ENVIRONMENTAL EFFECTS ON THE GROWTH OF BROADLEAVED TREES INTRODUCED UNDER PINE STANDS IN SRI LANKA

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A thesis submitted to the University of Edinburgh for the degree of

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DECLARATION

I hereby declare that this thesis has been composed by me from the results of my own work, except where otherwise stated, and that no part has been presented for a higher degree.

N.D.R. WEERAWARDANE

November, 1996

DEDICATED

To the Forest Department of Sri Lanka

&

To my parents N.D. Chandrasena and W.P. Chandrani,
and my wife, Pabasara S.M. Nakandala

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ABSTRACT

Central highland areas of Sri Lanka are environmentally important since they consist of sloping lands with watersheds. In these areas, about 20,000 ha of degraded grasslands have been planted with *Pinus caribaea* with the objectives of protecting soil and water resources while producing timber and pulp. However, later on it was realized that this exotic species was not achieving the expected objectives satisfactorily although it established well in these difficult areas. The main problems associated with *Pinus* plantations are slowly decomposing needle litter which accumulates on the forest floor attracting fire in the dry seasons and destroying the litter itself along with undergrowth development if any, and exposing the soil surface in sloping lands which generally increases soil erosion and possibly hampers the expected soil improvements. Moreover, it was found later that timber and pulpwood produced by thinnings in this species have not a sufficient demand in the country resulting in delay in appropriate thinnings. This left a high density of tree stocking in most of the plantations, further affecting the ecological balance in the area.

To help resolve these problems, it was decided to gradually convert some of these plantations into other species by underplanting suitable broadleaved trees. The present experiments were carried out at five different sites to study the condition in more detail and evaluate the performance of broadleaved species *Alstonia macrophylla*, *Swietenia macrophylla*, *Toona ciliata* (*Cedrela toona*), *Khaya senegalensis* and *Michelia champaca* under pine overstorey canopy. Various treatments were designed to study the effects of light, soil micro-climate improvements and reduction of root competition from pine trees on the survival and early growth of underplanted tree species. These treatments included mulching of seedlings with pine needle litter, trenching around seedlings, mycorrhizal inoculation of the top soil around seedlings and some of the combinations of these treatments. Different thinning methods and thinning levels of pine trees with varying light intensities were also tested in the experiments. In addition, physical and chemical soil analyses were carried out.

Results indicated that *Alstonia* growth was very satisfactory under pine overstorey where row thinning of pine trees had been done with considerable canopy opening. Mulch treatments significantly improved the height and diameter growth by 20% and 28% respectively while trenching and mycorrhiza application showed no response at this site. Total dry matter accumulation, Relative Growth Rate (RGR) and Net Assimilation Rate (NAR) were also significantly improved by mulch treatments. *Khaya* plants were grown under a row thinned pine stand which was a comparatively dry site and mulching improved growth rates of seedlings by 47% and 20% for height and diameter respectively. These growth increases were almost doubled when mulching was combined with trenching. Dry matter production, RGR and NAR were also improved with these treatments and root:shoot ratio was reduced. Mycorrhizal inoculation showed improvements of RGR, NAR and reduction in Leaf Area Ratio (LAR) of these plants. *Toona* which was grown under a uniformly thinned stand in a much wetter site did not perform well, and failed to show significant height and

diameter growth improvements to any of the treatments. However, mulch treatments favoured its leaf growth compared to the control, showing higher leaf area and Leaf Weight Ratios (LWR). *Swietenia* showed about 61% increase to the combined treatment of mulch, trench and mycorrhiza in terms of height growth during the shorter period of this experiment. Survival was very high in all species except *Toona*. Mulched conditions generally favoured the growth of all species particularly in the less wet sites. Observations suggested that it also improved soil micro-climate in terms of moisture, nutrients and aeration of topsoil.

Different uniform thinning levels at higher elevations of pine from 30 to 10 m^2 basal area increased direct light level from 18% to 58%, and indirect light levels also followed the same pattern with slightly lower values as measured by hemispherical photographs. *Alstonia*, *Toona*, *Swietenia* and *Michelia* all responded positively to increasing light levels with growth being less in all species under 30 and 20 m^2 basal area. *Swietenia* and *Alstonia* tended to show much reduced growth with light levels below 50% full sun. Under mid elevations *Alstonia* indicated sufficient light conditions around 59% full sun with row thinning while *Swietenia* indicated about 53% or low light would be suitable for its height growth at mid elevations. *Khaya*, on the other hand, indicated light levels above 50% are beneficial for its growth although it can tolerate low light conditions.

These results may be useful adding to the understanding of these difficult environments and for introduction of these species into pine or any other overstorey species with appropriate silvicultural practices.

CHAPTER 1

GENERAL INTRODUCTION

1.1 SRI LANKA, PINE PLANTATIONS AND THE NEED FOR THEIR CONVERSION TO BROADLEAVES

Sri Lanka covers an area of about 65,000 sq km and is located between latitudes 5° 54' and 9° 52' N and longitudes 79° 39' and 81° 53' E. The country consists of two main topographic divisions, a highland area in the interior and lowland plains surrounding it. The elevation of the lowlands is generally less than 100 m while the highlands rise up to above 2000 m.

Climate is tropical and maritime with the rainfall distribution characterised by monsoon winds. The country can be divided roughly into a northern and eastern Dry Zone and south western Wet Zone merging into an Intermediate Zone in between. The Dry Zone occupies almost two-thirds of the country and consists mainly of flat and undulating country where annual rainfall varies from 760-1500 mm. The Wet Zone has an annual rainfall ranging from 2000-5000 mm and consists of a narrow coastal plain and very rugged mountainous areas culminating at 2750 m. The mean annual temperature varies from 28°C near sea level and decreases upward to about 18°C at 2000 m elevation.

The natural forest cover in the country in 1994 was around one fourth of the total land area (Bandaratilake, 1994), having dwindled rapidly in the last few decades due to population increase, economic growth and their related contributing factors. It has been estimated that closed canopy natural forest cover will decline from about 24% in 1992 to about 17% by 2020 (Forestry Master Plan, 1995). The country is presently attempting actively to protect the remaining natural forests due to their biological and environmental values which cannot be replaced completely by forest plantations. However, forest plantations are also being established on a large scale in order to meet the timber and fuelwood demand in the country while also expecting environmental benefits and relieving the pressure on the natural forests. The most serious consequences of deforestation and forest degradation are generally reported as reduction of biodiversity, irregular water supply, shortened life span of irrigation channels and reservoirs, soil erosion with associated loss of soil fertility, increased

scarcity of wood and fuelwood and other forest produce. Tropical deforestation in a wider context is discussed in the next Chapter. Major forest plantation species in the country are teak (*Tectona grandis*), conifers (*Pinus* species), eucalypts (*Eucalyptus* spp) and mahogany (*Swietenia macrophylla*). In addition, various other species are planted on a relatively small scale. Afforestation in the country is usually done in degraded lands since fertile ground is used mainly for agricultural purposes.

Central highland areas are environmentally important since they consist of sloping lands with watersheds which are important for intensive agricultural work practised in those areas. Therefore afforestation should aim at protecting the soil from erosion and maintaining soil fertility, preferably improving it, while producing timber or fuelwood. In environmentally sensitive areas, ideally, site protection should be given priority rather than timber production. The control of soil erosion has been identified as one of the primary objectives of afforestation programmes in critical watershed areas, as forest cover with a good canopy and well developed litter on the forest floor can generally reduce soil erosion and improve the soil. The lands available for afforestation in the uplands are mainly covered with grass (Plate 1.1b) and generally have degraded soils and other unfavourable micro-climatic conditions due to initial deforestation and subsequent exposure, burning, grazing and accelerated erosion for many decades. Weil (1982) carried out an extensive study of the*patana* soils in the uplands and found that erosion in these sites has decreased soil organic matter and nutrients including nitrogen, phosphorus and exchangeable bases. He also indicated shallowness and rockiness as limiting factors for tree growth in some sites. Investigations made by the Forest Department of Sri Lanka have indicated that large scale afforestation of these *patana* grasslands with most indigenous species tried is difficult due to site degradation, however, establishment of exotic species such as pine has been very successful.

Pine was introduced into Sri Lanka more than 20 years ago, and they are the species most extensively planted in the highland areas with an extent of around 20,000 ha. The most widely planted pine species is *Pinus caribaea* var.*hondurensis*, while *Pinus patula* has also been planted at higher elevations of over 1200 m on a smaller scale (see Plate 1.1a). These species have shown a greater ability to establish and grow successfully than most other species under existing adverse conditions in available afforestation sites. Initial growth rates are very rapid; *P. caribaea* can attain 3 m by the second year in the wet highlands. Its mean annual height growth rate is maintained at around 1.2 m up to the 11th year, although apparently by the 10th year

overcrowding and crown competition sets in (Perera, 1989a). This species has been planted in the highland åreas with the main objectives of watershed protection, soil erosion control, stabilizing the slopes and pulpwood and/or timber production.

Establishment of a forest cover has been achieved successfully by these plantations. However, some of the other objectives of pine plantations have not been achieved successfully due to various reasons which were not perceived originally. One of the main drawbacks has been the lack of demand for pine pulp and thinnings in Sri Lanka. For this reason the State Timber Corporation was reluctant to harvest pine, and as a result harvesting schedules were very much delayed, causing lot of environmental problems.

Another critical issue with regard to reforestation with pine is the apparent fast depletion of water reserves during dry periods in watershed areas. Although pine's contribution to this is not scientifically proven, it is strongly believed that pine is at least partly responsible. It seems that it is not only the species of pine but also its silvicultural management which can affect the hydrology of these lands. Possibly lack of proper silvicultural management of these plantations may be the main contributing factor for this. Lack of management, mainly thinning, is due to the fact of the poor economic returns from thinnings mainly due to low density wood (see section 2.2). Lack of sufficient thinning at the right time has resulted in overcrowded stands of trees, possibly lowering the water table excessively in this ecosystem. In fact, overstocking with delayed thinning affects the timber properties of the pine itself, since the diameter growth will be hampered by mutual competition.

Furthermore, delays in thinning of the stands lead to heavy stocking with a dense mat of needles which attracts and spreads fire easily. Slow decomposition rate of pine litter also contributes to accumulation of litter on the forest floor (see also section 2.7). Dense litter mats of long, wiry needles provide an ideal fuel for forest fires due to their loose packing, low moisture content and high content of volatile inflammable compounds. Such fires may bring about serious ecological consequences, including being unfavourable for soil erosion control. A combination of shade and repeated burning contributes to little or no undergrowth in most of these plantations, particularly in the drier areas (see Plate 1.2a,b). Also, the seasonal dry spells coupled with high evapotranspiration in heavy stocked stands, particularly in the drier Intermediate Zone, could cause moisture stress intense enough to suppress undergrowth development in these plantations (Perera, 1989b). Accumulation of a

thick mat of needles may itself obstruct natural growth of seedlings underneath these trees.

When the fire destroys the undergrowth and needle litter the soil will be exposed (Plate 1.2b) to the direct impact of rain drops which may seal off the soil surface, decreasing infiltration capacity. This has been reported by various authors e.g. a ground fire study in pine stands by Sony et al (1985). In a hot ground fire, colloidal organic matter in the surface mineral layer may be destroyed, accompanied by a loss of structure and a reduction in porosity (Fuller et al, 1955). Fire can also reduce infiltration by the plugging of macropores with ash, by the formation of a charred crust and by the development of a water-repellent hydrophobic ash layer (Savage, 1974). Reduction in infiltration may reduce ground water recharge and increase surface runoff, which can lead to greater soil erosion. Also, high erosivities have been recorded under forestry plantations with a tall canopy and without ground cover due to increased size and velocity of raindrops under the canopy (Young, 1990). High erosivities coupled with high overland flow in sloping lands enhance soil erosion, further deteriorating the soil.

Nutrients accumulated in pine needles will not readily be available to other plants, due to the slow decomposition rate of needles. When the litter is burnt, a part of the nutrients accumulated, mainly nitrogen and sulphur, will be lost directly through volatilisation during the fire (Kraemer and Herman, 1979). Other nutrients returned to the soil in the form of ash such as phosphorus, potassium, calcium and magnesium will be in a highly mobile form and can quickly be lost by leaching (Grier, 1975) and washing off in sloping lands during heavy rains. Moreover, organic matter in the top soil layers will be destroyed by fire (especially by hot fires) which is extremely harmful for soil fertility maintenance and nutrient cycling. Therefore repeated fire can progressively deplete these sites of nutrients causing further degradation of the soil. This is discussed further in section 2.8. Fire may also cause destruction of the soil seed bank, so that recurrence of fire will progressively diminish the floristic potential of these sites causing ecological retrogression (Perera, 1989b). Other possible major effects of fire are reduction of soil faunal activities which may also affect soil fertility and physical properties, and destruction of pine plantations themselves in younger stages. An indicative model of possible ecological consequences is given in appendix I.

In view of the above situation, many ecologists and environmentalists and also the general public in the country have objected to the growing of monoculture pine plantations. Due to the pressure from interested groups, the Forest Department in Sri Lanka has now virtually stopped establishing pine plantations and is seeking ways of better utilization of existing plantations and possible conversion of these plantations into broadleaves in environmentally important areas, as an alternative management plan. Various authors have suggested the possibilities of planting broadleaves under existing pine plantations (e.g. Bandaratilake, 1988; Gunatilleke, 1989; Baldwin, 1991). Some studies on underplanting in other countries are discussed in section 2.4. Lack of ability of pine to protect the soil sufficiently in some situations due to associated fires and also due to its restricted timber uses warrant attempting gradual conversion of pine into other broadleaved species.

However, besides these disadvantages pine has some advantages as well. It is one of the few species which can grow in degraded site conditions and establish a forest cover which can be considered important. Its well established root system can bind the soil and protect it to some extent but apparently not the topmost soil layer. Its unfavourable environmental effects can be alleviated, at least to some extent, by sufficient thinning. Moreover, if pine forest cover had not been established it would have not been possible to plant valuable broadleaves as tried in the present study. Also, ectomycorrhizal associations of pine may be useful in efficient nutrient cycling in these plantations, reducing possible nutrient losses due to leaching. Therefore it can be speculated that pine has created a relatively better situation compared to similar lands without any forest cover by improving the micro-climate and as a result the introduction of other species are generally facilitated.

The subject of selecting potential broadleaves and their establishment methods under pine overstorey canopy remain largely uninvestigated so far and if methods can be successfully developed, the situation will undoubtedly be improved. It should also be noted with the proposed underplanting that some of the best pine trees can be retained until the end of the pine rotation period thus encouraging the growth of some individuals in the stand while maintaining the beneficial effects of the pine. In view of the above situations, the research branch of the Forest Department identified underplanting as a priority research area. Some initial observations even without proper thinning of the overstorey have given encouraging results. Due to various problems associated with this species and and its environment, the possibilities of converting them to broadleaved mixed stands were investigated to assist the forestry

by looking at aspects of the ecology and growth of the young trees being established by the Forest Department, Sri Lanka. The aim was to provide some insight into the factors that might be influencing survival and growth of underplanted species. Accordingly the present study investigates the response of different broadleaved species to the above- and below-ground environment existing under the pine overstorey canopy manipulated by various treatments.

Ecologically, a mixture of species is generally preferable to a monoculture and the resulting diversity has substantial long term benefits (see section 2.9 for details). It can also be noted that self-regenerating broadleaves can be environmentally more important, even if they are monocultures, since the natural regeneration means that clear-felling of the forest can be avoided, assuring sustainability with a continuous forest cover in environmentally sensitive ecosystems. All species used in the present study have a self-regeneration capacity at least to some extent and also have a higher timber value than pine. The Forestry Master Plan newly formulated for the country in 1995, depicts a forest policy which recognizes that forestry resources should be used in a sustainable manner both in terms of the continued existence of important ecosystems and in the flow of forest products and services. Thus mixed pine/broadleaved stands in the initial stages and perhaps subsequently a mixed broadleaved stand might satisfy these requirements in a better way and harmonise the relationship between the forests and the environment in hilly areas.

The literature survey done on the related fields of the present study cast light on some of the available knowledge in respective areas of science. The general description of tropical deforestation and the status of *Pinus caribaea* in reforestation programmes gives some background information about the subject area and its core species. Evaluation of some underplanting practices in both tropical and temperate areas introduce the concept of this practice and its uses in various countries for various purposes. Details of different types of underplanting and related practices give a closer look on how these practices have been adopted successfully in the past. The major factors which contribute for survival and growth of underplanted species were discussed in relevant sections to emphasize the importance of investigating site specific problems. Some of the important areas were response of broadleaves to understorey light levels, litter decomposition, nutrient dynamics and importance of mycorrhiza. Final section on mixed species plantation establishment highlights the importance of species mixtures in terms of ecological and economical basis to satisfy the future requirements of establishing sustainable forests.

The present study addresses the scientific areas of identification and overcoming the problems associated with above- and below-ground environment for the successful growth of broadleaved tree species planted under an overstorey canopy of a single species plantation crop. The literature survey revealed that one of the weaknesses with respect to this area of study is lack of sufficient information on understorey tree growth under plantation conditions in the tropics. Most of the information in the tropics is on natural forest conditions, which cannot be directly applied to plantation conditions, although it may be indirectly very relevant. Further, information on underplanting in coniferous stands in the tropics is sparse at present. A very partial understanding of the importance of mulching and mycorrhiza to improve soil micro-climate in forest seedling establishment was also considered an important drawback. Identification of suitable species for underplanting on these very difficult pine sites, and their response to various light levels under the overstorey canopy, were of urgent need in Sri Lanka, where little experience has so far been obtained. Site-species matching and compatibility of mixing pine and broadleaved understorey species also needs to be investigated in order to develop sustainable forest ecosystems. Information is especially needed for the highland areas where lands are prone to soil erosion and fire damage and for indegenious species which might be tested at a later stage.

Lack of research evidence on the type of underplanting carried out in the present study led to the design of appropriate experiments. This consisted of information on suitable species, site species matching in the present study area, ways of improving soil environment under existing conditions and methods of reducing overstorey root competition. Additionally, the intensity and method of thinning of the overstorey to suit the requirement of different underplanted species, suitable solar radiation levels for understorey plants were also included.

1.2 OBJECTIVES OF THE STUDY

This study explores the performance of five different broadleaved species under an overhead canopy of pine in different climatic areas within the central highlands of Sri Lanka. The main objective was to assess the effects of soil and canopy treatments on the early performance of broadleaved species planted under pine. The effects of different thinning regimes and thinning methods of pine overstorey were also studied, as well as the relationships between the solar radiation levels and growth of

broadleaves. The results will guide the selection of species for underplanting programmes with pine in the country.

The specific objectives were to determine:

a) Effects of mulching, mycorrhiza application and trenching and their different combinations on height, diameter and volume growth of *Alstonia macrophylla*, *Khaya senegalensis*, *Toona ciliata* and *Swietenia macrophylla*.

b) Effects of the above treatments on dry matter production and its allocation to different plant parts, by growth analysis including the calculation of root:shoot ratio, relative growth rate, net assimilation rate, specific leaf area, leaf area ratio and leaf weight ratio.

c) Effects of uniform overhead canopy thinning on performance of *Alstonia macrophylla*, *Toona ciliata*, *Swietenia macrophylla* and *Michelia champaca* in a single site, and row thinning on performance of *Alstonia macrophylla*, *Khaya senegalensis* and *Swietenia macrophylla* in different sites.

d) Effects of different light levels on the growth of underplanted tree species in the various experimental treatments.

Five field experiments were carried out in different sites in order to address the above specific objectives.

Hypotheses tested under the present study were as follows:

1) Broadleaved trees can be successfully introduced to pine stands located in various different climatic zones in the upland areas of the country. *Alstonia*,*Khaya*, *Swietenia* and *Toona* are some of the possible candidates to be used in underplanting in these pine stands.

2) Growth of underplanted species is affected by root competition from pine overstorey trees for soil moisture and nutrients.

3) Growth of underplanted species can be improved by the practices of mulching, trenching and introduction of mycorrhizal fungi, or with certain combinations of these treatments.

4) Different thinning methods and thinning intensities of pine overstorey will influence the growth of understorey trees.

5) Variation in the solar radiation level received by the understorey canopy due to various treatments will affect the growth of broadleaved species.

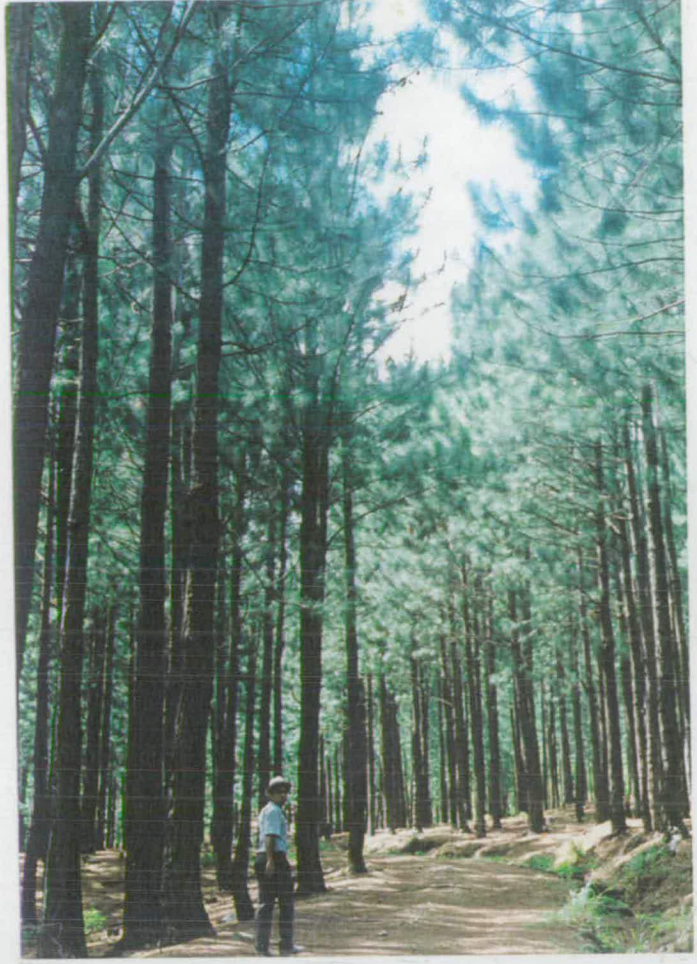

Plate 1.1 : a) A view of a pine plantation at Galaha, Sri Lanka.
b) Grasslands used for the establishment of pine plantation (one of the latter can be seen on the top of the hill).

Plate 1.2 : a) Fire damage to pine plantations.
b) Pine forest floor after burning.

CHAPTER 2

GENERAL LITERATURE REVIEW

2.1 TROPICAL DEFORESTATION

Forests covered about 31% of the world's land area in the 1970s and 64% of this forested area was closed forests (Kallio et al, 1987). Closed tropical forests are estimated to hold between 50-90 % of the world's bio-diversity (Reid and Miller, 1989). Of the various types of forests in the world, tropical forests play a particularly large role in ameliorating the climate, protecting the soil and producing diverse timber and non-timber products. In many cases the farming systems of the tropics benefit from soil and water conservation services provided by forests in their vicinity and from trees on site. Most tropical forest ecosystems are biologically diverse communities and have distinctive micro-climates, characterised particularly by their effects of absorption of solar radiation, and the turbulence generated by air flow over the foliage and light quality and quantity on the forest floor (Unsworth, 1992). Some natural forests are still existing in tropical countries and they play vital roles for communities particularly in hilly areas providing water. Natural forests include rainforests, seasonal forests, tropical dry forests, woodlands, riverine forests, mangroves, fresh water swamp forests and cloud forests. These have been classified according to differences in climate, soils and constituent species. Gradual depletion of these forests throughout the world may cause considerable impacts on the environment.

