dry period in the month of April and May 1989. After 17 months (second count) survival of the seedlings of *Dipterocarpus confertus* was 2787/6800 = 40.98% and after 35 months (after the third count) survival was 1820/6800 = 26.77%. Seedling survival at each count is shown in Table 21 and Figure 22.

When distribution patterns (as shown in Fig. 23 A and 23 B) are compare d, it can be seen that mortality of seedlings tends to be clumped. When the data from the sporocarp inventory were plotted in the same way, a relationship become visible between the appearance of sporocarps and the survival of the seedlings. The appearance of sporocarps is an indication of the availability of inoculum propagules for the seedlings.

Spatial relationships between the appearance of sporocarps and the survival of seedlings is shown in Figure 23. The number of surviving seedlings was counted and related to the distance to the nearest sporocarp. The results are presented in number of surviving seedlings decreases with increasing distance from a sporocarp location. Only at a distance of less than one metre was the number of the seedlings found to increase with increasing distance from the sporocarp. This result shows a strong relationship between the availability of the fungal inoculum from which the seedlings obtains its ectomycorrhizal infections and the survival of seedlings after the food sources from cotyledons are depleted.

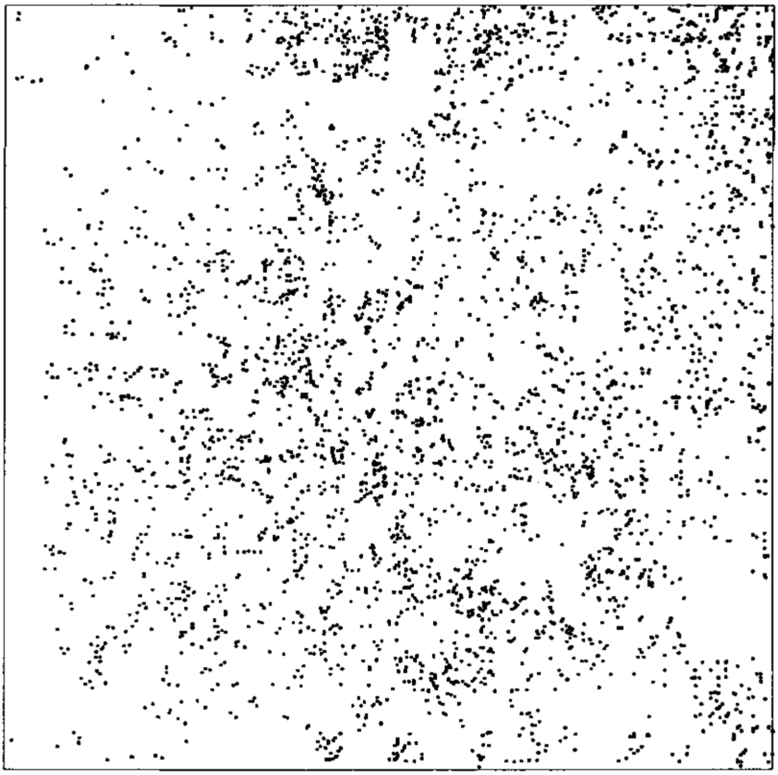


Figure 21. Distribution of surviving *Dipterocarpus confertus* seedlings four months after fruitfall.

Table 21. Survival of *Dipterocarpus confertus* seedlings over 35 months observations.

Observations	Number of surviving seedlings	Survival (%)
germinated seedlings (0 months)	6800	100% with assumption all within a short period germinated
observ. I (4 months)	3471	51.04
observ. II (17 months)	2787	40.98
observ. III (35 months)	1820	26.77

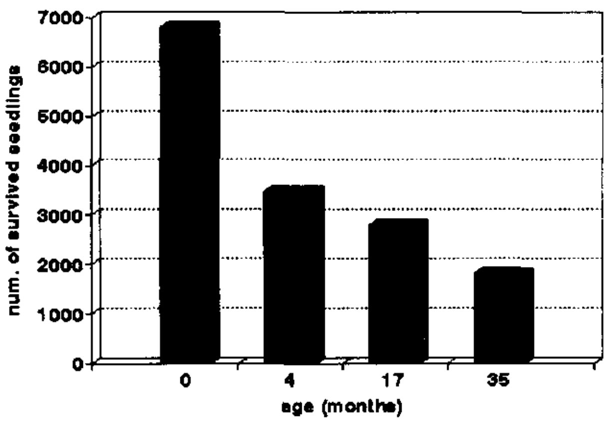


Figure 22. Survival of *Dipterocarpus confertus* seedlings after 35 months.

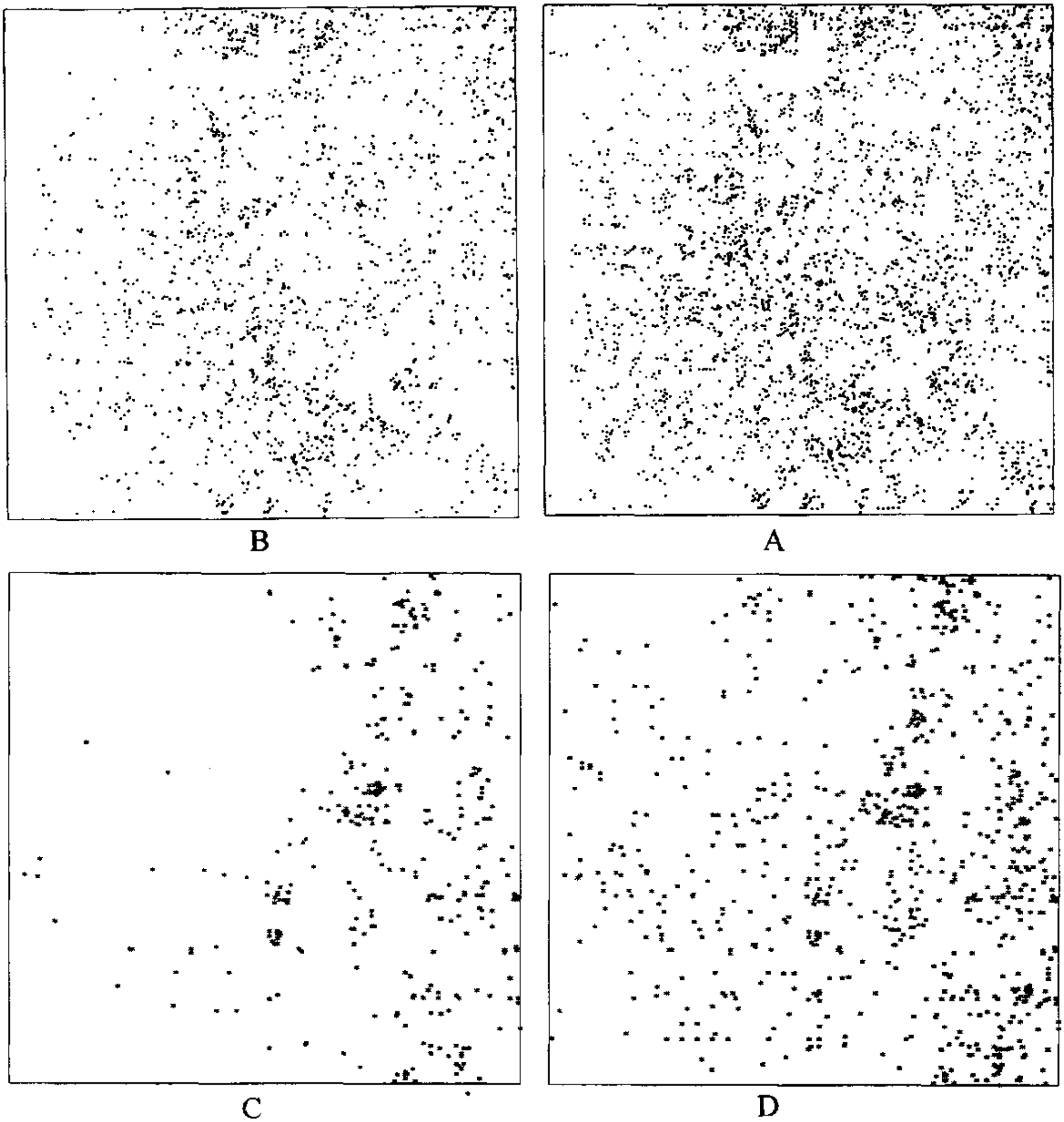


Figure 23. Spatial correlation between ectomycorrhizal sporocarp appreance and seedling survival. A: survived seedling till 1990; B: survived seedling till 1992; C: sporocarp appearance till 1990; D: sporocarp appearance till 1992.

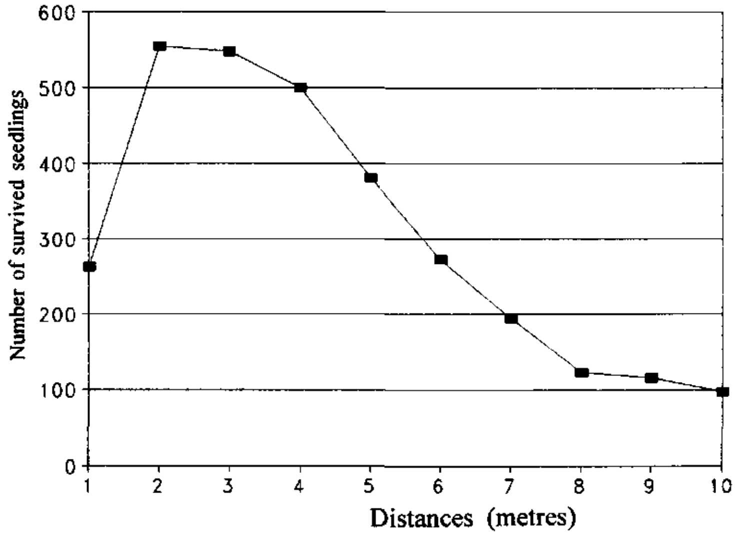


Figure 24. Correlation between the numbers of surviving seedlings and their distance from the location of sporocarp appearance.

4.3.2 Correlation between seedling growth, light and ectomycorrhizae

The distribution and intensity of light on the forest floor over the entire plot is shown in Figure 25. The figure shows that the areas of lowest light intensity tend to be continuous (conjunction) which shows the effect of canopy covering in the plot. The areas of highest light intensity are scattered due to light penetrating through the canopy gaps. In the whole plot, 40% of the area received an average light intensity of less than 2 %, 54% received a light intensity of 2 to 5% and 6% received a light intensity of 5 to 12.5%.

The number of seedlings observed in each light class is presented in Table 22.

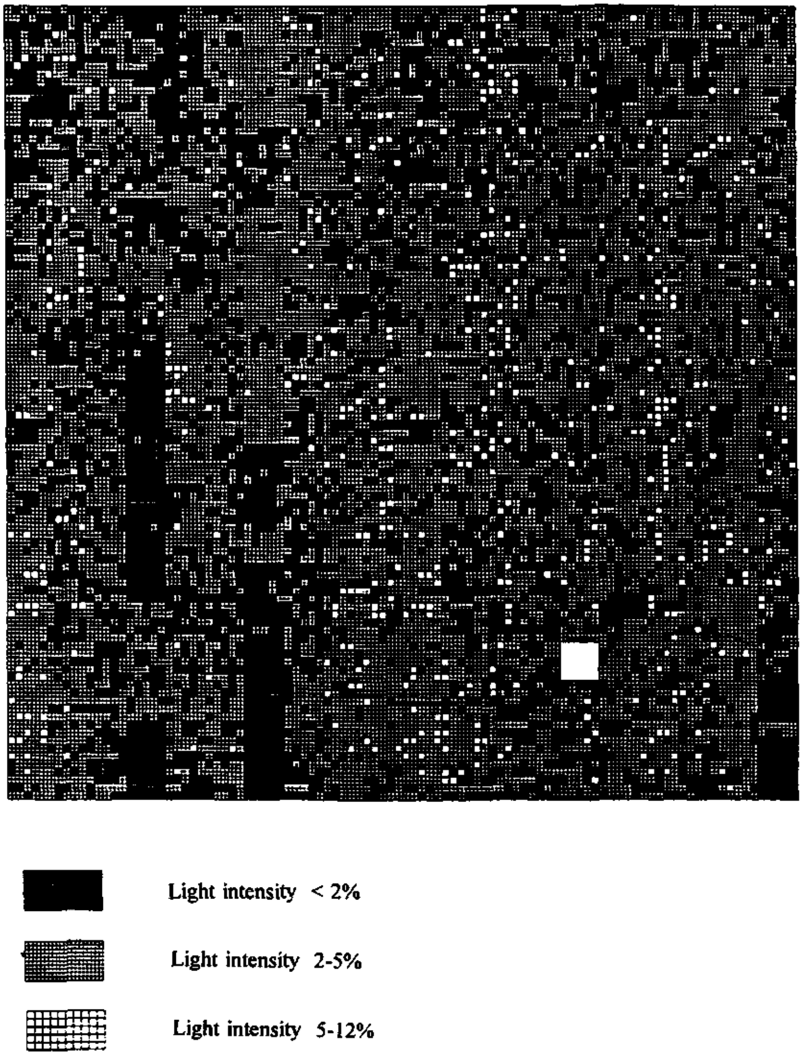


Figure 25. Light distribution in the regeneration plot as recorded by direct measurement on the forest floor (white square is not measured).

Table 22. Number of *Dipterocarpus confertus* seedlings recorded under different light intensities in the regeneration plot for every observation (see 4.2.4).

Light-Cls (PAR)	Light Intens.[1]	Area[2] (m2)	Density[3] (/100m2)	Obsv.I	Obsv.II	Obsv.III
<20	<1.0 %	419	27	115	82	52
20-40	2.0 %	3617	33	1187	951	621
40-60	3.0 %	2674	37	988	798	524
60-80	4.5 %	1885	36	688	543	359
80-100	6.0 %	877	34	295	238	145
100-120	7.0 %	302	30	90	80	54
120-140	8.0 %	50	52	26	19	11
140-160	9.5 %	91	34	31	29	18
160-180	10.5 %	49	35	17	15	12
180-200	12.0 %	7	43	3	3	3
>200	>12.5 %	4	50	2	2	1

Notes : 1) % light intensity is calculated from PAR measured in the plot divided by light measured outside the plot (PAR = 1800 mmol/m2/s).

2) Area of light is counted from the number of 1 m2 square in each light class range .

3) Density is calculated as the number of seedlings surviving at first count (Obsv.I) divided by area of the light class in which they occur.

Regarding the growth of *Dipterocarpus confertus* seedlings in the plot (whole population), the result of regression analysis showed that there was no significant influence upon the growth of the seedlings of tested factors such as light intensity, distance to the mother trees, availability of mycorrhizal propagules, soil nutrients and soil physical properties.

4.3.3 Correlation between seedling growth and soil chemical and physical properties

The variance analysis of the soil chemical data showed that there was no significant difference between the map unit with respect to Na ($F=2.05$; $P<0.16$), Ca ($F=0.84$; $P<0.53$) and P ($F=5.68$; $P<0.12$). Significant differences between map units were found with respect to content of sand ($F=45.58$; $P<0.001$), silt ($F=14.51$; $P<0.001$), clay ($F=41.66$; $P<0.001$), C ($F=12.47$; $P<0.001$), N ($F=23.93$; $P<0.001$), C/N ratio ($F=23.91$; $P<0.001$), pH ($F=18.67$; $P<0.05$), Mg ($F=40.12$; $P<0.001$), Al ($F=131.07$; $P<0.001$) K ($F=8.09$; $P<0.05$), and cation exchange value ($F=44.87$; $P<0.001$). Regarding soil nutrient properties in relation to the growth of the seedlings, regression analysis showed that there was no significant relationship between them.

Soil physical analysis showed there was no significant difference between map units with regard to water at field capacity ($F=1.28$; $P<0.31$) and available water ($F=1.52$; $P<0.23$). The bulk density at different depths was significantly different between map unit ($F=14.94$; $P<0.001$). Regression analysis of soil nutrients and physical properties exhibited no relation to the growth of the seedlings.

Soil nutrient contents and physical properties of the plot are shown in Table 23 and Table 24. Descriptions of two soil pits of the plot are presented in Appendix 4.

These tables show that the nutrient status of the plot is very low compared to common standards of soil nutrients (Appendix 1).

Regression analysis of physical soil data against growth of the seedlings showed there was no significant difference for any parameters between different map units, except for bulk density. This means that there is no influence of the physical soil properties on the growth of the seedlings. It may be noted from the chemical soil analysis that the data show very low to medium amounts of soil nutrients, very low pH, low amounts of exchangeable bases and high aluminium saturation according to the common standards (Van Bremen *et al* ., 1990)

4.3.4 Correlation between light, rainfall and appearance of sporocarps.

There were a total of 941 sporocarps encountered over the observation period, consisting of 89 undetermined species from 22 genera, 24 of which were indentified (Appendix 2). The genera were *Amanita, Aphelaria, Heimiella, Phyloporus, Russula, Boletus, Cortinarius, Lycoperdon, Hydnum, Clitocybe, Inocybe, Laccaria, Boletinus, Paxillus, Cantharelus, Hebeloma, Agaricus, Lepista, Lepiota, Ramaria and Strobilomyces, Tylopilus*. The dominant genera were *Amanita, Boletus* and *Russula*. There were eight species of dipterocarps in the plot which were suspected to be associated with the above ectomycorrhizal fungi. The dipterocarp species in the plot were *Dipterocarpus confertus* Sloot., *Dipterocarpus humeratus* Sloot., *Shorea smithiana* Sym., *Shorea parvifolia* Dyer., *Shorea leprosula* Miq., *Shorea laevis* Ridl., *Hopea mengerawan* Miq., and *Cotylelobium malayanum* Sloot..

Table 23. Average values of chemical soil analysis of the regeneration plot for the five map units.

Soil	Depth	Texture			pH		Organic Contents			HCL 25%		Bray	Exchangeable Cation (NH4-Asetat 1N pH 7)							KCl 1 N	
Mapunit	(cm)	Sand (%)	Silt (%)	Clay (%)	H20	KCL	C (%)	N (%)	C/N ratio	P_2O_5 (mg/100g)	K20 (mg/100g)	P_2O_5 (ppm)	Ca	Mg	K	Na	total	CEC	Base sat (%)	Al (m.e.)	H+
u.m.1.3	0-10	47.00	37.33	15.67	3.93	3.37	2.25	0.12	18.33	7.00	11.67	1.20	0.43	0.33	0.15	0.07	0.99	8.56	11.33	3.91	0.27
(1)	10-20	45.67	37.00	17.33	4.10	3.60	1.04	0.07	14.33	4.33	6.33	1.80	0.14	0.17	0.07	0.04	0.43	6.77	6.33	3.92	0.27
ust.3.3	0-10	45.67	38.00	16.33	3.90	3.40	2.63	0.13	20.00	8.33	12.00	2.13	0.18	0.45	0.17	0.04	0.84	9.00	9.33	3.95	0.26
(2)	10-20	44.00	38.33	17.67	4.10	3.57	1.27	0.08	15.67	5.33	9.67	1.47	0.44	0.23	0.11	0.03	0.81	6.94	11.67	3.96	0.30
u.m.5.3	0-10	45.00	39.33	15.67	3.87	3.33	2.92	0.15	19.00	8.00	12.67	1.83	0.29	0.41	0.18	0.05	0.93	9.11	10.33	4.04	0.32
(3)	10-20	40.67	41.00	18.33	4.03	3.53	1.26	0.08	15.67	5.00	9.00	0.70	0.17	0.25	0.11	0.04	0.57	6.97	8.00	4.03	0.31
ust.5.3	0-10	30.00	48.00	22.00	3.80	3.30	2.80	0.18	15.67	11.00	14.67	1.23	0.19	0.39	0.19	0.05	0.82	11.81	7.00	5.46	0.44
(4)	10-20	28.00	46.00	26.00	3.97	3.60	1.23	0.11	11.33	7.33	11.33	0.57	0.20	0.21	0.11	0.07	0.59	9.15	6.33	5.48	0.43
c.f.5.3	0-10	35.67	46.00	18.33	3.83	3.27	3.33	0.16	21.33	9.00	13.33	4.20	0.29	0.53	0.18	0.08	1.13	10.50	10.67	4.48	0.43
(5)	10-20	35.00	41.67	23.33	4.00	3.43	1.35	0.08	17.33	5.67	9.67	1.27	0.22	0.30	0.14	0.05	0.71	7.70	9.33	4.49	0.41

Table 24. Average values of physical soil analysis of the regeneration plot for the five map units.

Soil	Depth	Water Content (vol %)				Bulk	Water Hold. Cap. (pF2.5-pF4.2)		
Mapunit	(dm)	pF0	pF1.8	pF2.5	pF4.2	Density	(vol %)	(mm)	total (mm)
u.m.1.3	0.5	57.74	31.58	25.02	9.15	1.14	15.87	7.94	7.94
(1)	1.5	57.48	34.38	26.03	13.07	1.18	12.97	19.45	27.38
u.st.3.3	0.5	61.54	28.73	21.02	12.34	1.02	8.68	4.34	4.34
(2)	1.5	53.18	29.44	20.36	10.43	1.26	9.92	14.88	19.23
u.m.5.3	0.5	57.74	29.98	23.32	13.07	1.12	10.26	5.13	5.13
(3)	1.5	53.10	29.81	21.49	13.07	1.16	8.41	12.62	17.75
u.st.5.3	0.5	62.28	29.56	22.75	9.39	1.00	13.36	6.68	6.68
(4)	1.5	55.06	30.36	21.72	12.04	1.16	9.68	14.52	21.20
c.f.5.3	0.5	61.62	25.67	20.61	11.01	1.06	9.60	4.80	4.80
(5)	1.5	51.68	30.48	21.85	11.26	1.28	10.59	15.88	20.69

The number of species and the number of mushrooms which appeared every year during the observation period is presented in Table 25.

Table 25. Number of species and number of mushrooms that appeared in the year 1989 to 1993 in the one-hectare plot in the Wanariset forest.

Year	Number of species appeared	Number of mushrooms
1989	12	53 *)
1990	28	114
1991	88	482
1992	45	210
1993	25	85

*) observation from November to December 1989 only.

The correlation between daily rainfall and the daily appearance of sporocarps during the observation period is shown in Figure 26. From the graph it can be seen that there is only a weak correlation between rainfall and sporocarp appearance.

There is also a weak correlation between monthly rainfall and monthly sporocarp appearance. Regression analysis of these correlations (R^2) of each year gives $R^2 = 0.05$ for the year 1990, $R^2 = 0.20$ for 1991, $R^2 = 0.31$ for 1992, and $R^2 = 0.29$ for 1993. These correlations are presented in histograms (Figures 27 to 30).

Different seasonal patterns of appearance were exhibited by different species of mushrooms. *Amanita, Russula* and *Boletus* appeared almost throughout the year, whereas *Hydnum, Paxillus, Laccaria* and *Cortinarius* appeared at certain times when most of the ectomycorrhizal fungi produced sporocarp in the plot. This was correlated with the time of flushing of the trees in the forest. The temporal sequence of the sporocarp appearance for all species hence is likely to exhibit a peak season as does the flowering of dipterocarp trees.

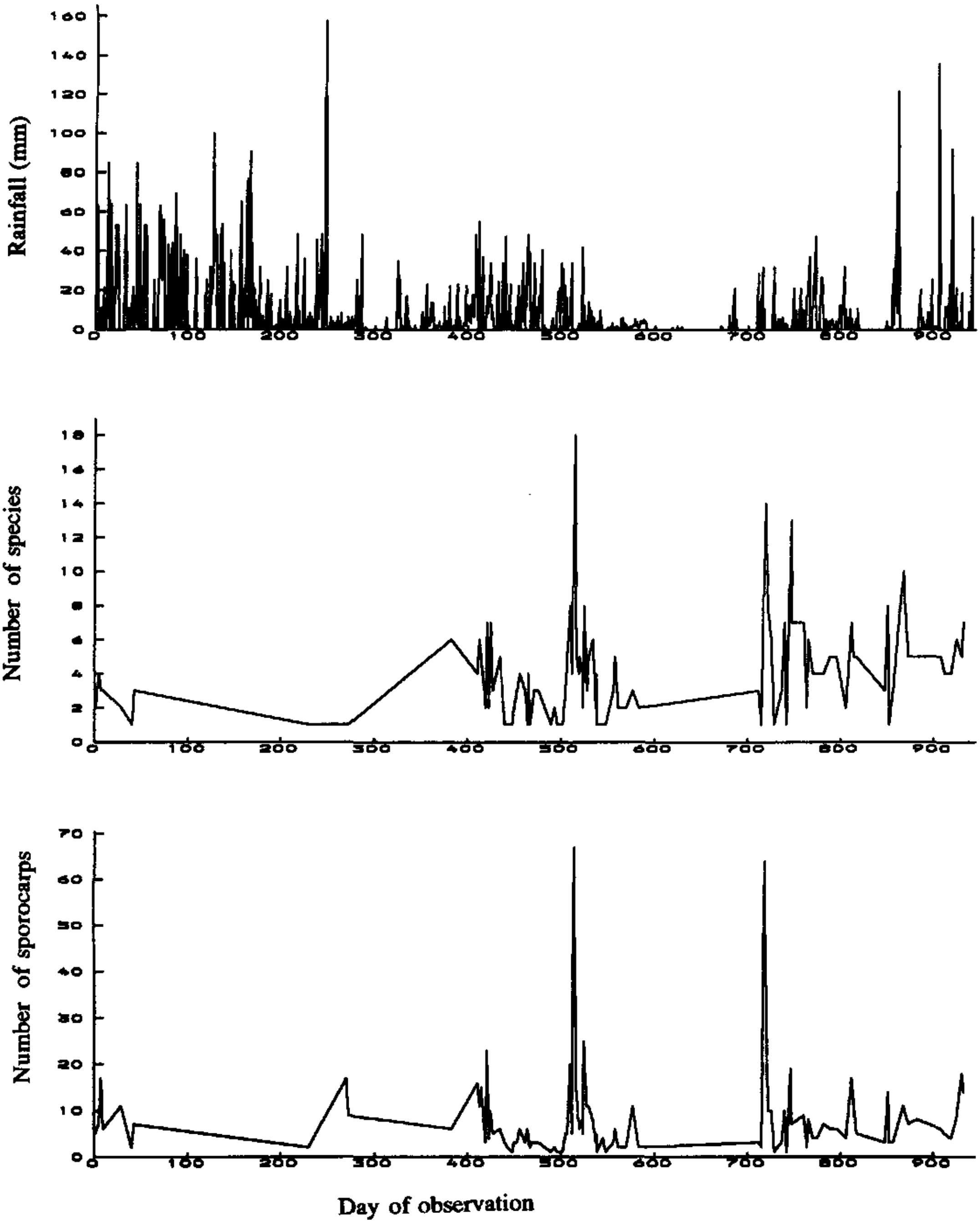


Figure 26. Graphical correlation between daily rainfall and daily appearance of sporocarps.

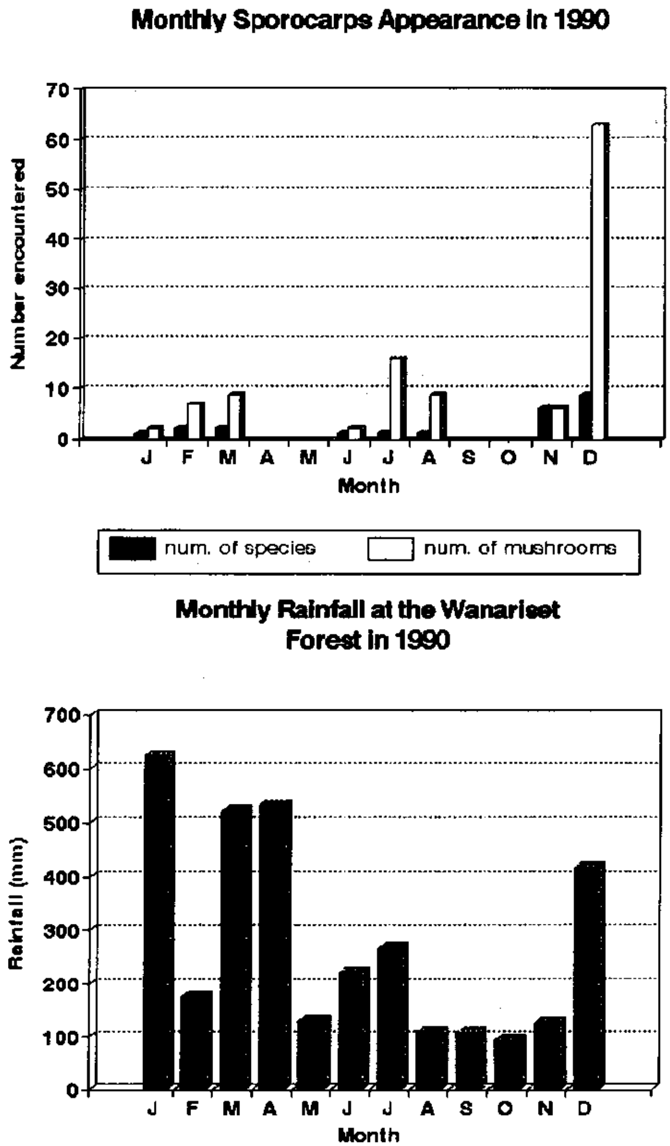


Figure 27. Histogram of monthly rainfall and monthly sporocarp appearance in 1990.

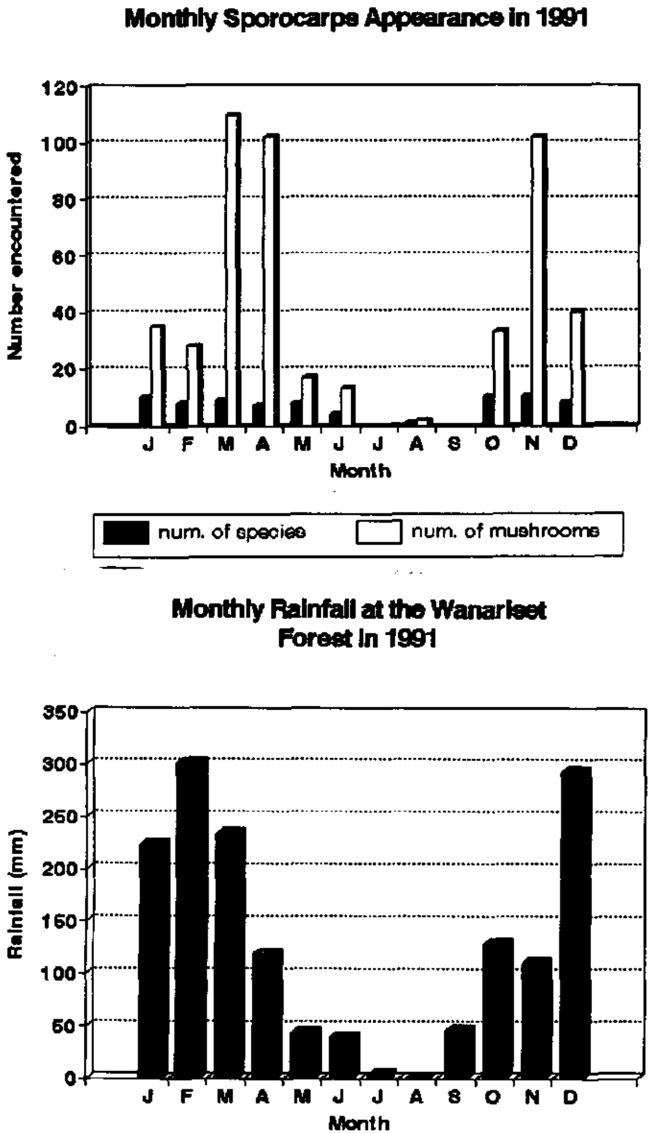
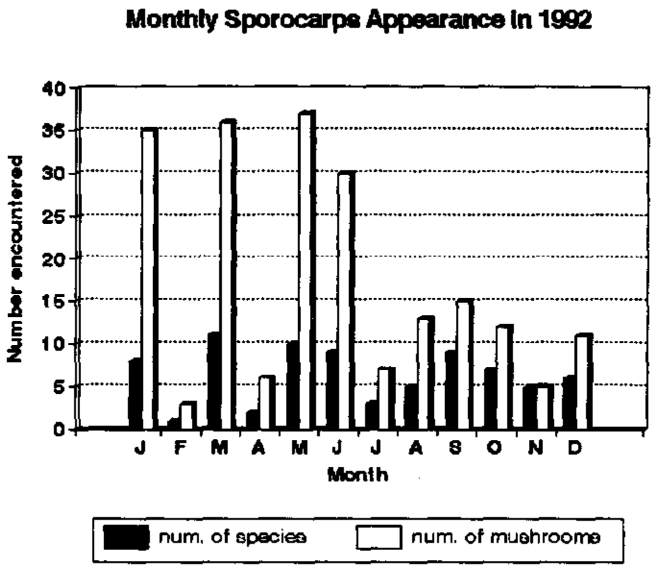


Figure 28. Histogram of monthly rainfall and monthly sporocarp appearance in 1991.



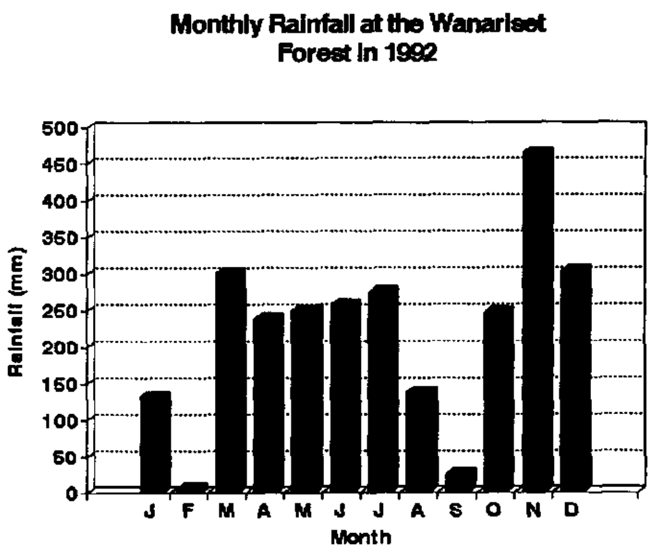
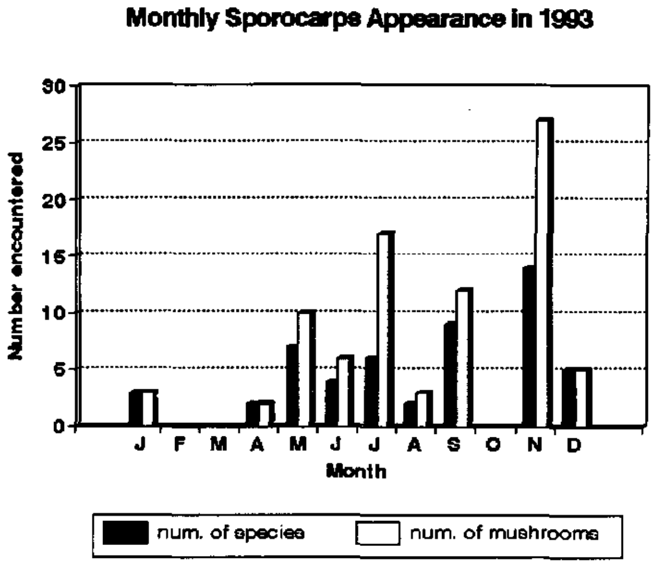


Figure 29. Histogram of monthly rainfall and monthly sporocarp appearance in 1992.



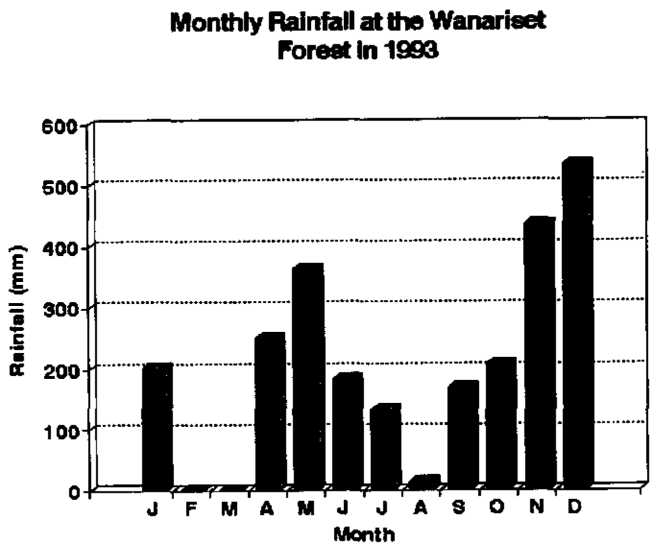


Figure 30. Histogram of monthly rainfall and monthly sporocarp appearance in 1993.

There was no correlation shown between the number of sporocarps which appeared and the amount of light reaching the forest floor. The number of mushrooms appearing in each light intensity region is presented in Table 26.

Table 26. Number of sporocarps appearing in the area of the different light intensity regions.

Light intensity (%)	Area in the plot (m2)	Density (/100m2)	Number of Sporocarps encountered
<3.0%	6710	10.0	669
3.0 to 7.0%	2762	8.0	223
7.0 to 10.0%	352	10.5	37
10.0 to 12.5%	151	14.5	22

4.4 Discussion

Seedling survival of dipterocarps has been discussed thoroughly by Whitmore (1984) who reported large differences in survival rate between species. Survival of *Dipterocarpus confertus* seedlings in this experiment is higher than recorded in previous studies over the same time span. Khoon (1981), however, found 75.9% survival of *Shorea pediculata* in a coastal hill side dipterocarp forest after 2.5 years. He found that leaf predators were the main factor responsible for the mortality. An interesting aspect of his results was that there was no influence of light quality (classified as open, sunflecks and shade) on mortality, which is in accordance with the present experiment. Results from other experiments, however, showed that the mortality of seedlings in the first years was due to the lack of light after germination (Burgess, 1972; Chai, 1973; Fox, 1973). Light is expected to have an indirect influence upon the survival rate through its effect on ectomycorrhizal formation on the roots of the seedlings. Results from Burgess's experiment, however, showed that the mortality of the seedlings in the first year was mainly due to the lack of light after seedling germination and probably to lack of mycorrhizal infection.

Results from the present experiment show that the presence of mycorrhizal inoculum might influence the survival of naturally regenerated *D. confertus* seedlings. Data relating the presence of sporocarps to the numbers of surviving seedlings showed there was a decline in seedling survival with increasing distance from the mushrooms. This indicates the importance of mycorrhizal infection for seedling survival. These results are not in accordance with results from a previous experiment by Becker (1983), who doubted whether mycorrhizal infection affects seedling survival. He thought so because he observed no root hairs in some of the seedlings of *S. leprosula* and *S. maxwelliana* in his experiment. Dipterocarp seedlings have no root hairs, but only fine roots. Most plants dependent on mycorrhizae do not have root hairs (Baylis, 1975). It is quite possible that what Becker thought of as root hairs were actually fine roots. Under natural conditions, dipterocarp species growing in the understorey have very poor and superficial roots. It is possible that observations indicating no fine roots in Becker's experiment might be due to the harvesting procedure of seedlings from the forest probably not being perfect. This would result in the fine roots remaining in the soil, especially for seedlings growing in clay soil.

The chance of a seedling becoming infected after germination depends on the availability of mycorrhizal fungal propagules in the forest soil. The propagules of ectomycorrhizal fungi in the forest soil can be either spores, ectomycorrhizal roots or fungal hyphae. In natural forests, however, most seedlings quickly become infected by mycorrhizal fungi already established in association with adult trees (Read, 1991). Results from the present experiment support the claim that most surviving seedlings exist where mushrooms appear. The sporocarp appearance was used as an indicator of the availability of living mycorrhizal roots. It is not known in this experiment whether seedlings were infected by spores or by mycelial strands. Since the air currents on the forest floor are very weak, spores may not be distributed far from the sporocarps. In the equable climate of rain forest understorey, moreover, the fungal spores might moreover lack dormancy (Ashton, 1989). Therefore mycelial strands from living mycorrhizal roots are thought to be the main sources for seedlings to become infected (cf. Fleming, 1983).

The question arises as to when the seedlings are becoming dependent upon ectomycorrhizal symbiosis? After germination, seedlings rely on food sources from their cotyledons for a certain time, until their leaves can produce carbon compounds by photosynthesis. Unfortunately, very little information is available on the time it takes for seedlings to become independent from their cotyledons under natural conditions. One hypothesis is that mycorrhizal dependency is related to the size of the seed. Larger seed size decreases mycorrhizal dependency or vice versa (Allsopp and Stock, 1992). In general, however, this independence will start as soon as the first green leaf of the seedlings (a pair of leaves for dipterocarp species) reaches maturity to start active photosynthesis or when the food resources in the cotyledons are completely depleted (Dr. G.M. Lechon, 1993 personal communication). This time can vary because of differences in seed size between dipterocarp species and also differences in germination type (see Vogel, 1980). In germination experiments with *Shorea curtisii* it was found, for example, that the starch content of cotyledons disappears within 20 days (Cockburn and Wong, 1969). During the period of depletion of carbohydrates from the cotyledons, light is not a critical factor for the seedlings to become established in the forest. Therefore a very dense carpet of seedlings is often found on the forest floor shortly after a mass flowering season (Ashton, 1964; 1982; Fig. 31).

In the first two years severe natural selection occurs with few seedlings surviving. Availability of ectomycorrhizal inoculum to the seedlings is one of the most important factors involved in this selection. When seedlings become infected they will start to exploit nutrients from the soil. This is the time for seedlings to start carrying out photosynthesis. If they do not, seedlings become stunted without any growth until they become either infected or start to die slowly (Smits, 1982). Seedlings of dipterocarp species growing in greenhouses could survive for four years without growth and start to grow rapidly as soon as mycorrhizal inoculation was introduced (Smits, 1982; Hanafi *et al.*, in press). Even when fertilizer and light were introduced the seedling could not be stimulated to grow (Yasman, 1986 unpublished data). These results point out that seedlings of dipterocarp will not actively photosynthesise as long as there are no ectomycorrhizae introduced. For temperate tree species, ectomycorrhizal symbiosis especially in case of facultative mycotrophs, could become less important if availability of nutrients, especially nitrogen and phosphorus are not limiting factors (Richards, 1987; Bagyaraj, 1989).

Sporocarp appearance observed in this plot was used as an indication for the availability of ectomycorrhizal fungal propagules below ground. This parametric relationship has been confirmed in temperate mycorrhizae. The amount of mycorrhizae underground shows a positive correlation with the number of sporocarps appearing above ground. This has been confirmed in the mycorrhizae of Douglas fir plantations (Jansen, 1988) and in *Pinus sylvestris* (Termorshuizen and Schaffers, 1989) in the Netherlands. However, this relation is not always exhibited due to the fact that not all mycorrhizal fungi form sporocarps regularly (Menge and Grand, 1978; Danielson and Pruden, 1989). However, as far as the availability of mycorrhizal fungal propagules is concerned, a relationship between the appearance of sporocarps and the availability of mycorrhizal roots below ground is expected. Therefore these assumptions were used as a basis to relate the location of appearance of the sporocarps in the forest to the chance of the seedlings becoming infected by mycorrhizal root propagules.

Since not all ectomycorrhizal fungi form fruiting bodies regularly, availability of mycorrhizal propagules may be much greater than can be observed from sporocarps. Mycorrhizal fungal propagules for dipterocarp seedlings on the forest floor can also originate from mycorrhizal roots of non-dipterocarp species. However, non-dipterocarp ectomycorrhizal propagules (originating for instance from the Fagaceae and some Myrtaceae) are unlikely to be potential inoculum sources (cf. Becker, 1983) in the plot, because their growth is suppressed under emergent trees. Therefore, the appearance of sporocarps is thought to be an

Figure 31. Dense dipterocarp regeneration (*Shorea polyandra*) at Pulau Laut (South Kalimantan) after the mass flowering season.

indication of ectomycorrhizal fungi associated with upper storey dipterocarps.

The light intensity reaching the forest floor was very low. About 40 percent of the area in the plot had a light intensity of less than 2% of full sunlight (Table 26). This light intensity is considered to be a limiting factor for mycorrhizal formation. According to Nylund and Unestam (1982), the initial phase in the sequence of events of ectomycorrhizal formation appears to be controlled mainly by the host. In the early stage of seedling growth where most carbohydrate sources derive from the cotyledons, the infection of root tips by mycorrhizae may occur and is not limited by low light intensity. Thereafter, when carbohydrates reserves have diminished, light becomes more important due to a greater utilization of carbohydrates by both mycorrhizae and plants. Therefore, even under low light intensity in natural forests, seedlings may be able to form mycorrhizae if roots meet mycelial propagules from germinated or nearby established ectomycorrhizal hyphae. However, this initial period of primary infection is restricted by the limited carbohydrate level of the seedlings, as soon as carbohydrate reserves from the cotyledons are depleted. Secondary infection after this will depend upon carbohydrate production by photosynthesis in the seedlings. Under natural conditions the mechanism of mycorrhizal infection by fungal propagules is facilitated, as seedlings become integrated into the network of mycelial strands and so are potentially able to utilize nutrients or carbohydrate from carbohydrate pool in the soil at a considerable distance from their own root systems.

The dipterocarp species growing in the plot (Appendix 3) included *D. confertus* as well as *Shorea smithiana, Hopea mengerawan, Shorea laevis, S. leprosula and S. parvifolia* which are also considered to be potential sources for mycorrhizal infection for the seedlings of *D. confertus*. If the seedlings of *D. confertus* do indeed form mycelial networks with other species of mother trees this may influence the growth of the seedlings in the same way as with their own mother trees. This may be an explanation as to why there was no influence changing with respect to distance from the mother trees, as found in a further experiment (cf. Chapter 5). Similarly the lack of influence of light intensity on the growth of seedlings due to the effect being diminished by the existence of different mother trees in the plot, and by ectomycorrhizal guilds.

The results of the soil data analyses showed that there were no significant relations between the soil nutrients and the physical soil properties of the plot and the growth of *Dipterocarpus confertus* seedlings. There are two possible explanations. First : that all parameters measured in these chemical and physical soil data show too little variation in too small an area to distinguish their effect on growth of the seedlings. Secondly : that methods used to classify the soil map units which are used for soil sampling for chemical and physical analysis are not suitable for small plots. The method used here was the standard method described by Van Bremen *et al.* (1990) based on guidelines for soil and site classification from FAO. It is suggested by the present author that in order to analyze soil properties in a small plot it may be much better to sample the soil systematically rather than to classify the soil into map units and then take samples based on that map unit.