Deforestation usually refers to permanent conversion of forest lands to non-forest use. It is not a simple process and involves a number of different agents and causes. The amount of tropical deforestation has increased from 11 million hectares per annum in the 1970s to about 17 million hectares per annum in the 1980s (Rietbergen, 1993). Deforestation rate as a percentage of existing forests has doubled from 0.6% in 1980 to 1.2% in 1990 (Dembner, 1991). This fast rate of depletion has been mostly attributed to population increase and resulting problems such as clearing the land for agriculture, settlement schemes, development programmes, logging etc. In addition to these social impacts, naturally occurring changes such as due to wind and fire damage also influence the depletion to some extent. Forest depletion loss has not been

replenished by reforestation instead, timber extraction rate has exceeded the rate of reforestation (WRI, 1992). Destruction of forests and other human-accelerated environmental changes have contributed to regional climate changes, ozone depletion in the stratosphere, land-use changes, toxification of the bio-sphere, invasion of exotic species and widespread loss of biotic diversities (Likens, 1992). Deforestation alone has contributed to soil degradation, changes in water flows and increased sedimentation of rivers, reservoirs and irrigation systems etc. The nature and magnitude of the resulting ecological effects depend on the initial forest environment, the way in which it is used and managed, the purpose for which it is cleared (Mather, 1990).

Of the estimated 12 million hectares of forest plantations in the tropics, almost 80% consist of fast-growing species used for fuelwood, paper pulp, woodchips and low-quality timber; only 2.5 million hectares have been planted with slow-growing hardwood species for the product of high-quality sawnwood (Panayotau and Ashton, 1992). This trend of planting trees with fast growing exotic species may not only cause shortages of high quality timber but also land degradation in most of the areas. Another important fact in present forest practices is lack of sustainability; only 1 million hectares are reported to be under sustained yield management for timber production out of estimated total global area of 828 million hectares of productive tropical forests (Poore et al, 1989). Instead of managing these forests for single product as happened in the past, multiple use management has been stressed more recently, which is aimed at combining economic profitability, social acceptability and ecological sustainability (Panayotau and Ashton, 1992). These authors further advocate that this type of management requires modifications of existing silvicultural practises and logging technologies to protect the environment.

In addition to the environmental consequences being experienced due to deforestation, the clear-cutting method of forest harvesting is considered to lead to environmental damage. It causes soil erosion, due to exposure to heavy rains and winds particularly in fragile lands, changes in micro-climate, stream damage, wild life disturbances in some instances and even aesthetic injury, despite its many advantages. The erosion removes nutrients and fine soil particles from the soil, causes fertility decline in the site itself and excessive sedimentation in reservoirs and stream channels. Further, in certain areas, decomposing slash left may increase the amount of dissolved chemicals and plant nutrients in the water that may encourage extensive bacteria and algae growth, which can reduce the amount of dissolved oxygen in water

causing harmful effects on fish (Robinson, 1975). Another important aspect of clear-felling is removing of a large proportion of total biomass from the site which may cause gradual land degradation with disrupted nutrient cycling, particularly in the tropics, since a considerable proportion of the total nutrients in these ecosystems are contained in the tree biomass rather than in the soil (Mather, 1990). The use of alternative methods such as shelterwood systems may be useful in such situations.

2.2 *PINUS CARIBAEA* MOR. IN TROPICAL REFORESTATION

Pinus caribaea Mor. is indigenous to Central America and the Caribbean region in the latitudinal range between 12° N and 27°N and is mostly found on the Central American coastal lowlands and several islands in the Caribbean region (Lamb, 1973). Although its distribution is predominantly coastal some populations are found in inland locations up to 800 m altitude (Barnes, 1988). It has three recognized varieties: *P. caribaea* var. *caribaea* Barrett and Golfari occurs in western Cuba, *P. caribaea* var. *bahamensis* Barrett and Golfari is found in several islands in the Bahamas and Turks and Caicos islands and *P. caribaea* var. *hondurensis* Barrett and Golfari forms discontinuous stands in Central America extending from north-eastern Nicaragua, through north and central Honduras and eastern Guatemala to northern Belize (Barnes, 1988).

It is an important exotic plantation species and is now widely planted throughout the tropics (Greaves, 1981). It has been extensively studied in provenance trials, growth trials and general behaviour. Exploration, collection and evaluation of Central American pines have been done for more than 25 years by the Oxford Forestry Institute (Barnes, 1988). The species has shown the ability to grow in hot lowlands, infertile sites, eroded areas and savannas. In its natural region it grows in acid soils having pH 4-5 and low in nutrients, provided texture permits good aeration. Its great resistance to fire reduces risks of total destruction after the third or fourth year and also from the pole stage onwards variety *hondurensis* is more resistant than *Pinus oocarpa*. On suitable sites it can achieve a mean annual increment of 21 to 28 m^3/ha up to the 13^{th} year (Lamb, 1973 and Greaves, 1981). Gibson et al (1983) reported that *P. caribaea* var *hondurensis* is superior to other varieties of *bahamensis* and *caribaea* in most of the sites. Other important tropical pine species are *P. patula, P. kesiya, P. oocarpa* and *P. merkusii*. A sub-species of *P. patula* was later identified as *P. patula* ssp *tecunumanii* which is reported to have outstanding growth rates with straight stems and clear boles (Eguiluz-Piedra, 1986).

Workers in various countries have reported the performance and drawbacks of *P. caribaea.* It has been successfully introduced to the Northern Territory of Australia due to the fact of flat terrains available for planting, suitable temperatures and moisture regimes, low cyclone and fire hazards and low pest infestation (Eyre, 1987). Applegate and Nicholson (1988) have reported its use in sylvi-pastoral systems in north eastern Australia. However, Golkin and Cassels (1989) reported in Malaysia that pine was disqualified to be included in large scale pulpwood production programme due to its slow growth rates and high maintenance costs. In India, Chowdhary et al (1987) reported that *Pinus caribaea* is fast growing and yields large quantities of long-fibred pulp which is used for paper industry. Cuevas et al (1991) compared the above- and below-ground organic matter allocation in a tropical pine stand of 11 years and broadleaved secondary forest and found that in pine above-ground litter was very much higher than the dead root fraction while in the broadleaved forest it was the opposite. A similar trend was found for above-ground tree biomass. This indicates accumulation of a slowly decomposing needle layer of pine in contrast to broadleaved forests and also possible nutrient removal by its harvesting and their possible consequences. Lack of sufficient seed production was experienced in Sri Lanka. Zobel et al (1987) reported that no flowering occurs at high elevations, except between 9°N and S latitudes, however in Australia heavy flowering has been observed.

Although pine plantations are generally healthy in Sri Lanka some of the important pest and diseases have been reported in plantations elsewhere. Proctor (1967) noted die-back starting from the tip and advancing down the stem and attributed it to boron deficiency associated with drought stress and possible inadequate land preparation before planting. Another cause of die back was reported in Tanzania (Wormald, 1975) due to fungal infections by *Diplodia* spp. which has reduced survival and growth and caused stem deformation. Needle blight disease caused by *Cercospora pini-densiflorae* also can seriously affect exotic plantations (Pancel, 1993). In SE Asia shoot or tip moth damage has become serious after establishing large scale plantations in countries such as Philippines, Thailand and Vietnam (Speight and Speechly, 1982). Shoot boring resulted in malformation of trees and bark boring caused death of young plants. The incidence of damage was high in low altitudes and in degraded soils. *P. caribaea* var. *hondurensis* is much more susceptible to early feeding by shoot moth than the var. *cubensis* of the same species (Speight and

Speechly, 1982). In central America, *Dendroctonus* beetle has been reported to be a major pest (Pancel, 1993).

Pines are softwood species and some of which have very low wood density. Rapid early growth of pine can lead to reduction in wood quality by formation of higher percentage of juvenile wood. The corewood or juvenile wood of pine is regarded as undesirable because of its impact on both solid wood, pulp and paper products. Although it is preferred for some pulp and paper products it is not suitable for papers requiring high tear strength (Cown, 1992). Plumptre (1979) has also reported that pine grown rapidly in tropical plantations producing low density juvenile cores of rather low quality wood. Wood from the juvenile core tends to distort badly and a large proportion of the outer wood has to be discarded as slabs and edgings. This results in getting the timber marketed at values of the lowest quality. He reported that one way of improving wood qualities is having a long rotation but this would not be financially viable. Zobel et al (1987) reported that this species in exotic environments shows good survival and growth rate but the wood is not suitable for most purposes mainly due to extra-low wood density. According to Hughes (1971) wood density can be influenced by silvicultural treatments. Lower elevation planting sometimes produces denser wood than those in high elevations. In its indigenous range, or when grown where there are definite wet and dry seasons, the wood is reported to be normal with specific gravity between 0.45-0.55, however, when grown under very suitable conditions wood density of var. *hondurensis* is extremely low having values between 0.25-0.35 (Zobel and Van Buijtenen, 1988). Lamb (1973) has reported that irregular distribution of resin, a large core wood of specific density under 0.4 which is unsuitable for construction purposes, susceptibility of wood to blue stain after felling the trees and inferior quality pulp produced from *P. caribaea* var *hondurensis* are some of the drawbacks of wood quality of this tree species.

2.3 GENERAL CHARACTERISTICS OF TREE SPECIES SELECTED FOR THE STUDY

2.3.1 *Alstonia macrophylla* Wall. (Apocynaceae)

Source : Dassanayake and Fosberg (1983)

This is a species introduced to Sri Lanka, probably from its native region of Malaysia. It is naturally distributed from Indo-China to the Moluccas; and in northern Malaya it is found in secondary jungles (Corner, 1940). The species has been grown in the

country for a long time and is now widespread and naturalized, particularly in the Wet and the Intermediate zone areas (see section 3.1.1). It is quite common in private lands in these zones since people favour the species for some of their timber requirements. It grows well in fertile lands but also can be found growing in degraded lands though the growth is not so satisfactory. It is considered to be a pioneer hardwood species but has shown the ability to grow under some shade conditions. In early attempts to grow the forest species in impoverished soils in the country, this had been recorded as one of the best species (Holmes, 1946). This species has not been planted in large scale plantations in the country until recent years. Linked with this, sufficient growth information of this species is lacking in the country.

It is a moderate sized tree with a cylindrical trunk. Latex is found in the leafy shoots and in inflorescences. Leaves are arranged generally 4 in a whorl and are large, shiny yellowish green, turning yellow when withering. It produces small white fragrant flowers in small stalked terminal clusters. Fruit is a long hanging cylindrical pod. Pods split open and contain many small flat seeds with a tuft of silky hair at each end. Seeds can germinate naturally once they are fallen on a suitable ground showing high natural regeneration capacity.

Its growth is fast and though it does not grow to large sizes, it produces a very straight bole with little taper, making it very suitable for transmission poles. The timber is heavier, harder and stronger than the local relative, *Alstonia scholaris*. The timber is now widely used locally for furniture making and other industries though it is not as high a quality as that of ordinary mahogany (*Swietenia*). The wood is durable and seasons well and is used in beams, joists, rafters, floors and household implements (Siapino, 1983). In some countries, leaves of the tree which contain alkaloids are used for medicinal preparations (Ratnayake, et al 1987).

2.3.2 *Toona ciliata* M. Roem. (Meliaceae)

Source : Dassanayake et al (1995)

A synonym to this species is *Cedrela toona* Roxb. and is indigenous to India, Burma and Thailand (Webb et al 1984). It is an introduced species in Sri Lanka and is now naturalized particularly in mid and high elevations. In the country it is widely found in private lands where people grow it as a timber species. It prefers fertile and well-drained soils with neutral to acidic conditions and growth is slow in infertile lands. It requires shade for its early growth but later becomes a light-demander.A related

species, *Cedrela mexicana* has been planted in small scale in the country and has been recommended elsewhere for mixed planting with conifers for rain forest sites (FAO, 1986).

The tree grows to a height of about 30-35 m with a fairly straight bole. Its leaves are pinnate and the tree is deciduous in certain periods of the year. Fruit is a pendulous, valved capsule about 2-3 cm long dehiscing from the apex. The seed is light and brown in colour and germination is quick and easy. The tree bark is regularly and evenly furrowed or fissured longitudinally. All parts of the tree smell strongly when cut or crushed.

The species has not been planted in commercial plantations in the country and therefore growth information is generally lacking. However, local people are quite familiar with the species and its growth requirements, and it grows successfully in private lands.

Sawn timber is widely used, mainly for furniture making, ceiling and other light construction work, and planks are also used for decorative purposes. Round wood can be used for plywood and veneer production. The timber is light weight, pinkish in colour and very fragrant.

The tree is susceptible to shoot borer attack by *Hypsipyla robusta* (see section 2.3.4) which affects the straightness of the tree. Planting the tree in mixture with other species and in optimum sites where growth is vigorous have been observed to reduce the susceptibility to this attack in the country.

2.3.3 *Khaya senegalensis* A. Juss (Meliaceae)

Source : Keay (1989)

A synonym for this species is *Swietenia senegalensis* and some vernacular names are Senegal mahogany, dry zone mahogany and African mahogany. Its origin is considered to be west and central Africa (Webb, 1984). The species has been introduced to the country from Africa during the 1960s and planted in an arboretum in the Intermediate zone, according to the Forest Department records. However, large scale planting started quite recently in the Intermediate and the Dry zone areas. It is considered to be drought resistant and less susceptible to shoot borer attack than ordinary mahogany, *Swietenia macrophylla*.

It is a deciduous tree growing up to 20-30 m height with pinnate and oblong leaflets. Flowers are white, and fruit is a 4 valved capsule about 4 cm diameter. The seed is flat and winged, about 4 cm long and requires no pre-treatment for germination and good fresh ones germinate quickly. The bole is usually short but in deep wet soils it is fairly straight and exceeds 10 m while under less favourable conditions the tree is low branched, nevertheless attains very large diameters (FAO, 1986). The bark is dark grey covered with small scales.

Natural regeneration occurs around mother trees by seeds, and propagation by root suckers is also possible. For good growth it requires nutrient-rich and wet soil but can withstand long dry periods. It is reported to have the ability to effectively check transpiration under dry conditions by closing stomata (Okali and Dodoo, 1973) which shows the adaptation to dry conditions. It can also withstand waterlogging conditions and because of that it can grow on flood-prone banks of water courses in savannas (Irvine, 1967). The tree is shade bearing when young and light demanding later on. In open lands it is heavily crowned and often shows poor form but may be improved when underplanted or planted at close spacing in plantations. Early growth is fast but becomes slow later on, in dry situations (FAO, 1956).

The timber is excellent and wood is deep red brown, hard and can be sawn easily. The wood takes a good polish and can be used for furniture and cabinet making and other light construction work (Webb, 1984). It is only moderately hard and heavy, though the heaviest timber of all African mahoganies (*Khaya* species) and can be used for most of the work for which mahogany (*Swietenia macrophylla*) is used (Irvine, 1967).

The tree contains a gum and the bark yields a brown dye. The dried and powdered bark is used for medicinal purposes. The leaves are used for fodder for animals in some countries (FAO, 1986).

2.3.4 *Swietenia macrophylla* King (Meliaceae)

Source : Dassanayake et al (1995)

Swietenia macrophylla is indigenous to central and South America from latitudes 22° N to 19°S. It occurs naturally under a considerable range of environmental conditions from tropical dry forests to tropical moist forests. It is reported to grow up to an

elevation of about 1500 m in the natural habitat and wood of the highland timber is said to be of high quality also with best growth development of trees than that from lowlands. It can withstand drought while also having the capacity to grow in wet and inundated areas. Deep, well drained, neutral to alkaline, fertile soils with an abundant supply of soil moisture are preferred with maximum growth development although it can adapt to a range of site and plant associations probably due to its genetic plasticity for various leaf adaptations (Lamb, 1966). Snook (1993) showed that it can survive fires and hurricanes in Mexico while Gullison et al (1996) demonstrated its ability to withstand flooding in Bolivia better than many other species in its natural habitats. Since it regenerates after episodic and ephemeral disturbances regeneration occurs infrequently and stands are composed of even-aged and even-sized cohorts that regenerated together (Boot and Gullison, 1995). Unless silvicultural treatments are undertaken to increase growth it is assumed that it will take somewhat between 105 and 148 years for these trees to reach commercial size in natural forests (Gullison et al, 1996).

This species is reported to be a pioneer species, being light demanding and relatively fast growing (Whitmore, 1990). Natural regeneration occurs in sites where almost full overhead light available, in canopy gaps, agricultural clearings or after disturbance by fire or strong winds (Snook, 1993). Conversely, Ramos and del Amo (1992) described it as a late secondary forest species though it prefers much sunlight (eg. 68% of full sunlight in comparison to 17% and 37% levels). Also, it does not tolerate root competition from other species (Negrero-Castillo and Mize, 1983) and that may be the reason it grows in canopy gaps or disturbed areas where higher levels of sunlight is available possibly with lesser root competition. Lamb (1966) also reported that dense shade and root competition are unfavourable for its reproduction and seedling growth is not tolerant to extended drought; the first year is the most critical period for its establishment. Although it is classified as a pioneer species mainly due to these characteristics, it also has some characteristics of shade tolerant climax species such as comparatively large seed size, quick germination of seeds without dormant period, lack of live seed bank in the soil (instead a seedling bank), production of hard timber, long life span and large size of the tree. In accordance with Ramos and del Amo (1992), Gullison et al (1996) also describe it as a light demanding climax species.

This species was introduced to Sri Lanka about 1880 from the British Honduras and first established in plantations in 1897 at a forest reserve in the Intermediate zone as

mentioned in the Forest Department records. Since then it has been planted quite extensively in most of the Intermediate and Wet zone areas and is now naturalized in the country.

The species does not thrive at high elevations in Sri Lanka and is therefore generally planted below 1500 m. In the country, mahogany has generally been planted under the canopy of other broadleaved species for a long time. It has been underplanted in jak (*Artocarpus heterophyllus*) plantations in the Intermediate zone areas and later mahogany has dominated the site. In other areas degraded natural forests have been line-planted with mahogany with varying degrees of success. Due to its shade requirements during early stages it is not planted in open lands as a monoculture plantation, however it becomes a light demander subsequently. Its shade requirement for early growth and liability to a shoot borer attack have generally restricted its wider scale planting. It is tolerant of a broad range of soil types, though growing best on soils which are deep, well drained, with gentle slopes and a neutral to slightly alkaline pH. Young seedlings are not tolerant to extended drought.

Mahogany is attacked by the well known pest *Hypsipyla* spp shoot borer, a nocturnal moth whose larvae attack the terminal shoots of trees up to the pole stage, causing repeated branching. It is generally found that the attack is less severe when the tree is planted under shade. Suratomo (1977) reported that the degree of infestation decreased with increasing age and height of the host, and therefore advocated close space planting to encourage height growth.

It is a more or less deciduous tree with a heavy, dark green, dense crown. The leaf contains 3-6 pairs of opposite leaflets, the end single leaflet being the biggest. The trunk is usually buttressed and bark is dark grey, ridged and fissured. Young leaves are pink in colour but soon turn green, old leaves turn orange brown to dull scarlet when they wither. Seed can be stored for up to one year under dry, cold and airtight conditions. No pre-treatments are required for seed germination. Seedlings require full shade for the first 2-3 weeks and then 50% shade for about one month (Pancel, 1993).

With full light, a well drained soil and abundant moisture, seedlings can reach a height of about 50-100 cm within 6 months, although under shade they may only grow 15 cm in their first year (Wenban-Smith, 1993). The natural regeneration capacity is very high but seedling growth is limited under heavy shade conditions and

sufficient canopy opening is required for satisfactory sapling growth. Under insufficient light conditions seedlings may persist for many years, growing very slowly. It has been observed that most rapid growth occurs under complete overhead light with side protection from other trees.

Swietenia produces very valuable timber and is categorized in the country as a luxury timber species. The timber is used mainly for furniture making in the country and its finishing properties are excellent. There is a high demand for its timber and therefore people are planting it in their private lands. It is regarded as the most valuable tree in tropical America and as one of the premier cabinet woods in the world (Cown et al. 1989). Roundwood can be used for veneer-plywood production. In an economic analysis of 43 rain forest species to be planted in Australia, Russell et al.(1993) concluded this species as one of the most valuable tree species.

2.3.5 *Michelia champaca* Linn. (Magnoliaceae)

Source : Dassanayake and Fosberg (1987)

An introduced species to Sri Lanka, this has been planted in private fields for quite a long period. It is an evergreen tree, found wild in the Eastern Himalayas, Assam and Burma and cultivated throughout India. Like most of the other species mentioned previously this species has not been planted in plantations since the growth is usually poor under degraded and exposed site conditions. It prefers fertile soils and some shade in early stages of growth. Under full sunlight the height growth is not much stimulated but shade encourages early height growth with a straight stem. In one Indian forest species study (Tharper et al., 1992) this species was recorded as having high level of root colonization by VAM fungi which can be very important for seedling vigour.

The tree has a dense crown and the bark is grey and smooth. The leaves are dull green, the flowers are yellow or orange and the fruit is a round capsule. Seeds of *Michelia* contain oils which are thought to be responsible for shortening the viability period, for seeds lose viability within a few weeks and normally have poor keeping qualities. The soft tissue which surrounds the ripe fleshy seed is generally palatable to birds and this helps in the natural spread of the seeds. Seed germination is otherwise generally poor unless proper seed treatment is done.

The species is valued for its timber which is used for making furniture while tree branches can be used for firewood. It can also be used in plywood industry as it produces good cylindrical logs. Trees can be felled for timber at the age of about 25-30 years and at this age it can attain a mean annual increment of 8.3 m^3/ha (Ghosh and Singh, 1981). The same authors mention that it produces a high leaf biomass (e.g. 21% of total biomass in first 4 years) which may be beneficial in soil fertility improvement since it sheds a lot of leaves during its growth.

2.4 UNDERPLANTING

2.4.1 Introduction

Underplanting refers to planting or occasionally sowing a species under the overhead canopy of the same species or another species, generally of older age, thereby developing at least two storeys on the same land. This structure is an intermediate stage between multi-storied natural forest and single storied, even aged monoculture plantations. It is generally believed that two or more layers of tree canopies are ecologically more sound in terms of site protection than single layered canopies.

Depending on the objective, the two layer structure formed in the first stage can be managed later on either for the underplanted species thereafter to take over the overstorey and become a single storey or to have two or more canopy layers permanently on the same land. Underplanting and subsequent management of the canopies in a forest plantation are generally considered more difficult than that of a single species. Success usually depends on the species selected for overstorey and understorey, their growth rates and mutual compatibilities, site quality and other environmental factors and the method of management of the different stories. In particular, if the overstorey is not managed properly the growth of the undercrop can be severely affected and can lead to failures.

Underplanting can be done to achieve economic or ecological objectives, or both. In some cases economic disadvantages can be compensated for by ecological benefits such as soil erosion control, long term ground cover, maximum utilization of sunlight and soil resources etc.

Presently underplanting is practised in many countries usually to raise more productive shade bearing tree species which need shade at least for early growth, or

where the overstorey is unproductive or uneconomical and needs to be gradually replaced.

Some of the possible advantages of underplanting can be listed as follows :

1. Land utilization will be maximized by maximum uses of available resources :
   - Available sunlight will be more fully utilized by different canopy layers.
   - Soil nutrients will be tapped and recycled by different layers of roots in different species with different demands on soil.