Regarding the lack of significant relationships between seedling growth and the variables measured, there are some possible explanations for this. First, growth of seedlings is influenced by root competition with other species, which was not determined in this experiment. Second, a non significant difference in seedling growth may have been due to the fact that many seedlings in the plot being attacked by top borers (see Figure 32) that may explain why seedling height at the third measurement did not increase or was even less than the first and second measurements (data not shown). Top borer pests that particularly attack dipterocarp seedlings of the genus *Dipterocarpus* have indeed been observed in the Wanariset forest (Smits *et al.*, 1990). A third possibility is that seedlings have great variations in height at the first measurement due to differences in seed size, which caused differences in food reserves. Regression analysis of growth of

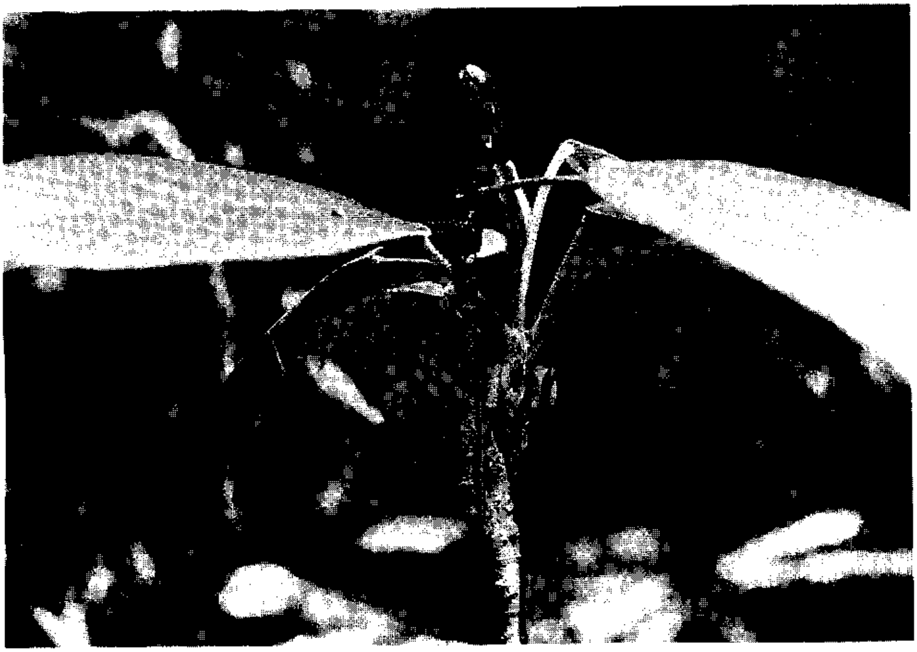


Figure 32. Top damage of *Dipterocarpus confertus* seedlings in the natural forest caused by top borer.

seedlings growing in different map units showed that there were significant height differences between the map units at the first measurement. This result suggests that there was quite some variation in seedling size at the time of measurement. This variation could not be traced as a result of either genetic or environmental factors.

Very little is known regarding the causes of sporocarp production by mycorrhizal fungi. In temperate zones, increasing soil temperature may increase the production of sporocarps (Agerer, 1985). In tropical rain forests, the fluctuation of soil temperature is not great. In some open spots in the Wanariset forest where the light or sunflecks are much higher than other places, sporocarp occur more frequently (Smits, 1994). Data from the present experiment show that there is no correlation between light intensity reaching the forest floor and the number of sporocarps appearing. The light penetrating the canopy might not be sufficient to raise soil temperature sufficiently to create significant temperature differences between different regions due to very low light intensity reaching the forest floor. If there is an effect of soil temperature, however, the increase in soil temperature seems to be the initial factor rather than the main determinant factor. Other factors such as carbohydrate level in the fungal mycelia, or physiological aspects of the host plant might be involved. My observations were that most of the mushrooms in the genera *Amanita* and *Russula* started to develop during the night and I often observed that the pileus (cap) of the mushroom was still closed at 8.00 am. On the contrary, it was often found that the genus *Lactarius* normally started to develop during the day time. In the day time the fluctuation of soil temperature due to sunflecks penetrating through the canopy gap is small, especially during the rainy season. Measurement of fluctuation of soil temperature in the forest floor at 5 cm depth shows that fluctuation in a day is less than 0.5 °C in the rainy season and 1 to 1.5 °C when the soil moisture was very low. The daily soil temperature in day time varied from 24 to 27 °C.

In plants, it has been shown that during the daytime carbon is transported from the leaf to the root, and at night carbon sources come from starch breakdown. It is possible that most of the sporocarps start to develop at night when the starch in the root system is broken down and fungi have the chance to develop. If this occurs during the rainy season when there is no limitation of water for photosynthesis, a lot of carbohydrates will be transported (and may be accumulated) by the root systems. When these carbohydrates are broken down afterwards, this may be a good time for ectomycorrhizal fungi to form fruiting bodies. In temperate zones the appearance of mushrooms usually commences at the end of the summer and during the autumn, at the time when a lot of carbohydrate is transported to the root system of a tree. In temperate regions most of the studies suggest that soil temperature and soil moisture may be the main factors determining whether or not the mushrooms form fruiting bodies (Wasterlund and Ingelog, 1981; Agerer, 1985).

Rainfall could explain the variation in sporocarp appearance in temperate forests (Dahlberg, 1991), but there was no significant correlation between rainfall and sporocarp appearance in the present experiment. Precipitation is not the only factor that determines the appearance of sporocarps. Under normal conditions in tropical forests with no major difference between dry and wet seasons, the occurrence of sporocarps is related to the flushing of the trees (Smits, 1994). An indirect effect of precipitation might come about by increasing the photosynthetic ability of the host tree by increasing the available water in the soil, which is also needed for ectomycorrhizal fungi to develop further.

There can be variations in soil moisture at the time of sporocarp appearance for different ectomycorrhizal fungi. For instance, *Russula* spp. and *Amanita* spp. mostly appear when the soil moisture is about 60 to 80%, while *Boletus* spp. and *Hydnum* spp can appear at a soil moisture of 50% (Yasman, 1993). Some species even appear in the dry season when the soil moisture is very low.

It is difficult to arrive at firm conclusions regarding the specificity of ectomycorrhizae, since the experiment was carried out only during the seedling stage. It is often found in dipterocarp nurseries that many species of mycorrhizal fungus can infect seedlings of different tree species. Later on, mycorrhizal succession will probably take place when the seedlings are planted out in the field. It is strongly influenced by substrate, competition and age of the tree (Last *et al.*, 1992; Smits, 1994). As long as descriptions of the mycorrhizal type cannot be used for species determination, it is difficult to see the degree of specificity. Nevertheless, the long term observations on sporocarp appearance in the natural forest show that certain groups of mycorrhizal fungi, especially from Boletaceae, Amanitae and Russulaceae, tend to associate with certain species of dipterocarps.

Based upon the numbers of ectomycorrhizal fungi that have been described, the results show that specificity of mycorrhizae in a dipterocarp species for the moment appear likely to be at a genus level of fungi or higher. Worldwide, there are about 5000 fungi capable of forming ectomycorrhizae (Marx, 1991) and in temperate forests, for instance in the Netherlands, about 1100 ectomycorrhizal fungi can be associated with a few tree species. In dipterocarp forests, however, after more than 7 years of observations in the area of the Wanariset forest, we have been able to distinguish 172 unidentified species of fungi associated with some of at least 42 species of dipterocarp trees. Possibly other ectomycorrhizal fungi species associate with Fagaceae and Celastraceae.

In dipterocarp mycorrhizal fungi, it is not clear whether early stage fungi and later stage fungi can be distinguished as long as the observation of sporocarps is restricted to the natural forest only. This research is only now underway in East Kalimantan. For temperate mycorrhizae, for instance in pine mycorrhizae, later stage mycorrhizal fungi do not infect the seedlings in plantations (Last *et al*, 1983), but more species among these late stage fungi can infect plants in nursery. This seems also to be the case in dipterocarp mycorrhizae where almost all introduced mycorrhizal inocula collected from old-growth forests do form ectomycorrhizae in the nursery. None of the seedlings collected from wildlings near their mother trees have ever shown deficiencies of ectomycorrhizae in the nursery. It is not yet clear how important mycorrhizal succession in dipterocarp regeneration is in comparison with temperate mycorrhizae. In temperate mycorrhizae, this may become important for selection or breeding highly efficient fungi with a combination of late stage fungi and early stage fungi both introduced in the nursery (Bowen, 1994).

Other factors, such as light intensity, did not influence the growth of the seedlings in the natural regeneration plot. In many gap experiments, however, the influence of light is of primary importance because the differences in light intensity between the control and the created gaps are very great and are linked to other factors such as soil water content, relative humidity, and temperature. In this plot no gaps were present or created during the study period, so the differences between the subplots in the plot were small.

4.5 Conclusions

- There was a positive correlation between the availability of ectomycorrhizal fungal propagules (indicated by the appearance of the sporocarps) and the survival of the dipterocarp seedlings after germination. The growth of the seedlings, however, did not reflect a significant influence of the variables measured such as light intensity and soil nutrient status in the plot. From the sporocarp appearance it could be seen that there are certain groups of mycorrhizal fungi associated with dipterocarp species. These were found to be specific, at least at the level of genus or higher. The appearance of sporocarps seems to be controlled by the host plants rather than by environmental factors such as soil moisture content, soil temperature and light reaching the forest floor. Although the light intensity reaching the forest floor was very low, the seedlings growing in the understorey still possess mycorrhizal roots which they may obtain from hyphae growing out from ectomycorrhizae on the mother tree. The seedlings became infected soon after seed germination when food resources from cotyledons were not yet depleted. The main source of mycorrhizal infection for the seedlings is living mycelium in the rhizosphere.

CHAPTER 5

PHOTOSYNTHESIS AND CARBON BALANCE OF *Dipterocarpus confertus* Sloot. SEEDLINGS IN NATURAL FOREST.

5.1 Introduction

Dipterocarps are among the few species in natural forests that can prolong their growth in the understorey where the light intensity is very low for growth and for the formation of ectomycorrhizae on seedling roots.

Light penetrating to the forest floor consists of diffuse light and sunflecks. This light has different spectral qualities as a result of the light passing through the canopy (Sasaki and Mori, 1981). The leaves in the upper layer canopy absorb red and far red light, and therefore the light near the forest floor contains less red wavelengths (Bazzaz, 1989). The quantity of light available for seedlings growing in the understorey depends on the architecture and the quantity of vegetation and the amount of light intercepted by the leaves and branches of the upper canopy (Pearcy, 1983). Most of the understorey plants may be able to efficiently use both diffuse light and sunflecks as they are classified as shade tolerant species. These types of light are important in maintaining a positive carbon balance in understorey species (Pearcy and Calkin, 1983). Many shade tolerant species possess physiological and morphological adaptations which enable them to survive under low light intensity (Crawford, 1989). Physiological adaptations of seedlings growing in the understorey include maintaining a low rate of photosynthesis, low light compensation point and low leaf conductance to CO_2 (Boardman, 1977; Langenheim *et al.*, 1984; Bazzaz, 1989).

There is little information available as to how such mechanisms work in dipterocarp species which are adapted to low light intensities on the floor of mixed dipterocarp forests. Seibert (1990) summarized results from experiments concerning the influence of light intensity on the growth of some dipterocarp species. Seibert concluded that dipterocarps need moderate light intensities of 30 - 70% of full sunlight. These results come from experiments carried out in a greenhouse which may not representing field conditions. Measurements of light intensity in a natural dipterocarp forest (Chapter 4), however, showed that the light intensity on the forest floor (where most of the surviving seedlings occur) ranged from 0 to 12.5% of full light. Under these light conditions seedlings growing in the understorey do not reach their maximum photosynthetic rate. Ectomycorrhizae are assumed to play an important role in the mechanism by which seedlings maintain their carbon balance through mycelial interconnections with mother trees (Chapter 3 and 4).

In general, plant photosynthesis is very sensitive to variations in light intensity and ambient concentrations of CO_2, two of the principal resources involved in the process. Light is the most critical factor for seedlings in natural rain forests since CO_2 sources can be enriched from soil respiration (Crawford, 1989). Other factors that influence photosynthesis are temperature, nutrients and water status of the soil and of the plant and also air pollution (Mooney, 1986; Evers *et al.*, 1991). Therefore it is necessary to measure photosynthetic capacity as well as dark respiration of the seedlings growing in the understorey under the actual light from diffuse light or sunflecks.

This experiment aims to study the photosynthetic capacity of seedlings under natural conditions in order to be able to estimate the carbon balance of the seedlings and so draw conclusions as to whether seedlings under very low light intensity are able to produce their own photosynthetic products to survive or even to grow in the natural light environment. The carbon balance of the seedlings growing in the understorey will be used as an indication of the nursing effect of the mother tree upon the seedlings. As a comparison, measurements of photosynthesis of the same species under controlled conditions in which light is not a limiting factor, were made in order to asses to what extent physiological adaptations may influence the process. Measurements were also taken of the seedlings planted in the natural forest.

5.2 Materials and Methods

5.2.1 Selection of seedlings for measurement

Seedlings of *Dipterocarpus confertus* were used in this experiment. There were two different sources of the seedlings. For measurements under natural conditions, seedlings were selected from those growing under four different mother trees in the regeneration plot described in Chapter 4. Only seedlings growing within the crown projection area of each mother tree were selected (Fig. 33). The other source of seedlings was from seeds which originated from the fruiting season of 1990. The latter ones were used for planting in the forest and in the greenhouse. The seeds germinated in the greenhouse before transplanting them to the field along the procedures to reduce risk of spontaneous infection as described in Chapter 3 for *Shorea lamellata*. No mycorrhizal inoculations were made. The seedlings were planted near two of the mother trees, namely MT1 and MT4 (see Fig. 33).

5.2.2 Data collection

In order to obtain gas exchange data in the field, a portable photosynthetic measurement device (built by the Analytical Development Company (ADC)) consisting of a Leaf Analyzer Chamber (type LAC-3) equipped with a Parkinson

Leaf Chamber (PLC) were used in the forest (see Box 2 : LAC-3 and PLC). This apparatus works automatically and obtains data on net photosynthesis and CO_2 concentration, stomatal conductance, and temperature. The leaf analysis chamber LAC-3 is designed for open system measurements, where a leaf is placed in a chamber and a flow of gas of known carbon dioxide (CO_2) and water vapour content is passed through the chamber and monitored. The photosynthetic and transpiration rates are determined from the flow rate and the changes in carbon dioxide and water vapour content of the air passing through the chamber. All calculations were done by the computer in the apparatus.

Three different measurements on the seedlings were done both in the forest and in the greenhouse experiment. The first measurement concerned seedlings growing in the natural forest. Seedlings were divided into 4 blocks, based on the position of the seedlings relative to their mother trees. There were four mother trees in the forest under which the seedlings were situated. Block 1 (MT1 = mother tree 1) consisted of 44 seedlings, Block 2 (MT2 = mother tree 2) had 20 seedlings, Block 3 (MT3 = mother tree 3) 40 seedlings and Block 4 (MT4 = mother tree 4) 25 seedlings.

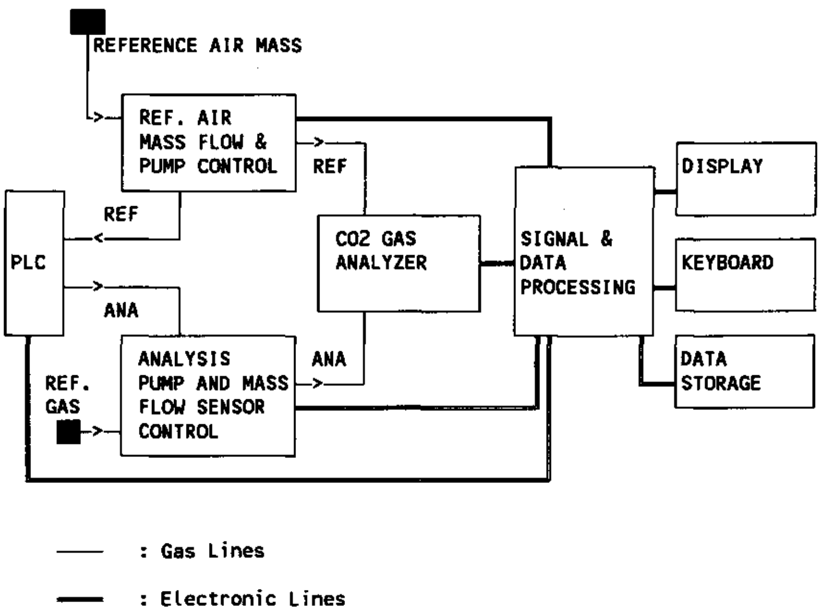
Another measurement was done on seedlings of the same species, planted in two different blocks in the plot. Measurements were done one year after plantation.

In Block A planted seedlings were isolated from the root system of the mother tree by digging a ditch around a 6 x 6 meters plot. In Block B the seedlings were planted close to the buttresses of the mother tree without isolating the seedling roots from the mother tree root system by digging. The assumption was made that, if the mother trees nurse their seedlings underneath, the nursed seedlings will differ in their physiological reaction to light in comparison with the ones not nursed. By isolating the seedling from its mother tree it is expected to react more sensitively to light.

For comparative purposes, measurements were also taken of photosynthesis of *Dipterocarpus confertus* seedlings in the greenhouse, growing under different light intensities created by different layers of green polyvinyl netting (cf. Chapter 2). The source of the seedlings (see above) the same mother tree under which the seedlings had been planted in or out side the ditch. The results of these measurements were analyzed separately. The parameters recorded for photosynthesis consisted of photon flux density (PFD) in Photosynthetically Active Radiation (PAR) in micromol/m^2/second, stomatal conductance, CO_2 consumption (parameters of net photosynthesis), and transpiration. These values were displayed automatically by the apparatus at the time of measurement.

Box 3. LEAF CHAMBER ANALYZER AND PARKINSON LEAF CHAMBER
(LCA-3 and PLC)

The leaf chamber analysis system type 3 is a battery powered portable integrated system for the measurement of transpiration and photosynthesis. The unit incorporates a controlled air supply for a PLC (Parkinson Leaf Chamber), a differential, auto-zeroing, solid state carbon dioxide analyzer and data processing and data storage capabilities. The LAC-3 is designed for use in 'open system' measurements. The open system consist of a system where a leaf is placed in a chamber and a measured flow of gas of known carbon dioxide and water vapour content is passed through the chamber. The photosynthetic and transpiration rates are determined from the flow rate and change in the carbon dioxide content of air passing through the chamber. Schematically, the system of the apparatus works as follows (after the accompanying manual by the ADC):



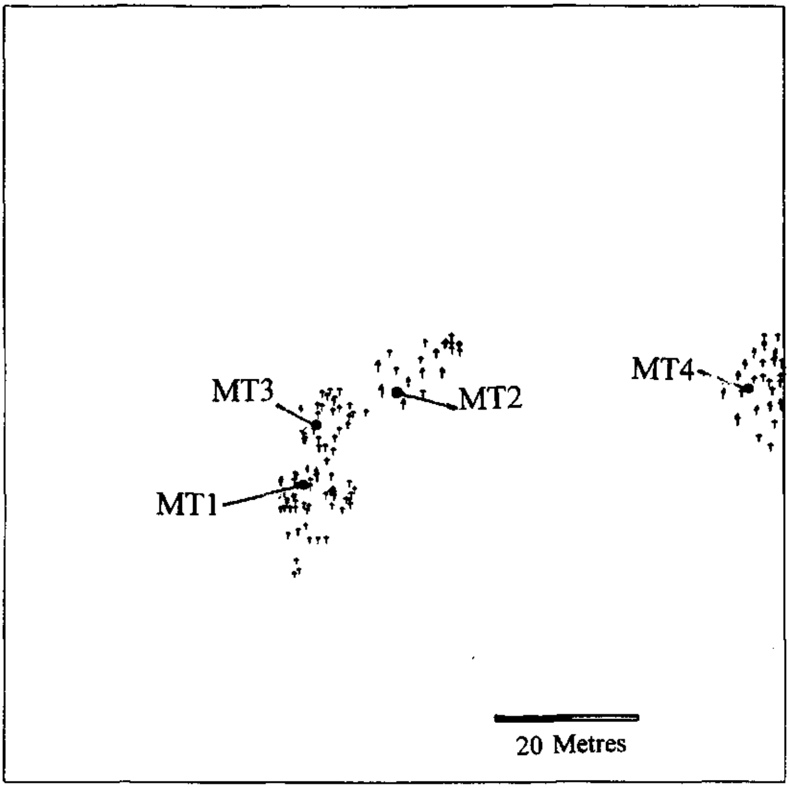


Figure 33. Distribution of the selected seedlings of *Dipterocarpus confertus* used for measurements of photosynthesis (● = position of mother trees).

Measurements of the above parameters were made during clear, non-cloudy days. The measurements were done between 10.00 a.m and 2.00 p.m during the period of September 1991 till March 1992 and May 1992 till July 1992. In this way, the seedlings received the maximum amount of light both in terms of light intensity and time of the day.

To get information on global radiation in the area, data from the closest climatological station, i.e. Balikpapan Airport ca. 30 km from the study area, were used to estimate the light a seedling may receive during the experiment (Appendix 5). This weather station is the only one which has global solar radiation data.

To calculate the carbon balance for every monitored seedling, the light reaching the seedling in one day must be cumulated. The light each seedling gets was measured from 8.00 a.m till 5.00 p.m. at 15 minute intervals. Measurements were done on days when there were no clouds between January 1992 and

September 1992. Later, during the period of April 1993 till August 1993 the same data were gathered once more, but then on every day except for rainy days.

On four occasions within a four-year period, the height was determined for all seedlings growing under the mother tree and used for photosynthesis measurements. On the fourth occasion, the diameters of the seedlings were measured as well. For the present study, no growth measurements were made of either the planted seedlings in the plot, or the seedlings in the greenhouse.

Since all the seedlings measured from MT1 to MT4 in this experiment were growing in the same plot as described in Chapter 4, soil data and organic horizon data in that plot were also used for the data analysis in this experiment.

5.2.3 Carbohydrate determination of the seedlings

In order to obtain information as to whether or not there was starch accumulation in the seedlings growing in the understorey, and as to how far the gradient of starch accumulation in seedlings reached in relation to microclimate (e.g.light) and distance of seedling to mother tree, a carbohydrate analysis was carried out in seedlings used for measurements of photosynthesis. The procedure of handling the sample, sample analysis and calculations followed the methods of Doorduin (1991, unpublished report) and Evers *et al.*, (1991).

Due to great variability in microclimate, such as in light intensity that each of the seedlings receives and which may cause great fluctuations in starch accumulation, the seedlings were shaded three days before harvesting using green mosquito netting to homogenize conditions of the seedlings before analysis. Carbohydrate content of roots and shoots were analyzed separately. The distances of the seedlings from their mother trees were measured and the time of harvesting of the seedlings were also noted. The harvesting was done at 6.00, 9.00, 12.00, 15.00, 18.00 and 24.00 hours.

Starch determination of the roots had a quantitative as well as qualitative aspect in this experiment. A high quantity of starch under unfavourable conditions indicates nourishment from other sources, e.g. by the mother tree. It has been proven in temperate tree species that starch accumulation in the root may increase due to water stress (Dr. P. Evers, 1992 personal communication). Therefore, it was necessary to prevent confusion between stress effects and nourishment. This required the sampling of seedlings under favourable conditions during the rainy season, without water stress. The data from this analysis were used for a comparison between self-supporting and non self-supporting seedlings to find out whether the non self-supporting seedlings had accepted carbohydrate that was not produced by their own leaves.

Following the starch and total carbohydrate determination, the results were classified based on both the distance of each seedling from the stem base of their mother trees and the time of harvesting. The mean values of starch contents and total carbohydrate contents of the seedlings were calculated from this classification.

5.2.4 Data analysis

The data were analyzed using the Genstat statistical package (Lane *et al.*, 1987; Payne *et al.*, 1987). The regression analyses of the correlation between the parameter measured and the growth of the selected seedlings were made to test the influence of the parameter upon the growth. The fitted curve of the photosynthesis-PFD relationship used a rectangular hyperbola with linear-divided-by-linear curve with the general form of $Y = a + b/(1 + dX)$ (Payne *et al.*, 1987), in which Y is the photosynthesis rate in micromol CO_2/m^2/second, X is Photon Flux Density (PFD) in micromol photon/m^2/second, and a,b and d are constant values. This curve consists of two linear phases, the first being the light limited phase of CO_2 assimilation and the second being a light saturated phase as an asymptote (Blackman, 1905 cited by Barber and Baker, 1985). The biochemical efficiency of the photosynthesis by the plant can be tested by using the angle of the light-limited phase. This angle can be calculated from the derivative (Y') from the photosynthetic-PFD response curve as $Y' = -bd/(1+dX)^2$.

The number of hours out of 24, during which the seedlings received a light intensity below and above the compensation point were calculated from the light measurement data. This enabled calculation of the carbon balance by means of the distinction between the number of hours of light (PFD) below the compensation point multiplied by the value of dark respiration (Rd) and the number of hours of PFD above the compensation point multiplied the value of the maximum photosynthetic rate (P_{max}).

5.3 Results

The correlations found between the parameters measured are presented in a matrix in Table 27. Organic layers (litter, humus and fermentation) and soil nutrients were represented by soil map units using the data from the experiment described in Chapter 4. There were no mother trees in the soil map unit 3. The results show a highly positive correlation between thickness of litter layer and fermentation layer, and a highly negative correlation between regression coefficient of the growth and distance of the seedlings to the stem base of their mother trees.

Regression analysis of the variance of the parameters measured with relation to the regression coefficient of the growth of the seedlings is presented in Table 28.

5.3.1 Correlation between photon flux density of PAR, photosynthesis and photosynthetic efficiency of dipterocarp seedlings

From the data collected on clear days between December 1991 and July 1992, the maximum photosynthetic rate was 4.6 micromol/m^2/sec and the minimum was -3.9 micromol/m^2/sec. A fitted curve of the relation between Photon Flux Density (PFD) in micromol/m2 and photosynthetic rate for all seedlings is shown in Figure 34. A curve was fitted by using the equation of 'linear divided by linear' $Y = a + b/(1+dX)$ (Payne *et al.*, 1987), in which Y is the photosynthetic rate and X is PFD. The equation of the curve is $Y = 2.809 - 3.609/(1+0.013X)$.

Table 27. Correlation matrix between the parameters measured in the experimental plot.

Parameters	1	2	3	4	5	6	7	8
Regr.coeff. (1)	-							
Light received by seedlings (2)	0.096	-						
Distance from mother tree (3)	-0.404	0.017	-					
Thickness of ferment. layer (4)	0.132	-0.171	-0.051	-				
Thickness of humus layer (5)	0.157	-0.037	-0.076	-0.079	-			
Thickness of litter layer (6)	0.235	-0.024	-0.022	0.722	0.176	-		
Soil map unit-2 (7)	-0.350	0.224	0.253	0.132	-0.120	-0.065	-	
Soil map unit-4 (8)	-0.083	0.126	0.012	-0.486	0.320	-0.381	-0.175	-
Soil map unit-5 (9)	0.266	-0.223	-0.224	0.260	-0.221	0.333	-0.612	0.000

Table 28. Summary of accumulated analysis of variance of the parameters measured in the experiment.

Parameters	df	F value	P
Distance from mother tree	1	23.64^{+++}	0.001
Soil map unit/Soil nutrient	3	5.40^{++}	0.002
Thickness of litter layer	1	4.72^{++}	0.032
Mean distance	1	3.09^{+}	0.082
Reciprocal distance to mother tree	1	1.13	0.291
Residual	96		

Note : $^{+++}$ very highly significant at $p<0.001$
$^{++}$ highly significant at $P<0.005$
$^{+}$ significant at $P<0.01$

When the values of measurements around different mother trees are fitted, the result are as shown in Figure 35. These results are slightly different. The equations of the photosynthesis curve for each mother tree are shown in Table 29.

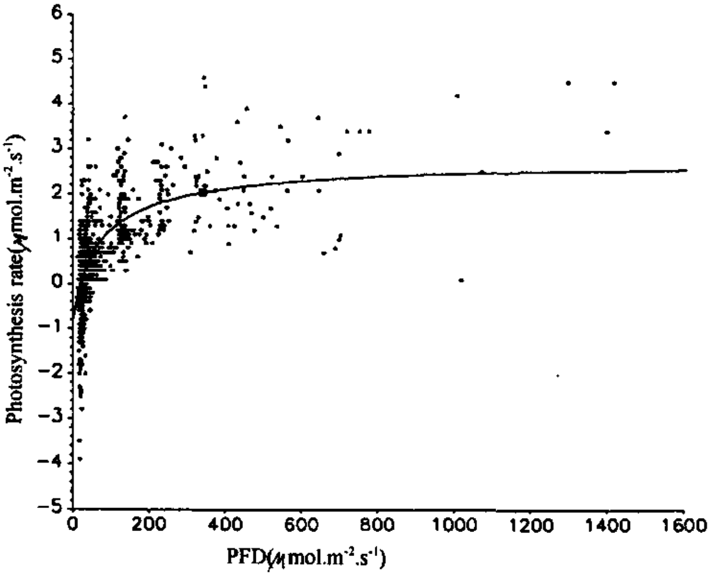


Figure 34. Photosynthesis-Photon Flux Density (PFD) response curve of *D. confertus* seedlings for all measurements.

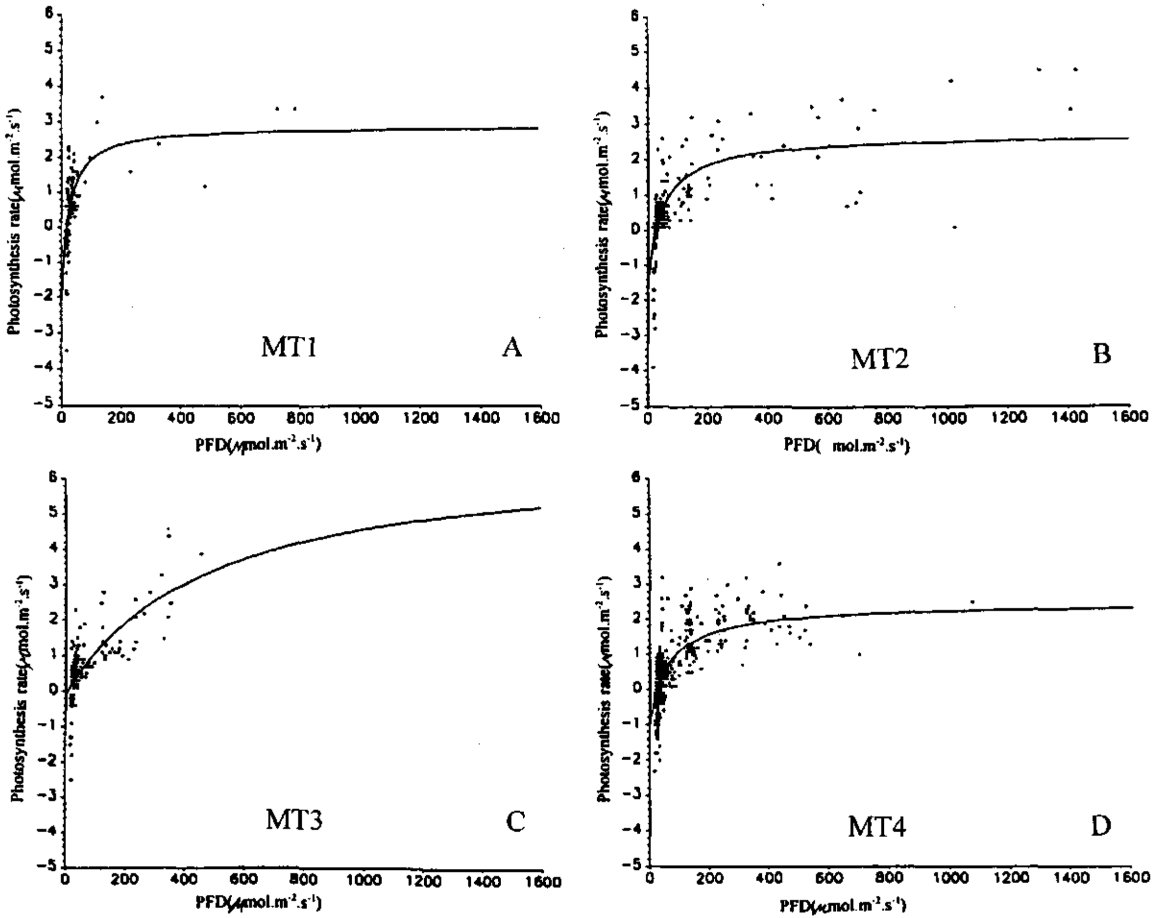


Figure 35. Photosynthesis-Photon Flux Density (PFD) response curve of *D. confertus* seedlings from different mother trees.

As a comparison, the fitted curve of photosynthesis-PFD response for planted seedlings in the natural forest is shown in Figures 36 and 37.

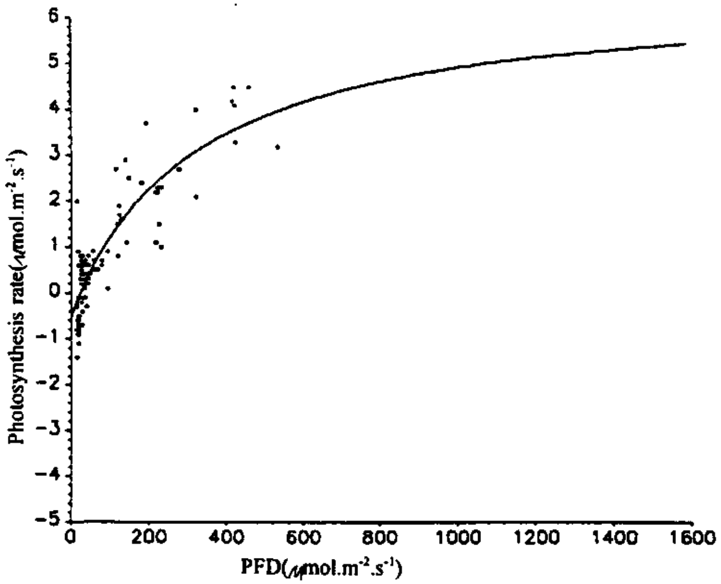


Figure 36. Photosynthesis-Photon Flux Density response curve of *D. confertus* seedlings planted without physical separation from the root system of their mother tree.

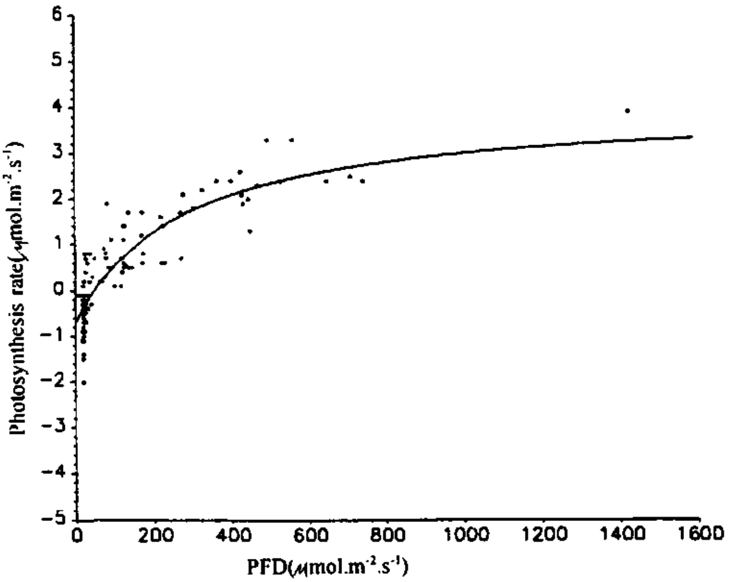


Figure 37. Photosynthesis-Photon Flux Density response curve of *D. confertus* seedlings planted isolated from the root system of their mother tree.

Table 29. Equations of photosynthesis-PFD response curves for seedlings growing below different mother trees.

Mother tree	Equation for fitted curve
MT1	Y = 2.762 - 4.278/(1+0.020X)
MT2	Y = 2.974 - 5.085/(1+0.038X)
MT3	Y = 7.080 - 7.340/(1+0.002X)
MT4	Y = 2.533 - 3.502/(1+0.015X)

Photosynthetic maxima, dark respiration, light saturation points and light compensation points for seedlings growing under different mother trees derived from the equation of each curve are presented in Table 30.

Table 30. Maximum photosynthesis, dark respiration, light saturation point and light compensation point of seedlings growing beneath each different mother tree.

Details	MT1	MT2	MT3	MT4	All seedlings
Equation for photosynthesis-PFD fitted curve	Y=2.762-4.278/(1+0.020X)	Y=2.974-5.085/(1+0.038X)	Y=7.080-7.340/(1+0.002X)	Y=2.533-3.502/(1+0.015X)	Y=2.809-3.609/(1+0.013X)
Photosynthetic maximum	2.726	2.974	7.080	2.533	2.809
Dark respiration	-1.520	-2.111	-0.260	-0.969	-0.800
Light saturation point	709	874	5254	1776	1899
Light compensation point	27.5	18.7	18.4	25.5	22.00

Results from the mother tree 3 (MT3) have very high constant values of a and b and light saturation point. This might be due to the fact that fewer data were available, especially for high light intensities (Fig 35 C). For the interpretation respecting the entire population of seedlings, general curves from measurement of all seedlings of the four mother trees were used (Fig. 34). It was found that the maximum photosynthetic rate was approximately 2.809 micromol/m²/second, and the minimum (reached when X = 0) was -0.8 micromol/m²/second. From this curve it was determined that the light compensation point of seedlings growing in the understorey was reached at a light intensity of 22 micromol/m²/second.

In crop production the angle formed by the tangent of the curve at the compensation point is used to estimate the "biochemical efficiency" of the plant in photosynthesis. The value of this angle can be calculated by a derivation from the equation of each mother tree. Higher values indicate that plants are biochemically more efficient than plant with lower values. The analysis of data of different plots showed that there were no significant differences in the angles (tangent values) of these curves. Hence the photosynthetic efficiency of seedlings growing near different mother trees is the same.

Regarding the relationship between stomatal conductance and photon flux density (PFD) (Figure 38), the regression analysis indicated a very weak correlation between stomatal conductance and photon flux density (R^2 = 0.13).

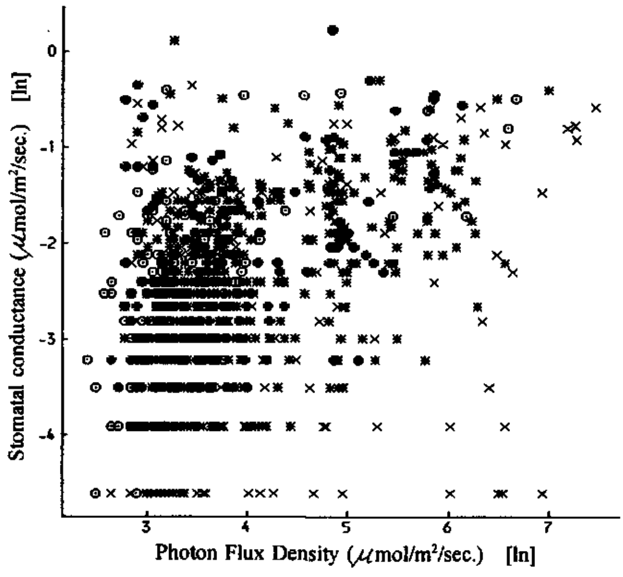


Figure 38. Relationship between stomatal conductance and Photon Flux Density of seedlings growing in the understorey (•: MT1; x: MT2; ⊖: MT3 and *: MT4).

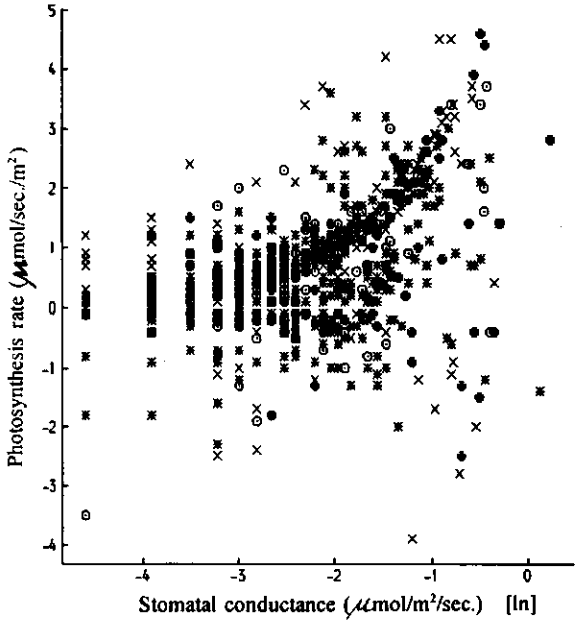


Figure 39. Correlation between photosynthesis and stomatal conductance of *Dipterocarpus confertus* seedlings in the understorey (•: MT1; x: MT2; o: MT3 and *: MT4).

The relation between stomatal conductance and photosynthesis of *Dipterocarpus confertus* seedlings in the understorey is shown in Figure 39.

For comparison, the photosynthesis of seedlings growing in a greenhouse was measured and the results are shown in Table 31. The equation of the curve is Y = 26.2 - 26.4/(1+0.027X). The compensation point of these seedlings lies at a light intensity of 28.3 micromol/m²/second. This value is only slightly different from the compensation point of seedlings in the natural forest. This means that the compensation point of each species has a narrow range. On the other hand, seedlings under favourable conditions have a dark respiration rate lower than that of seedlings under natural conditions. The maximum photosynthetic rate, however, shows a large difference between seedlings under different environmental conditions. The maximum photosynthetic rate of seedlings in the greenhouse experiment was 26.2 micromol/m²/second and the minimum was -0.2 micromol/m²/second. The summary of maximum photosynthetic rate, light compensation point, dark respiration and light saturation point for seedlings growing both under natural conditions and in the greenhouse is presented in Table 31.

During the period of measurements both of seedlings growing beneath different mother trees and of seedlings growing in the greenhouse, the maximum and minimum photosynthetic rates were recorded (Table 32). The results show that seedlings growing in the greenhouse have higher values of maximum photosynthetic rate (P rate) and dark respiration (Rd), while the PFD to reach the minimum P rate is also higher than that in seedlings growing under natural conditions. This result suggests that physiological adaptations of the seedlings growing under different environmental conditions change the photosynthetic apparatus of the leaves causing them to react differently to light.

Table 31. Photosynthesis measurements of *Dipterocarpus confertus* seedlings growing in the greenhouse and in the natural forest.

Details	**Greenhouse**	**Natural forest**
Equation	Y=26.2-26.4/(1+0.027X)	Y=2.808-3.609/(1+0.013X)
Maximum photosynthetic rate	26.2 micromol/m^2/sec.	2.809 micromol/m^2/sec.
Dark respiration	-0.2 micromol/m^2/sec.	-0.8 micromol/m^2/sec.
Light saturation	PFD :709 mmol/m^2/sec.	PFD :1899 mmol/m^2/sec.
Light compensation point	PFD :28.3 mmol/m^2/sec.	PFD : 22 mmol/m^2/sec.

5.3.2. Correlation between growth of seedlings, distance to mother trees and soil organic matter.

Regression analysis of seedling growth shows a highly significant relationship between growth and distance of seedlings from their mother tree ($F_{1,102} = 19.90$; $p < 0.001$). The second rank of significance is thickness of the litter layer ($F_{1,96} = 4.72$; $p < 0.05$) and the third is soil nutrients of different map units ($F_{3,96} = 5.40$; $p < 0.05$). The correlation matrix between all the factors measured shows a significant relation between mean values of the litter and fermentation layers ($R^2 = 0.722$). There was no significant influence of the light that seedlings received upon the growth of the seedlings.

Table 32. Maximum and minimum photosynthetic rates of single *Dipterocarpus confertus* seedling per different mother tree recorded during the period of measurements

Mother Tree	P. rate (mmol/m²/sec.)	PFD (mmol/m²/sec.)	Date	Time
MT1	Max: 4.50 Min: -3.93	1420 19	19/3/92 13/3/92	14.27 10.22
MT2	Max: 3.65 Min: -3.46	237 18	14/3/92 25/3/92	11.34 10.17
MT3	Max: 4.58 Min: -2.50	471 19	25/3/92 12/2/92	12.52 10.12
MT4	Max: 3.58 Min: -2.30	433 18	21/4/92 19/3/92	11.29 13.30
Green-house	Max: 8.7 Min: -1.6	1168 40	10/2/92 23/1/92	10.43 11.47

5.3.3 Carbohydrate accumulation in seedlings of *Dipterocarpus confertus*

Carbohydrate analysis of the roots and the above ground part (stem) of *Dipterocarpus confertus* seedlings growing at different distances from their mother trees in the natural forest is presented in Table 33. The carbohydrate contents of the roots and the stems in relation to the distances from the mother tree are shown in Figure 40 and 41, and in relation to the time of harvesting in Figures 42 and 43.

Table 33. Mean starch and total carbohydrate (CHO) content (g/100 g Dry Weight) of seedlings growing at various distances from the foot of their mother tree.

	Root		Stem	
Distance (m)	Starch (g/100g DW)	Total CHO. (g/100g DW)	Starch (g/100g DW)	Total CHO. (g/100g DW)
1.5	0.22±0.07	0.40±0.10	0.29±0.07	0.82±0.12
2.0	0.29±0.09	0.80±0.05	0.35±0.06	0.85±0.09
2.5	0.29±0.06	0.71±0.05	0.34±0.11	0.73±0.11
3.0	0.36±0.03	0.73±0.09	0.66±0.10	1.13±0.17
3.5	0.59±0.06	0.91±0.11	0.90±0.09	1.23±0.14
4.0	0.55±0.06	0.88±0.13	0.81±0.14	0.88±0.12
6.0	0.46±0.09	0.67±0.09	0.52±0.04	0.72±0.11
10.0	0.36±0.07	0.53±0.11	0.52±0.11	0.73±0.09

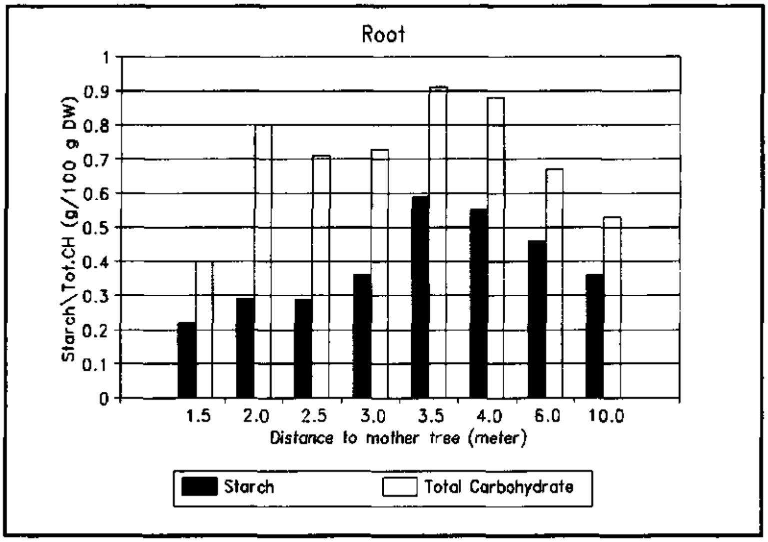


Figure 40. Mean starch and total carbohydrate content of the roots of *Dipterocarpus confertus* seedlings growing at various distances from their mother trees.