2. More effective long term soil cover can be given than in a single species plantation, thereby protecting the soil from erosion and degradation.

3. Shade bearing tree species can be raised under the overstorey of another species which provides shelter.

4. Sensitive species can be protected from harsh environmental conditions such as intense solar radiation, low air humidity, high winds, too much soil moisture evaporation, frost damage etc.

5. Incidences of pests and diseases can be reduced in certain situations, eg. shoot borer attack in Meliaceae plants and root diseases in some tree species.

6. Fire risks can be reduced by mixing different species.

7. Litter breakdown can be improved where it is too slow.

8. Understorey tree form may be improved.

9. Unproductive or uneconomical tree stands can be gradually replaced with another species without exposing the soil too much as in the case of clear felling.

Possible disadvantages include :

1. Tree species may compete with each other for soil moisture and nutrients, especially if they are not properly managed.

2. Low light levels can reduce the growth of the understorey .

3. Under heavy shade, tenderness of plant tissues may be increased with such as internodal elongation.

4. Management of two or more canopy layers may be more difficult and felling may cause damage to the undersorey.

5. The practice may not be economically attractive.

6. Unforeseen problems may crop up due to management difficulties and species incompatibilities.

2.4.2 Underplanting in Sri Lanka

Some forms of underplanting have been practised for a long period in the country. Most of this work has been done in normal silvicultural practices rather than on an experimental basis. Some of these practices have gained wider application after long term experience.

One of the best example of underplanting in the country is enrichment or line planting of *Swietenia macrophylla* (mahogany) in degraded natural forests. This practice has been carried out for a long period and successful mahogany stands have been established. *Swietenia* needs to be always underplanted due to its shade requirement for early growth and to reduce *Hypsypyla* shoot borer attack. Line planting is done by clearing a strip in scrub forests and planting the tree seedlings along a line. This practice is done to improve the conditions of degraded forests and hence the term enrichment planting.

In the past, jak (*Artocarpus heterophyllus*), a valuable timber and fruit species, has been underplanted with *Swietenia macrophylla.* In later stages it has been developed to a mixed species stand since the overstorey jak was not completely removed. Later still, mahogany dominated the stand, probably suppressing the original overstorey due to its fast growth rates and profuse natural regeneration capacity.

Swietenia macrophylla has been planted under *Pinus caribaea* plantations as a pilot study of investigating the possibilities of underplanting. Planting was done without

sufficient thinning of pine. At the age of 8 years the mahogany has reached a height of 8-9 m under moderately heavy shade with an average diameter of about 9 cm, while trees under light shade reached 5-6 m height with 5 cm diameter. Another study has been started in a pine stand adjacent to a large natural forest, which influenced the micro-climate of that stand, to find out the possibility of gradually converting pine to more desirable broadleaved forests. The species selected in this study have been mainly rain forest species including *Shorea* spp, *Dipterocarpus* spp, *Mesua ferrea, Pericopsis mooniana, Caryota urens* and *Swietenia macrophylla.* Cane (*Calamus* spp), a climbing vine, which is in high demand for handicrafts such as basket weaving and furniture making has been planted in pine stands quite successfully in wet areas. However, due to animal damage this species is not widely planted now.

Some early studies have been done on underplanting in dry natural forests. The timber species *Berrya cordifolia* and *Azadirachta indica* have been planted under the shelter of other species. Burning before planting and trenching around the seedlings to control root competition, and combinations of these two treatments have been tried out for these two species. The best growth was obtained by burning with trenching, followed by trenching alone, burning alone and controls without burning and trenching. This indicates root competition effects when underplanted, particularly for soil moisture in the dry season (Rutnam, 1959). Another early study (anonymous, 1945) has shown the species *Myristica laurifolia* cannot be grown successfully in full open sunlight owing to attacks by scale insects followed by root fungus. Recently, *Berrya cordifolia* has been planted under the canopy cover of scrub forests in the dry areas.

Various types of underplanting have also been done within agro-forestry practice. One of the best examples is planting perennial crop tree/shrub species such as coffee (*Coffea* spp), cloves (*Syzygium aromaticum*), nutmeg (*Myristica fragrans*) and cacao (*Theobromo cacao*) under the canopy of coconut trees (*Cocos nucifera*); which in agro-forestry is called intercropping rather than underplanting. This practice has been extensively studied and is now recommended for coconut growers in the country (Liyanage et al, 1984).

Another important example from the country are the perennial tree 'home gardens' where timber, fruit and other trees of economic value are planted in mixtures and have thrived well in an ecologically balanced way for centuries (Ranasinghe and Newman, 1993). Seedlings of various species are regenerating naturally under the

existing canopies in these systems, and this type of tree mixtures are found in some other tropical countries as well e.g. Indonesia.

2.4.3 Underplanting in other tropical countries

In the past, in most tropical countries, underplanting has been done mainly in natural degraded or scrub forests as enrichment planting to improve those forests. This type of practices have been carried out for a long period while in recent times underplanting in forest plantations has been tried out. Also, with the recent developments in the field of agroforestry various types of underplanting have been tested with trees as mentioned in the previous section. Forest home gardens are also a common feature in most of the wet climates in the tropics.

In India, Sen (1965) reported that degraded forests can be enriched with teak (*Tectona grandis*) and other valuable forest species. Teak has given very good results when the overwood was successively removed. Another early study by Venkataramany (1956) reported that sowing or planting a subsidiary tree species under an existing stand can lead to better soil cover, minimizing soil erosion, increase the production of the site and provide early returns by heavy thinning of the overwood etc. *Swietenia macrophylla* and *Toona ciliata* have been successfully underplanted and dense line planting has been recommended to minimize damage by browsing animals.

Studying a large number of species under the canopy of degraded natural forests in India, Rai (1990) has reported that *Dipterocarpus indicus*, *Mesua ferrea* and *Vataria indica* are promising species for underplanting. In another study by the same authors, *Persia macrantha*, *Hopea parvifolia* and *Calophylum tomentosum* have performed well and they concluded that only major rain forest species can grow well under heavy shade. Semi-deciduous species such as *Acrocarpus fraxinifolius* and *Toona ciliata* have initially performed well but did not grow later probably due to their greater light requirements in later stages.

Ahmad et al (1989) reported that rattan (*Calamus manan*) planted under a Malaysian pine forest has given successful results. The same rattan species under*Shorea* species has been reported to give favourable return on investment (Rauf, 1982). Line planting or group planting of *Shorea parvifolia* under non-commercial trees in Malaysia has given similar results in terms of growth but group planting has given better survival

(Tang and Chew, 1980). Removing overhead shade 3-6 months after planting has been recommended. In another study, Ang (1991) reported that *Shorea parvifolia*, *Alstonia angustiloba* and *Endospermum malaccense* grew better in open sites than in forest sites, indicating their light preferences.

Heavy shading is not tolerated by species such as *Cedrela odorata* though it grows under shade in early stages as reported by Siagurua and Taurereko (1988) and Siagurua et al.(1987) in Papua New Guinea. However, Kriek (1968) has reported *Cedrela odorata* as one of the promising species for underplanting in tropical high forests in Uganda, in addition to the other suitable species of *Acrocarpus fraxinifolius*, *Cordia alliodora* and *Terminalia* species. These studies indicate that overhead canopy manipulation to alter the light environment is required for better growth of under planted species.

Ray and Brown (1995) reported that seedling survival of broad leaved species is better under the shade of degraded dry forests than in open areas in the Caribbean. Plants in open areas were susceptible to drought stress and subsequently mortality occurred. Further, he suggested planting seedlings under the shade of a fast growing species such as *Leucaena leucocephala.* Beneficial effects of underplanting have been experienced in mangrove plantations of *Sonneratia* and *Avicennia* spp in Bangladesh by Siddiqi et al (1992). Plants in open areas were suffering due to geomorphological changes, species succession and insect infestations. Some commercially important species have been proposed for large scale underplanting.

The use of *Alnus japonica* as a nurse crop in reforestation of *Pinus kesiya* seedlings has been reported by Penafiel et al. (1980) in the Philippines. Underplanted seedlings have shown greater height growths, shoot dry weights and nitrogen contents in needles than plants in open areas.

It should however be noted that in tropical areas underplanting is carried out in various ways, particularly to restore degraded natural forests and most of the results are not usually reported since they are mainly normal planting practices rather than experiments. Therefore, in order to give a description about various underplanting methods and their success, some experiences obtained in temperate countries are discussed in the following section.

2.4.4 Underplanting in temperate climates

Different types of underplanting have been carried out in different situations. The objectives generally have been to replace uneconomical tree stands, to reduce insect or disease incidences, to satisfy shade requirements of an understorey crop etc. Broadleaves under conifers, conifers under broadleaves, conifers under conifers and broadleaves under broadleaves have been planted and a description of examples of underplanting in broadleaves and coniferous stands is given below:

2.4.4.1 Underplanting in coniferous stands

Various types of coniferous stands have been underplanted in different ways in different countries mainly in Europe, Russia and USA. Fisher (1993) reported that in Germany, oak (mainly *Quercus petraea*) can be successfully introduced to understocked and non uniform stands of *Pinus sylvestris* either by underplanting or by encouraging natural regeneration. A similar study by Preuhsler et al. (1994) reported that old *Pinus sylvestris* stands of 80 years old can be regenerated by sowing oak or underplanting with various other species such as beech (*Fagus sylvatica*). In this study, oak was reported to grow well under both light and heavy shelters. Comparatively young stands of *Pinus sylvestris* of age 40-50 years have been underplanted with beech in some other studies where pine overstorey has been removed when about 90 years old and beech has been retained to grow as the main crop (Ditmar and Knap, 1986). Successful underplanting of the same species by other species such as *Abies grandis* and *Thuja plicata* were reported by Niefnecker (1992). Beneficial effects of underplanting of *Pinus sylvestris* have been reported by Gerold (1987), recording 10 fold current annual increment and 140% total mean volume increment at the age of 120 years, as compared with plots which were not underplanted.

In Russia, underplanting has been tried for a long time with the general objectives of stabilizing the ecosystem, reducing the damage by foliage eating insects, lessening the incidences of root disease and improving fire resistance in plantations. Broadleaved species have been planted as rows or regular groups which were surrounded by other broadleaved species in certain cases. Group planting has been particularly done when the pine was suffering from the root disease caused by *Fomes annosus* (Bernadzki et al., 1984, Onis'kiv, 1977). Davidenko and Nevzorov (1978) also reported that mixed plantations are superior to pure plantations in controlling

root diseases. In another Russian study of underplanted species (about 100 years old Scots pine with an understorey of 50 years old spruce), the diameter at breast height (DBH) of spruce was found to be significantly correlated with distance to the nearest spruce or pine stem showing the importance of tree competition effects on diameter growth (Yurgenson and Yurgenson, 1984).

Interception and transmission of the precipitation in an underplanted environment was studied by Chmyr and Skiba (1979) in a *Picea abies* stand underplanted with Norway spruce. Results indicated that interception can be considerable and thus restrict the moisture supply of the underplanted spruce and to avoid this it was suggested that overhead canopy should be sufficiently opened.

Fenger (1975) suggested raising a new crop of pine trees beneath widely spaced trees retained from the previous crop of pine in South African plantations to suppress the young trees to a limited degree to reduce the effects of low density juvenile cores formed in the first 10 years. He found that young suppressed trees favourably compare with old mature trees both in density and percent latewood.

Advantages of underplanting in terms of improved nutrient availability are reported by Bevage and Richards (1970) and Richards (1962). *Araucaria cunninghami* usually shows nitrogen deficiency when planted in open areas but the problem can be overcome by planting under pine stands suggesting that the pine may facilitate mobilization of nitrogen, or that the nitrogen requirement is lower under shade in *Araucaria*. The advantages of under/inter planting with nitrogen fixing species and mutual benefits have been reported by various other researchers (eg. Preuhsler and Rehfuess, 1982).

Hiley (1956) suggested that pure Japanese larch stands can be converted to two storied high forest at the age of 25 after heavy thinning and underplanting. At the age of 50 the larch is clear felled and the under crop itself should be thinned so that it in its turn can also be underplanted, carrying the system forward indefinitely. He reported such a system would have the advantage of selection system without its disadvantages. Magnuski (1987) has obtained better results of underplanting with row planting of the under crop in comparison to group planting, and also reported that increment loss through tree removal for underplanting is far outweighed by the benefits of conversion.

Underplanting has been carried out in insect-damaged and defoliated *Pinus sylvestris* stands after manipulating the overhead shelter to give relative diffuse light ranging from 90-60% of that in the open (Wagner, 1994). Results have shown beech and Red Oak (*Quercus rubra*) were best under shelter whereas *Quercus robur* and birch (*Betula pendula*) were best in the open. Alder (*Alnus incana*) failed under shade, which shows the different ability of various broadleaved species to grow under overhead shelter. Schenk (1994) reported the possibility of underplanting snow damaged spruce (*Picea abies*) with *Fagus sylvatica*. Plantations on unsuitable sites and/or with unsuitable provenances can be enriched by underplanting as suggested by Malcolm (1957) in a study of underplanting European larch stand with Douglas fir and *Abies grandis*. These studies show that underplanting is a viable method of restoring conifer stands damaged by external factors.

Underplanting has been successful in some situations to control some disease incidences as reported by Rowan et al (1975) in Georgia where fusiform rust was significantly reduced in *Pinus taeda* seedlings when planted under the old trees of the same species and the results were attributed to low tissue area exposed to infection or modification of micro-climate and soil fertility by the overstorey.

2.4.4.2 Underplanting in broadleaved stands

In Germany pure oak stands have been converted to mixtures with beech since 1865 by underplanting or allowing natural regeneration of beech (Gurth and Kruse, 1988). *Pinus sibirica* has been tried under 26-30 year old broadleaved stand by Ermolenko (1990) in Russia and experience suggested that thinning and root severing of broadleaved species around underplanted seedlings should be done. When poplar was underplanted with Norway spruce under 57% and 43% canopy cover, the spruce height increment was twice as great in the more open stand (Turlyuk, 1984). Turlyuk (1983) found that when spruce was planted under birch, spruce growth was limited more by root competition from the overstorey than by canopy effects. With similar field studies, Gryazev (1975) concluded that underplanting in broadleaved stands such as birch, alder and aspen was a suitable method of establishing *Picea abies*.

Emmingham et al. (1989) has reported that conifers beneath broadleaved stands in Texas could shorten time to conversion to more valuable stands. They suggested thinning the broadleaved stand to final crop spacing before planting the conifers which could increase growth and marketable volume of broadleaves while releasing

the site resources necessary to support conifers. This is supported from another study by Wendel (1971) in Virginia, suggesting the most efficient method of converting hardwood stands in poor sites to *Pinus strobus* is to underplant the stand and remove the overstorey after 5-10 years. Another study in the same state suggested that underplanting can be a viable means of regenerating oak (Tworkoski et al, 1986). In a study on underplanting *Pinus taeda*, *Pinus palustris*, *Pinus elliotti*, *Pinus virginiana* and *Juniperus virginiana* under a low grade hardwood stand in Mississippi it was found that seedlings given immediate release from hardwood competition by thinning the overhead canopy were almost 3 times taller than as those on unreleased plots, and *Pinus taeda* was the best species showing high tolerance to overhead competition (Williston and Huckenpahler, 1958).

In an attempt to underplant a poor *Quercus garryana* stand with Douglas fir, it was revealed that considerable success can be achieved if the overstorey trees were carefully and properly managed, and the two species were not incompatible (Hall et al , 1959). Ferguson (1963) found in broadleaf/conifer mixed stand underplanted with *Pinus taeda* seedlings that survival and height growth were retarded in direct proportion to the basal area of the overtopping trees.

Tarrant (1961) observed the beneficial effects of interplanting Douglas fir and *Alnus rubra* plants, where the volume of mixture was more than twice that of pure Douglas, and also the nitrogen content of Douglas fir seedlings were higher indicating that *Alnus* has contributed to increased growth of it. Some desirable and undesirable effects of underplanting were observed by Brown (1955) in a beech plantation raised under shelter. He reported that height growth was not affected and a promising stem form was developed by a continuing overhead shade which intercepted 70-80% of the light, but diameter growth was retarded. However, on the other hand, when the under crop was released from shade 7 years after planting, vigorous height and diameter growth was developed, but with an undesirable frequency of forks and other blemishes.

Lower costs of weeding have been experienced by Davies (1966) when *Picea sitchensis* seedlings were planted under open birch scrub. Henriksen and Sanojca (1983) achieved successful control of epicormic branch formation with shade effects when the understorey beech was 30 year old and the overstorey *Quercus robur* was 70 years old.

Proper selection of species is important for the success of underplanting. Shade tolerance, fast initial growth, good form, and self pruning characteristics were preferred for understorey species to be underplanted in a logged-over indigenous forest in New Zealand (Anonymous, 1963). In this study *Acacia melanoxylon* was selected as one of the best species, a species which is planted in highlands of Sri Lanka as well.

2.5 FACTORS INVOLVED IN SURVIVAL AND GROWTH OF UNDERPLANTED TREE SEEDLINGS

Many factors are involved with the survival and growth of underplanted species, particularly light availability and root competition for water and nutrients. These factors directly affect the early establishment of the underplanted seedlings and also interact with each other to produce specific micro-climatic conditions at a particular site.

Since underplanting involves planting seedlings under an overhead canopy, light plays a major role for the growth of these plants. Species adapted for low light levels at least for early growth (shade tolerant species) are generally suitable for this purpose. At later stages, most species require more sunlight and therefore canopy manipulation may be required by thinning or pruning of trees. Light quality, including the red:far-red ratio, also plays an important role in plant growth. Effects of light environment and thinning of overstorey trees for understorey seedling growth are discussed in detail in Chapter 7.

Understorey environment can also be strongly affected by root competition for water and nutrients. Established trees of the overstorey will generally pose root competition effects on growing seedlings in the understorey as compared to the situation where seedlings are growing in open lands without weed competition. Weed competition is usually less intense under pine overstorey, particularly before thinning and in early stages after thinning of pine trees. Therefore, control of below ground competition may be required depending on the site and the overstorey conditions, and the ability of understorey to withstand competition. Trenching around seedling is one of the possible method for controlling root competition in the seedling rooting zone. Placing mulch around the growing seedling can also be generally beneficial to improve the conditions in the rooting zone. Soil moisture conservation from mulching is particularly important in dry periods and it may also help in improving the nutrient

status of the plants. The below ground competition effects and ameliorative effects of trenching and mulching are discussed in relevant sections of Chapters 4 and 5. Other micro-climatic effects such as soil surface temperature and soil fertility levels are discussed in Chapter 8. Nutrient availability in relation to mycorrhizal infection, litter decomposition and forest fire are discussed in Sections 2.6, 2.7 and 2.8 respectively. Wild animal damage is another problem sometimes experienced in certain areas. Plant herbivores with little else to eat in pine plantations have damaged underplanted seedlings in some situations, for example cane plants were damaged by porcupines and *Albizia* plants by deer in Sri Lanka. Thus various factors may be involved in the successful growth of underplanted seedlings.

2.6 MYCORRHIZA IN REFORESTATION

As mentioned in section 2.1, extensive deforestation in the tropics has led to land degradation and a variety of related problems. Once these lands are degraded it is commonly found that they can hardly support the growth of most of the local species any more. This is generally believed to be due to decline in soil fertility which is not favourable for the growth of these species. Miller and Jastrow (1992) reported that under disturbed environments mycorrhizas may be a limiting factor for plant growth. Despite this fact, sufficient attention has not yet been given to the role of mycorrhiza on plantation establishment in the tropics. For example, in Sri Lanka mycorrhizal inoculation is done only for the planting of pine species. Apparently, one of the main reasons for this is the ability to reforest those lands with exotic tree species with considerable success (e.g. acacia and eucalypt plantation establishment).

Mycorrhizal infection, which is a mutualistic association between certain fungi and plant roots, is believed to be widespread in natural ecosystems. Reeves et al (1979) showed that in a natural community in Colorado, 99% of plants were endomycorrhizal whereas in a disturbed site less than 1% of plants were mycorrhizal, and emphasized the importance of re-establishing mycorrhizal fungi to produce stable ecosystems. Once natural forest cover is depleted the mycorrhizal inoculum potential declines in those sites due to lack of host species. Soil erosion after deforestation also contributes to the lowering of spore density (Perry et al, 1987). Mycorrhizas also play an important role in the plant succession. The late successional trees of moist tropics are usually obligately mycorrhizal while trees of earlier successional stages (pioneers) and those in relatively fertile sites are often facultatively mycorrhizal. Trees growing in highly infertile lands are predominantly ectomycorrhizal (Janos,

1980). Out of the two main types of mycorrhiza, it is generally thought that ectomycorrhizas predominate in temperate species while endomycorrhizas (vesicular-arbuscular mycorrhiza) mostly occur in the tropics. However, many tree species of the Dipterocarpaceae and Caesalpinoideae form ectomycorrhizal associations (Janos, 1980) while some others like eucalypts form both ecto- and endomycorrhizal associations (Chilvers et al, 1987). Ectomycorrhizas are characterized by the presence of a mantle of fungal hyphae enclosing the end-roots and usually a Hartig net of intercellular hyphae. Vesicular-arbuscular (VA) mycorrhizas form external hyphal networks in the soil and arbuscules extensively within the cells of the cortex (Bolan, 1991). It has been observed that the latter show little host specificity (Janos, 1980).

Mycorrhiza may improve seedling survival and growth by enhancing uptake of nutrients and water, lengthening root life and protecting against pathogens (Harley and Smith, 1983). They can have advantageous effects on plants during times of stress such as drought, by increasing the fitness of plants (Allen and Allen, 1986). In some instances even hormonal changes of the higher plant are reported to be controlled by these fungi (Allen et al, 1982). In addition to these effects within the plants, Tisdall (1994) showed that mycorrhizal hyphae (especially VA fungi) can stabilize macro-aggregates in the soil, while other organisms and chemicals stabilize micro-aggregates. Soil aggregation helps in soil aeration, drainage and plant growth.

Facilitation of nutrient absorption is one of the great advantages to higher plants offered by these fungi. The fungal hyphae have a large surface-to-volume ratio and can explore a large volume of soil more intensively than plants (Allen, 1991). They are particularly important in phosphorous (P) absorption. P is often not readily available to plants since it is frequently at low levels and/or fixed in the soil by alluminium (Al) and iron (Fe) as insoluble phosphates and therefore a means of P solubilization is very important in such soils. Bolan (1991) reported that mycorrhiza increases nutrient uptake especially P by exploring a large volume of soil, solubilization of soil P and faster movement of P into mycorrhizal hyphae. However, if P is not limiting the growth of plants, the fungus may not a play a major role and can become a carbon drain (Allen, 1991). Nutrient uptake of different groups of mycorrhizae was studied by Marschner and Dell (1994) and reported that ectomycorrhizae can take up P, NH_4^+, NO_3^- and K while endomycorrhizae absorb P, NH_4^+, K, Ca, SO_4^{2-}, Cu and Zn. They also found that VA fungi can deliver up to 80% of P, 25% of N and 10% of K of plant requirements, however, consuming 10-20% of net photosynthates from them. Another recent report by Northurp et al

(1995), showed that ectomycorrhiza has the capacity to utilize organic N in dissolved form, in contrast to mineral forms such as ammonium and nitrates, thereby minimizing N availability to competing organisms and reducing N losses from leaching and denitrification.