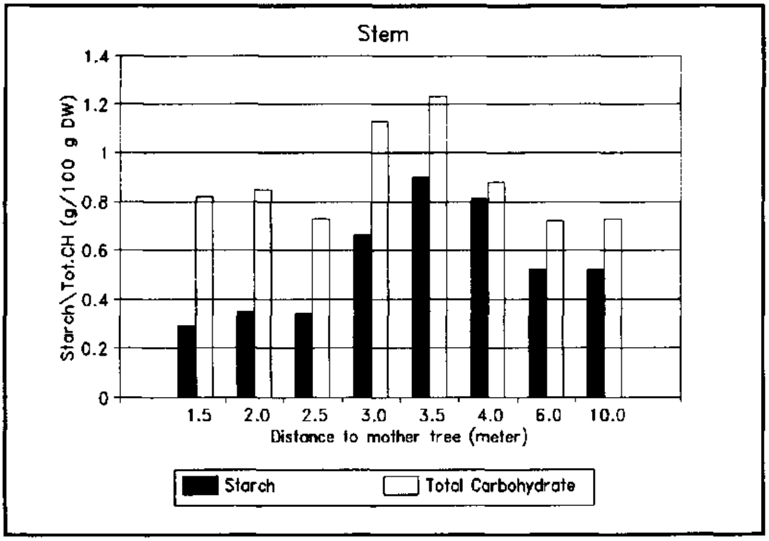


Figure 41. Mean starch and total carbohydrate content in stems of *Dipterocarpus confertus* seedlings growing at various distances from their mother.

Table 34. Mean starch and total carbohydrate content (g/100 g Dry Weight) of seedlings harvested at different times of the day.

	Root		Stem	
Time of harvesting	Starch (g/100gDW)	Total CHO. (g/100gDW)	Starch (g/100gDW)	Total CHO. (g/100gDW)
6.00	0.10±0.02	0.46±0.06	0.29±0.08	0.51±0.09
9.00	0.37±0.04	0.65±0.08	0.56±0.09	0.86±0.10
12.00	0.42±0.05	0.73±0.08	0.61±0.07	0.85±0.09
15.00	0.34±0.02	0.72±0.05	0.38±0.06	0.84±0.10
18.00	0.33±0.03	0.76±0.03	1.02±0.09	1.37±0.15
24.00	0.40±0.07	0.84±0.08	0.52±0.08	0.85±0.08

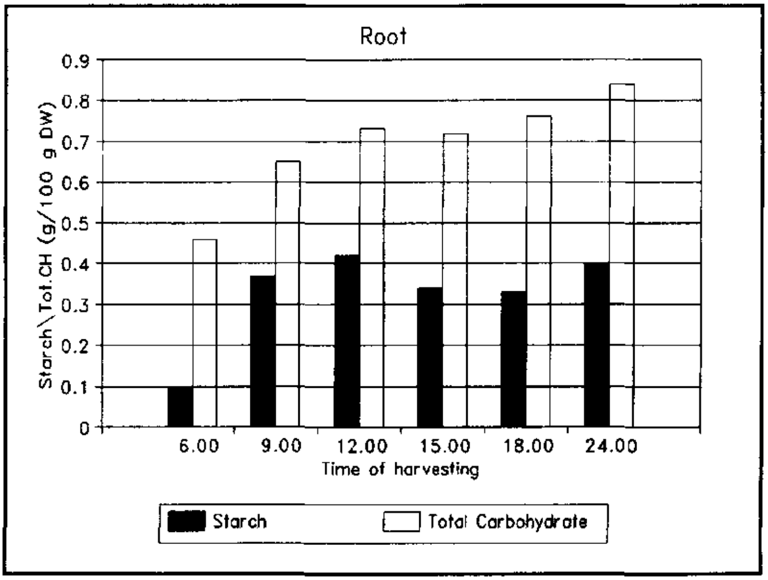


Figure 42. Mean starch and total carbohydrate content in the root of *Dipterocarpus confertus* seedlings harvested at different times of the day.

In general, results from carbohydrate analysis show that the starch and the total carbohydrate contents in the stem/shoot is higher than in the root. When the seedlings are classified on the basis of the distance from their mother tree, results show that the highest starch and carbohydrate contents occurred in the roots and stems of the seedlings grown between 3 and 3.5 m from the foot of the mother trees. The lowest starch and total carbohydrate content was found in the seedlings grown 1.5 m from their mother tree.

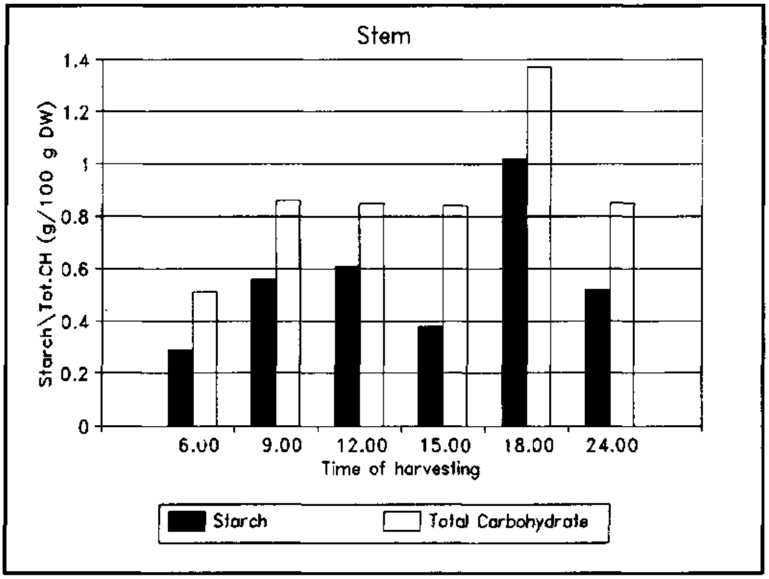


Figure 43. Mean starch and total carbohydrate content in the stems of *Dipterocarpus confertus* seedlings harvested at different times of the day.

Regarding the effect of time of harvesting of the seedlings, the highest starch content of the root was found in seedlings harvested at 12 am, while in the stem it was highest at 12 pm. The total carbohydrate content was highest when the seedlings were harvested at 12 pm for the root and 6 pm for the stem. The starch and the total carbohydrate content was lowest for both the root and the stem of seedlings harvested at 6 am.

5.3.4 Estimation of the carbon balance of *Dipterocarpus confertus* seedlings growing under natural forest

The number of hours that seedlings received a light intensity above the compensation point (PFD above 22.00 mmol/m^2/sec.) was much lower than the number of hours below the compensation point (PFD below 22.00 mmol/m^2/sec.) (Table 36) apportioned over 24 hours a day. Calculation of the mean values for all light measurements gave 2.66 hours above the compensation point and 21.34 hours below the light compensation point. These results reveal that 89 % of the light received by seedlings was below their light compensation point and only 11 % of the light was above their light compensation point. When these results are compared with the solar radiation data (Appendix 5) it is likely that this figure is a little bit of an overestimate, because the solar radiation of the study area varied from 0 to 100%, whereas most of the light measurements were done on clear days.

Unfortunately, the data on solar radiation obtained for the study area are little precise because they were obtained by the use of the Campbell-Stokes apparatus which only records the solar radiation of light intensities above 120 W/m^2 (Bruin, 1993) or the approximate equivalent of 545 micromol/m^2/sec. of PAR (1000 micromol/m^2/sec.= c. 220 W/m^2). The range important for the current study starts from 3 micromol/m^2/sec. and higher.

The average PAR measured between 8.00 to 17.00 hours with intervals of 15 minutes during the whole observation period for different mother trees is presented in Table 35.

When Y values (net photosynthesis) are fitted against X values (PFD) of average light intensities for different mother trees (Table 35) into the equation presented in Table 29, the results obtaining a negative carbon balance of seedlings growing under different mother trees as MT1= -33.906, MT2= -37.224, MT3= -7.638 and MT4= -21.81 micromol/m^2 during the daytime from 8.00 till 17.00 hours.

Although the results from light measurements of the seedlings below mother tree MT3 are similar to those of seedlings below other mother trees, the value of P_{max} and dark respiration are much higher than the others, resulting in a positive carbon balance for these seedlings. The high value under mother tree MT3 may be due to a lesser number of measurement of photosynthesis at high light intensity. For all measurements, however, the carbon balance for all seedlings is negative if based on the value of P_{max} and dark respiration calculated for 24 hours a day.

Table 35. Average PAR measured from 8.00 to 17.00 hours every day with intervals of 15 minutes for different mother trees during the observation period.

Time of measurement	Average light under MT1	Average light under MT2	Average light under MT3	Average light under MT4
8.00	3.4	3.3	3.5	5.0
8.15	4.5	4.2	4.2	4.5
8.30	5.3	5.4	5.7	6.7
8.45	6.7	6.3	6.5	6.9
9.00	9.5	8.1	8.0	8.7
9.15	9.7	11.5	8.3	10.2
9.30	17.7	13.2	8.7	13.5
9.45	16.2	14.5	12.6	13.5

Table 35 (Continued)

10.00	11.7	15.3	14.5	12.1
10.15	16.3	16.0	16.5	17.4
10.30	18.4	17.1	23.4	21.2
10.45	19.0	23.6	22.4	21.6
11.00	20.9	27.5	37.0	28.8
11.15	34.0	29.9	45.0	36.3
11.30	43.0	32.0	34.0	43.5
11.45	45.0	44.0	39.0	42.7
12.00	56.0	56.0	59.0	57.0
12.15	58.0	42.0	42.3	47.8
12.30	56.0	66.0	65.0	68.6
12.45	67.0	72.0	89.4	79.2
13.00	78.0	75.0	77.4	76.8
13.15	87.0	77.0	42.0	64.3
13.30	78.0	87.0	71.9	45.9
13.45	58.0	70.0	56.0	60.3
14.00	56.0	54.0	39.0	27.9
14.15	58.0	45.0	34.2	35.7
14.30	43.0	34.0	20.0	28.7
14.45	41.0	34.0	21.0	32.0
15.00	20.0	21.0	22.9	21.3
15.15	23.0	21.0	12.0	18.7
15.30	19.0	17.0	19.3	18.4
15.45	11.0	13.0	7.9	11.6
16.00	7.0	6.0	5.4	6.4
16.15	3.3	3.8	4.1	3.9
16.30	3.1	3.5	5.1	4.7
16.45	3.0	3.5	3.8	4.6
17.00	2.5	3.3	3.9	4.1

Table 36. Estimation of carbon balance for seedlings below different mother trees and for the whole seedling population.

Measurements of the seedlings of mother tree (1)	Estimation of the carbon balance calculated for 24 hours per day						
	Sum of hours where PFD above 22.00 mmol/m²/sec. (2)	P_{max} (3)	Day P (per 24 hours) (4) (2)x(3)	Sum of hours where PFD below 22.00 mmol/m²/sec. (5)	Dark respiration (R) (6)	Day R (per 24 hours) (7) (5)x(6)	Net Carbon Balance (8) (4)-(7)
MT1	3.90 h	2.726	**10.63**	21.10	-1.520	-32.07	**-21.44**
MT2	2.14 h	2.974	**6.36**	21.86	-2.111	-46.15	**-39.79**
MT3	2.50 h	7.080	**17.70**	21.50	-0.260	-5.59	**+ 12.77**
MT4	2.10 h	2.533	**5.32**	21.90	-0.969	-21.22	**-15.90**
Average for all measurements	2.66 h	2.809	7.47	21.34	-0.800	-17.07	**-9.60**

5.4 Discussion

An interesting aspect in this experiment was that different light intensities reaching the seedlings did not cause differences in the growth of the seedlings. This means that under natural conditions the very low light intensity reaching the forest floor may not be a critical factor for growth of seedlings since the seedlings are connected to the mycorrhizal mycelial network of their root system. This result is not in accordance with the findings by Osunkoya *et al.* (1993) that even small differences in light environment can effect plant growth. Their study, however, used gaps of different sizes in the forest interior with varying canopy densities. In the current study, no gaps were used or created, the differences in light condition being mainly due to forest canopy gaps which have little effect on the understorey light regime because of the high ratio of canopy height to gap diameter (cf. Canham *et al.*, 1990)

The distance of seedlings from their mother trees had a very strong influence on their growth, showing the importance of the mother trees to their offspring in the understorey. Seedlings growing close to the mother trees grew faster than seedlings far away. It can be concluded that the mycorrhizae of mother trees may provide nutrition to the seedlings through hyphal inter-connections that facilitate faster growth than in seedlings without hyphal connections to the mother tree. If distance from mother trees is interpreted as influence of their root system, this result suggests that seedlings obtain nutrition from their mother tree by exploiting the greater amount of carbohydrates that big trees produce under favourable light conditions. This result is in accordance with results described in the Chapter 3. The highly significant importance of the litter and fermentation layers lies in the fact that mycorrhizal hyphae or rhizomorphs may decompose litter, so permitting ready uptake of nutrients by their mycelia.

Although ectomycorrhizal fungi show low ability to decompose litter on the forest floor due to the polyphenole content of the litter (Richards, 1987), other microorganisms or saprophytic fungi on the forest floor may play an important role in the early stages of decomposition of litter to form the fermentation layer. The litter and fermentation layer on the forest soil has shown to be more important for dipterocarp mycorrhizae than the humus layer. These results suggest that when the fermentation layer decomposes further, becoming the humus layer, the nutrient availability of the humus layer may not be sufficient for plants because non mycorrhizal plants and plants with other forms or root symbiosis might compete for the same nutrients. At the fermentation stage nutrients are only accessible to the ectomycorrhizal roots. Alexander (1989) indicated that delayed breakdown of organic matters in the forest may establish conditions in which ectomycorrhizae are likely to be the most effective competitors for nutrients.

Most ectomycorrhizal tree species are able to associate with a wide range of mycorrhizal fungi in adapting to different soil and other environmental conditions. Regarding the soil substrate preferred by mycorrhizal fungi, two different classes of ectomycorrhizal fungi can be distinguished. First are soil inhabiting fungi like *Laccaria* and second are litter inhabiting fungi like *Russula, Laccaria* and *Cortinarius,* species that are better adapted to exploit litter for nutrients (Hilton *et al.*, 1989). Litter inhabiting fungi like *Russula* species produce significant quantities of surface phosphatase that may take up phosphate from organic matter. In the sporocarp observations (Chapter 4) it was shown that litter inhabiting fungi were more numerous than soil inhabiting fungi. This may lead to an explanation of the significant influence of the litter and fermentation layers upon growth of seedlings of *D. confertus*, rather than other factors.

Compared to the results obtained from the nursing experiment (Chapter 3) in which seedlings very close (less than 2 metres) to the mother tree grew more slowly than seedling at a distance of 2 to 4 and 4 to 6 meters, such relationship is not clearly shown in this experiment. An indication from carbohydrate analysis in this experiment, however, is that the highest starch and total carbohydrate occurred in the seedlings growing between 3.0 and 3.5 metres from the closest buttress of their mother trees. The inconsistency between these two experiments (especially with respect to growth) might be due to the fact that under dense natural stands of mother trees, their primary and secondary root systems may inter-cross in the rhizosphere, which is presumably not the case in the nursing experiment (Chapter 3), because the mother trees grew isolated from each other.

Photosynthetic rates of *D. confertus* seedlings acclimated in the greenhouse differ nearly nine-fold as to P_{max} and only slightly as to the light compensation point seedlings acclimated under shade in natural forest. This result suggests that physiological adaptation of the seedlings is an important factor explaining the behaviour of photosynthetic apparatus of the plants. In this view, physiological adaptation is not only the reaction of the leaves to the different light conditions, but other environmental factors such as competition and soil condition might be important in this mechanism too. Such physiological adaptation of the seedlings in the understorey, as found in this current study, showed that there are some differences in photosynthetic rate between planted seedlings connected to their mother tree and planted seedlings isolated from their mother tree (Fig. 35 and 36).

The relationship between stomatal conductance and photosynthesis did not indicate a reciprocal causative effect between these two as is often found in steady state measurements. The increasing of photosynthetic rates is not followed by the increasing of stomatal resistance. This is in accordance with the results found by Wood and Turner (1971), and Roden and Pearcy (1993) in which stomata were unresponsive to changes in PFD and play a minor role in the understorey photosynthesis. This might be due to the capacity of understorey plants to fix CO_2 after short illumination. The capacity of post-illuminance CO_2 fixation allowing the leaves of the seedlings to continue assimilation after the sunflecks have passed (Pearcy, 1990). During this time the importance of stomatal openings are not a primary limitation.

Post-illuminance carbon fixation is an important component of the total carbon gain of the understorey plants, especially during short sunflecks (Pearcy, 1988). In the current study, the effect of post-illuminance was not measured although this might contribute to the carbon gain of *Dipterocarpus confertus* seedlings in the understorey. However, it is not likely to be the main source of assimilated carbon in the seedlings. This is supported by the data for carbohydrate analysis, where high concentrations of carbohydrate were found in the stem as well as in the roots of the seedlings harvested after 6 pm. Light data show that before 9 am and after 4 pm, most of the light reaching the forest floor was of very low intensity. There were no fluctuations in light intensity at this time that could be important for post-illuminance fixation.

Although the carbon balance of the seedlings growing near different mother trees varied, especially below the mother tree MT3, where they had a positive carbon balance, measurements under other mother trees and for all seedlings revealed on the average a negative carbon balance for all populations of *Dipterocarpus confertus* seedlings. This population approach avoid the large errors caused by interpretation of the individual photosynthesis measurements in populations of the same species as found by Troeng and Linder, (1981). The negative carbon balance from auto-photosynthesis by the seedlings is unlikely to enable the seedlings to maintain either mycorrhizal symbiosis or growth. However, there are a considerable number of seedlings that can maintain their growth under very low light intensity (see mortality rates, Chapter 4). The results suggest that the seedlings growing in the understorey which have a negative carbon balance may replenish their carbon deficiency from the carbon pool originating from photosynthesis of adult, fully illuminated trees. The inter-connections between the roots of the trees through mycelia are thought to be of primary importance in this mechanism.

For seedlings growing under their mother trees, the importance of inter-connection of mycelia implies at least two possibilities for transfer of carbon. First, it is not very clear in this experiment whether carbon flow goes directly toward the seedlings, as part of normal carbon allocation of photosynthates to the root of the tree or, second seedlings may benefit by utilizing the high concentration of carbon in the soil within the area of the root system of their mother trees. The first possibility suggests that only the seedlings integrated in the mycelial network would benefit from high carbohydrate allocation from fully illuminated crowns, whereas the second possibility suggests that any seedlings within an area of high concentration of carbohydrate might benefit no matter whether they become integrated in the mycelial network or not. The high carbohydrate content of the seedlings growing between 3.0 to 3.5 meters from their mother trees, where most the fine roots exist, suggests that the first possibility is more likely than the second.

There are some constraints upon using the measuring apparatus in the field, especially when the air humidity is very high after rain. Measurements could not be taken when it was raining or for one day after rain, due to the higher humidity. All of the measurements in the forest in this experiment were done when the humidity at the forest floor was below 90% (mostly around 70 to 80%). Another limitation was that the measurements could not be done at very low light intensities (below 10 micromol/m^2/sec). This gave problems in measuring dark respiration, which is the major handicap in using portable photosynthesis devices in the field (Dr. J.McP. Dick, 1994 from ITE Edinburgh, personal communication). The results obtained show that respiration of seedlings in natural forest fluctuates less than the fluctuation of the photosynthetic rate measured at different light intensities (PAR). Dark respiration used for calculation of the carbon balance of the seedlings was derived from the equation for photosynthesis and PFD curve. The use of extrapolation is questionable in this case, because the actual rate of CO_2 fixation is generally lower than the extrapolated rate (Brix, 1968). Laverenz (1988) has indicated the difficulties in making good estimation of dark respiration. By fitting non-rectangular hyperbola to the gas exchange data, he found out that at very low PFD the curves are not linear as a result of what is called the Kok effect. For tropical tree species, however, Ramos and Grace (1990) have proven the error to be very small and to make very little difference in dark respiration between measurement and extrapolated values. Therefore in this experiment the value of dark respiration as obtained from extrapolation is thought to be reliable enough.

5.5 Conclusion

Natural regeneration of *Dipterocarpus confertus* revealed that the distance between a seedling and its mother tree is linked to the growth of seedlings in the understorey. The importance of litter and the fermentation horizon for the growth of seedlings suggests that ectomycorrhizal roots might recycle nutrients more rapidly than endo-or non-mycorrhizal roots.

Photosynthesis-PFD response assessed by measurements under natural conditions indicated that the light compensation point in seedlings is about 22.00 mmol/m^2/sec which is slightly different from the seedlings growing in the greenhouse which have a light compensation point of 28.30 micromol/m^2/sec.. Although the photosynthesis-PFD responses of the seedlings growing near different mother trees were different, the "biochemical efficiency" of those seedlings was not significantly different.

About 11% of the light received by the seedlings in the understorey exceeds the light compensation point and 89% of the light is below the light compensation point, calculated over 24 hours. This amount of light would not allow seedlings growing in the understorey to maintain a positive carbon balance. Therefore, seedlings growing in the understorey must correct a carbon deficit, as is assumed by obtaining carbon produced by the mother tree which has a fully illuminated crown. In this way, ectomycorrhizal roots are thought to play an important role by inter-connecting the seedlings and mother tree through mycorrhiza mycelia.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

6.1 The role of light, nutrients and ectomycorrhizae in dipterocarp regeneration.

The importance of light for the formation of ectomycorrhizae in temperate trees has been discussed thoroughly (Björkman, 1942; Handley and Sanders, 1962; Hacskaylo, 1973; Nylund, 1988). The current study has proven that development of ectomycorrhizae in dipterocarp seedlings too is influenced by the light intensity received by the seedlings (Chapter 2). The number of infected roots increases with increasing light intensity. This is in accordance with the results obtained by Johnson (1976) that seedlings in the understorey may reduce their amount of mycorrhizal infection in the presence of heavy shade with minimal effect on their growth (including root growth). However, the physiology of how light regulates ectomycorrhizal formation was not examined in this study, i.e. whether or not increasing light intensity causes an increase in the rate of photosynthesis and translocation of carbohydrates to the root or vice versa, whether or not that mycorrhizal infection might stimulate translocation of carbohydrates to the root and increases the net photosynthesis (see Walander, 1992).

There is a certain level of light that is closely related to the photosynthetic capacity of the host plant to build up the carbohydrates required by mycorrhizal fungi (Stenström and Unestam, 1987). The light intensity must exceed the photosynthesis/respiration compensation point of the host plant in order to provide a sufficient flow of carbohydrates to the fungus in order to maintain the long-term symbiosis. Very little is known about the amount of carbohydrates required by different mycorrhizal fungi. Some fungal species have been shown to have different carbohydrate and nutrient sink capacities (Stenström and Unestam, 1987; Gagnon *et al.*, 1988; Hadi and Santoso, 1987; Omon, 1994). The results of the present study suggest that certain fungi predominantly associate with host plants that experience very low light intensity (low carbohydrate production), while some other fungi were mostly found to be associated with host plants that experience high light intensity. As has been demonstrated in Chapter 2, light demanding *Shorea leprosula* seedlings can form many more mycorrhizal types than shade tolerant *Dipterocarpus confertus* seedlings. This result indicates that co-selection of fungal symbiont and host plants is heavily influenced by the light conditions experienced by the green plant after seed reserves have been depleted.