Many environmental factors affect the inoculum potential and infection of mycorrhiza in forests e.g. soil chemical status, soil pH, presence of heavy metals, soil moisture, soil temperature, organic matter and soil microflora (Bowan, 1994). VA fungal spores can persist longer in soil when desiccated as reported by Perry et al (1987). The infected fungal species in early stages of a forest may be replaced by other fungi in later stages (Mason et al, 1983). In forest plantations, silvicultural operations disturbing the soil environment such as clear cutting and slash burning are reported to be less favourable for mycorrhizas. Parke et al (1983) found in a temperate climate that mycorrhizal formation was reduced by 20% and 40% in clear-cut and clear-cut + burnt soils respectively compared to undisturbed soils. In contrast, Schoenberger and Perry, 1982 reported that Douglas-fir trees formed significantly more mycorrhiza in a clear cut but unburnt site than in an undisturbed forest site. In forest floor studies Harvey et al (1976) reported that ectomycorrhiza in contrast to VA are predominantly concentrated in or immediately under litter horizons. Gadgil and Gadgil (1975) found in forest litter studies that mycorrhizas under *Pinus radiata* stands were slowing down the litter decomposition rate probably due to their successful competition for moisture and nutrients with obligate saprophytes by direct physical and chemical antagonism. Though this may be an adaptation of mycorrhizal fungi in competitive situations for nutrients, it can interfere with nutrient availability for other species.

In plant communities, ecto-mycorrhizas have been found to be forming hyphal connections between roots of the trees of the same or different species. These interconnections help to transfer carbon (C) between plants particularly when there is a concentration gradient induced by shading of some plants (Finlay and Read, 1986a; Heap and Newman, 1980). When seedlings are growing in shade under an overhead canopy, below the light compensation point, they believed that mycorrhiza is supplying C from other trees through these hyphal connections. However, Finlay and Read (1986b) found that P transfer is unidirectional and is not so transferred from plant to plant by fungi. Spatial and temporal linkages of plants by ectomycorrhiza can reduce plant competition for resources and promote forest recovery. However, management practices that create intense disturbances and loss of organic matter can

decrease the ability of plants to form such linkages (Amaranthus and Perry 1994). This indicates that in natural stands or in mixed plantations with natural regeneration mycorrhiza may play vital roles influencing the plant growth by mediating interactions among plants.

According to the above discussion it is clear that due consideration should be given for mycorrhizal research in forests to identify their role under local conditions and to use them for maximum benefits for plants, particularly when they are planted under harsh environmental conditions which are often encountered nowadays in reforestation in the tropics. Simple techniques such as adding soils for nursery plants from forested soil may be done for hardwood species, as successfully done for conifers in many tropics. Such inoculation may enhance seedling survival (Amaranthus and Perry, 1987) in addition to better growth. It can also help trees to compete successfully with grasses and herbs for resources (Bowan, 1980) under plantation conditions. However, much work is still to be done to discover the most suitable fungal species and strains that form effective mycorrhizas with a particular tree species and genotypes (P.A. Mason, personal communication)

2.7 LITTER DECOMPOSITION AND NUTRIENT CYCLING

Litter decomposition is extremely important in maintaining the nutrient level in forest ecosystems. It releases minerals and non decomposable humic and other substances. High rates of litter decomposition is generally experienced with most species in the tropics which leads to a quick return of nutrients to the soil. However, litter constituents such as phenolics and low amounts of nutrients can significantly reduce this rate in some instances. Slow rates of decomposition can result in the accumulation of large nutrient stocks in the soil surface and become unavailable to plants for a longer period, temporarily immobilising them. Additionally, litter accumulation pauses fire risks in drier areas of tropics as will be described in Section 2.8. Litter decomposition is mainly regulated by the climatic factors, soil moisture, soil micro-organisms, soil fauna and the chemical nature of litter.

Numerous researchers have studied litter decomposition in various tree species, however, some of the processes involved seem to be not yet clearly understood. The chemical constituents in the litter which are responsible for decomposition have been in debate and these include lignin, polyphenols, nutrient (N or P) contents, the C:N ratio and also lignin:N and polyphenol:N ratios. Fogal and Cromack (1977) showed

that lignin is mainly responsible for decomposition of Douglas-fir out of other chemicals. Palm and Sanchez (1990) reported that polyphenols influence the rate of decomposition more than percentage N or percentage lignin. Polyphenols are resistant to decomposition and apparently may control N release from the litter. Meanwhile Oglesby and Fowness (1992), studying chemical composition on nitrogen mineralization from the green manure of tropical legume trees, showed that the best chemical index of N release was the initial polyphenol:N ratio. Taylor et al (1989) and Flanagen and Van Cleve (1983) reported that N content of leaves and C:N ratio are the best predictors of mass loss rate in forest litter and was substantially better than lignin:N ratio while some others (e.g. Staaf and Berg, 1982) have shown that P or C:P ratio is a limiting factor for decomposition.

Most N in tree leaves is in organic form but this N is immobilized during the first stage of decomposition, and if decomposition is slow this may lead to a deficiency of N for tree growth (Attiwill and Adams, 1993). In contrast, significant amount of phosphorous (up to 50% or more) is in inorganic form in the foliage of some tree species (Chapin and Kedrowski, 1983) and this can be readily leached from fresh litter (Polglase et al, 1992). In India, Bahuguna et al (1990) reported that in eucalypt leaf litter N, P and K nutrients are highly leachable and this promotes microbial activity and litter decomposition. Carlyle and Malcolm (1986) also suggested that P and K could be leached from senescing foliage of trees in relatively large amounts but N loss was probably low. Phosphorus is the element most likely to be limiting in tropical forests growing on well weathered soils (Attiwill and Adams, 1993) and during decomposition, N and P are not readily released as shown in some temperate and tropical studies. Staff and Berg (1982) reported that in Scots pine needles the nutrients are retained in the order of Mn,Ca,K,Mg,S,N,P during the first 1.5 years and there was a net increase of N and P thereafter. Studying nutrient release pattern in tropical highlands, Lisenework and Michelsen (1994) showed that nutrient release pattern was K>Mg>Ca>N=P.

Coniferous leaf litter is reported to be more resistant to decomposition than that of broadleaved trees (Millar, 1974). Though there are some advantages of litter accumulation (e.g. it can function as a mulch protecting the soil), it can bring about unfavourable effects such as creating a high fire risk (see section 2.8) and temporarily immobilizing nutrients. After burning, released nutrients will be leached easily as they are in soluble form. In pine litter, needles constitute about 60 to 80 % and others such as cones and branches and bark etc amounts to the balance as reported by Millar

(1974). However, the needle percentage in litter may vary in different areas. Cones and branches seems to be more resistant to decomposition than leaves which may further delay decomposition. Slow decomposition of litter such as that of pines also restricts nutrient availability in the forest floor. For example, in pine forests in Mediterranean climates it has been found that net mineralization did not take place within 2 1/2 years (Wesemael , 1993).

In the decomposition stages of pine litter, starch, hemicelluloses and amino acids are initially decomposed while lignin is decomposed at a later stage. Microflora are believed to be responsible for primary decomposition. Their action is to breakdown complex polysaccharides into assimilable monosaccharides. The fungi are mainly responsible for this and other organisms such as protozoa, bacteria and actinomycetes are also responsible (Millar, 1974). Polyphenols form complexes with the protein of the needle mesophyl cells immediately before litter fall, which then show considerable resistance to microbial decay (Handley, 1954). Litter decomposition is also influenced by micro-arthropods (Abbot and Crosslay, 1982) which helps in the initial breakdown of material. Mycorrhizas are reported to suppress litter decomposition in *Pinus radiata* which may be an adaptation which conserves nutrients from leaching and volatilization which contribute to the formation of raw humus as a result of low microbial activity (Gadgil and Gadgil, 1975).

Nutrient re-translocation seems to occur in leaves of various tree species to varying degrees. Mo et al (1995) reported that 50% of N and 20%P of the fresh foliage in a pine forest in China were re-translocated before leaf fall, while Ca was not. 30% of K was also lost before leaf fall but this was mainly attributed to leaching. In another study in India, Lisanework and Michelsen (1994) showed that exotically grown tree species such as eucalypts and *Cupressus* produce low quantities of litter, and re-translocate nutrients during senescence producing low quality leaf litter, whereas native species had a less efficient within-stand nutrient cycling which enhanced nutrient availability to other plants, promoting undergrowth development. Thus, low decomposition rates and tight nutrient cycling mechanisms seem to be better adaptations of the exotic species in degraded lands. To improve litter decomposition in such situations, mixing species would be beneficial. Mixed litter is reported to decompose in a different manner from pure litter by developing hyphal 'bridges' of fungi between different types of litters thereby moving nutrients between them and levelling differences (Ineson and Mctiernan, 1992)

2.8 EFFECTS OF FIRE ON FOREST FLOOR

Fire has been a major problem in tropical plantations degrading and depleting forests, and in turn causing many environmental hazards. Considerable economic losses have been experienced due to burning of young plantations. Fire is usually experienced in intensively managed monoculture plantations during dry periods and additionally, litter accumulation of some tree species such as pine and teak tend to aggravate the situation. Repeated and uncontrolled fires have considerably contributed to forest depletion in the tropics. The usual causes of fire include clearing of lands with fire for agriculture, burning of grasslands for cattle grazing and arson due to social unacceptability of tree species. Goldammer (1988) reported that increasing rural populations have largely contributed to increasing the incidence of fire, and if these man-made fires were eliminated, many of the monsoon forests of SE Asia would be reverted to evergreen rain forest biomes. According to Wormald (1992) the incidence of fire in forests is growing rapidly around the world; in Europe and North America the extent of forest area burned is estimated to be 4 million ha and in Brazil it was over 200,000 ha between 1983 and 1988. Raison (1980) reported that intensive forest management practices, including clear felling, slash burning and short rotations lead to serious declines in productivity in Australian forests, and intense slash burning was suspected to be much more significant than harvest of biomass. In Sri Lanka, fire is a serious problem during dry periods particularly in pine forests situated mainly in upland hilly areas. The high incidence of fire in degraded lands such as grasslands and savannas is a major obstacle to the restoration of forest cover.

Fire in pine plantations in Sri Lanka, as described in Chapter 1, causes destruction of forest litter layer, ground cover vegetation and consequent accelerated soil erosion, in addition to destruction of young forest plantations (see Appendix I). Most tropical pines are pioneers and are usually planted in degraded sites and show distinct adaptations to fire environment. Its thick bark protects it from fire when it is sufficiently grown and the inflammable litter layer eliminates ground vegetation competition. Goldammer (1988) reported that regularly occurring fires in natural ecosystems favour the fire-adapted pines which replace fire-sensitive broadleaved species. In natural environments in the Philippines it has been reported that the altitudinal distribution of natural pine is extended in mountainous zones due to the effect of fire (Kowal, 1966). Such fire-climax pine forests occur in countries such as India, Burma, Vietnam, Philippines and Indonesia (Goldammer, 1993).

Fire plays major roles in ecosystems with effects on plant community structure and composition, and on soil erosion and nutrient cycling. Due to the effects of destruction of species not tolerant of fire, it causes a reduction in bio-diversity in the ecosystems. In fire prone areas such as savannas, fire has prevented regeneration of some tree species causing gradual genetic erosion in natural habitats. Fire can cause undesirable effects on soil seed bank, insects, small animals and mycorrhizal fungi. Long term impacts of frequent fires lead to considerable erosion because of the complete or partial removal of the protective litter layer before the monsoonal rains in the tropics. Serious erosion losses were reported by Bell (1973) in teak plantations. Stadtmueller (1990) has shown that fires are catastrophic for the environment and soils, causing physical, chemical and morphological changes, destroying soil fauna and flora, and increasing erosion. In the Philippines, grassland burning has been considered a critical problem in watersheds increasing peak flows, soil erosion and suspended sediments downstream (Dano, 1990). Moreover, fire can reduce soil infiltration rates when the soil pores are filled with fine material which accelerates erosion under some topographic and climatic conditions (Wormald, 1992). Kellman (1984) reported that inherently infertile soils are generally more fire prone than that of more fertile soils due to the slowness with which closed cover trees and shrub species are established on these soils.

Fire directly consumes part or all of the above ground plant material and litter and when they are burned it liberates nutrients tied up in the plant tissues. As a result nutrients from the organic matter can be more available in the soil, and/or removed from the site by volatilization or wind effects during the burn. Trabaud (1994) reported that C and N are the elements largely lost in a vegetation fire and N was particularly susceptible to volatilization. Significant amount of gaseous N can be lost above 300°C (Debano and Conrad, 1978) but some N can be left in the ash (Christensen, 1973). Christensen also reported that soil heating and combustion transform N into readily available forms for plants. After fire, soil bacterial number is reported to build up rapidly and may encourage nitrification and improve the N status of soil (Raison, 1979). P can also be volatilized from combustible fuel and blown away, and the degree of transfer depend on factors such as temperature, the forms of P in the fuel, the cation contents of the ash and the amount of ash transport. Volatilized P forms phosphoric acids and can be redeposited in rainfall (Raison et al. 1985a,b). K can also be lost in the fire. Although it is not volatilized as N, a significant amount can be lost above 550°C (De Bano and Conrad, 1978) and a part can be redeposited as ash (Trabaud, 1994). However, redeposited ash on the soil

surface can be easily washed off or the K leached down, particularly on steep slopes. Smith (1970) reported that Na, P and Ca were greatly leached in the first 3 months after the fire.

Increased soil temperatures after fire, with increased pH and availability of cations, may result in higher rates of decomposition and mineralization of organically bound N (MacLean et al, 1983). Increased mineralization of nutrients due to fire may lead to leaching of them before plants take them up. S losses during burning have been reported to be critical in the long term maintenance of forest productivity (Klock and Grier, 1981). In a jack pine area in the temperate zone, Smith and Sparling (1966) reported that a surface fire can record a mean temperatures of 300°- 400°C, with extremes up to 600°C or more. These values may be much higher in tropical areas with higher ambient temperatures especially if there is less soil moisture.

Improvements in soil structure, nutrients and soil organic C have been reported under *Eucalyptus* plantations when they were protected from fire (Basu and Aparajita-Mandi, 1987; Kushalapa and Kushalappa, 1987). Soil organic matter is generally responsible for holding and slowly releasing nutrients to plants. Burning of forest biomass can increase pH, Ca, K, and Na and base saturation of soil whereas total C, C/N ratio and CEC decreases. Relative order of nutrient loss in a forest fire was estimated by Trabaud (1994) in the order of Na>Ca>P>K>Mg. Slightly different results were obtained by Oya and Tokashiki (1984), reporting nutrient addition to the soil after burning was in the order of K_2O>CaO>Na_2O>MgO>P_2O_5, representing only 35%, 12%, 8%, 14%, and 1% respectively of the total amounts stored in the forest biomass.

Fire damage in plantations can be minimized by controlled burning. It may, in fact, be beneficial for some plantations in releasing immobilized nutrients to the soil. However, it is not practised in pine plantations in Sri Lanka, probably due to difficulty in controlling fire in steep and undulating terrain and the scattered nature of plantations in a large area. Goldammer (1988) reported that integrated concepts of prescribed burning and sylvipastoral systems may offer a new approach toward solving this problem. The establishment of mixed plantations with appropriate tree mixtures might significantly contribute to reduce the fire risk due to mixed types of litter on the forest floor.

2.9 MIXED SPECIES PLANTATIONS

Intensive forest management for the production of timber, pulp and fuelwood has favoured the use of single species plantations throughout the world. These have simplified stand structures and when appropriately chosen and well managed can provide uniform, predictable outputs. The harvesting techniques are also much simpler, particularly if clear cutting is done at the end of the rotation period. However, there have been some unfavourable impacts of these monoculture plantations, while the expected benefits of mixtures have led to interest in establishing mixed plantations in various countries. Species mixtures are not a new type of forest and indeed they are generally present in natural ecosystems. In addition, they have been planted successfully in mixed tree gardens in the tropics for centuries. Enrichment planting in secondary forests has also been practised in the tropics for creating mixed forests. Nevertheless, mixtures have not yet been widely used in plantation forestry probably due to complexities associated with management and harvesting of such forests.

Some of the problems associated with single species plantations are: risk of yield reductions in subsequent rotations due to deterioration of site quality, catastrophic outbreaks of insects or diseases (Ball et al, 1995), soil erosion due to clear felling, slow rates of litter breakdown resulting in disruptions of nutrient re-cycling and enhanced fire risk. In clear-cutting methods in the tropics, the exposure of soil to direct rainfall and sunlight results in greatly increased erosion, while higher soil temperatures can kill fine roots and root mycorrhizal symbionts. Also the thin layer of organic litter and humus will be liable to increased rates of decomposition reducing soil nutrient holding capacity (Whitemore, 1981, Panayotou and Ashton, 1992). Some of the research experiences of second rotation yield decline in single species plantations and possible causes have been compiled by Wormald, 1992. The main factors associated were low nutrient status, low moisture availability and loss of organic matter from the soil as well as soil compaction, weed competition and pest and disease problems. However, he quotes some reports having recorded higher yields in plantations than estimated which has been attributed to increased temperature, carbon dioxide and rainfall, and higher mineralization rates.

In Swaziland, Robinson (1973) has reported that there was a tendency to decline in the vigour of pine as a consequence of low biological activity as evidenced by a build up of litter, absence of earthworms and lack of mycorrhiza. He also reported that the

problem of litter accumulation is particularly acute in close canopy softwood stands in the tropics and sub-tropics, but is less of a problem in open stands having an understorey of broadleaf species which promotes the breakdown of forest litter. Panayotou and Ashton (1992) reported that a number of potential problems associated with monoculture plantations cast doubt on long-term sustainability in the humid tropics. Absence of biodiversity, land degradation due to short term and continuous cropping and pest and diseases are some of the important facts. The absence of a dormant period (cold or prolonged dry period) in much of the humid tropics allows uninterrupted reproduction of insects and diseases which can cause epidemics.

The main advantages of mixtures were reported by Ball (1995). A mixed stand may be more stable - less susceptible to wind blow, less liable to attack by insects or disease and maintaining or increasing the fertility of the site. They can take advantage of synergies that may exist between species or the potential for conserving the biological diversity at the species level. The possible capacity of mixtures to use the site more efficiently giving higher biomass output or insurance against partial or complete loss of one species or of its markets can be economically attractive. Some of the important social facts include aesthetics, soil and water conservation and supplying a wider range of products. Advantages were also recorded by other researchers such as rooting zones of different species can occupy different soil strata (Lamb and Lawrence, 1993), greater amount of solar energy can be captured due to their different canopy strata and different light requirements (Kelty and Cameron, 1995). Species may have differing phenologies of root or shoot growth and therefore competitive demand for soil water and nutrients may be lower than that of a monoculture plantations. In general, mixtures of local species will have a more aesthetic appearance and may result in broader community support. In cases where soil is poor in nutrients, a mixed stand can improve the survival and growth of a species when combined with a suitable accompanying species (Matthews, 1989).

Synergy between species has been reported when nitrogen fixing tree species are mixed with non-nitrogen fixing tree species. In Hawai, when N-fixing*Paraserianthes falcataria* was planted mixed with fuel wood species *Eucalyptus saligna* in a N-deficient site, higher yields were obtained from the*Eucalyptus* due to capturing more nutrients and through the higher nutrient cycling capacity of*Paraserianthes* (Binkley et al, 1992). DeBell et al (1989) reported that the N concentration of*Eucalyptus* foliage increased as the number of *Paraserianthes* trees were increased in the

mixture. Soil N content was also higher under *Paraserianthes* trees. In comparison with pure species plots, the mixtures generally have relatively higher yields with the additional advantage of including other species of high economic value. Pest damage was less severe in some species in the mixtures and establishment costs were lower for the slower growing species (Montaginini et al, 1995). Severity of pest infestation is generally lower in mixtures, but can sometimes be increased if a resistant species planted with a highly susceptible species (Smith, 1986, Perry and Maghembe, 1989). Risch (1981) reported that mixtures of interplanted crops support lower densities of insect populations.

When mixtures combine tree species that differ in growth requirements and production, they can reduce inter-specific competition and can sometimes outyield mono-specific stands (Kelty, 1992). Further, when the canopy is stratified in mixtures with a rapidly growing overstorey and a slow-starting but highly productive species in the understorey, they are likely to exhibit greater total productivity than pure stands of shade-intolerant species, forming one of the most successful types of mixed planting (Smith, 1986). If the trees in the upper canopy are not too dense they grow more rapidly in diameter than if crowded into the single canopy of a pure plantation while the understorey canopy can influence stem form and self pruning of upper canopy species (Burkhart and Tham, 1992).

In a Douglas-fir and Red Alder mixture and pure plantations, Binkley (1984) reported that the mixture showed higher mortalities on fertile lands while pure conifers recorded poor growth in infertile lands than the fertile site or in mixed stand. Kelty (1992) reported that two or more species need to use resources differently if they are to co-exist on the same site. In some cases reduction of competition for resources can increase the yield of the mixture over a single species stand on lower yielding sites but that is not necessarily so in higher yielding sites. Conifers/broadleaved mixtures are sometimes planted in lowlands of Britain with the benefit of nursing effects, increased profitability and flexibility while in uplands, they have been planted to alleviate difficulties associated with poor sites (Kerr et al, 1992).

Vandameer (1989) identified two basic types of beneficial interactions between species, namely complementary and facilitative interactions. In complementary interactions two species exhibit reduced competition in mixture compared to that in monocultures thereby utilizing resources more efficiently, while in facilitative interactions one species positively affects the growth of another in mixture. Results of

such interactions in forest species have been summarised by Kelty and Cameron (1995). They reported that in mixtures, differences among species in tree height, crown architecture and leaf area density can result in the development of a stratified canopy causing spatial separation of light interception between species. Differences in phenology of leaf development can also cause a temporal separation. Similarly, uptake of nutrients and moisture might be partitioned in space by species having differences in depth of rooting.

Species mixtures can be broadly categorised into two types (Wormald, 1992); two layered or single layered canopies. A two layered canopy can be either a temporary mixture with the end result of a monospecific stand, or a permanent mixture with the end result of a multi-specific stand. A single layered canopy is generally a permanent mixture with the end result of a multi-specific stand. Usually the mixtures consist of two species and the management of more species are usually more complicated. However, a mixture of several different species have been successfully established in Sri Lanka at Sundapola. Some of the species are mahogany (*Swietenia macrophylla*), teak (*Tectona grandis*), jak (*Artocarpus integrifolia*), *Mesua ferrea* and *Berrya cordifolia* which have been established at the beginning of this century or even before. All species have grown well and now supporting the natural regeneration under their canopies. These species have been planted initially in a secondary natural forest. After the establishment of better canopy cover and the subsequent opening of the upper canopy, other local species (which were there originally) have also grown to larger sizes and are now self regenerating. At present the upper canopy consists of mainly *Swietenia*, *Tectona*, *Berrya* and *Artocarpus* and the second lower canopy consists of species such as *Mesua*, *Semecarpus* spp and *Pterospermum* spp (personal observations). This forest also provides excellent habitat for birds and animals, and furthermore, the green understorey and damp soil cover in the plantation does not easily catch fire as can happen in mono-specific plantations.

The skills required to manage mixed plantations, particularly mixtures of dominants and co-dominants, are greater than for managing monospecific plantations. Badly timed interventions or incompatibility of species used may result in malformation of stems or possibly a natural reversion to a monospecific condition. One of the main disadvantage often ascribed to mixtures is the higher cost involved in intensive management. However, in certain situations, self thinning may reduce the need for management interventions compared to plantations of single species. Complexities of harvesting operations can also be a problem in mixtures (Burkhart and Tham, 1992).

In certain situations mixed species plantations may experience failures due to unsuitable combinations of species, inadequate considerations of stand dynamics and growth behaviour and poor silvicultural treatments etc. It is clear from past work that the nature of interactions among species controls differences in production and the advantages and disadvantages appear to be site specific. Plantations established for site improvement, watershed management, rehabilitation of degraded soils, nursing more important species and amenity can frequently be established as mixtures (Wormald, 1992).

CHAPTER 3

MATERIALS AND METHODS

3.1 EXPERIMENTAL SITES

The sites selected for the present study were in the central highlands of the country where most of the pine plantations are concentrated. Pine plantations are quite widely distributed throughout these upland areas. Five sites were selected from this area, three of them were in Kandy Forest Division (Panwila, Deltota and Galaha) while the other two were in Nuwaraeliya and Badulla Forest Divisions (Watawala and Kinigama respectively). Climatic data of rainfall, temperature and relative humidity are given in Tables 3.1 and 3.2, and Figures 3.1, 3.2, 3.3 and 3.4.

The pine plantations selected for the study were those belonging to the Sri Lanka Forest Department which is solely responsible for establishing forest plantations in the country.

3.1.1 Panwila - *Alstonia macrophylla*

The site is located in the agro-ecological area known as the Mid Country Wet Zone (MCWZ). This zone receives a rainfall of more than 2000 mm per year which is well distributed throughout the year and as a result long dry periods are not usually experienced (see Table 3.1). The altitude ranges from 300-900 m above sea level (a.s.l). The site conditions may vary in different areas with respect to altitude, land terrain and soil types.

The Panwila site is situated at 7° 20' N and 80° 43' E latitude and longitude respectively. The site altitude is 575-600 m. It is about 25 km NE from the nearest main city of Kandy. In the Forest Divisions of the country it belongs to Panwila Beat in Teldeniya Range of Kandy Division. The main rainy seasons are from November to January and May to August while a short dry period is experienced around February.

Major soil groups are Reddish Brown Latosols, Immature Brown Loams and Red-Yellow Podzolic soils. The slope of the land is 25-30° with a westerly aspect. The site conditions are fairly uniform.

Pine overstorey was about 14 years old in late 1993 at the initial stages of the experiment and had a tree density of about 510 trees per ha and a basal area of 13.0 sq m per ha after thinning for underplanting. The growth of pine trees in the site was moderate with a narrow crown allowing much sunlight to penetrate on the ground. The pine trees in the site were thinned along the rows; two adjacent rows out of each four rows. Pine trees had been planted approximately along the contour. Some sparse undergrowth mainly consisting of grass was observed under the trees particularly after thinning of the pine stand.

3.1.2 Deltota - *Khaya senegalensis*

The site is located in the agro-climatic area of Mid Country Intermediate Zone (MCIZ). This zone receives less rainfall than the MCWZ; between 1750-2500 mm. The spread of rainfall over the year is not uniform with a marked dry period, generally in February and from May to August. Some dry winds are also experienced in the dry season. The altitude range is the same as that of MCWZ.

The experimental site is situated at 7° 9' N and 80° 41' E at an altitude of between 975-1000 m a.s.l. The higher altitude makes it little cooler than the previous site, particularly during the windy days of the dry period. The site is located about 35 km SE from Kandy. The site belongs to Galaha Beat in Kandy Range of Kandy Division.

Major soil groups in the area are Reddish Brown Latasols, Immature Brown Loams and Reddish Brown Earths. The site is in a gentle slope of 8-12° with more uniform site conditions and with a westerly aspect.

The growth of pine trees in this site was fairly good and trees were about 15 years of age at the time of the beginning of the experiment. The stocking density was about 486 trees per ha and basal area was about 28.0 sq. m after the thinning for the present experiment. About 50% of the initial stocking was removed to facilitate underplanting. The method of thinning was similar to the Panwila site.

3.1.3 Watawala - *Toona ciliata*

This site is located in the agro-ecological area of Up-Country Wet Zone (UCWZ) which receives quite a high rainfall. The rainfall is well distributed throughout the year. The altitude is higher than 900 m which makes the climate comparatively cooler than other climatic zones.

The selected experimental site is in Watawala which is at 6° 52' N and 80° 31' E. The area receives a rainfall of around 5000 mm, the highest of all the experimental sites. A short dry spell is experienced in February or so. The site elevation is between 1025-1075 m a.s.l. The site is located about 56 km SW of Kandy and belongs to Norton Bridge Beat of Hatton Range of Nuwaraeliya Division.

Major soil groups are Red Yellow Podzols and Mountain Regosols. The site conditions were not very uniform, however care was taken to minimize within block variation as far as possible. The slope of the site is 20-25° with easterly and north easterly aspects.

The pine overstorey here was about 12 years old and had not grown yet to large sizes. The density of trees after thinning was about 700 trees per ha with a basal area of about 18.0 sq.m. The thinning of trees was done in a random and uniform way in contrast to row thinning in other two sites described earlier. There was a good undergrowth here mainly consisting of some perennial shrubs. A higher rainfall with less frequent burning due to very short dry period encourages undergrowth here.

3.1.4 Galaha - *Swietenia macrophylla*

This site is located in the boundary of MCIZ and MCWZ. The experimental site is in Galaha where latitudes and longitudes are 7° 11' N and 80° 39' E. The elevation is 850 a.s.l. while the rainfall is around 1800 mm.

The site is in Galaha Beat of Kandy Range of Kandy Division situated about 25 km SE from Kandy. The slope of the site is very gentle with a slope of 2-10° and as a result having fairly uniform site conditions. The aspect of the slope is north westerly and south easterly. Major soil groups are same as in the Deltota site.

Pine overstorey was about 15 years old at the begining of the experiment. The opening of the canopy for underplanted strips has been higher here compared to previously mentioned sites; three adjacent rows were removed out of each six rows but still maintaining the same intensity of 50% thinning as that of other sites. In this trial wider gaps were formed to increase sunlight for undergrowth and minimize root competition between pine and underplanted seedlings. The stocking density of trees in this trial plot was about 555 trees per ha with a basal area of about 23.0 sq. m per ha.

3.1.5 Kinigama - Mixture of species

Kinigama is located in the agro-ecological zone of Up-Country Intermediate Zone (UCIZ). This zone has a marked dry period ranging from June to August.

Kinigama site is on 6° 48' N and 80° 09' E . The elevation is 1350 m a.s.l. It receives a rainfall of about 1500 mm per year. It is about 10 km NE from Bandarawela and belongs to Kinigama Beat of Haputale Range of Badulla Division.

Major soil groups in the area are Red Yellow Podsols. The experimental site was on a slope of about 20° where aspect is westerly.

The overstorey of pine was about 16 years old when the broad-leaved species were underplanted. Pine was thinned down to different levels of basal area to provide different levels of light for the undergrowth. Felling trees were selected in order to have uniform thinning throughout the plot. The thinning levels were 10, 15 and 20 sq. m per ha of basal area. Unthinned control plot was having a basal area of about 30 sq m per ha. The site had undergone annual burning during most of the dry periods before the trial was started.

3.2 SPECIES SELECTION

The species selected were *Alstonia macrophylla*, *Swietenia macrophylla*, *Khaya senegalensis*, *Toona ciliata* and *Michelia champaca*. A description of the characteristics of these species is given in Chapter 2.

All five species selected are common introduced species in the country except*Khaya senegalensis* which was begun to be planted on a large scale only recently. The

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species are widespread at least in a certain geographical area in the uplands. All of the species have been generally observed to be capable of growing under shade at least in the initial periods of growth while demanding more sunlight in later stages.

Apart from shade tolerance, other important requirement for the selection of species for planting under pine was the ability to grow under infertile or moderately fertile soil conditions which is the general situation under most of the pine plantations.

Within the above limitations of shade and tolerance of moderate to low soil fertility, only a limited number of broad-leaved species were available for planting. Most of the other available broad-leaved species generally prefer fertile soil conditions (those rich in nutrients and organic matter) with better micro-climatic conditions except some exotic species such as *Eucalyptus* and *Acacia* which can grow in infertile lands but under full sunlight. Species trials have been conducted for almost all valuable native tree species and much time and efforts have been spent on this for about two decades in early years of forestry research in Sri Lanka. There were only a few species which has showed promise but they were more suited for small scale planting in special sites and not for large scale plantation forestry in difficult sites (Vivekanandan, 1988).

Pine itself has been planted in the lands which have been degraded after clearing the original forest cover a long time back. These lands possibly have been used for some shifting cultivation or any other form of agriculture after clearing the natural forest and subsequently abandoned after the fertility declined. Once a land falls into this situation it is extremely difficult to restore soil fertility in a short time and to grow local species there. However, pine grew in these lands satisfactorily and it is expected that some improvement in soil in terms of physical or chemical properties or both has been achieved under it during the last 15 years or so. However, again the soil condition may have been altered by the influence of fire; depending on the severity and frequency of it. Usually the soil is better in the Wet zone pine areas where fire is less frequent. Therefore, experience suggests that more opportunities for the success of broadleaved species lies in the wetter areas than in dry areas.

Under the above situation the selected species were considered to be some of the potential candidates for planting under pine and consequently included in the experiments.

3.3 TREATMENTS AND EXPERIMENTAL DESIGNS

The treatments selected for this series of trials were basically same except in two trials which are described below.

3.3.1 Panwila, Deltota and Watawala trials

The species selected were *Alstonia macrophylla, Khaya senegalensis* and *Toona ciliata* respectively. The treatments applied were as follows :

i) Control - without any treatments
ii) Mulching
iii) Mycorrhiza application
iv) Trenching
v) Trenching and mulching
vi) Trenching and mycorrhiza application

Mulching was done mainly with pine needles and sometimes with addition of weed material when the plots had been weeded. Mulch material was placed on the top of the soil around the plants up to a distance of about 50-75 cm from the base of the plant and with a thickness of about 50-75 cm. Mulch was replaced during assessment visits whenever it had been displaced by winds and rain water. The aim of the mulching treatment was to improve soil micro-climate by improving soil moisture status, lowering soil surface temperature and reducing possible soil moisture and temperature fluctuations in the seedling rooting zone.

Trenching was done, more or less in a circle, about 75 cm away from each seedling. The depth of the trench was about 20-25 cm. Pine roots were severed when they were encountered in digging the trenches. The trench was back-filled with soil after opening, to minimize any water deficits to the seedlings. Also, the opening was kept to a minimum whenever possible. Trenching could not be done by just driving a spade without opening up the soil due to its hardness and the gravels found in some areas. The trench was initially somewhat opened with a mammoty and then dug deep using a crow bar. Trenching was done at the beginning of the experiment and re-opened in about five to six months later. Trenching was expected to reduce possible pine root competition with underplanted seedlings thereby reducing the risk of soil moisture and nutrient depletion from the seedling rooting zone.

The mycorrhiza treatment was applied by introducing presumed infected soils to the rooting zone of seedlings. Mycorrhiza infected soil was collected from around larger trees of the same species in some other sites. The collected soil was applied in 3-4 holes made around the seedlings and covered with normal soil to avoid possible displacement by rain water and also to reduce contamination of other plots. Uninfected soils were further protected by digging drains around the plots and thereby diverting any surface water flow during the rains. It was assumed that there may be hardly any endo-mycorrhizal spores in pine soils due to a lack of relevant tree species in pine soils for a considerable period and a lack of mature trees of respective species in nearby areas except in *Alstonia*, and also the annual burning of pine litter on top of these soils which can destroy any spores existing. Mycorrhiza addition might possibly improve better nutrient status and have other beneficial effects in the soil environment.

Trenching was combined with mulching and mycorrhiza treatments, to study possible interactions. Trenching and mulching treatment was so designed to further improve the possible soil micro-climatic conditions in the seedling rooting zone than what is achieved when they are applied alone. The same benefits were expected by combining the trenching and mycorrhiza treatments. Combined treatments were limited to these two due to experimental limitations.

Control treatment was included to compare the other treatment effects with it so that the treatment effects can be clearly identified.

The above three trials were planted in late November or December in 1993. Major monsoonal rains are received in most part of the country during this period, and therefore most of the forest planting is done in this period. *Alstonia* and *Toona* seeds were sown in germination beds and later transplanted to polythene tubes when they grew to a sufficient height of about 2-3 cm. *Khaya* seeds were directly sown on to polythene bags due to their bigger size. The size of the polythene tube was 22 x 10 cm of flat dimensions (about 700 cu.cm). The potting media used were normal soils collected from unused lands which consisted of some topsoils. Seedlings thus raised in nurseries for about 5-6 months were later taken to the field for planting. Field planting was done by digging pits of about 25 x 25 x 25 cm dimensions. Weed control was done once during the experimental period in each of these trials. Weeding included removing all weeds along the planted strip of broadleaves and slashing those

in between these strips in the Panwila and Deltota trials. In the Watawala trial, weeding was done around the plants and slashing in the rest of the area.

3.3.2 Galaha trial

Galaha trial with the species of *Swietenia macrophylla* was designed to have the same treatments but in a slightly different way as follows;

i) Control
ii) Mulching
iii) Mycorrhiza application
iv) Trenching
v) Mycorrhiza, trench and mulching

Here treatment five was designed to include each of the single treatments in one to test the combined effect of all. This was different from other experiments mentioned above, though the aim of the treatments was basically the same.

The seedlings were raised in a nursery by sowing the seeds in a germination bed and subsequently planting them in polythene tubes. Sufficiently grown seedlings were out planted later on in the area of the experimental plots in December 1994. The nursery practices were same as those mentioned in the previous section. The preparation of planting holes and field planting were done in the same way as that of previously mentioned experiments. No weeding was done in this trial since weed growth was sparse.

3.3.3 Kinigama trial

Kinigama trial which consisted of four different species and four different overstorey thinning regimes had treatments as follows:

i) Species :
   a) *Alstonia macrophylla*
   b) *Swietenia macrophylla*
   c) *Toona ciliata*
   d) *Michelia champaca*

ii) Thinning regimes : a) 10 sq m basal area
b) 15 - do -
c) 20 - do -
d) 30 - do- (control - with only pre-commercial thinning done earlier)

Each thinning plot consisted of about 50 m by 50 m area where middle core of 25 m by 25 m was used for establishing species sub-plots leaving a buffer zone of 25 m all around the core plot. In this trial, three of the species tested separately in previous trials were brought together into one site and tested under different light levels, with the addition of *Michelia champaca*. The seedlings were raised in a similar way to the other experiments. *Michelia champaca* seeds were sown direct into polythene bags and later planted in the field. Weeding was not necessary in this trial during the experimental period.

3.3.4 Experimental designs

Experiments were designed to find any effects and interactions of treatments imposed on the underplanted trees. Ideally, if all the possible treatment combinations were included, the experiments would have been set up according to a fully factorial design which would have enabled all the possible treatment interactions to be assessed. However, limitations of uniform space and the desirability of keeping the experiment from getting too big led to the chosen lay outs. Trenching was regarded as the main treatment and therefore it was included in all experiments designed initially. Mulching and mycorrhiza treatments were regarded as secondary treatments and trenching was combined with mulch and mycorrhiza treatments separately to have treatment combinations. No mulch plus mycorrhiza treatment was included since they were expected to be less important. Control treatment was included in order to compare it with these single or combined treatments, thus having 6 treatments altogether.

The two experiments of *Swietenia* at Galaha and thinning levels at Kinigama were started one year later taking advantage of experience with other three experiments established earlier. In the *Swietenia* experiment it was decided to have a three factor combined treatment consisting of all basic treatments included in other experiments in addition to three simple treatments and the control. In the thinning experiment a complete design was adopted including four species with four thinning levels where

each thinning level included all four species in order to find out their interaction effects.

Analysis of variance was used to separate out effects of treatments from the other variations inherent in the site and plants. A covariate was added to these analysis making it analysis of covariance in order to take into account initial variations of plant height, diameter etc. This analysis helps in reducing experimental error in addition to the replication of treatments. Estimation of the proportion of solar radiation received by each plot was also used as an covariate wherever appropriate.

In each experiment described above the treatments were arranged in Randomized Complete Block (RCB) designs. The Panwila, Deltota and Watawala trials consisted of 18 plots in each site while Galaha trial had 15 plots. In each experiment, an experimental plot consisted of about 25 plants at a spacing of about 2 x 2 m. There were three blocks and the treatments were randomized in each block. In the Kinigama trial the treatments were arranged in the same design but in factorial combinations so that each species had all four thinning regimes. In this trial the thinning levels were randomized within the blocks and different species were randomized within each thinning regime. The trial consisted of 48 plots. Plant spacing was 1 x 1 m. A thinning plot consisted of about 50 x 50 m and the core plot of 25 x 25 m were used for experimental purposes excluding the border rows. Each plot had 24 plants.

Having different blocks in these experiments should separate out some of the possible variations introduced by soil fertility differences within the experimental area and also to find out whether the treatment effects are changed by natural soil fertility differences (interactive effects) particularly along the slopes. To achieve these objectives, blocking was done down the slope and treatments across the slope thereby minimizing the variation within the blocks.

The present set up of the experiment, however makes the species confounded with the site. This was unavoidable since different species had been planted at different sites. The sites selected were those established for normal plantation programmes and experiments were set up accordingly. Species suited were those generally suited for planting in understorey environment as described in section 3.2. The sites were selected from those having more or less uniform plant size also with sufficient number of plants.

3.4 GROWTH MEASUREMENTS

Growth measurements of underplanted species were done in terms of height, diameter, biomass production and leaf area. In all trials except Kinigama all the plants were used for non-destructive measurements since plots were arranged alone underplanted strips without leaving gaps between plots which resulted in no edge effects of plots. Thus sample size for these measurements were about 25. In the Kinigama trial, plants only in the core plot were used for measurement. The data collection was usually completed in 1-2 days. It was done at different time periods in the different species of different experiments.

Heights were measured in seedlings on the upper side of the slope at about 3 month intervals throughout the experimental period. A meter ruler or a retractable height measuring rod was used for this measurement. Measurements were taken from the base of the plant to the end of the main stem. The data were recorded to the nearest 1.0 centimetre.

The diameter measurements were taken using calliper. Measurements were done at the base of the plants at a marked a point and if any swellings were present they were avoided by taking measurements just above them. These measurements were taken at the same time as height measurements were done. Diameter was recorded to the nearest millimetre.

Biomass production was measured in plants by destructive methods at two times during the experiment; one at the beginning and other at the end of the experiments. At each measurement about 5-6 plants were destructively sampled from each plot which were selected randomly from medium sized plants. This amounted to about 15 to 18 plants from each treatment of an experiment thus representing all blocks. Fresh weights of plants were measured in the field just after digging out the plants. The leaf, stem and root biomass were recorded separately. Dug out plants were taken to a laboratory about 20-30 km away where they were air dried for a day or so and then oven dried at about 105° C for about 24 hours. Dry weights of leaf, stem and roots were measured separately using an electronic balance. Leaf area was measured with a leaf area meter (LICOR portable area meter: model LI-3000) before oven-drying the leaf materials. Total leaf area was measured in sampled plants. The leaves used for leaf area measurements were left fresh until measurements were done by not

detaching them from the plants during the transport to the laboratory and measurements were taken before air drying the material.

3.5 LIGHT MEASUREMENTS UNDER THE CANOPY

Hemispherical canopy photographs were taken to quantify the relative light levels (percentage of full sunlight) near the canopy of underplanted species. These photographs were useful to measure both direct and indirect (diffuse) light levels. The measurements were taken at selected seedling locations at the initial stages and at the end of the experiments.

A Nikon FM 2 camera with Nikkor 8 mm Fish eye lens was used for taking photographs. The Fish eye lens (hemispherical lens) was used to take photographs at a wide angle of 180°. Kodak Tmax 100 (film speed 100) black and white films were used for all photographs.

Procedure of photographing : The camera was loaded with above film and fixed on a tripod with the lens pointed upward. The camera body was levelled horizontally using a bubble level. The top of the camera was oriented towards the magnetic north with the help of a compass. The hemispherical lens was focused on infinity and its filter was set to the clear position which marked as L1BC. The camera data back (Nikon MF 16) was set to print the day of month and time when photographs were taken. This was useful to identify the photographs later on and also to find the up side of the photograph which was directed towards the magnetic north.

The required height of light measurements were taken by changing the height of tripod. Height was measured from the ground level to the top edge of the glass surface of the lens. The heights selected were 1.5 m for *Alstonia* and *Toona*, and 1.3 m for *Khaya* and mixed species trial at Kinigama in the first height measurements. At the second light measurements the heights were same except in *Alstonia* where height was increased up to 1.7 m to accommodate the considerably increased height of most plants.

The aperture size or f number for photographs was determined using a spotmeter (Minolta Spot Meter). The exposure time of the spot meter was usually set to 120 (increased if the foliage was moving due to wind) and the film speed to the respective ISO number of the film used. A spot reading was taken of the sky through a gap of

the canopy as close to the zenith as possible. This reading was used to set the f number of the camera. The shutter speed of camera was automatically selected to the respective exposure time.

After the camera assembly was properly positioned and the exposure settings were done as described above, the photographs were taken using the camera self-timer. It was made sure that no objects except trees were present above the camera level which otherwise could have spoiled the photographs.

Photographs were taken preferably on evenly overcast days. During sunny days they were taken before about 10.30 am and after about 3.00 pm to avoid direct sunlight on the lens which could reduce the sharpness of photographs.

The films were processed at university lab in Edinburgh and negatives were later scanned using a slide scanner (Microtek 35T) connected to an IBM compatible computer, giving a final image diameter of 1000 pixels. Images were digitized directly from film at a resolution of 1024 dots per sq. inch. After scanning, the image was analyzed using the customized software package designed with the Optimas image analysis package Optimas 5.1 (Optimas Corporation, Washington). Analysis consisted of calculating direct and indirect levels of total solar radiation received at the location of photographing. The level of solar radiation thus calculated was a proportion of the total solar radiation which would have received without any overhead canopy. The direct light level calculations were done by the computer using solar tracks drawn on the image. Thus the light level received during different time of the year could be calculated depending on the position of the solar tracks. The indirect light level was calculated based on concentric circles drawn at constant distances throughout the image by the computer.

Major assumptions made in the methodology are: a standard overcast sky exists in the experimental area (this is usually valid for tropical areas where the sun's movement takes it high in the sky), atmospheric transmissivity is a constant (taken as 0.65), penumbral effects and light reflections from the leaves are negligible.

3.6 OTHER RELATED MEASUREMENTS

3.6.1 Soil physical and chemical properties

Soil samples were collected from different experimental sites for physical and chemical property analysis. Three soil samples were taken from each replicate randomly and composite samples were made for each replicate representing upper, middle and lower slopes of the sites. Average values of the samples were calculated for each site. Disturbed samples were taken using a trowel for chemical analysis. Undisturbed samples were collected using soil cores for water holding capacity and soil bulk density measurements. Soil chemical analysis, water holding capacity and soil texture by particle analysis method were done by the Institute of Fundamental Studies laboratory.

a) Soil Physical properties :

Water holding capacity : A block of undisturbed soil was saturated, left for 48 hours to allow all gravitational water to flow out and then weighed. The soil block was then oven-dried for 24 hours at 105 °C. By this method soil total water holding capacity was determined on weight to weight basis and converted to weight to volume basis using respective bulk density values of each site.