Due to carbohydrate limitations in the root systems of seedlings under natural conditions, new root tips can not develop until the seedlings experience better light conditions. This means that under natural conditions there will be less secondary infection by other fungi or by spread of fungi already present on the root system that allows them to develop a greater dominance among the other ectomycorrhizal types present on the root system.

Development of plant root systems is determined by such factors as soil fertility, water in the soil, carbohydrate level in the root system as well as in the soil. It was observed that the development of root systems in the greenhouse was much more ample than root systems of the same species under natural conditions. This result implies that the amount of ectomycorrhizae formed under natural conditions is much lower than ectomycorrhizal formation under favourable conditions in a greenhouse where the light intensities are generally more favourable for small seedlings, leading to more available carbohydrates for the ectomycorrhizal establishment.

Considering the amount of mycorrhizal roots in natural forests where light intensity is very low, it is assumed that seedlings of dipterocarp species will have a low level of infection as well. But for survival seedlings must have ectomycorrhizae, otherwise they will exhibit symptoms of chlorosis. Light may not be of primary importance in the initial phase of mycorrhizal infection. Carbohydrate in the host seedlings originating from the cotyledons suffice for initial infection. Secondary infection, however, will rely on the carbohydrates made by the photosynthesis of the host seedlings.

It might be possible that fungi with a high demand for carbohydrates infect seedlings growing under unfavourable light conditions if the seedlings fulfil their carbohydrate need via carbohydrates supplied through the ectomycorrhizal hyphae connected to roots of fully illuminated mother trees. In such case, carbohydrates are a limiting factor for formation of ectomycorrhizae in the seedlings.

By growth data analyses of seedlings it was shown that there was no significant difference in growth of the seedlings in different light regions in the natural forest. On other hand treatment with different light intensities in the greenhouse experiment resulted in different growth rates. It needs to be noted that the light intensities in the greenhouse were all above the compensation point while those in the forest were mostly under the compensation point. This result suggests that light is not a critical factor for survival and early growth of dipterocarp seedlings under natural forest conditions.

Based upon the outcome of many gap experiments done in forests it has been suggested that light is the most important factor determining the growth of seedlings in the understorey (Holmes and Cowling, 1993; Osunkoya *et al.*, 1993; Bongers and Popma, 1988; ter Steege, 1993). In this current study there were no artificial gaps created in the forest. The different amounts of light reaching the seedlings were a result of small canopy openings which on the average may be assumed not to differ overmuch between the sites in the plot. Therefore differences in the growth rate of the seedlings in the plot may not have been clearly expressed. Therefore clear discrimination must be made between the gap studies and studies of seedlings in the understorey, only receiving light from sun flecks passing through the much smaller canopy openings above (Oldeman, 1992, his Fig. 2A). Results from gap studies can not be extrapolated to fit the conditions of an almost closed crown canopy.

In strong contrast to the absence of a correlation between the light intensities in the understorey and the survival and growth of the seedlings, the appearance of sporocarps, as an indication of the availability of mycorrhizal inoculum in the forest soil, was proven to have a positive correlation with the survival of the seedlings. Therefore the failure of dipterocarp seedlings to form mycorrhizae can be considered to be one important factor for high seedling mortality. In other mycorrhizal plants this high mortality of the seedlings is only common in nutrient-poor soils under better light conditions (Fenner, 1987).

Another important factor that determined the growth of dipterocarp seedlings in the experiments here described (Chapter 5) was the different soil nutrient status as represented by different map units. Further analysis of soil nutrients showed they were significantly different between the map units for certain soil factors and their ratios, especially C/N ratio, percentage of sand, silt and clay, pH , C, N and available P, K, Ca and Mg. However, none of these elements significantly influenced the growth of the seedlings, although these elements are considered the most important for the growth of ectomycorrhizal roots. The values of these elements showed that their availability in the plot was very low to low according to the common standard (Appendix 1). This may be the reason why their influence on the growth of seedlings was not significant. Similar results for adult dipterocarp trees were obtained by Eijk-Bos *et al.* (1995 in prep.) and Van Bremen *et al.* (1991) and Oldeman and Iriansyah, (1993), not revealing any clear correlation between soil nutrients and tree growth. There was a relation with soil texture and water retention capacity.

Although the thickness of organic horizons, especially litter and fermentation layers, revealed a significant influence on the growth of the seedlings, there was no correlation between the soil nutrients and the thickness of the organic horizons. These results suggest the importance of ectomycorrhizae in nutrient cycling through hyphae that enable them to absorb the nutrients directly from litter and fermenting organic material (Stark,1971) so that relatively little enrichment with nutrients from decomposition takes place in the mineral soil. Endomycorrhizal and non- mycorrhizal root are unlikely to do so (cf. Janos, 1983). Direct uptake of nutrients from litter is supposedly an active process, meaning that there is a high need for carbohydrates that the plants do not seem to get from autophotosynthesis. This aspect will be discussed in the next part of this chapter in more detail.

The correlation between thickness of litter layers and growth of the seedlings is supported by the fact that most of the species of mycorrhizal fungi observed in the plot were litter inhabiting fungi (Chapter 4). The same is true for the quantity of sporocarps of litter inhabiting fungi encountered. However, no special analysis of the locations of the sporocarp and the thickness of the litter was made. The ability of ectomycorrhizal roots to recycle the nutrients from litter and the fermentation stage might imply that the efficiency, in terms of access to the nutrients in the organic matter, of ectomycorrhizal tree species is greater than in endo- or non-mycorrhizal species. Endomycorrhizal hyphae also tend not to extend far from the roots, whereas ectomycorrhizal hyphae can penetrate deeper and faster in the litter layer. This might provide ectomycorrhizal trees a better competitive position for obtaining nutrients on nutrient-poor soils as is the case under most of the dipterocarp forests. Perhaps this advantage may also be linked to the stronger dominance of ectomycorrhizal trees, as expressed in terms of basal area, in the higher diameter classes (Smits, 1992, 1994).

6.2 Dipterocarp ectomycorrhizae : indicative evidence for the nursing role of mother trees

Obligately mycorrhizal plants normally do not respond to fertilizer application when they do not form mycorrhizal roots (Vozzo and Hacskaylo, 1971). This an indication of the dependence of dipterocarp species upon ectomycorrhizae. Another experiment showed that dipterocarp seedlings without mycorrhizae did not grow, though fertilizers were added to the soil, whereas introduction of mycorrhizal inocula can speed up the growth and induce the plants to produce green leaves after one month (Figure 44). In other cutting experiments of dipterocarp species without mycorrhizae under different soil conditions, all of the seedlings had stunted growth and produced small yellowish leaves (Yasman and Smits, 1987). This means that dipterocarp seedlings can not exploit the nutrients in the soil unless they have ectomycorrhizal symbiosis in their roots. This may be different in temperate mycorrhizae where the trees are less dependent upon mycorrhizae, especially on soil rich in available phosphate and nitrogen.

Once ectomycorrhizal roots are established, a sufficient flow of carbohydrate from host plant to fungus must occur in order to maintain the symbiosis in the long term. Seedlings collected from natural forest, however, never show ectomycorrhizal deficiency (Smits, 1986). This means that the amount of mycorrhizae associated with the roots is unlikely to be the most critical factor for seedlings growing in the understorey in the natural forest. When the seedlings are infected, even a small part of the root is enough for them to initiate photosynthetic processes in the leaves. It has been observed (personal observation) in a greenhouse that seedlings originating from seeds growing in sterile soil are stunted in growth until they are infected from spores blown in the air or infected from mycorrhizal

Figure 44. Response of originally non-ectomycorrhizal *Shorea assamica* seedlings two months after introducing NPK fertilizer and ectomycorrhizal inocula. A: neither fertilizer, nor ectomycorrhizal inocula; B: inoculated with ectomycorrhizal roots; C: Inoculated with soil containing many ectomycorrhizal rhizomorphs; D: NPK fertilizer added.

roots of neighbouring plants. The work of Smits (1994) with perforons showed that even the initial establishment of one or two small ectomycorrhizae led to immediate and dramatic growth responses of the dipterocarp plants. Smits and Struycken (1983) showed that dipterocarp explants needed certain vitamin additions like thiamin in the medium. Thiamin or a precursor thereof, they suggested, might be supplied by the associated ectomycorrhizal fungi. The dramatic growth responses of dipterocarps after ectomycorrhizal inoculation (see also Figure 44) therefore may less be the effect of nutrient uptake rather than stimulation of certain physiological processes in the associated green plant.

The obligate character of the dipterocarp ectomycorrhizal association is also obvious from the strong correlation between survival and growth of the seedlings under the mother trees related to distance from the stem base of the mother tree. Seedlings growing at larger distances from the mother tree tend to have lower survival and rates growth (see Chapters 3 and 5). This can be best explained in terms of the need for ectomycorrhizal fungi after germination of the seedlings. The strong correlation with the sporocarp phenology as mentioned above also supports this hypotheses.

The transport pathway of photosynthates from the above-ground plant parts to the root, and the inter-plant connection of root systems of mycorrhizal plants by mycelia have been demonstrated experimentally in the laboratory (Read *et al.*, 1985). A number of studies have suggested that this interplant connections through mycelial networks might also occur under natural conditions, though the effect of the physico-chemical environment in the rhizosphere may result in other reactions than the studies in laboratories have revealed (Erland *et al.*, 1990).

When seedlings of dipterocarps germinate on the forest floor, they usually start to grow under conditions of low light intensity and they will act as a carbon sink where photosynthates from the mother trees will be transported. This was confirmed by Brownlee *et al.* (1983) in an experiment with *Pinus sylvestris*. They found that the mycorrhizal mycelial strands act, not only as infective propagules, but also as pathways for the transport of assimilates from one plant to another. They demonstrated that labelled assimilate were distributed by the donor plant to the young seedlings, particularly to the recently formed mycorrhizal roots of the younger seedlings.

The results of Brownlee *et al.* (1983) also indicated the importance of carbohydrate from the mother tree for the initiation of mycorrhizal infection of seedlings. In order to infect the roots of seedlings, there must be a gradient of carbohydrates between the mycorrhizal source and the target seedling roots (Allen and Allen, 1992). This might rely on the photosynthetic capacity of the mother tree which, in natural forests often is in the upper canopy layer. For instance, Smits *et al.* (1987) mention that dipterocarp trees only start flowering after their crowns are fully illuminated and therefore can become mother trees producing off-springs. This means that a tree that may potentially be used as a source of mycorrhizal propagules must be a tree which has a fully illuminated crown. However, this mechanism of transfer of carbohydrates via mycelial interconnections may be more complex still and show differences between seedlings of different species near the same mother tree. Non-ectomycorrhizal trees are an unlikely source of carbohydrates transported through the mycelial network since the uptake of carbohydrates from the roots necessitates the presence of a well developed Hartig net (Harley and Smith, 1983). Non-dipterocarp ectomycorrhizal trees with fully illuminated crowns first of all are rare in the mixed dipterocarp forest and second were found to have few ectomycorrhizal sporocarps of the same fungi as found connected to dipterocarps (personal observation). Therefore, ectomycorrhizal mycelia from non-dipterocarp species are unlikely to act as a pathway for carbohydrate transfer to dipterocarp seedlings. However, this transfer might occur between different species within the family of Dipterocarpaceae since species and genera within this family are genetically rather similar (Ashton, 1969; Somego, 1978).

In the mixed dipterocarp forest where Dipterocarpaceae may make up 80 % of the tree crowns in the upper canopy (Ashton, 1982), ectomycorrhizae might play a significant ecological role in the energy flow in the ecosystem through their below ground mycelial network. Smits (1994) showed that the Dipterocarps may make up close to 50% of the total basal area. If an estimated 15 to 30% of the total assimilated carbon in coniferous (100 % ectomycorrhizal trees) forest is allocated to the ectomycorrhizal fungi (Vogt *et al.*, 1982; Fogel and Hunt, 1983) and this would be also valid in dipterocarp forests, this carbohydrate allocation might be equally proportional to the percentage of the carbohydrates locked up in the total wood volume of dipterocarp trees in this forest. Assuming that primary production of dipterocarps in the forest ecosystem is proportional to their crown canopy occupation it can be estimated that some 80 % of the energy cycling in the lowland dipterocarp forest ecosystem is accounted for by the single family of the Dipterocarpaceae. Since there are relatively few ectomycorrhizal species in the tropical rain forest of Southeast Asia, it may be assumed that the energy flows will be dominated by flows in and amongst individuals of the families Dipterocarpaceae and Fagaceae (also cf. Oldeman, 1994). This may provide an explanation for the dominance of Dipterocarpaceae in the region of South East Asia because to the efficiency of ectomycorrhizae in nutrient cycling.

In the present study some evidence was found that dipterocarp seedlings growing in natural forests within an area of the crown projection of the mother trees might benefit from carbohydrate translocated from the crown of their mother tree as long as the seedlings are integrated into its mycelial network. Although the evidence provided here cannot directly prove the flow of carbohydrate from sources of the mother tree to the seedlings as recipient, indirectly it has been demonstrated in the current study that the growth of seedlings is faster when the seedlings grow closer to the root system of their mother trees (Chapter 3 and 5). Also the clumped distribution of surviving *Shorea lamellata* seedlings under a mother tree (see Chapter 3) indicates some form of support, possibly through mycorrhizal root connections.

Measurement of photosynthesis of *Dipterocarpus confertus* seedlings shows that, in natural forest, the seedlings reach their compensation points at a photon flux density (PFD) of 22 mmol/m^2/sec. of Photosynthetic Active Radiation (PAR) and 28.3 mmol/m^2/sec. for the seedlings grown in the greenhouse. The maximum photosynthesis can be nine times higher for the seedlings in the greenhouse than in natural forest. There was no difference in the biochemical efficiency of the seedlings originating from different mother trees. Light measurements on seedlings growing in the natural forest revealed that 89% of the light received was below the compensation point and only 11% of the light was above the compensation point, as measured over a 24 hour period. When this figure was related to the maximum value of photosynthesis and dark respiration, it showed that the seedlings in the understorey probably are not able to maintain a positive carbon balance.

From the data on carbohydrate and starch content of stems and roots of the seedlings growing at varying distances from the roots of the mother trees (Table 33) it was learned that the highest carbohydrate and starch contents were reached at 3 to 3.5 meters from the large roots, where fine roots and therefore their associated ectomycorrhizae were present in highest densities. This was found to be consistently so for both the situation in the roots as well as the stem parts analyzed. These results therefore support the hypothesis of carbohydrate provision through the ectomycorrhizal connections.

Figure 45 (see below) is based upon the analyses of the root and stem total carbohydrate and starch contents. From Figure 45 it can be seen that with increasing distance the ratio of starch to total carbohydrates increases. This indicates as well that relatively more directly available carbohydrates are available closer to the fine roots. This again supports the hypothesis of carbohydrate provision through the ectomycorrhizal connections.

What we also can see from Figure 45 is, that the ratio of starch to total carbohydrates is higher in the stem than in the roots. This indicates that available carbohydrates not only originate from the leaves but also enter the plant through the roots. Under normal conditions of sufficient autophotosynthesis this is the other way around. Therefore this observation also supports the hypothesis.

From the starch and carbohydrate analyses of roots and stems of the seedlings sampled with varying harvesting times of the day (see Chapter 5 graphs 41 and 42), it was learned that total carbohydrates in both stem and root were more abundant during dark periods as compared to daytime samples. This means that during the night additional carbohydrates reach the plant, of course not originating from photosynthesis. This again points in the direction of root uptake of carbohydrates by the seedlings. The fact that it takes place after the light decreases under the compensation point indicates that this sugar originates from the transport of carbohydrates from elsewhere. It probably comes from the mother tree, since this transport is normally higher during the night time (Dickson, 1991).

From the following Figure 46, which is based upon the above-mentioned graphs 42 and 43, we can see that the concentrations of starch and carbohydrates in the stem display a slightly lower ratio of starch to total carbohydrates, indicating a higher availability of carbohydrates resulting from photosynthesis. The total

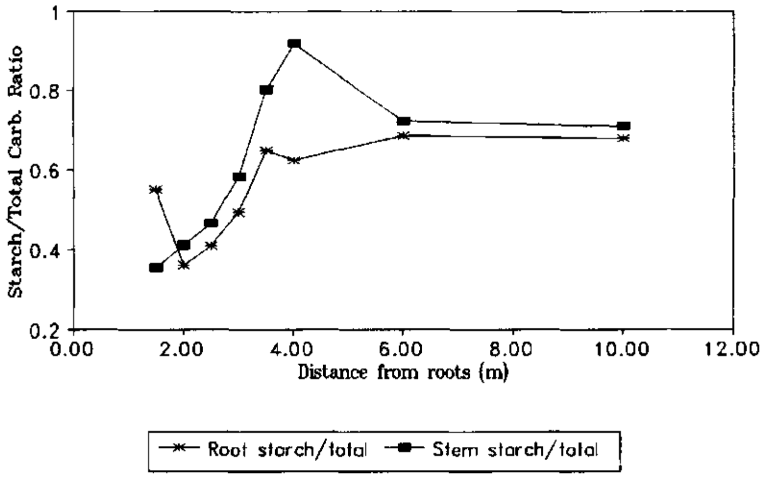


Figure 45. The ratio of starch to total carbohydrate content of *Dipterocarpus confertus* seedling stems and roots previously growing at various distances from the roots of the mother tree.

carbohydrates also rise slightly during the midday hours but the level is still far under that of the period after dark. It only goes down in the early morning, just before sunrise. This indicates that the translocation processes of carbohydrate take place in periods of hours rather than days.

From Figure 46 we also see that the availability of sugars, as expressed by the relatively lower starch:total carbohydrate ratio, is especially high in the roots. This again indicates an upward transport of externally gained carbohydrates in the seedlings. Again, as mentioned for Figure 45, the generally higher availability of non starch carbohydrates indicates an upward transport of these compounds.

The seedlings growing in the understorey of the forest are not able to maintain a positive carbon balance based upon the sole amount of the light they receive from sunflecks and possible resulting post-illuminance effect and from diffuse light. This was demonstrated in Chapter 5 where it was learned that the cumulative dark respiration was higher than the cumulative autophotosynthesis. Nevertheless there are still a considerable number of seedlings surviving under these unfavourable conditions of a deficitary carbon balance. Therefore it is suggested that these surviving seedlings obtain such carbon from their mother trees to survive as well as to maintain mycorrhizal symbiosis. The present study does not concern the question, whether or not the seedling carbohydrate deficit continues to be

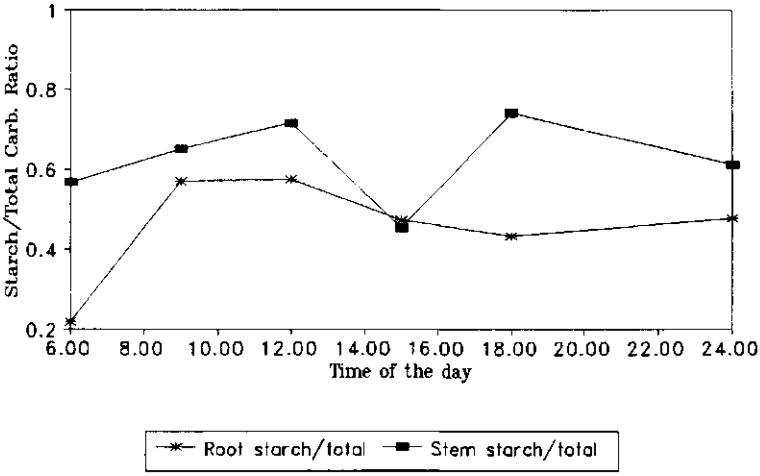


Figure 46. The ratio of starch to total carbohydrate in *Dipterocarpus confertus* seedling roots and stems during various harvesting times during the day and night period.

compensated for by their mother tree until the seedlings have the opportunity to receive more light, for instance because of senescence of crowns in the upper crown canopy or the sudden development of a gap because of tree fall (chablis).

6.3 Dipterocarp ectomycorrhizal specificity: some evidence.

Specificity of dipterocarp ectomycorrhizae in the present study is not considered as the ability of a single species of ectomycorrhizal fungus to associate with a single tree species. Many ectomycorrhizal fungi have been shown to have more or less the same inoculum potential when such fungi are introduced in the nursery. Although early- and late-stage fungi in temperate mycorrhizal succession have shown different inoculum potential (Deacon *et al.*, 1983), this does not mean that late-stage fungi may not be able to form mycorrhizae with seedlings. Fleming (1983) found that mycelial strands of late-stage fungi can infect the seedlings in the forest. In the case of inability of later-stage fungi to form mycorrhizae with the seedlings, this may be due to some later-stage fungi requiring much more carbohydrate than early-stage fungi (Frankland, 1992).

It is difficult to judge the degree of specificity of ectomycorrhizae from the seedling stage since most of the seedlings from natural forests never show ectomycorrhizal deficiency when they are transferred to the nursery. Therefore Smits (1994) proposed to define specificity of ectomycorrhizae in dipterocarps as a degree of specificity found under a certain set of environmental conditions in which he only referred to the natural forest. Such limitations refer to ecological specificity rather than absolute specificity that may never occur in mycorrhizal symbiosis.

Dipterocarp trees, especially those of the genera *Shorea, Dipterocarpus* and *Dryobalanops*, though sometimes also species of *Cotylelobium* and *Vatica,* are commonly found in a clumped distribution. Some authors think that this typically clumped distribution is related to the limited availability of ectomycorrhizal inoculum (Smits, 1983; Ashton, 1982). On the one hand, some of these typically cluster-forming species, such as *Shorea laevis,* prefer to grow on hill tops or ridges while some others, such as *Hopea rudiformis* and *Dipterocarpus tempehes* mostly prefer to grow or are more abundant on relatively wet sites. Other dipterocarps typically grow in heath forest, such as *Shorea albida*, while *S. balangeran* may not grow well or compete well in dryland forest. The latter two *Shorea* species have been observed to have typical brown coloured ectomycorrhizae of an appearance which is present only rarely in other dipterocarp species. It is possible that these differences in growth habit of different dipterocarps may be related to different preferences of their associated ectomycorrhizal fungi.

Some ectomycorrhizal fungi have shown different abilities in absorbing nutrients (Hadi and Santoso, 1985; Omon, 1994) and they may have different tolerances for heat in the soil (Marx and Bryan, 1971; Guinberteau, *et al.*, 1989), or different tolerances for surviving or functioning under drought stress (Guehl *et al.*, 1992). This could all be related to the specialization of ectomycorrhizal fungi to a certain set of environmental conditions. In this sense the ecological specificity might very well occur in dipterocarps.

Another observation supporting ecological specificity is the fact that some dipterocarp species and sporocarp species combinations appeared in areas geographically far apart with relatively similar site conditions in terms of soil, climate and temperature. The observations on sporocarp appearance in the present study show that fruiting bodies of ectomycorrhizal fungi that occur in the Wanariset forest were also found to occur in the Sungai Wein protection forest, the Bukit Soeharto forest and the ITCI concession area, some of these locations being at more than 40 kilometres from our plot. Notably the typical sites (e.g. slopes or tops of ridges) were also consistent for the occurrence of ecologically specific combinations.