Soil bulk density measurements : Undisturbed soil samples were taken from metal cores driven into the soil of upper 15 cm excluding humus layer. The metal cores were about 6 cm diameter and 5 cm long. The samples were then oven dried for 24 hours and dry weights were obtained. The metal core volume was also measured. The bulk density of each sample was calculated from these values. Replicated samples were taken and average values were calculated to minimize the effects of possible variations. The bulk density measurements were used as a guide to soil compaction and porosity.

Total soil porosity : This was measured from dry bulk density measurements and particle density values which were generally taken as 2.65 g /cm^3. Total porosity on volume basis was thus calculated as [1-(dry bulk density / particle density)] x 100. The porosity values give an indication of the volume of air held by soils which is related to soil compaction and rooting ability.

Soil structure : The structural features of size, shape and stability of soil aggregates were assessed. The size of the aggregates was measured and their shape was determined by comparing with standard shapes. The aggregate stability was assessed by dropping them for a distance of about 1 m and observing their ability to break into pieces. The soil structure was thus assessed in different layers in soil profiles.

Soil texture : Particle size analysis was done to determine the proportion of clay, silt, and sand of different soils which provides a basic indication of soil physical and chemical properties. Standard methods of sieving and sedimentation techniques were used for this. In soil profile studies the texture was determined in different layers by finger texturing method which gives quick and useful results.

b) Soil chemical properties :

Soil samples were taken from the upper 20 cm of the soil using a trowel for the chemical analysis. Methods described by Coninck (1987) were used for most of the analyses.

Soil pH : Measured in a soil:water suspension using soil pH meters (Metrohm 702 SM Titrino) with calomel electrodes. The pH meter was calibrated by Metrohm buffer solution of pH 7.0 and 4.0. Twenty millimeters of distilled water or 1 M KCl solution was added to 20 g of air dried soil samples and the suspension was stirred during 1/2 hour. The pH value was read after 1/2 hour.

Total N : Determined by micro-kjeldahl method in which all forms of N were reduced to ammonium by digestion in an acid and then separating it by steam distillation. The distilled ammonium was then titrated with hydrochloric acid to determine the N level. The amount of N present was expressed as a percentage of soil by weight.

Available P : Determined by the standard Olsen method where P was extracted by sodium bicarbonate. The amounts of P detected are given in ppm.

Exchangeable bases (K, Na, Mg, Ca) : The nutrients were extracted with ammonium acetate and then analyzed by atomic absorption spectrophotometry method.

Organic carbon : The organic matter was oxidized with a solution of potassium dichromate and sulphuric acid and then titrating with 0.02 N HCl. Values were expressed as a percentage of soil by weight.

CEC : The exchangeable cations were leached by an ammonium acetate solution and then titrated with an acid (0.02 N HCl) according to the method described by the Soil chemistry Department of the International Rice Research Institute. The calculated values were given as milli equivalents per 100g of soil.

C: N ratio : This was simply calculated from C and N values determined as described above.

c) Surface soil temperature : Surface soil temperature was measured with a hand held non-contact thermometer (Infrared thermometer, IT-330, Japan). The thermometer was pointed to the soil surface where measurements were to be done and the readings were directly read from the equipment.

3.7 DATA ANALYSIS

Growth data collected at different time intervals were used to assess the patterns of growth of different tree species and sites under different treatments. Results were analyzed using Analysis of Variance (ANOVA) or Analysis of covariance (ANCOVA) wherever appropriate. When results were shown to be significant at $p=0.05$ or $p=0.01$, Tukey's test (Steel and Torrie, 1980) was used for individual mean comparisons with the control. This is one of the most widely accepted and commonly used methods of multiple mean comparison, though there is no agreement as to the "best" procedure to routinely employ (Zar, 1996). In cases where total treatment effects were non-significant, but showing a marked effects of certain treatments (for example in mulch treatments) as indicated in plotted graphs of time vs growth, a factorial analysis was done by partitioning the overall sum of squares of treatments into main treatments of mulching, trenching and mycorrhiza application with or without the respective treatment, as suggested by Parker (1973) and Zar (1996). Several results were tested for normality by plotting graphs before analyses were done. In certain cases, equality of variance was tested by the Fmax test of homogeneity (Heath, 1995). Volume data were $\log_{10}$ transformed and percentage values were arc-sine transformed before analysis of variance. The results of analyses

are given in the text wherever appropriate and ANOVA/ANCOVA Tables are presented in Appendices II - IV.

A limitation in multiple comparison tests arises when a large number of comparisons are made as these may lead to a "Type I error". In other words, the greater the number of comparisons are made the greater is the chance of getting a significant result even with no real differences among treatment means. On the other hand, if the test is made too stringent, a "Type II error" can result, where actual significant differences are overlooked.

Some other commonly used methods for mean comparison are Least Significance Difference (LSD), Duncan's New Multiple Range Test (DNMRT), Orthogonal Contrast method, Dunnett test, Scheffe's Multiple Contrast test etc. The LSD procedure canot be used for comparing all possible means but can be used in a restricted way. For example, it can be used to compare adjacent means where means are arranged in order of magnitude (Little and Hills, 1978). DNMRT method tests all possible pairs of means and this is generally used for the comparison of unstructured treatments such as species or provenance comparisons. When pre-planned comparisons are not appropriate, this method can be used. Orthogonal Contrast method is another useful method for mean comparisons, if it corresponds to the structure of treatments but is not essential if the pre-planned comparison does not fit into such a test (Thattil and Nadesalingam, 1991). Tukey's test is applicable when a limited number of comparisons are made according to the objectives of the experiments, for example, when treatments are compared with a pre-planned control and gives a good balance between risks of "Type I" and "Type II" errors. Dunnett test can also be applied in the same way. Scheffe's test also provides a multiple comparison procedure but is less powerful than Tukey's test (Zar, 1996). Accordingly, Tukey's test was used for mean comparison procedure in the present experiments as appropriate and is applicable to pair wise comparisons of means (Steel and Torrie, 1980). This method consists of calculating a critical value and applying it to differences between pairs to be compared.

Standard error bars denote the standard deviation of sample means and it contain a range of values within which it is 68% confident that the population mean can lie. On the other hand, confidence interval contains a range with 95% confidence limits with two standard deviations and gives more precise information than the standard error while also giving a test of significance. Least significant difference bars also provide

a means of comparing treatment means at a particular level of significance. In the present study, standard error bars are presented in the graphs to indicate the variation of overall treatment means in a particular experiment.

Analysis of covariance was used to reduce the experimental error associated with the covariate as described by Gomez and Gomez (1984). In the present experiments ANCOVA was used to improve the precision of data by eliminating the effects of initial height, diameter or volume measurements. These parameters were used as one covariate. The average light level experienced in each experimental plot was used as a second covariate in the same manner. Since the light covariate was non-significant in all experiments, except in *Swietenia* height growth, it was excluded from the analyses.

Growth analysis

The growth analysis parameters of Relative Growth Rate (RGR), Net Assimilation Rate (NAR), Leaf Area Ratio (LAR), Leaf Weight Ratio (LWR) and Specific Leaf Area (SLA) were calculated using plant dry weight and leaf area measurements.

RGR, which is the rate of increase in plant dry weight per unit of dry weight per unit time, was calculated using the following equation (Hunt, 1978):

$$RGR\ (g\ g^{-1}\ unit\ time^{-1}) = (\ln W_2 - \ln W_1) / (t_2 - t_1)$$

(where W_1 and W_2 are mean plant dry weights during the first harvest (t_1) and the second (t_2) harvest respectively).

NAR is the rate of increase in plant dry weight per unit of leaf area per unit time. It was calculated from the following equation (also Hunt, 1978).

$$NAR\ (g\ cm^{-2}\ unit\ time^{-1}) = [(W_2 - W_1) / (t_2 - t_1)] \times [(\ln A_2 - \ln A_1) / (A_2 - A_1)]$$

(where W_1 and W_2 are the plant dry weights and A_1 and A_2 are mean plant leaf areas at the first harvest (t_1) and second harvest (t_2) respectively).

LAR is the leaf area per unit of total plant dry weight ($cm^2\ g^{-1}$) and was calculated from the leaf area and total dry weight measurement. LWR is the leaf dry weight per unit of total dry weight of plant, ($g\ g^{-1}$). SLA ($cm^{-2}\ g^{-1}$) was derived from leaf area

and leaf dry weight measurements, and is an indicator of leaf area per unit of leaf dry weight.

RGR and LAR can be resolved into separate components as follows:

$$RGR = NAR \times LAR ; \qquad LAR = LWR \times SLA$$

LAR is a morphological index of plant growth while NAR is a physiological index closely related to photosynthetic activity of the leaves (Evans, 1972). NAR determines the balance between photosynthetic and respiratory rates per unit leaf area.

Analysis of fish eye photos is described in section 3.5. Data were analysed using Minitab statistical package and they are presented in Tables which include appropriate mean values of data with either treatment standard error or overall standard error for all treatment means.

Table 3.1 Monthly and annual rainfall (mm) for different sites.

Site*	Year	Month												Total
		Jan	Feb	Mr	Apr	Ma	Jun	Jul	Au	Sep	Oct	Nv	Dc	
1	1991	153	79	77	129	45	256	140	83	84	337	168	241	1792
	1993	16	53	50	80	229	288	165	73	43	422	385	351	2155
2	1994	97	25	05	75	10	40	25	86	293	361	301	175	1493
3	1991	277	46	135	68	178	50	23	44	151	143	206	193	1514
	1993	52	31	43	23	94	87	40	42	138	258	288	221	1317
4	1991	101	110	89	159	354	849	536	561	333	800	308	117	4317

* 1. Kandy - (Galaha, Panwila) 3. Bandarawela -(Kinigama)
2. Deltota 4. Watawala

Source : Site 1,3,4,5 - Met. Dept., Sri Lanka, Site 2 - Forest Dept

Table 3.2 Monthly averages of air temperatures(°C) for different sites.

Site*	Year	Month											
		Jan	Feb	Mr	Apr	Ma	Jun	Jul	Au	Sep	Oct	Nv	Dc
1	1991	24	24	26	26	26	25	25	25	25	24	24	24
	1993	23	24	26	27	26	25	24	24	25	25	25	24
2	1991	19	19	21	21	22	22	22	22	22	21	20	19
	1993	18	19	20	21	22	22	22	22	22	21	20	19
3	1991	15	16	17	17	18	16	16	16	17	16	16	15
	1993	15	15	16	17	17	17	15	16	16	16	16	16

*1. Kandy - (Galaha, panwila and Deltota)
2. Bandarawela - (Kinigama)
3. Nuwaraeliya - (Watawala)

Source : Met. Dept., Sri Lanka

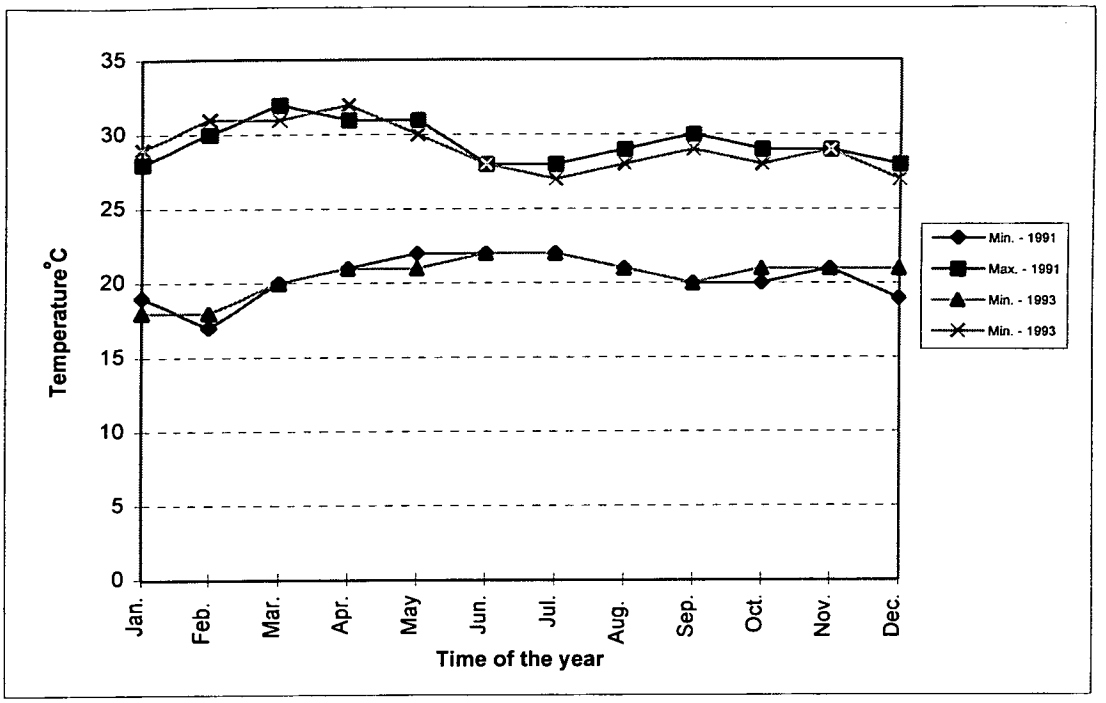


Figure 3.1 : Maximum and minimum air temperatures for the Galaha, Panwila and Deltota sites (data from met. station, Kandy).

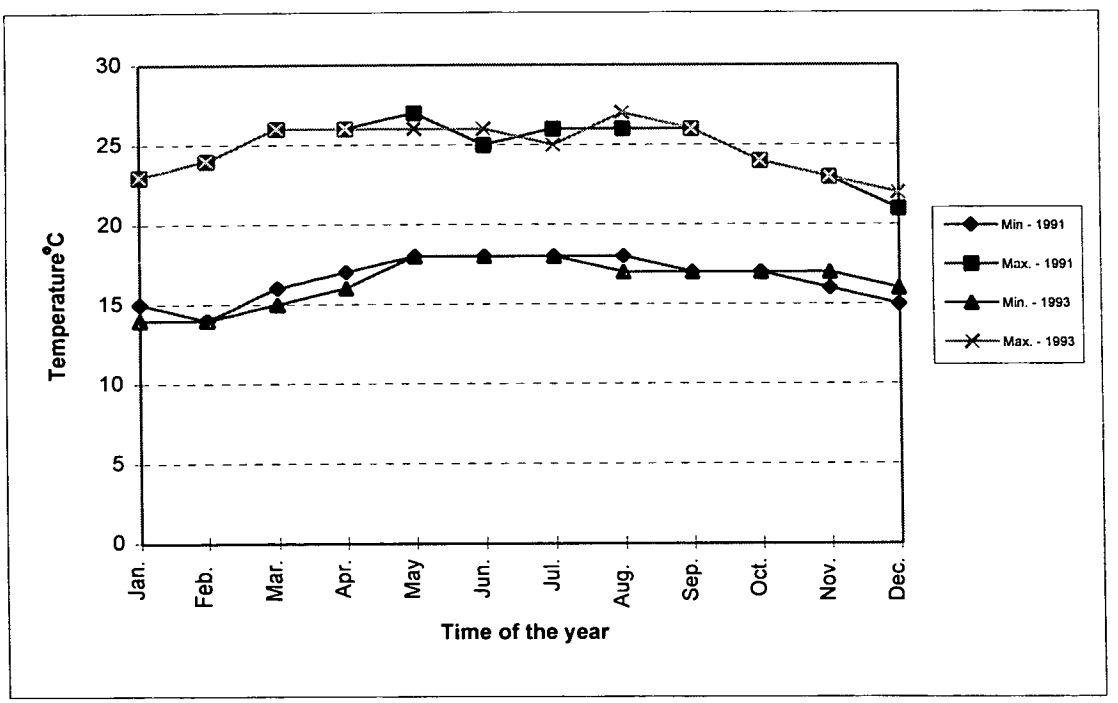


Figure 3.2 : Maximum and minimum air temperatures for the Kinigama site (data from met. station, Bandarawela).

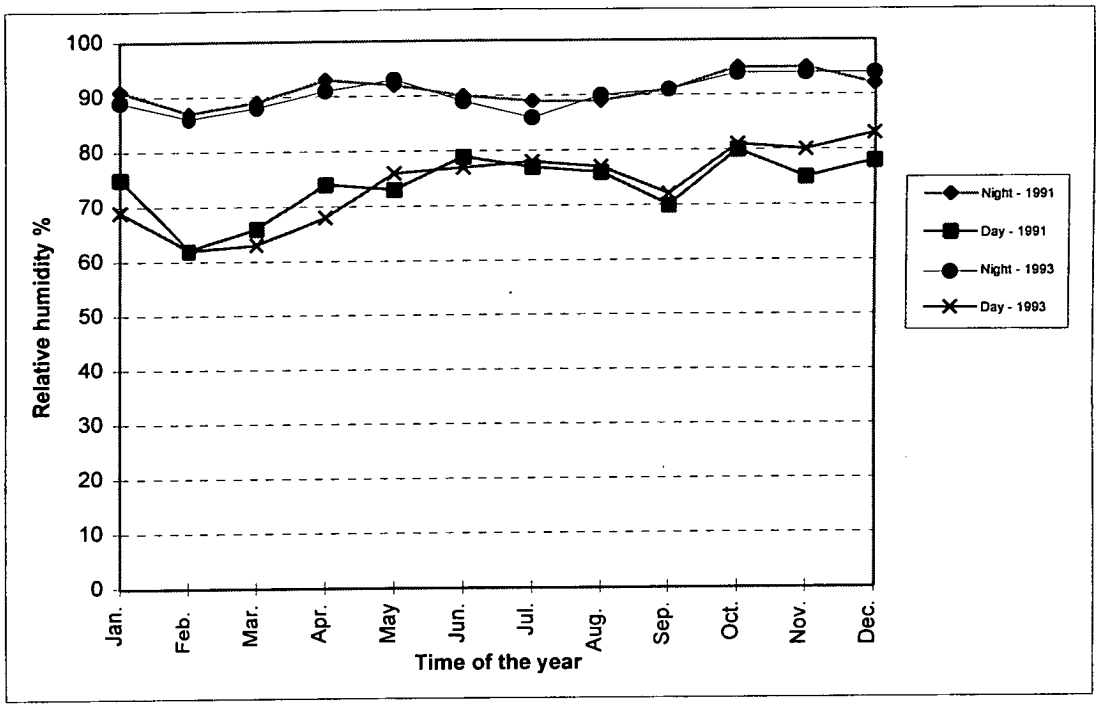


Figure 3.3 : Mean monthly relative humidity for the Galaha, Panwila and Deltota sites (data from met. station, Kandy).

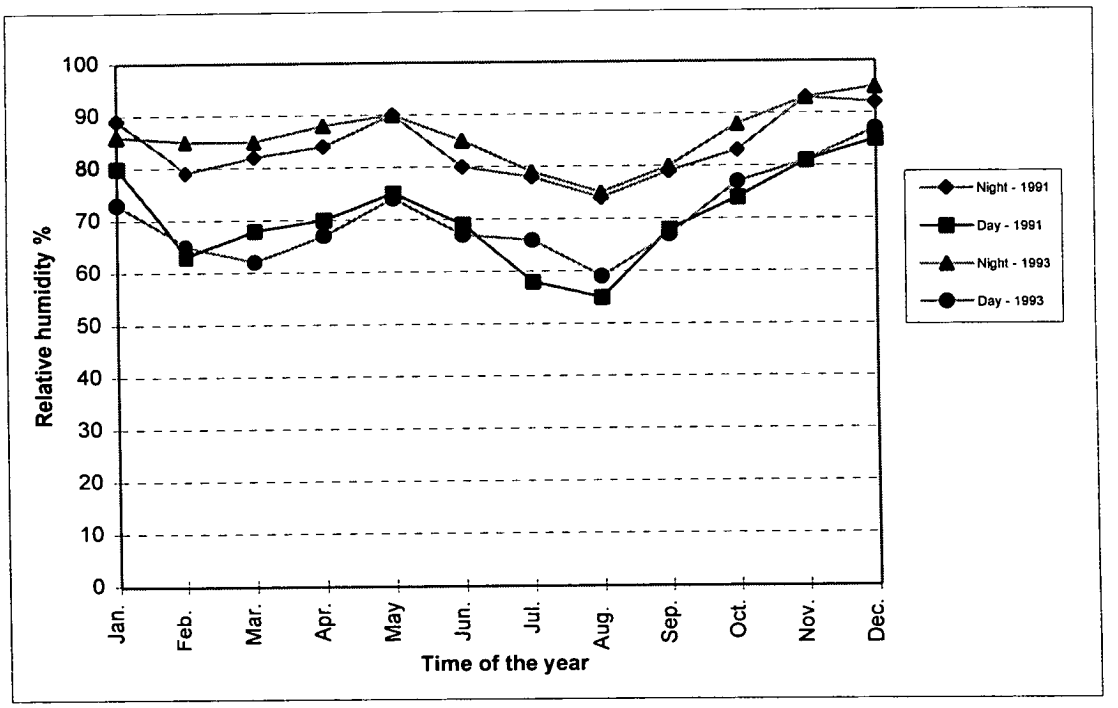


Figure 3.4 : Mean monthly relative humidity for the Kinigama site (data from met. station, Bandarawela).

CHAPTER 4

GROWTH RESPONSES OF DIFFERENT BROADLEAVED SPECIES TO MULCH, TRENCH AND MYCORRHIZA TREATMENTS UNDER PINE OVERHEAD CANOPY

4.1 INTRODUCTION

Tree seedlings planted under an overhead canopy of other trees are generally under more competition from other trees than those planted in open land. Therefore, competition effects in terms of light, water and nutrients play important roles in the growth of such seedlings. In the present experiments thinning of overstorey pine was done to increase light levels for understorey plants and to reduce root competition effects of pine. Different treatments were carried out in the trials to minimize root competition effects from pine trees for water and nutrients and to improve soil micro-climate in the rooting zone of underplanted seedlings. The basic treatments were mulching, trenching and mycorrhiza application as described in Chapter 2. Mulching was mainly supposed to reduce soil moisture depletion effects, reducing temperature fluctuations in the surface soil layers and improving nutrient status in the rooting zone while trenching was designed for minimizing pine root effects for water and nutrients in the seedlings. The mycorrhizal treatment was mainly to improve nutrient uptake efficiency of growing seedlings as described in section 2.6. Growth in terms of height, diameter and notional volume of the species of *Alstonia macrophylla*, *Khaya senegalensis*, *Toona ciliata* and *Swietenia macrophylla* under the above treatments are discussed in this Chapter. Notional volume was calculated to integrate the effects of diameter and height growth increments, which gives more realistic values for the comparison of treatments. The growth measurements were commenced at about 6 months after field planting up to the age of about 2.0 years. They were taken at about 2.5 to 3 month intervals to closely monitor the growth responses in different treatments of the experiment. Most of the discussions depend on the final measurement.

The results were analyzed by analysis of variance (ANOVA) or analysis of covariance (ANCOVA) wherever appropriate. Mean initial height, diameter and volume were taken as covariates in ANCOVA in respective analyses. Mean light level was taken as a second covariate and it did not affect the analyses in *Alstonia*,

Khaya and *Toona*. However, it was significant in height growth of *Swietenia*. Comparison of means separation was done with Tukey's test when the overall treatment effects were significant. In case where the overall treatment effects were non-significant, but with a pronounced effect of some treatments (e.g. mulch in most cases) as shown by growth curves, a factorial analysis was done to separate out the treatment effects using ANOVA or ANCOVA (see section 3.7). Notional volume was calculated by squaring the diameter values and multiplying them with corresponding height values. These values were transformed to normal logarithmic values before analysis of variance in order to minimize variation which is normally introduced in squaring the values. Results of ANOVA Tables are given in Appendix II.