From inoculation experiments it was learned that there can be large differences in growth between seedlings of the same mother tree inoculated by different ectomycorrhizal fungi in the nursery. Figure 47 shows a dramatic example at the Wanariset nursery where inoculation with some different ectomycorrhizal fungi resulted in different growth rates of seedlings. In this instance *Shorea* *leprosula* inoculated with *Amanita* sp. indet. 19 is growing faster than when it is inoculated with *Lactarius* sp or *Russula* sp. (Figure 47). Hence, we may assume that certain fungi provide the plant with a higher survival potential than others, and therefore may lead to some degree of plant-fungus specificity which again may be further influenced by the special relation with the site or substrate (Smits, 1994).

Figure 47. Different growth responses of *Shorea leprosula* seedlings inoculated with different ectomycorrhizal fungi in the nursery. A: inoculated with *Russula ebumeolata*; B: inoculated with *Lactarius subpiperatus*; C: inoculated with *Amanita sp. indet 19.*

Long-term observations of the appearance of sporocarps in the Wanariset forest showed that the most important ectomycorrhizal fungal genera are *Amanita, Boletus* and *Russula*. These three genera are more often encountered than other genera, such as *Cortinarius, Lycoperdon, Hydnum, Clitocybe, Inocybe, Laccaria, Boletinus, Paxillus, Cantharellus, Hebeloma, Agaricus, Aphelaria, Heimiella, Lepista, Lepiota, Phylloporus, Ramaria, Strobilomyces* and *Tylopilus*. Over more than four years of observation, 941 mushrooms in 22 genera appeared in a one hectare plot. The trigger mechanism of sporocarp appearance in the natural forest is not yet known. The data show that there was a weak correlation between precipitation and sporocarp appearance.

What is the importance of specificity of ectomycorrhizae in dipterocarps ? The family of Dipterocarpaceae counts a large number of species which show great differences in growth, in site preference as well as in commercial value. Most of the commercial timber tree species in this family belong to the main genera such as *Shorea* (Meranti), *Dryobalanops* (Kapur) and *Dipterocarpus* (Keruing), while some others belong to the genera *Hopea* (Balau), *Anisoptera, Cotylelobium* and *Vatica* (Resak). Species of the latter genera like species of *Cotylelobium* and *Vatica* tend to have less commercial value due to their short and poorly formed stems.

The differences in increment have important consequences for silviculture of the different species. Some ectomycorrhizal fungi have shown different abilities in promoting a faster growth of some dipterocarp species. Therefore the ongoing selection program for the production of superior quality dipterocarp planting stock for large scale planting activities now being developed at the Wanariset forestry research station in East Kalimantan, Indonesia, has to concern itself with the selection of suitable species combinations of ectomycorrhizal fungi and certain dipterocarps to reach optimal performance on selected sites. This selection program is bound to combine long-term experiments with inoculation experiments needs sporocarp inventories under natural forest as well as under plantation forest or secondary forest so as to assess the importance of succession processes in ectomycorrhizal fungi in dipterocarp plantations.

Taken into account all the aspects discussed in the present study related to the regeneration of dipterocarp seedlings it can be concluded that light or soil conditions do not represent the main factors for successful dipterocarp regeneration under a closed forest canopy, but that dipterocarp seedling survival is mostly related to the presence of mycorrhizal inoculum and consequent support of the seedlings through the ectomycorrhizal mycelial connections with roots from mother trees that have well-illuminated crowns in the upper canopy.

6.4 The limitation of the approaches.

One should be careful in drawing general conclusions for all dipterocarp species based upon the data collected in the present study which only involved a limited number of dipterocarp species. However, it is hoped that the outcome presented here may be valid for closely related species of Dipterocarps. This hope is especially strong in view of the fact that Dipterocarpaceae are a family of tree species which shows a great morphological as well as genetical constancy within the genera (Ashton, 1969; Somego, 1978).

6.5 The importance of the results for practical application.

It has been proven in previous experiments as well as in the present study that the importance of mycorrhizae in the dipterocarp forest ecosystem is much greater than previously thought. The experience with artificial regeneration as well as natural regeneration of dipterocarp forests shows that the failure of seedlings to establish in the field was not only due to technical problems but also due to the lack of understanding of the influence of microorganisms such as mycorrhizae upon the growth and performance of seedlings in the field. It has been shown that dipterocarp species are obligatorily ectomycorrhizal. Since the problem of planting stock production has been solved by means of planting stock production through wildlings and cuttings, the problem remains of how to grow seedlings in the field.

The seedlings collected from natural forest have shown no mycorrhizal deficiencies, whereas nursery stock produced from cuttings has to be inoculated by suitable mycorrhizal fungi in order to obtain an optimal growth in the field. The method of inoculation by using soil collected from underneath or nearby the mother tree has proven to be a practical method that can be applied in large scale dipterocarp nurseries.

In forest management it must be taken into account that logging operations change the microclimate of the forest ecosystem. Changing the soil temperature due to opening up the crown canopy leads to physical or physiological damage of the mycorrhizal symbiosis of the residual stands in the forest. On the other hand, the importance of residual stands as resources for inocula for germinated seedlings might determine the success or failure of natural regeneration after logging operations. Therefore, a sufficiently large residual stand with as much as possible evenly distributed mother trees must be retained, which is one of the key points in the Indonesian selective felling system to ensure the success of natural regeneration. The results of the present study also indicate that it may be better to not cut or kill large dipterocarp trees which are over their prime, the so-called trees of the past (Halle *et al.*, 1978), since they still have an important role in supporting the natural regeneration.

In natural forests, the presence of mycorrhizal fungi is not a limiting factor. The mycorrhizal fungi from the mother trees are thought to be the best for inoculation sources for the nurseries because these fungi have established through long evolution under strong competition and so are the best adapted fungi for such ecological conditions (see also Smits, 1994).

There are two main issues defined by the results of the current study that must be considered for practical application in forest practice in dipterocarp forests. First, mycorrhizal knowledge has to be applied in nursery practice in order to obtain good planting stock. The fact that some dipterocarp seedlings in the nursery do not show mycorrhizal deficiencies although no mycorrhizal inoculation was introduced is due to infection by common nursery fungi such as *Thelephora terrestris*. However, often these seedlings fail to establish after transplanting to the field. This is due to the unsuitability of the fungi that seedlings obtained from the nursery to perform well under field conditions with a different substrate and more interplant competition. Therefore it is strongly recommended that inoculation with fungi well-adapted to field conditions must be rule, in order to obtain better survival of the seedling after planting. Second, in the implementation of the Indonesian selective cutting system, the old forestry rule must be taken into account that the effect of changes in microclimate of the forest ecosystem determined the regeneration processes. This rule extends to dipterocarp ectomycorrhizae being sensitive to high soil temperatures. Negative effects of logging, especially the degree of crown opening, must be reduced in order to maintain a favourable microclimate for better growth of residual stands and their root symbiont rules. However, this should not be done to such a degree that light becomes a limiting factor for better growth of the seedlings.

The Indonesian selective felling and replanting system (TPTI) rules that at least 25 trees per hectare of the commercial species must be left in the forest after selective felling for the next rotation (Soerianegara, 1972; Armitage and Kuswanda, 1989). These trees (called "core trees") must be evenly distributed over the logged area. This rule seems to be relevant to the findings of this current study in which the distribution of the core trees might ensure that the germinating seedlings to obtain mycorrhizal infection with well-adapted mycorrhizae from the core trees. The hollow trees, however, that may not be harvested can also be considered as core trees in the TPTI system because these trees provide seeds as well as well-adapted ectomycorrhizal inoculum for better growth of dipterocarp seedlings.

SUMMARY

The present book on "Dipterocarpaceae: Tree-Mycorrhizae-Seedling Connections" deals with the role mother tree provide for their seedlings through their mycorrhizal connections between roots of the mother tree and the seedlings.

The book is the result of seven years of study in a lowland mixed dipterocarp rain forest in East-Kalimantan Indonesia. The book consist of six chapters.

The first chapter deals with a general introduction that provides an overview of some literature on Dipterocarpaceae and mycorrhizae with special reference to light.

Chapter 2 deals with the influence of light intensity on the formation of ectomycorrhizae in dipterocarp seedlings. In this chapter the results on experiments in the greenhouse are described. The outcome of these experiment reconfirms the importance of light for the formation as well as the number of ectomycorrhizae establishing on the root of the formerly non-mycorrhizal seedlings. Best growth and mycorrhizal development was attained at light intensities between 40 and 60% of full light. Also the indirect negative effect of the high light intensities upon top soil temperature and their consequent effects upon the performance of the associated ectomycorrhizae are discussed.

Chapter 3 reports on some field experiments in which non-mycorrhizal seedlings were planted at varying distances from an isolated growing mother tree of the same species in a natural forest. The monitoring of the survival and the growth of the seedlings indicated that those seedlings growing close to the root system of the mother tree outperformed the others. No correlations were found between the survival and growth with light intensity or soil nutrients the growing sites.

Chapter 4 deals with the relation between natural regeneration, ectomycorrhizae, light, soil nutrients and other physical factors. The results of four years ectomycorrhizal sporocarp collection and the monitoring of the survival and growth of 6800 *Dipterocarpus confertus* seedlings showed a strong correlation between the appearance of the sporocarp and the location of the best surviving seedlings. No correlation was found between light intensities and survival or growth of the seedlings. Sporocarp appearance was not influence by rainfall pattern although more sporocarp can occur after rainfall during certain period of the year. Factors which are potentially influencing sporocarp formation are discussed extensively. No correlation was found between soil chemical properties and the survival and growth of seedlings but some correlation existed with the presence of much organic matter.

Chapter 5 deals with the photosynthesis and the carbon balance of the same *Dipterocarpus confertus* seedlings. It was found that a strong correlation existed between distance of the seedling from the foot base of the mother trees and their growth. No correlation was found between light intensity and growth of seedlings. The photosynthesis measurement revealed that the seedlings had a negative carbon balance, cumulative dark respiration being higher than the cumulative photosynthesis. More than 89 % of the light received by the seedlings was below the compensation point light intensity. Starch and carbohydrate analyses of roots and stems of the seedlings showed that plants growing near the root of the mother tree had higher carbohydrate content. Available sugar was higher during the night than during the day time and was relatively always higher in the roots.

Chapter 6 deals with general discussion and conclusion of the research. The review of earlier chapters leads to the conclusion that the presence of ectomycorrhizae on the seedlings is more importance for the survival and growth of the seedlings than light intensity or other soil properties under closed canopy in a natural dipterocarp forest. The result form the earlier chapters also provide evidence for the nursing role of the mother trees, carbohydrates produced in the fully illuminated crown of the mother tree are being transported to the seedlings through ectomycorrhizal connection. This chapter also discusses the specificity of ectomycorrhizae and provide some indication that there is certain degree of ecological specificity present in Dipterocarpaceae and fungi relationship.

At the end of Chapter 6 some practical conclusions are drawn with regard to the importance of the research findings for forest management in mixed dipterocarp forest. Old trees can still have an important role in supporting dipterocarp seedling regeneration and this aspect should be included in selective harvesting system in mixed dipterocarp forest.

SAMENVATTING

Het huidige booek over "Dipterocarpaceae : Tree-Mycorrhizae-Seedling Connections" betreft de rol van de moederbomen voor hun zaailingen via de schimmerverbindingen tussen de wortels van de moederbomen en de zaailingen.

Het boek is gebaseerd op de resultaten van zeven jaar onderzoek in een laagland tropisch regenwoud gedomineerd door meranties in de Indonesische provincie Oost-Kalimantan. Het boek bestaat uit zes hoofdstukken.

Het eerst hoofdstuk betreft een algemene inleiding met overzichten van de literatuur op het gebied van Dipterocarpaceae and mycorrhizae met speciale referenties tot de rol van licht in deze relatie.

Hoofdstuk 2 gaat in detail in op de invloed van licht intensiteiten op de vorming van mycorrhizae op de wortels van zaailingen van Dipterocarpaceae. In dit hoofstuk worden de resultaten van kasproeven beschreven. De bevindigen uit deze proeven bevestigen het belang van licht voor de vorming zowel als de hoeveelheid ectomycorrhizaeop de wortels van de voormalig niet geinfekteerde zaailingen. De beste groei van de zaailingen en ontwikkeling van de ectomycorrhizae werd bereikt bij lichtintensiteiten varierend van 40 tot 60% van vol licht. Verder wordt in dit hoofdstuk ook het indirekte negatieve effekt van hoge licht intensiteiten op bodemtemperatuur van de bovenste lagen en als gevolg hiervan op het funktioneren van de geassocieerde ectomycorrhizae.

Hoofdstuk 3 rapporteert de resultaten van veldproeven waarbij niet geinfekteerde zaailingen werden geplant op verschillende afstanden van geisoleerd groeiende moederbomen van dezelfde soort onder natuurlijke bosomstandigheden. De overleving en de groei van de zaailingen was beter wanneer de zaailingen dichter bij de wortels van de moederboom groeiden. Er werd geen verband gevonded tussen het overleven en de groei van de zaailingen met de lichtintensiteit of de hoeveelheid organisch materiaal ter plekke.

Hoofdstuk 4 gaat over de relatie tussen natuurlijke verjonging, ectomycorrhizae, licht, bodemfaktoren en andere fysische faktoren. De resultaten van zes jaar verzamelen van ectomycorrhizae-paddestoelen en het volgen van de groei van 6.800 *Dipterocarpus confertus* zaailingen liet zien dat er een sterk verband bestaat tussen de plaatsen waar de paddestoelen verschijnen en de plaatsen waar de zaailingen het beste overleven en groeien. Er werd geen verband gevonden tussen licht intensiteiten en het overleven en de groei van de zaailingen. Het verschijnen van paddestoelen werd niet beinvloed door de variaties in regenval, maar normalerwijze verschijnen paddestoelen na zware regenval gedurende bepaalde periodes in het jaar. Faktoren die het verschijnen van de paddestoelen zouden kunnen beinvloeden worden uitvoerig besproken. Er werd geen verband gevonden tussen de chemische bodemeigenschappen en het overleven en de groei van de zaailingen maar er werd een zwak verband gevonden met de aanwezigheid van organisch materiaal.

Hoofdstuk 5 behandelt de fotosynthese en de suikerbalans van dezelfde *Dipterocarpus confertus* zaailingen. Een sterk verband bleek te bestaan tussen de afstand waarop de zaailingen groeiden van de wortels van de moederboom en de overleving en groei van deze zaailingen. Er werd wederom geen verband gevonden tussen de lichtintensiteit en de groei van de zaailingen. De metingen van de fotosynthese toonden aan dat de zaailingen een negatieve suikerbalans bezaten, de cumulatieve donkerademhaling zijnde hoger dan de cumulatieve fotosynthese. Meer dan 89% van het licht wat werd ontvangen door de zaailingen was onder het lichtcompensatiepunt. De suikeranalyses van wortels en stengels van de zaailingen lit zien dat die zaailingen die dichter bij de wortels van de moederboemen groeiden meer suiker bevatten. De beschikbare suiker was hoger gedurende de donkerperiode dan gedurende de dag en was relatief altijd hoger in de wortels.

Hoofstuk 6 bevat de algemene discussie en de conclusies van het onderzoek. Het overzicht van de voorgaande hoofdstukken leidde tot de conclusies dat de aanwezigheid van ectomycorrhizae op de wortels van de moederbomen belangrijker is voor het overleven en de groei van de zaailingen dan de lichtintensiteit of andere bodemeigenschappen onder een gesloten kronendak in een origineel merantibos. De resultaten van de voorgaande hoofdstukken geven ook bewijzen dat er een voedingsrol van de moederboom voor de zaailingen bestaat, waarbij de suikers die geproduceerd worden in de kroon van de moederboom worden overgebracht naar de zaailingen via de schimmelverbindingen. Dit hoofdstuk bespreekt ook de specificiteit van de schimmels van de Dipterocarpaceae en geeft indikaties dat een hoge mate van ecologische specificiteit bestaat in de relatie tussen schimmel en meranti.

Aan het eind van hoofdstuk 6 worden nog enige praktische conclusies getrokken met betrekking tot het belang van de huidige bevindingen voor het bosbeheer in gemengde Dipterocarpaceae bossen. Oude aftakelende bomen kunnen nog een belangrijke rol vervullen voor het ondersteunen van dipterocarp zaailingen en dit aspekt verdient geincorporeerd te worden in de selectieve oogstsystemen van deze bossen.

RINGKASAN

Tesis yang berjudul "Dipterocarpaceae: Tree-Mycorrhizae-Seedling Connections" membahas mengenai peranan pohon induk bagi anakannya melalui hubungan mikoriza antara akar anakan dengan pohon induknya pada hutan alam.

Buku ini merupakan hasil penelitian selama tujuh tahun di hutan alam campuran Dipterocarpaceae in Kalimantan Timur Indonesia. Buku ini terdiri dari 6 bab yang masing-masing isinya akan dijelaskan berikut ini.

Bab pertama membahas pendahuluan dan tinjauan pustaka mengenai Dipterocaraacae dan mikoriza khususnya dalam hubungannya dengan cahaya.

Bab 2 membicarakan pengaruh intensitas cahaya terhadap pembentukan ektomikoriza pada anakan Dipterocarpaceae. Hasil penelitian di rumah kaca ini kembali mengkonfirmasikan kepentingan cahaya terhadap pembentukan dan perkembangnan mikoriza pada akar anakan. Pertumbuhan anakan dan perkembangnan mikoriza yang paling baik didapat pada intensitas cahaya antara 40 dan 60% dari cahaya penuh. Pengaruh negatif tidak langsung dari intensitas cahaya tinggi terhadap suhu tanah lapisan atas dan akibatnya terhadap pertumbuhan dan mikoriza anakan juga dibahas dalam bab ini.

Bab 3 relaporkan hasil percobaan lapangan dimana anakan tanpa mikoriza yang ditanam dengan jarak yang berbeda dari pohon induknya dari jenis yang sama di hutan alam. Hasil pengamatan daya hidup (survival) dan pertumbuhan dari akan menunjukkan bahwa anakan yang tumbuh dekat sistem perakaran pohon induknya tumbuh lebih baik dari yang jauh dari akar pohon induknya. Tidak ditemui hubungan antara daya hidup dan pertumbuhan dengan intesitas cahaya dan kandungan unsur hara pada tempat tumbuh dalam percobaan ini.

Bab 4 membahas hubungan antara regenerasi alam dengan ektomikoriza, cahaya dan sifat-sifat tanah dan factor fisik lainnya. Hasil dari pengumpulan data pemunculan jamur di hutan alam selama lebih dari empat tahun dan pengamatan pertumbuhan dari 6.800 anakan *Dipterocarpus confertus* memperlihatkan hubungan yang kuat antara pemunculan jamur mikoriza dengan tempat dimana anakan banyak yang hidup. Tidak ditemui hubungan antara pertumbuhan dan daya hidup dengan intensitas cahaya. Pemunculan jamur ektomikoriza tidak dipengaruhi oleh pola curah hujan di hutan walaupun bisa terjadi banyak pembentukan jamur sesudah musim hujan pada keadaan tertentu dalam setahun. Faktor yang menyebabkan pembentukan atau kemunculan jamur dihutan alam dibahas juga dalam bab ini. Tidak ditemui hubungan antara sifat-sifat tanah dengan daya hidup maupun pertumbuhan tapi ada hubungan dengan kandungan bahan organik pada lantai hutan.

Bab 5 membahas mengenai fotosintesa and neraca karbon dari anakan *Dipterocarpus confertus* yang tumbuh di hutan alam. Ditemui hubungan yang kuat antara pertumbuhan anakan dengan jarak tempat tumbuhnya dari sistem perakaran pohon induknya. Tidak ada hubungan antara intensitas cahaya dengan pertumbuhan anakan. Hasil pengukuran fotosintesa menunjukkan bahwa anakan yang tumbuh dilantai hutan mengalami defisit neraca karbonnya dimana komulatif respirasinya lebih tinggi dari komulatif fotosintesanya. Lebih dari 89% cahaya yang diterima anakan adalah dibawah titik kompensasi cahayanya. Analisa karbohidrat dari akar dan batang akan memperlihatkan bahwa anakan yang tumbuh dekat pohon induknya mempunyai kandungan karbohidrat yang lebih tinggi. Ketersediaan gula lebih tinggi pada waktu malam daripada siang hari dan selalu relatif lebih tinggi pada akar anakan.

Bab 6 membahas diskusi umum dan kesimpulan dari hasil-hasil pada bab-bab terdahulu. Disimpulkan bahwa keberadaan ektomikoriza pada anakan jauh lebih penting untuk daya hidup anakan dan pertumbuhannya dari intensitas cahaya atau sifat-sifat tanah di bawah kondisi tajuk yang rapat di hutan Dipterocpaceae. Hasil dari bab-bab terdahulu juga menunjukkan bukti bahwa peranan pohon induk yang dalam posisi menguntungkan untuk cahaya dalam membantu pertumbuhan anakannya melalui hubungan mikoriza. Bab ini juga membahas beberapa aspek dari spesifisitas ektomikoriza dan memperlihatkan bahwa cukup indikasi ada tingkat spesifisitas ekologi dari hubungan antara Dipterocarpaceae dan jamur mikoriza.

Pada bagian akhir dari tulisan ini disampaikan beberapa aspek kepentingan praktis dari hasil penelitian dalam hubungannya dengan sistem pengelolaan hutan campuran Dipterocarpaceae. Pohon-pohon yang tua masih bisa memegang peranan penting dalam membantu proses regenerasi anakannya dan aspek ini sebaiknya juga dipertimbangkan dalam sistem tebang pilih yang diterapkan untuk hutan campuran Dipterocarpaceae.

GLOSSARY

Amphimycorrhizae : are mycorrhizae in which plant roots are infested with intracellular hyphae, often with distinctive clamp connections and minute haustoria-like organs, and all of the root surface is covered with a dense mantle of hyphae, et certain times bearing cystidia-like structures, without any apparent change in root morphology or cortex cell morphology (Smits, 1994).

ARC/INFO : one of the methods used in the Geographical Information System.

ASCII : American Standard Code for Information Interchange

Biochemical efficiency : the efficiency of the photosynthesis process of the green plant as affected by the internal biochemical substances in the green plants.

Cutting : planting stock obtained through vegetative propagation of stem or shoot (the rooted stem or shoot).

Crown metamorphosis: a programmed period of tree development in which repetition of the patterns displayed in early branching can be found back in each of the subcrowns that are building the whole crown of the tree (see Oldeman, 1990)

Diffuse light: light reaching the forest interior at low light intensity resulting from light filtered by the crown canopy, or transmitted or reflected light from the leaves.

Distal rooting : a development of the primary root system away from the main stem of the plant

Ectomycorrhizae : the mycorrhizae characterized by an external fungal sheath or mantle round the plant root, where the hyphal penetration between the epidermal and often the cortical cells form a Hartig net.

Ectendomycorrhizae : the mycorrhizae which may or may not possess a thick fungal sheath, although external hyphae on the root

	surface are always present, as are hyphal penetration between the epidermal and cortical cells constituting a Hartig net, and also penetration into active living cells.
Endomycorrhizae :	the mycorrhizae which do not form external sheaths or mantles but the hyphae of which penetrate both between and into the living cell of the cortex and epidermis.
ECM :	Ectomycorrhizae
Fruiting body:	*(see sporocarp), the overall spore-containing* reproductive structure in fungi, often clearly visible to the naked eye.
Hartig net :	the net like structure that is visible on cross sections of ectomycorrhizal root, consisting the fungl hyphae entering between epidermis and or cortex cell.
Hypha (hyphae):	one of the filamentous structures that constitute the mycelium of the fungus.
Herbarium :	a collection of dry preserved of plants or fungi.
Mass flowering :	peak flowering season of dipterocarp forest where most of the species flower during the same time span.
Mycorrhizae :	a symbiotic association of a fungus and the root of higher plants in which the fungus lives on or within the root.
Mycelium (mycelia) :	the vegetative body of most fungi; a mass of hyphae.
Mother tree :	the adult tree where the seeds of the offspring originated, its crown being part of the upper layer of the forest canopy.
Primary root system :	the main root system of the plant derived directly from the seedling root system.
Pyramidal:	typical shape of ectomycorrhizae, where the branches of the mycorrhizae are shorter near the end of the structure than near the base and attachment with non mycorrhizal roots.

PAR :	Photosynthetic Active Radiation, solar radiation in the 400 - 700 nm wave length.
PFD :	Photon Flux Density, the number of photons (400-700 nm) incident per unit time on a unit surface.
PMA (law) :	Penanaman Modal Asing (Foreign Investment Law)
PMDN (law):	Penanaman Modal Dalam Negeri (Domestic Investment Law)
Ramification :	branching system.
Rhizomorph :	a root-like aggregation of hyphae.
Rhizosphere :	the environment below ground very close to the root system of the plants and influenced by chemicals produced by the root.
Secondary root system :	the branches of the main root which develop later on after primary rooting has become mainly distal.
Sunflecks :	short bursts of light reaching the forest floor through canopy gaps.
Solarization:	heating, using the solar radiation or pasteurization, of the culturing media.
Sporocarp :	the "fruiting body" formed by fungi as a reproductive organ and containing of spores.
Succession :	the chronological sequence of different organisms colonising a particular substrate.
TPTI :	Tebang Pilih dan Tanaman Indonesia (The Indonesia Selective Felling and Replanting System).
VAM :	Vescicular Arbuscular Mycorrhizae or endomycorrhizae
Wildlings :	planting stock obtained by collecting wild seedlings from natural forest.

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Appendices

Appendix 1. Classification of chemical soil characteristics (From Van Bremen, H. *et al.*, 1990).

Classifications presented below originate from the folowing sources: Balsem and Buurman (1989), London (1984), PTT (1983), SSS (1962) and RePPProt (1987). They have been applied in the description of the soils in the plot.

Soil reaction (pH-H2O, 1:2.5)

extremely acid	<4.0
excessively acid	4.0-4.5
very stronghly acid	4.6-5.0
strongly acid	5.1-5.5
moderately acid	5.6-6.0
slightly acid	6.1-6.5
neutural	6.6-7.3
slightly alkaline	7.4-7.8
moderately alkaline	7.9-8.8
strongly alkaline	>8.5

Organic carbon (% C, Walkley and Black)

very low	<2.0
low	2.0-4.0
medium	4.1-6.0
high	>6.0

Organic nitrogen (% N, Kjeldahl)

very low	<0.1
low	0.1-0.2
medium	0.3.0.5
high	>0.5

Exchangable potassium (me K/100g fine earth)

very low	<0.1
low	0.1-0.2
medium	0.3-0.5
high	>0.5

Exchangable calcium (me Ca/100g fine earth)

very low	<0.1
low	0.1-0.3
medium	0.4-1.0
high	>1.0

Exchangable Magnesium (me Mg/100g fine earth)

very low	<0.1
low	0.1-0.3
medium	0.4-1.0
high	>1.0

Base saturation (%, pH 7)

low	<20
medium	20-60
high	>60

Aluminium saturation (%, pH soil)

very low	<20
low	20-40
medium	41-60
high	61-80
very high	>80

Cation Exchange Capacity (me/100g fine earth, pH 7)

very low	<5
low	5-16
medium	17-24
high	25-40
very high	>40

Total Phosphorus (mg P205/100g fine earth)

very low	<10
low	10-20
medium	21-40

Total Potassium

very low	<10
low	10-20
medium	21-40

Available phosphorous (ppm P205)

very low	<10
low	10-15
medium	16-25
high	26-35

Appendix 2. List of species of ectomycorrhizal fungi found in the regeneration plot of the Wanariset forest during observation period (Nov. 1989 till Dec. 1993).

Agaricus sp. indet. 01
Agaricus sp. indet. 02
Amanita cf verna
Amanita sp
Amanita sp. indet. 01
Amanita sychnopyramis Corner & Bas
Amanita borneensis
Amanita longistriata Imai
Amanita elata (Mass.) Corner & Bas
Amanita xanthogala Bas
Amanita cf. avellaneosquamosaa Imai
Amanita centunculus Corner & Bas
Amanita sp. indet. 08k
Amanita sp. indet. 09
Amanita similis Boedijn
Amanita sp. indet. 20
Amanita sp. indet. 21
Amanita sp. indet. 22
Amanita sp. indet. 26
Amanita sp. indet. 27
Amanita sp. indet. 30
Amanita sp. indet. 32
Amanita sp. indet. 36
Amanita sp. indet. 37
Aphelaria dendroides (Jungh.) Corner
Boletus aff. olivaceirubens Corner
Boletus emodensis
Boletus sp
Boletus sp. indet. 04
Boletus sp. indet. 05
Boletus sp. indet. 06
Boletus sp. indet. 07
Boletus sp. indet. 08
Boletus sp. indet. 09
Boletus sp. indet. 11
Boletus sp. indet. 13
Boletus sp. indet. 14
Boletus sp. indet. 16
Boletus sp. indet. 17
Cantharelus sp. indet. 01
Clitocybe sp.
Clitocybe sp. indet 01
Cortinarius sp. indet. 03
Cortinarius sp. indet. 04
Cortinarius sp. indet. 05
Hebeloma sp.
Hebeloma sp. indet. 01
Hebeloma vinosophyllum Hongo
Heimiella retispora (Pat & Baker) Murrill
Hydnum repandum
Inocybe sp. indet. 01
Laccaria laccata (Scop.:Fr) B.&Br.
Laccria sp. indet. 02
Lactarius piperatus
Lactarius cf. austrovolemus Hongo
Lactarius subpiperatus Hongo
Lactarius sp. indet. 06
Lepiota sp. indet. 03
Lepista sp. indet. 01
Lycoperdon cf. columnare
Paxillus sp. indet. 02
Phyloporus aff. infundibuliformis (Clemand) Sing.
Russula sp
Russula eburneoareolata Hongo
Russula sp. indet. 02
Russula sp. indet. 03
Russula cf. pectinatoides Peck
Russula senecis Imai
Russula cf. metachroa Hongo
Russula sp. indet. 07
Russula sp. indet. 08
Russula sp. indet. 09
Russula sp. indet. 10
Russula sp. indet. 11
Russula sp. indet. 12
Russula sp. indet. 15
Russula sp. indet. 16
Russula sp. indet. 17
Russula sp. indet. 19
Russula sp. indet. 20
Russula sp. indet. 21
Russula sp. indet. 26
Russula sp. indet. 28
Russula sp. indet. 29
Russula sp. indet. 33
Russula sp. indet. 35
Strobilomyces popypyramis Berk.
Tylopilus alboater (Schw.) Murrill
Tylopilus ballouii (Peck) Sing.

Appendix 3. Tree species of diameter above 5 cm occuring in the regeneration plot with their mycorrhizal status (ECM=ectomycorrhizae; VAM=endomycorrhizae; RH= Rhizobium; NK=not known or not observed)

Species (1)	Family (2)	Mycorrhizal Status (3)
Dipterocarpus confertus	Dipterocarpaceae	ECM
Dipterocarpus cornutus	Dipterocarpaceae	ECM
Cotylelobium malayanum	Dipterocarpaceae	ECM
Hopea mengerawan	Dipterocarpaceae	ECM
Shorea ovalis	Dipterocarpaceae	ECM
Shorea laevis	Dipterocarpaceae	ECM
Shorea smithiana	Dipterocarpaceae	ECM
Shorea leprosula	Dipterocarpaceae	ECM
Shorea pauciflora	Dipterocarpaceae	ECM
Vatica umbonata	Dipterocarpaceae	ECM
Macaranga lowii	Euphorbiaceae	VAM
Eugenia sp indet. 1	Myrtaceae	VAM
Drypetes kikir	Euphorbiaceae	
Mallotus penangensis	Euphorbiaceae	VAM
Ganua pallida	Sapotaceae	VAM
Canarium sp. indet. 1	Burseraceae	VAM
Pimeleodendron griffithianum	Euphorbiaceae	
Madhuca sericea	Sapotaceae	
Cleistanthus sp. indet. 1		
Phoebe grandis		
Popowia sp. indet. 1	Annonaceae	VAM
Knema cinerea	Myristicaceae	VAM
Aglaia sp indet. 1	Meliaceae	VAM
Memecylon diafolium	Melastomaceae	VAM
Ptenandra sp. indet. 1	Melastomaceae	VAM
Monocarpia sp indet. 1	Annonaceae	NK
Diospyros sp. indet. 1	Ebenaceae	NK
Hydnocarpus sp. indet. 1	Flacourtiaceae	VAM
Dacryodes rugosa	Burseraceae	VAM
Baccaurea sp. indet. 1	Euphorbiaceae	VAM
Eugenia sp. indet. 2	Euphorbiaceae	VAM
Diospyros borneensis	Ebenaceae	VAM
Polyalthia sp. indet. 1	Annonaceae	VAM
Baccaurea sp. indet. 2	Euphorbiaceae	VAM
Canarium sp. indet. 2	Burseraceae	VAM
Sterculia sp. indet. 1	Sterculiaceae	NK
Artocarpus sp. indet. 1	Moraceae	VAM

Appendix 3 (Continued)

(1)	(2)	(3)
Aporusa nitida	Euphorbiaceae	VAM
Knema sp. indet. 2	Myristicaceae	VAM
Payena lucida	Sapotaceae	VAM
Acmena sp. indet. 1	Myrtaceae	VAM
Aporusa aurea	Euphorbiaceae	NK
Durio acutifolius	Bombaceae	NK
Eugenia sp. indet. 3	Myrtaceae	NK
Hydnocarpus sp. indet. 2	Flacourtiaceae	VAM
Ochanostachys sp. indet. 1	Olacaceae	NK
?	Rubiaceae	NK
Knema latericea	Myristicaceae	NK
Sindora cf. velutina	Leguminosae	RH
Xylopia malayana	Annonaceae	VAM
Payena sp. indet. 2	Sapotaceae	VAM
Lithocarpus sp. indet. 1	Fagaceae	ECM
Eugenia sp. indet. 3	Myrtaceae	VAM/ECM
Eugenia sp. indet. 4	Myrtaceae	VAM
Dyera costulata	Apocynaceae	VAM
Rhodamnia cinerea	Myrtaceae	NK
Artocarpus sp. indet. 2	Moraceae	VAM
Garcinia sp. indet. 1	Guttiferae	VAM
Barringtonia sp. indet. 1	Lecythidaceae	VAM
Ixora sp. indet. 1	Rubiaceae	NK
Sterculia sp. indet. 2	Sterculiaceae	NK
Scaphium macropodum	Sterculiaceae	NK
Eusideroxylon zwageri	Lauraceae	VAM
Nephelium sp. indet. 1	Sapindaceae	NK
Santiria tomentosa	Burseraceae	VAM
Lithocarpus sp. indet. 2	Fagaceae	ECM
Artocarpus anisophyllus	Moraceae	VAM
Teijsmanniodendron sp. indet. 1	Verbenaceae	NK
Fordia sp. indet. 1	Leguminosae	NK
Sarcotheca diversifolia	Oxalidaceae	NK
Archidendron sp. indet. 1	Mimosaceae	NK
Gymnacranthera sp. indet. 1	Myristicaceae	VAM
Calophilum sp. indet. 1	Guttiferae	NK
Girronierra sp. indet. 1	Ulmaceae	ECM
Elaeocarpus sp. indet. 1	Elaeocarpaceae	NK
Palaquium sp. indet. 1	Sapotaceae	NK
Polyalthia sp. indet. 2	Annonaceae	VAM
?	Annonaceae	NK

Appendix 3 (Continued)

(1)	(2)	(3)
Prunus japonica	Rosaceae	ECM
Myristica sp. indet. 1	Myristicaceae	VAM
?	Sapotaceae	NK
Atuna excelsa	Chrysobalanaceae	VAM
Koompassia malaccensis	Leguminosae	RH
Xylopia sp. indet 2	Annonaceae	VAM
Xanthophyllum sp. indet. 1	Polygalaceae	NK
Pertusadina sp. indet. 1	Rubiaceae	NK
Aporusa aurea	Euphorbiaceae	VAM
Palaquium rostratum	Sapotaceae	VAM
?	Lauraceae	NK
?	Annonaceae	NK
Aquilaria mallaccensis	Thymeliaceae	NK
Alangium sp. indet. 1	Alangiaceae	VAM
Saurauia sp. indet. 1	Actinidiaceae	NK
Rhodamnia sp. indet. 1	Myrtaceae	VAM/ECM
Pertusadina sp. indet. 2	Rubiaceae	NK
Myristica sp. indet. 2	Myristicaceae	VAM
Porterandia anisophylla	Rubiaceae	NK
?	Lauraceae	NK
Payena sp. indet. 2	Sapotaceae	VAM
Eugenia sp. indet. 4	Myrtaceae	VAM
Baccaurea sp. indet. 3	Euphorbiaceae	VAM
Crypteronia sp. indet. 1		NK
Pyota sp. indet. 1		NK
Magnolia sp. indet. 1	Magnoliaceae	NK
Mierucos sp. indet. 1	Tiliaceae	NK
Gluta rengas	Annacardiaceae	NK
Knema sp. indet. 3	Myristicaceae	NK
Porterandia sp. indet. 1	Rubiaceae	NK
Knema sp. indet. 4	Myristicaceae	NK
Polyalthia sp. indet. 3	Annonaceae	NK
Santiria sp. indet. 2	Burseraceae	VAM

Appendix 4. Description and site information of two soil profile in the regeneration plot.

Profile number : 1

General site information and derived values

Site number	: Profile 1
Mapping unit	:
Pedon Classification	: Typic hapludults
Diagnostic horizons/features	: haplic, argilic
Greenwich coordinates	:
Elevation (m asl.)	:
Geomorphic component	: Upper slope
Slope gradient (%)	: 35 %
Slope shape, aspect	: Concave
Micro relief	: 25 - 50 m
Stoniness	: none
Parent material	: claystone, sandstone
Effective soil depth (cm)	: 120
Obstructive layer	: no
Water table	: not observed
Flooding frequency	: none
Soil draenage	: moderately well draened
Land use/vegetation	: Primary forest/Research plot

Appendix 4 (Continued)

Profile Description

Horizon	Depth	Description
Ah	0 - 5 cm	10 YR 3/4, exterior large peds;loam; fine to medium sub angular blocky structure; very friable (moist), non plastic and non sticky when wet; many fine to medium pores; many very fine to fine roots; clear and wavy boundary.
EB	5 - 18/20 cm	10 YR 6/6,exterior large peds moist; Clay loam; medium to coarse subangular blocky friable (moist), sticky and slightly plastic when wet; many fine to coarse pores; many medium roots, and moderate coarse roots; few, fine, faint 5 Y 8/1 irregular reduction, few fine faint mottles; gradual wavy boundary.
Bt1	18/20 - 41cm	10 YR 6/6, interior large peds moist; clay loam; coarse subangular blocky and slightly firm, sticky and slightly plastic when wet; 10 YR 7/3 irregular reduction few fine mottles; many fine to medium pores, moderate coarse pores by insect; moderate fine to medium and many coarse roots; irregular wavy boundary.
Bt2	41 - 70 cm	7.5 YR 5/8, interior large peds moist; clay; coarse subangular blocky and firm, sticky and plastic when wet; 5 Y 7/2, irregular reduction, few,fine faint mottles; moderate fine to medium pores; many coarse and few fine to medium roots; irregular wavy boundary.
Bt2g	70 - 97 cm	5 YR 5/8, interior large peds,moist; clay; coarse angular blocky very firm, sticky and plastic when wet; 2.5 Y 8/2, irregular reduction, many fine distinct mottles; few fine pores; moderate fine to medium roots; irregular wavy boundary.

Appendix 4 (Continued)

BCg	97 - 120 cm	5 YR 5/8, interior large peds moist; clay; angular blocky, friable, sticky and palstic when wet; 5 Y 8/4,irregular reduction many fine to medium prominent irregular reduction and, 5Y 8/1, few fine faint mottles.

Profile number : 2

General site Information and derived values

Site number : Propile 2
Mapping unit :

Pedon classification : Typic paleudult
Diagnostic hareraus/ features : Ochric,argilic

Greenwich coordinates :
Elevation [m asl.] :

Geomorphic component : Lower
Slope gradient [%] : 35 %
Slope shape, aspect : Straight
Micro relief : 25 - 50 m

Stoniness : No
Parent material : Sandstone, claystone

Effective soil depth : 140 cm
Obstructive layer : No

Water table : Not observed
Flooding frequency : None
Soil draenage : Moderately well draenage

Land use/ vegetation : Primary forest/ research plot.

Appendix 4 (Continued)

Profile Description

Horizon	Depth	Description
Ah	0 - 4/5	5YR 3/4,exterior large peds,moist; loamy sand, fine to medium weak crumb; non sticky wet, very frible moist; many fine to medium roots, many fine to medium and coars pores, irregular wavy boundary.
E	4/5 - 15	10YR 7/4,exterior large peds,moist; sandy loam, fine to medium weak sub angular blocky, slightly sticky and non plastic wet,very friable moist, many fine to medium coarse pores, many fine to medium and coarse roots, irregular wavy boundary.
Bt1	15 - 52	10YR 6/8,moist; sandy clay loam, exterior large peds, medium to coase sub angular blocky, friable moist,slightly sticky and non plastic wet, few coarse pores, many medium to fine roots and moderate coarse roots ; irreguler wavy boundary.
Bt12	52 - 85	10YR 6/8, Exteriar large peds moist; sandy clay loam; medium to coarse subangular blocky and slightly firm moist, slightly sticky and slightly plastic wet; 5 Y 8/3 (moist) intersperred in the matrix, moderate fine faint mottles; moderate fine to medium pores; many coarse roots; diffuse wavy boundary.
Bt21	85 - 122	7.5 YR 6/8, exterior large peds moist; sandy clay; medium to coarse subangular blocky and slightly firm wet; 5 Y 8/3 interspersed in the matrix (moist) many fine distinct mottles; moderate fine to medium pores; few fine to medium roots; diffuse wavy boundary.

Appendix 4 (Continued)

Bt22	122 - 140	7.5 YR 5/8, exterior large peds moist; clay; many coarse angular blocky and firm; sticky and plastic wet; 2.5 Y 8/2, interspersed in the matrix (moist) many fine to medium distinct mottles; few fine pores; few fine roots.

Appendix 5. Solar radiation (%) of Balikpapan area as indicator for the study area during the observation period.

Year	1991	1992						1993								
Date/Month	Dec	Jan	Feb	Mar	Apr	May	June	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
1	25	100	95	79	0	82	0	38	100	80	10	100	75	68	43	30
2	48	37	32	29	0	100	100	0	100	88	5	72	0	17	92	90
3	18	85	43	0	100	0	100	100	76	16	20	2	0	25	52	80
4	4	88	0	76	28	10	25	74	100	48	16	56	0	75	82	100
5	0	50	90	74	37	57	11	25	24	46	0	98	0	75	62	50
6	34	75	25	0	75	6	14	100	0	9	56	95	0	65	35	78
7	0	37	100	63	22	36	28	0	94	63	0	90	0	70	50	0
8	50	37	100	70	71	53	8	75	78	55	3	54	85	87	80	0
9	85	60	89	36	70	90	50	63	88	32	0	94	50	37	57	0
10	38	6	100	13	0	0	54	0	78	0	54	94	100	0	6	60
11	0	70	100	48	25	85	40	0	0	8	16	100	0	95	38	22
12	12	30	40	60	62	100	24	63	50	25	65	100	70	0	0	27
13	60	47	38	89	90	100	23	0	98	36	84	100	50	0	65	0
14	73	89	13	100	37	52	0	60	83	50	98	96	75	0	30	30
15	25	75	44	100	80	80	0	53	89	50	91	85	75	82	0	60
16	55	70	78	75	100	40	29	50	43	63	94	94	46	99	10	77
17	56	80	74	50	100	95	18	0	43	3	74	46	68	62	36	95
18	44	84	16	95	100	75	23	0	64	31	69	86	1	56	50	51
19	54	70	54	89	65	78	49	37	100	36	18	85	97	100	18	45
20	0	34	0	100	100	100	0	88	71	48	100	100	40	100	98	90
21	24	80	96	88	88	98	3	0	0	100	5	86	100	100	21	8
22	51	12	88	88	65	20	75	50	66	13	100	84	75	78	38	28
23	4	74	91	95	96	80	20	0	84	88	0	100	80	25	14	45
24	10	100	78	64	97	0	81	60	90	43	19	98	62	25	95	58
25	69	96	70	100	20	83	5	45	80	21	30	100	98	6	36	46
26	87	48	64	99	10	100	26	0	0	54	70	100	6	48	33	5
27	13	70	100	60	100	15	62	25	53	61	100	81	25	25	40	62
28	69	100	100	100	85	100	44	13	40	5	100	8	80	4	36	40
29	20	100	70	100	86	87	45	37	0	23	100	45	95	94	75	8
30	80	96		100	95	85	65	23	12	15	16	100	35	0	57	48
31	36	97		100		87			0		16	56		12		10

Curriculum Vitae

IRSYAL YASMAN, was born at Payakumbuh, West Sumatera Indonesia on July 10, 1960. He finished Primary School (SD) in 1972, Secondary School (SMP) in 1975 and Senior High School (SMA) in 1979. Then he studied Forestry at Faculty of Forestry at Bogor Agricultural University (IPB) and finished in 1984 with major field Wood Technology, especially wood drying and wood anatomy. After graduating from the University he followed a course for two months on forest management in Pontianak West Kalimantan in 1984. He worked in a plywood factory in Palembang from 1984 - 1985 as a head of the research and product development department. Since 1986 he is working for PT INHUTANI I, an Indonesian state forestry enterprise in the unit located in Balikpapan East Kalimantan. From 1986 - 1987 he worked as a counterpart from PT INHUTANI I in the cooperative project between the Indonesian Ministry of Forestry and Wageningen Agricultural University. During this period most of his research concerned vegetative propagation and mycorrhizae of Dipterocarpaceae. In 1986 he followed a course in tissue culture and plant physiology in Bandung, Indonesia. Since 1987 when the Tropenbos Kalimantan project (now known as The International MOF-Tropenbos Kalimantan Project) started at the Wanariset research station a research station, resorting under the Agency for Forestry Research and Development of the Indonesian Ministry of Forestry, he is a counterpart from PT INHUTANI I for the Propagation and stand establishment research group of this project. He is mostly doing research on regeneration and ectomycorrhizae of Dipterocarpaceae. During these times he has given many lectures to students and trainees concering nursery techniques for Dipterocarpaceae. In 1988 he followed a course on tree physiology at De Dorschkamp (now Instituut voor Bosbouw en Natuur Onderzoek, IBN-DLO) in Wageningen, The Netherlands, and in 1990 a course on ecophysiology at at the same institute. He started preparing his doctoral study research in 1988 and he passed his qualifying examination for admission to the PhD study at Wageningen Agricultural University (WAU) in 1990. During his research, he was supervised by his promotors Prof.Dr.Ir. R.A.A Oldeman (Wageningen Agricultural University) and Prof.Dr.Ir. Ishemat Soerianegara (Bogor Agricultural University). In 1987 he married Nita Safitri and they were blessed with two children, Luthfi Adytra (boy) and Milanda Afratya (girl).

February 1995
Irsyal Yasman