4.2 *ALSTONIA MACROPHYLLA* (PANWILA)

4.2.1 General performance and observations

Alstonia grew very well in this experiment showing fast growth rates (see Plate 4.1). Well distributed rainfall in the experimental area would have been conducive for its growth. The relatively light shade cast by the pines also seemed to be helpful for fast growth which continued throughout the experiment. During the study period it was generally free from pest and diseases. A few trees fell over due to instability in the slopy land associated with initial fast growth and shallow rooting and was obviously not due to related treatments. Trees started branching during the experimental period which did not affect the growth of leading shoot; first and second branching occurred at about 10 and 17 months respectively after field planting.

4.2.2 Survival, Height, Diameter and Notional Volume growth

Survival of this species was excellent in this trial indicating that the existing soil and light conditions were not limiting for it. All treatments showed a survival of 100 or nearly 100% (Table 4.1). Because of high survival percentage values recorded in all treatments, it was not necessary to do statistical analysis.

Height growth of *Alstonia* was very fast, reaching a height of about 2m at 2 years after field planting. Different growth rates were observed for different treatments. The best growth was achieved by mulch and mulch+trench treatments (Figure 4.1 and Table 4.1). The SE value of treatment differences was 11.1. Although, overall treatment differences were not significant at p=0.05 with ANCOVA, when mulch

treatments were separated and compared with unmulched treatments mulch effect was found to be significant at p=0.05 (Tables 4.2 and 4.3). Effects of mulching treatment on height growth became more pronounced with time showing about a 20% increase over the control at the final measurement. Both the mulch treatments were similar indicating that trench combined with mulch did not help in achieving additional height growth. The trench alone treatment was also similar to the control, confirming this. Comparatively less rapid height growth rates were recorded in all other treatments including control, mycorrhiza and trench+mycorrhiza treatments. All these treatment effects were more or less the same, showing no advantage over the control. Treatment effects, particularly mulch started showing differences compared to the control about 6 months after the application of the treatment. The covariate of initial height was highly significant at p=0.01 level (Table 4.3). The interaction effects of trenching vs mulching and trenching vs mycorrhiza were not significant (Table 4.3). The block effect in the experiment was non significant for height growth of this species.

Diameter growth showed broadly similar patterns to height growth (Figure 4.1), the best growth being recorded in the mulch and mulch+trench treatments (Table 4.1). Mulch effect in comparison to unmulched treatments were significant at p=0.05 level (Tables 4.2 and 4.3). Diameter increment in the mulch treatment was about 28% higher than the control which will be even higher for cross sectional area increment. Treatment effects were more pronounced with time and at the last measurement it was apparent that mulch treatment might be beginning to surpass the trench+mulch treatment. All the other treatments were found to be similar to the control recording lower values than mulch treatments. They were not statistically significant from each other. The effects of initial diameter (covariate) for the treatment effects and treatment interaction effects were not significant (Table 4.2 and 4.3). Block effect for diameter growth was also not significant.

Notional volume measurement showed that mulch effect was significantly different from others at p=0.05 (Tables 4.1, 4.2 and 4.3) with an increment of about 63% higher than the control. Effects of mulching treatments were very pronounced compared to others as shown in the Figure 4.2. Other treatment effects of trenching, mycorrhiza and their combination were not significantly different from the control indicating that they did not have effect on growth of this species in the present study. Instead, trench+mycorrhiza recorded somewhat lower values than the control or mycorrhiza alone, though these differences were not significant. This might suggest

that trenching had a slightly unfavourable effect during these early stages of *Alstonia* growth. Block effect was not significant. There was no significant interaction between treatments (Table 4.3).

Height and diameter relationship was almost linear showing continuous growth of both parameters with time (Figure 4.3). However, diameter growth was slowed down during the middle of the study period while height was continuously increasing. This generally overlapped with dry periods. In the mulch+trench treatment more diameter growth in comparison to height growth was observed during the later stages of the study. The slope of the regression line for these two parameters was almost the same in all treatments indicating height and diameter relationship was not much affected by treatments.

4.2.3 Discussion

These experimental results and observations show that *Alstonia macrophylla* performs well under the existing conditions of the pine stands in this experimental area. In this study with sufficient light available with adequate thinning of pine trees, it could show good growth under pine canopies even without any treatments. Mulching improved the growth of seedlings significantly, but not the treatments of trenching, mycorrhiza or their combinations. Mulch apparently improved the soil moisture level in the rooting zone during dry periods by conserving soil moisture received in the wet periods. This was clearly shown during field observations; under the mulch soil was wet for a longer period after rains than unmulched areas due to reduced soil moisture evaporation from the soil surface. Another possible effect of mulch would be the increased insect activities under it as noted in field observations which would have contributed to faster litter breakdown. Also, insects would have created more aeration in the rooting zone facilitating root growth and improving water infiltration. Also, mulch itself with more moisture retained for a longer period and warm conditions under it apparently helped in speeding up of litter breakdown. Leaching of nutrients from the mulch layer and lowered soil temperature underneath it may also have made some contributions for improved growth rates of *Alstonia.* A dense mat of feeder roots was observed under the mulch which was a marked response of plants to mulching within a short period, strongly indicating that the soil conditions were changed under it possibly making more soil moisture and nutrients available for plants than the control. Mulch effect was more marked in the two blocks of the experiment which were located on the upper slope rather than the third one on

Table 4.1 : The mean effects of different treatments on growth of *Alstonia macrophylla* at the age of about 2 years. (n = 60-75 trees per treatment)

Treatments	Survival %	Mean Height increment (cm)	Mean Diameter increment (cm)	Mean Notional volume increment (cu.cm)
Control	100.0	145	2.26	2251 (3.353)#
Mulch	98.5	175	2.89	3680 (3.536)
Mycorrhiza	100.0	151	2.25	2393 (3.322)
Trench	100.0	143	2.22	2181 (3.335)
Trench + Mulch	100.0	174	2.80	3541 (3.541)
Trench + Myco.	100.0	144	2.12	1965 (3.380)
SE	-	± 11.1	± 0.24	± 556 (± 0.075)
CV	-	9.1 %	11.9 %	34.5 % (3.8 %)

= Log_{10} transformed values

SE = Standard error for the overall treatments, CV = Coefficient of variation

Table 4.2 : Mean values of final measurements (at the age of 2 years) of main treatment effects of *A. macrophylla* in factorial analysis (Values are adjusted means by covariance analysis* and n = 60-75 trees).

Treatment	Mean Height growth (cm)			Mean Diameter growth (cm)			Mean Notional Volume growth (cu.cm)		
	1	2	SE	1	2	SE	1	2	SE
Mulch	231	198	± 10.7	3.90	3.30	± 0.26	3763	2309	± 603
Mycorrhiza	201	202	± 9.9	3.25	3.25	± 0.12	2316	2295	± 270
Trench	209	213	± 13.9	3.49	3.45	± 0.28	2846	2728	± 659

1 : with treatment; 2 : without treatment

SE : Standard error for each treatment

* covariate = initial mean values of each growth parameter.

Table 4.3 : Significance level of different treatments of *A. macrophylla* from analysis of covariance (ANCOVA).

Source	Height	Cov.	Diameter	Cov.	Notional volume	Cov.
Mulching	*	*	*	ns	*	ns
Trenching	ns	ns	ns	ns	ns	ns
Mycorrhiza	ns	*	ns	**	ns	**
Trench x mulch	ns	ns	ns	ns	ns	ns
Trench x myco.	ns	ns	ns	ns	ns	ns

Cov. = covariate I : Initial height

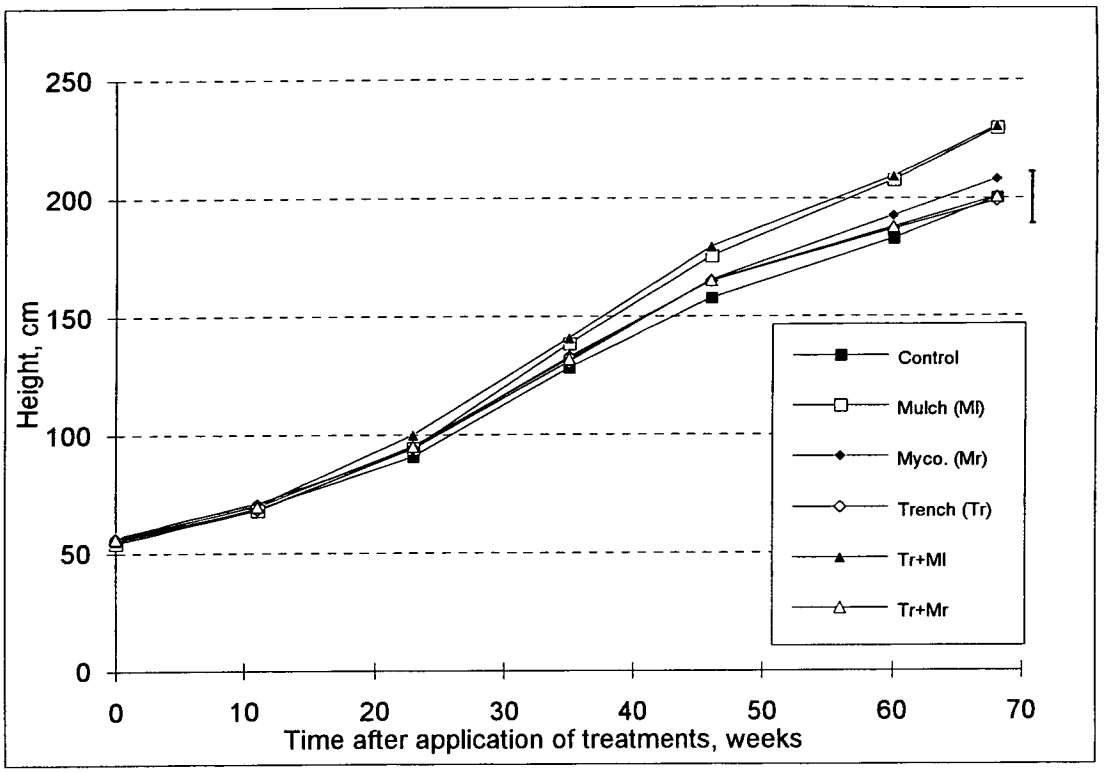
Significance level : ns - non significant

* - significant at 5 % level

** - significant at 1 % level

the lowest part of the slope which shows that the soil moisture was more deficient and plants benefited more from the mulch on the upper slope. The less effect of mulch in the lower slope apparently diluted the overall effect of the mulch treatment.

Trenching did not show any improvements in growth in terms of height and diameter of *Alstonia* probably due to sufficient soil moisture availability in this area for a longer period in the year and lack of strong root competition for water and nutrients from pine roots at least for early stages of its growth. Severed roots can regrow fast producing new adventitious roots which would have also reduced the effect of trenching (J. Jenik, personal communications). Another possibility would be that much of the pine roots severed during trenching would have been from felled trees in the thinning operations which was done just before planting tree seedlings and as a result this would have had a little impact on *Alstonia* growth. Mulch and trench interaction was non significant for all the parameters studied (Table 4.3.) indicating no additional benefits in their combination. As mentioned in the previous section a lack of response was observed in mycorrhiza treatment. In the area where this particular trial was conducted mature *Alstonia* trees were growing in adjacent areas. This would have contributed for building up of mycorrhiza inoculum potential in the



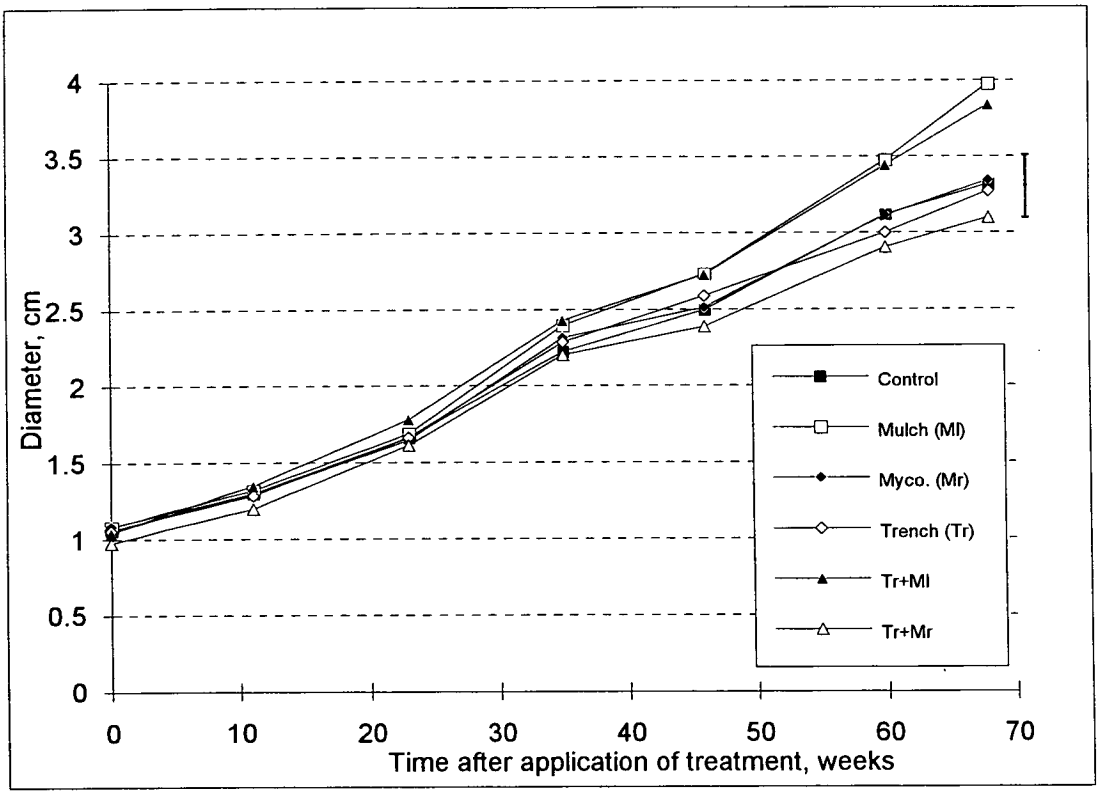


Figure 4.1 : Mean height and diameter growth of Alstonia macrophylla under different treatments during the experimental period. (above - height growth, below - diameter growth)
The bar represents ± one overall standard error value for any treatment at the final measurement (n = 60-75 trees per treatment)

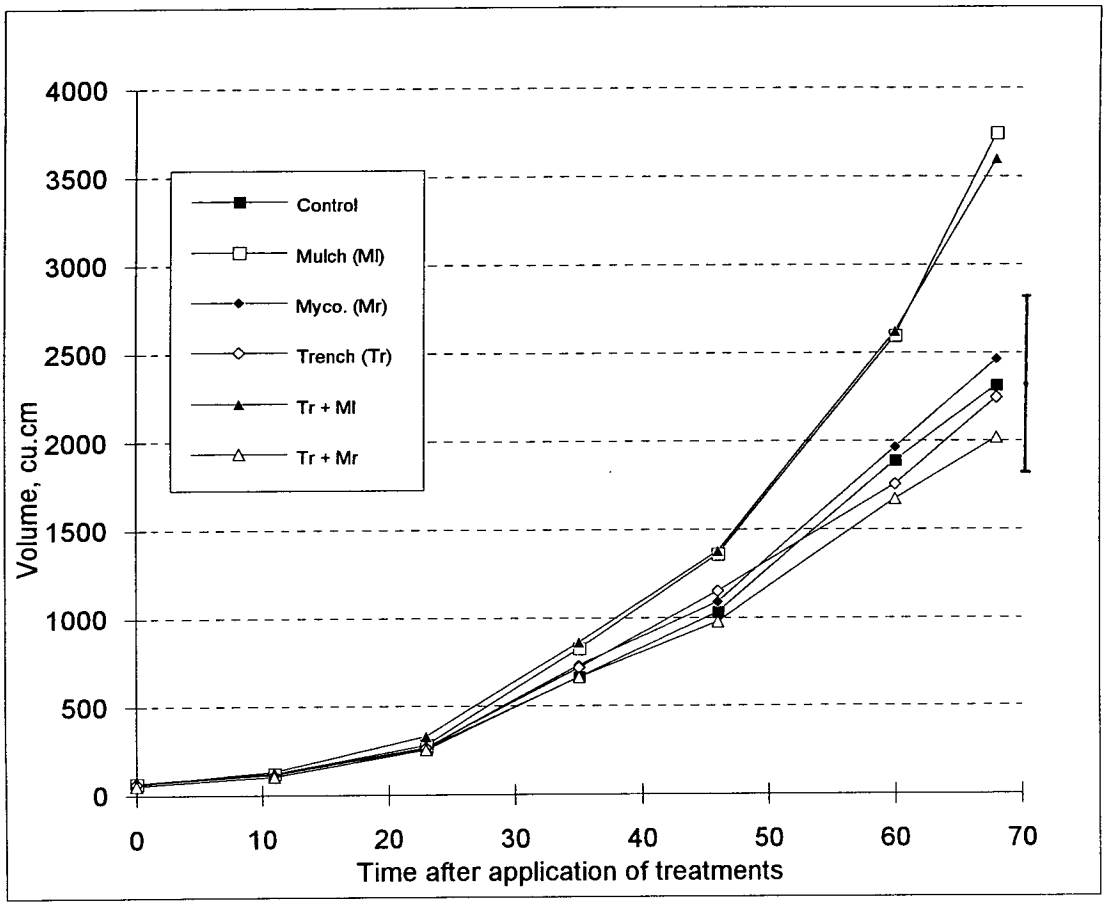


Figure 4.2 : Mean notional volume growth of Alstonia macrophylla under different treatments during the experimental period.
The bar represents ± one overall standard error value for any treatment at the final measurement (n = 60-75 trees per treatment).

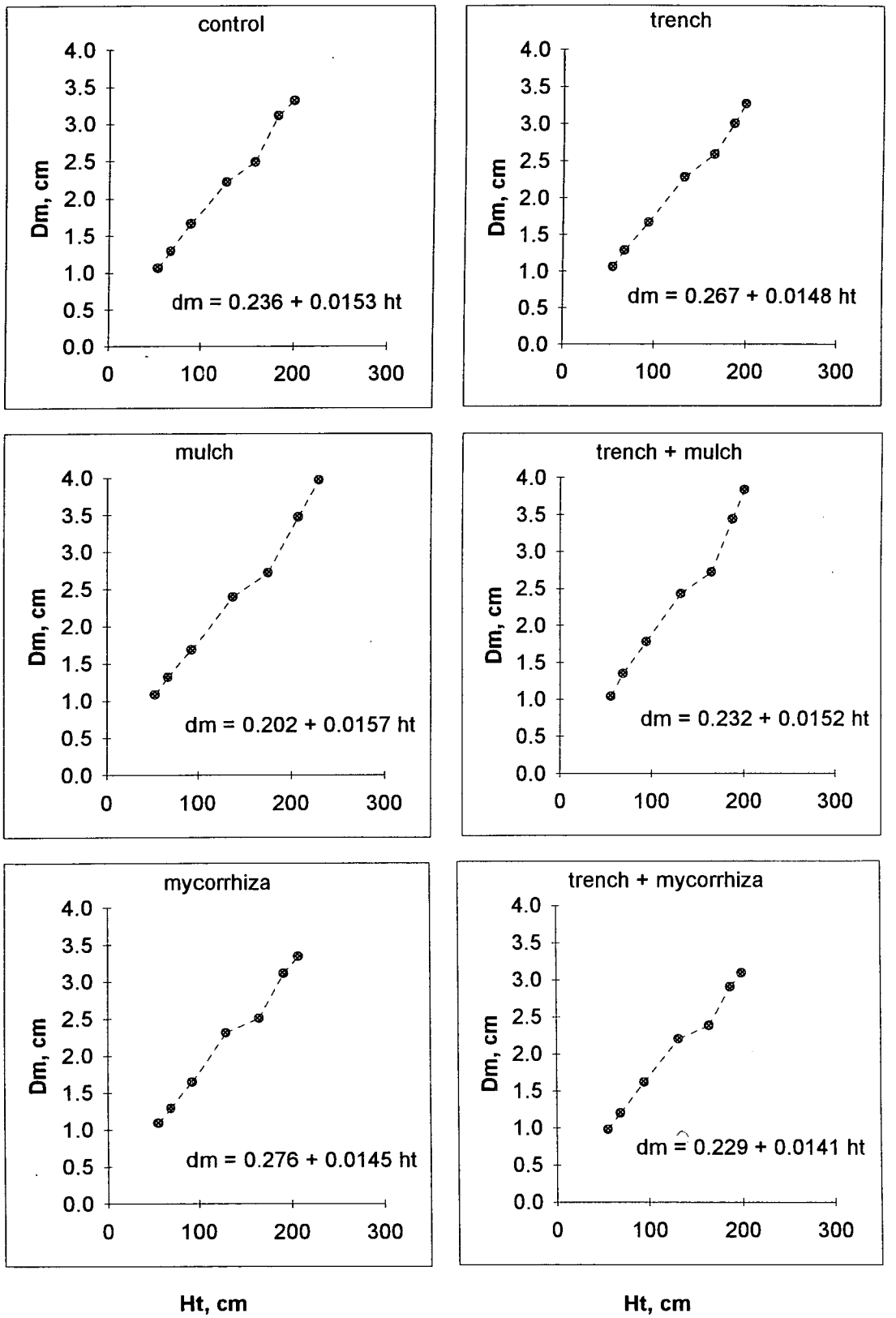


Figure 4.3 : Height (Ht) and Diameter (Dm) relationships of Alstonia macrophylla showing changing relationships with different treatments.
(the equations assuming a linear relationship, n= 60-75 trees per treatment)

area and as a result the control plots may have already had infection. This may have led to lack of added benefits to mycorrhizal inoculation. As mentioned elsewhere, general performance of trees even in control plots was satisfactory probably due to this reason. In some areas *Alstonia* was observed to be growing naturally under pine in limited scale and this shows its potential for planting under pine stands. Limited scale growth may be due to the effects of annual fire occurrences in dry periods in pine plantations.

Almost continuous increase of diameter/cambial growth and height growth were observed in the study indicating active growth of plants. Lowered diameter growth in the middle of the period which roughly overlapped with the dry period would have been due to lowered rates of dry matter production during this period or allocation of dry matter for some other functions of the plant.

4.3 *KHAYA SENEGALENSIS* (DELTOTA)

4.3.1 General performance

Khaya plants grew well in this trial although the growth rate was much slower than *Alstonia.* The initial growth of *Khaya* is generally slow but it can grow faster during later stages, as observed in other field plantations. It can tolerate shade in the early stages as mentioned in chapter 2. Its growth was induced during rainy periods but showed virtually no growth at other times, particularly in dry periods and as a consequence, growth was in sequential stages of development. During the height increment it produced young shoots with a flush of leaves induced by soil moisture build up during rains. The plants were healthy and showed no signs of pest or disease problems.

4.3.2 Survival, height, diameter and notional volume growth

Survival was 93% or above in all treatments and therefore a statistical analysis was not necessary as in the previous experiment (Table 4.4). High survival indicated the species' ability to establish under these conditions.

The height growth in different treatments varied considerably indicating significant treatment differences (Table 4.4 and Figure 4.4). The greatest height growth was recorded in mulch+trench treatment (84%) and the second greatest was in mulch

treatment (47%). This showed that mulch alone treatment effect was doubled with adding trenching treatment to it. However, only mulch+trench treatment was significantly different from the control at P=0.01 and mulch alone treatment was marginally significant at p=0.05 by the Tukey's test (Table 4.5). Mulch+trench treatment was not significantly different from mulch treatment at p=0.05 though they differed appreciably. This result was different from the performance of *Alstonia,* where trenching could not improve growth. However, in neither study did trenching alone improve height growth. Height growth was more marked between fourth and fifth measurements in the mulch treatments which occurred during a dry period where mulch would have helped conserving soil moisture and inducing growth in the presence of more sunlight than in cloudy wet periods. Among the other treatments there were no significant differences compared to the control. Nevertheless, mycorrhiza had slightly lower values and trench+mycorrhiza slightly higher values than the control. This suggests that effects of mycorrhiza might be improved when combined with trenching and although these two treatment effects were not significantly different at p=0.05 level. Most of the treatment effects became more prominent from about 8 months after application of treatments except in trench+mulch treatment where the effects became prominent from about 2.5 months after application of treatments (Figure 4.4). Interactions between treatments were not significant (Table 4.4). The block effect was not significant for height growth.

Overall treatment effect for diameter was significant at p=0.05 level and trench+mulch treatment was significantly higher than the control at the same significant level by Tukey's test as shown in the Table 4.5. Diameter growth had same trend as that of height growth except between fourth and fifth treatments where it slowed down to some extent. Mulch+trenching effect was clearly separated out from other treatments from nine months after treatment application. The diameter increment of this combined treatment effect was 40% while mulch alone was 20%, doubling the effect of mulch as similar to height increment values. However, in contrast to height growth, mulch treatment was unable to show significant differences from the control though it had consistently higher values than the control. It was clear also from these results that mulch improves diameter growth and in combination with trench can further improve these effects. The block effect was significant at p=0.05. Treatment interactions were not significant (Table 4.4).

Notional volume calculation integrated the effects of both height and diameter growth and this showed marked differences between treatments (Table 4.4 and

Figure 4.5). Calculated volume data were $\log_{10}$ transformed and the treatment differences were highly significant at p=0.001 level. Mean comparisons by Tukey's test showed that mulch treatment was significantly different at p=0.05 level while mulch+trench treatment was significant at p=0.01 level. Mulch in combination with trench greatly increased the volume growth by 114% more than the control while mulch alone was about 50% higher. These effects showed strong benefits of the mulching and trenching treatments for *Khaya* in Deltota site under comparatively dry conditions. Mulch+trench had consistently higher values than the mulch alone values. Mycorrhiza application had the lowest volume growth, even lower than the control and mycorrhiza+trench treatment was slightly above the control, however, these values were not significant. Block effects and interactions between treatments were also not significant.

Height and diameter growth relationship had a similar pattern in all treatments but with slightly different slopes according to regression analysis (Figure 4.6). Almost linear relationship was observed between the average values of these two except for some period where diameter increment was slowed down while height was increasing showing continuous growth of height values during most of the study period. However, it should be noted that these values were mean values of large number of plants, and individual plant growth was having several alternate growth and resting periods since this species grew in flushes of rapid height growth followed by dormancy of the terminal bud. Diameter increment was lower in comparison to height growth between fourth and fifth measurements as that of *Alstonia* which was experienced following a short dry period indicating some stress to plants during this period for their diameter growth. In later stages of the study mulch+trench treatment had more height growth in comparison to diameter growth. This relationship of height and growth showed that diameter growth was slowed down for some period which was common for most of the plants while average height growth of all plants was continuously increasing.

4.3.3 Discussion

The above results show that *Khaya senegalensis* can establish well under pine showing better survival rates and average growth of plants was continuously increasing though it was comparatively slow. Probably it would give better growth rates in lower elevations than the present study. As for *Alstonia* (section 4.2.3), mulching had a marked effect on growth of underplanted seedlings, particularly when

Table 4.4 : The mean effects of different treatments on growth of *Khaya senegalensis* at the age of about 2 years. (n = 60-75 trees per treatment)

Treatments	Survival %	Height increment (cm)	Diameter increment (cm)	Notional volume increment (cu.cm)
Control	93.9	19	1.0	143.5 (2.207)#
Mulch	95.7	28	1.2	215.0 (2.403)
Mycorrhiza	100.0	17	1.0	115.5 (2.166)
Trench	95.2	20	1.1	153.2 (2.261)
Trench + Myco.	92.8	22	1.1	164.2 (2.228)
Trench + Mulch	100.0	35	1.4	306.8 (2.494)
Significance of treatments	-	***	*	***
Significance of interactions				
a) Trench x mulch	-	ns	ns	ns
b) Trench x myco.	-	ns	ns	ns
SE	-	± 2.0	± 0.07	± 18.1 (± 0.033)
CV	-	8.2 %	5.9 %	14.9 % (2.3 %)

= Log_{10} transformed values

SE = Standard error for the whole treatments, CV = Coefficient of variation

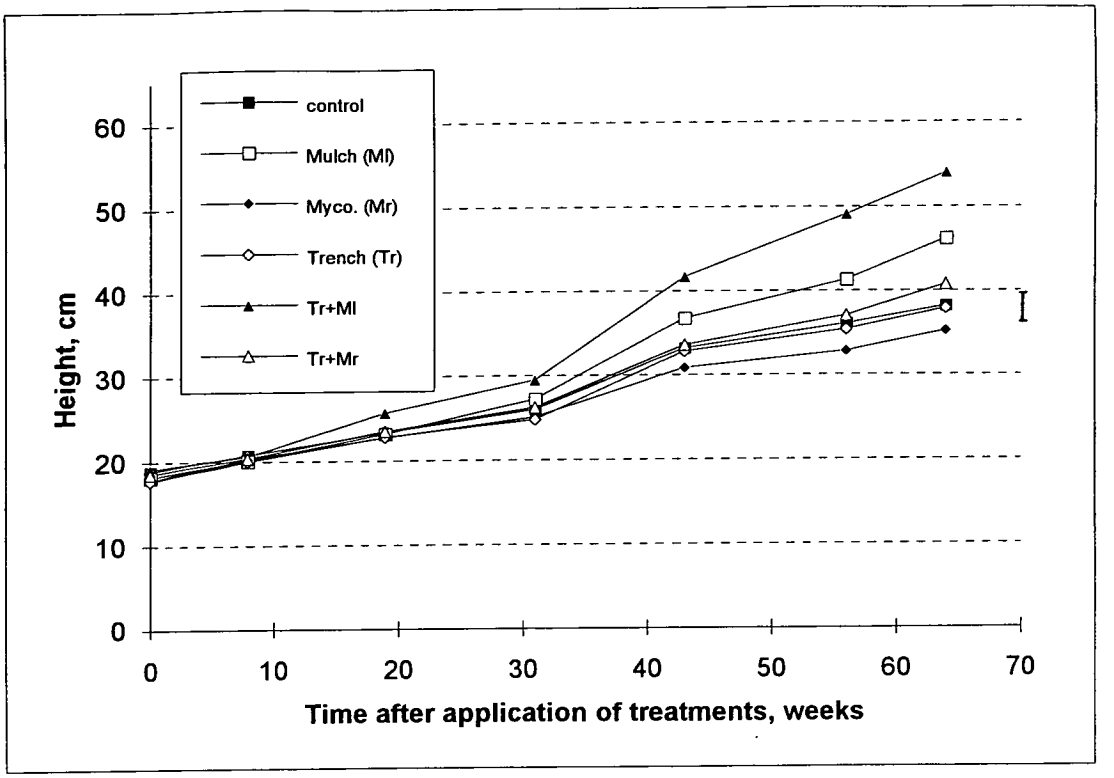
it was combined with trenching. Nevertheless, interaction between mulching and trenching was not statistically significant. Fine root development near the soil surface under the mulch was observed in this study as well, showing some morphological changes in roots in response to mulched environment. In this study trenching played a significant role for plant growth, in contrast to *Alstonia* site. The results were promising indicating trenching could double the effect of mulching. The present site was comparatively drier than the *Alstonia* site and indicated that trenching would

Table 4.5 : The results of mean comparisons of *K. senegalensis* from Tukey's test (Values are adjusted means by covariance analysis).

Treatments	Mean height (cm)	Mean diameter (cm)	Mean volume (cu.cm) (Log values)
Mycorrhiza	35.74 (a)#	1.946 (a)	2.166 (a)
Control	37.72 (a)	1.995 (a)	2.207 (a)
Trench	38.48 (a)	2.088 (a)	2.261 (a)
Trench+Myco.	40.84 (a)	2.076 (a)	2.228 (a)
Mulch	46.26 (b)	2.165 (a)	2.403 (b)
Trench+Mulch	53.30 (c)	2.352 (b)	2.494 (c)

- Values followed by the same letter are not statistically significant (Values with 'b' and 'c' letters are significantly different from each other as well as from 'a')

have been useful to create better conditions in the rooting zone probably by reducing water uptake in the rooting zone by pine roots. Root competition for nutrients would also have been reduced simultaneously. It suggests that probably mulch effect could be fully realized only when pine root competition was minimized or eliminated. Mycorrhizal treatment slightly lowered the growth and this may indicate that they were not efficient in promoting growth in the presence of pine roots. This can be further supported by increased growth when trenching was added to mycorrhiza treatment removing pine root effects in the seedling rooting zone, which produced better results than trenching alone or mycorrhiza alone treatments. It can also be noted that trenching alone was similar to the control indicating pine roots were not very competitive with planted seedlings in the absence of better soil moisture or probably nutrients. However, mycorrhizal effects cannot be confirmed in the absence of statistical significance of results. Some of the possibilities of mycorrhizal interactions are discussed in the light of other researchers work in section 4.6.



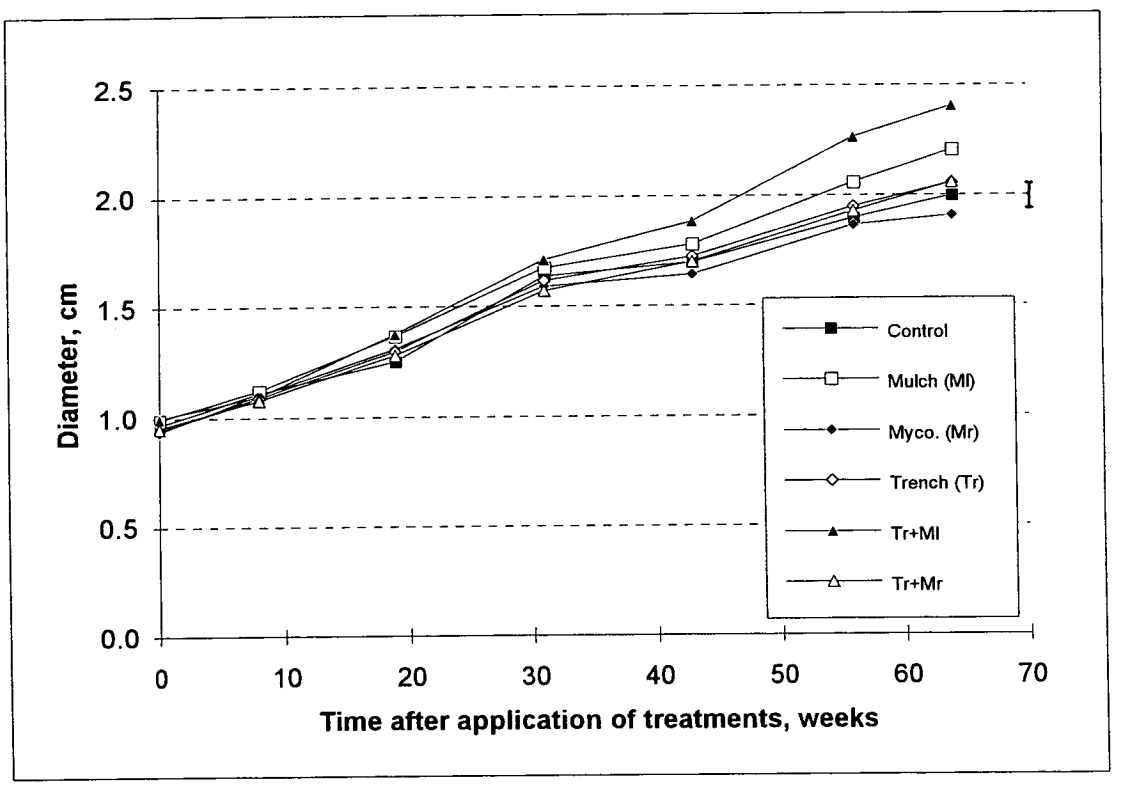


Figure 4.4 : Mean height and diameter growth of Khaya senegalensis under different treatment s during the experimental period. (above - Height growth, below - Diameter growth)
The bar represents ± one overall standard error value for any treatment at the final measurement (n = 60-75 trees per treatment).

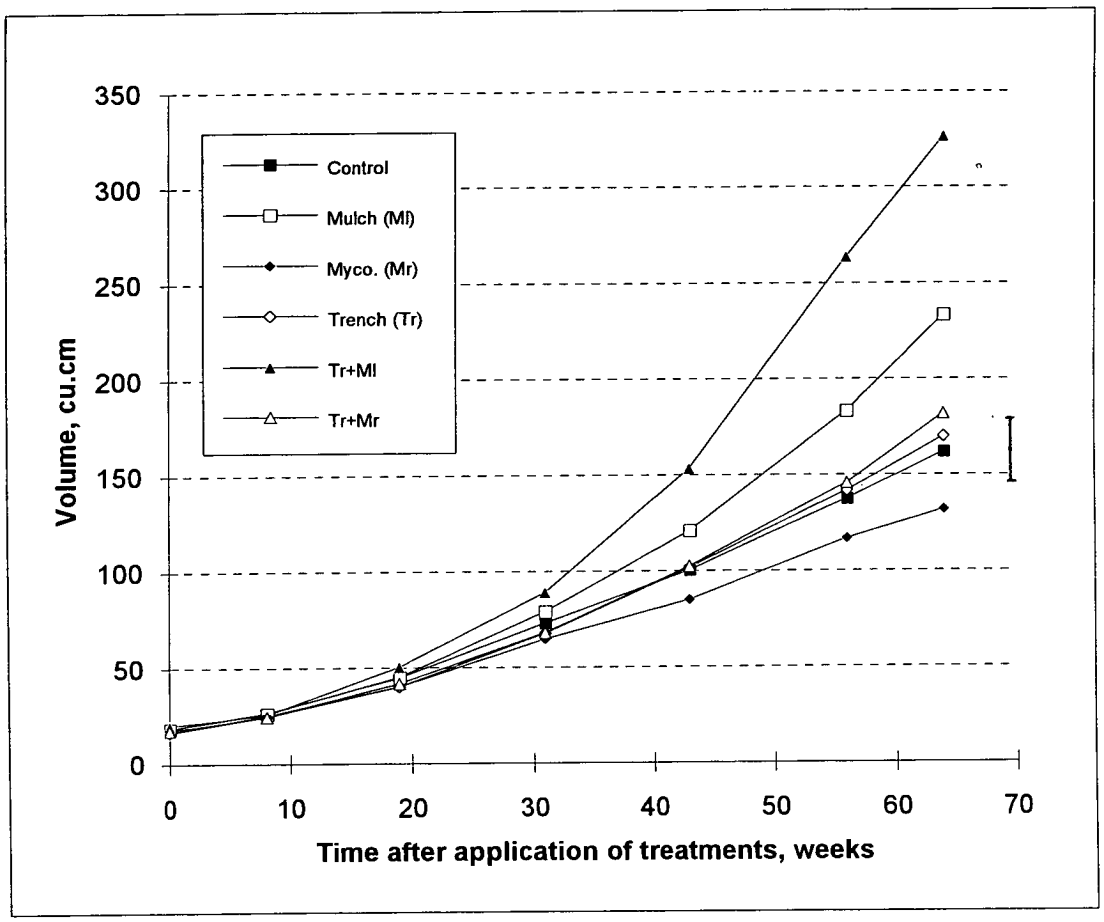


Figure 4.5 : Mean notional volume growth of Khaya senegalensis under different treatments during the experimental period.
The bar represents ± one overall standard error value for any treatment at the final measurement (n = 60-75 trees per treatment).

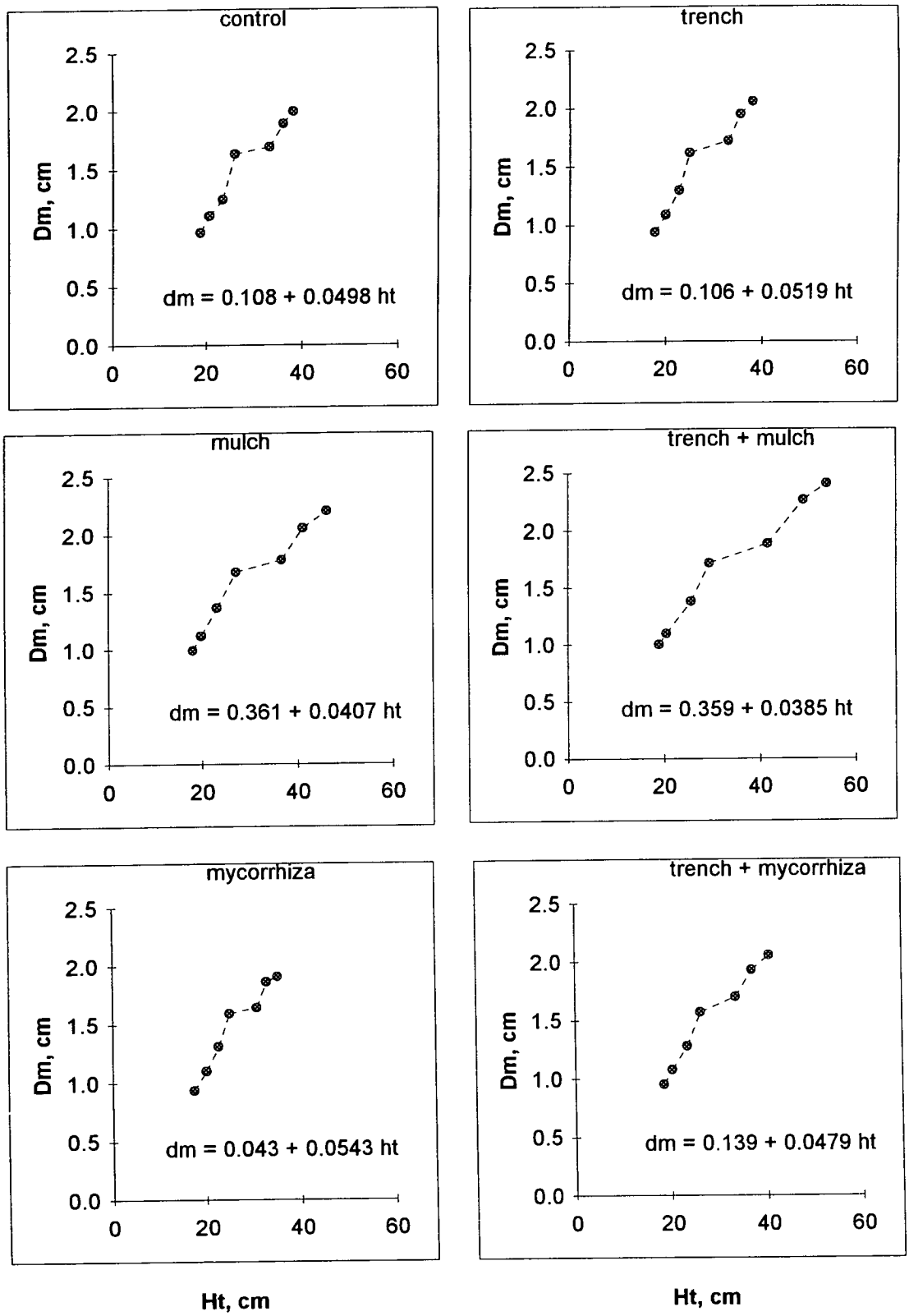


Figure 4.6 : Mean height (Ht) and diameter (Dm) relationships of Khaya senegalensis showing changing relationships under different treatments (the equations assuming a linear relationship, n = 60-75 trees per treatment).

4.4 *TOONA CILIATA*

4.4.1 General performance and observations

This species performed poorly compared to other species. The growth may have been affected due to too much rain received in the site and also possibly due to poor site qualities. However, *Toona* has been observed to be growing better in different sites in the same area. As mentioned elsewhere it usually prefers better soil fertility, and poor growth is attained in degraded sites. Some plants showed die-back; some of these died completely while others recovered later on. There was a lot of ground vegetation in this site, and it therefore, had to be weeded several times to reduce root competition.

4.4.2 Survival percentage, Height, Diameter and Notional volume growth

Survival percentage was comparatively low in this trial. It varied from 57-71% across the treatments (Table 4.6). Data were transformed using angular transformation but results however, were not statistically significant. The block effect was also non significant. This shows that survival was not affected by the treatments in this study.

Toona's response of height growth to different treatments were different from others. The treatment differences were not significant at p=0.05 by the statistical analysis (Table 4.6) and as a result the null hypothesis was not rejected. However, some trends in growth were observed in the graphs of Figure 4.7. This indicated that in the mulch treatment, height growth was not improved compared to the control in contrast to all other experiments. This may be due to impaired root growth of plants with too much of soil moisture. Mulching, in fact, reduced height growth by 25% though it was not significant. Trench alone treatment improved height growth by about 17%. Mycorrhiza treatment did not have any beneficial effects and in combination with trench it further reduced height up to about 33%. These interpretations are indications only and was not proven by the data analysis. However, trenching and mulching interaction was significant at p=0.05 (Table 4.6) indicating their combination can have some effects on the plants.

Diameter growth under different treatments were also not significant at p=0.05 level in this study (Table 4.6). In comparison to control treatment, trench treatment had the best diameter increment with about 23% greater diameter increment. There was a

rapid increase in diameter in this treatment between the third and fourth treatments. Both mulch treatments recorded slightly negative effects. Mycorrhizal treatments were not beneficial for diameter growth. There were no interactions between treatments for diameter growth.

Notional volume growth of plants showed fairly similar pattern to above results (Figure 4.8) and the treatment effects were not significant. Only trench treatment had positive effects of about 10% volume increment. Mulch treatments showed about 23% reductions in notional volume growth. Mycorrhiza and trench combined treatment also recorded about 30% volume reduction but was not so low when mycorrhiza was applied alone. The block effect was significant for treatments showing the variation existed between blocks.

Diameter and height relationship showed that it was more or less a linear relationship except in the mulch treatment where a slightly curvilinear relationship was observed (Figure 4.9). Both parameters were increasing with time though the growth of this species was not satisfactory.

4.4.3 Discussion

The results reported here clearly showed in this site that growth of *Toona ciliata* was not much improved with any of the treatments applied and in fact was poorer with some. However, a small positive response was noted for trenching treatments for both height and diameter growth though this was not significant. Thinning of pine in this trial was done in a uniform way rather than rows which might have created some root competition effects for growing seedlings for nutrients due to uneven spacing of pine trees compared to the position of seedlings. Some improvement in growth with trenching might be attributable to this. Under the conditions in this site soil moisture was not limiting at all due to heavy rainfall received which probably resulted in lack of or negative response to mulching. Too much soil moisture may create anaerobic conditions and may limit root growth. Limited root growth may in turn affect shoot growth. Mulch treatment is usually beneficial particularly when the soil would otherwise dry. However, surface feeder root development was observed under the mulch of this species as well, as that of other species, which indicate that even under heavy rainfall conditions plants could have had some benefits from the mulch probably in terms of some nutrient supply. There were also some evidence of interactions between mulching and trenching which may perhaps be important to

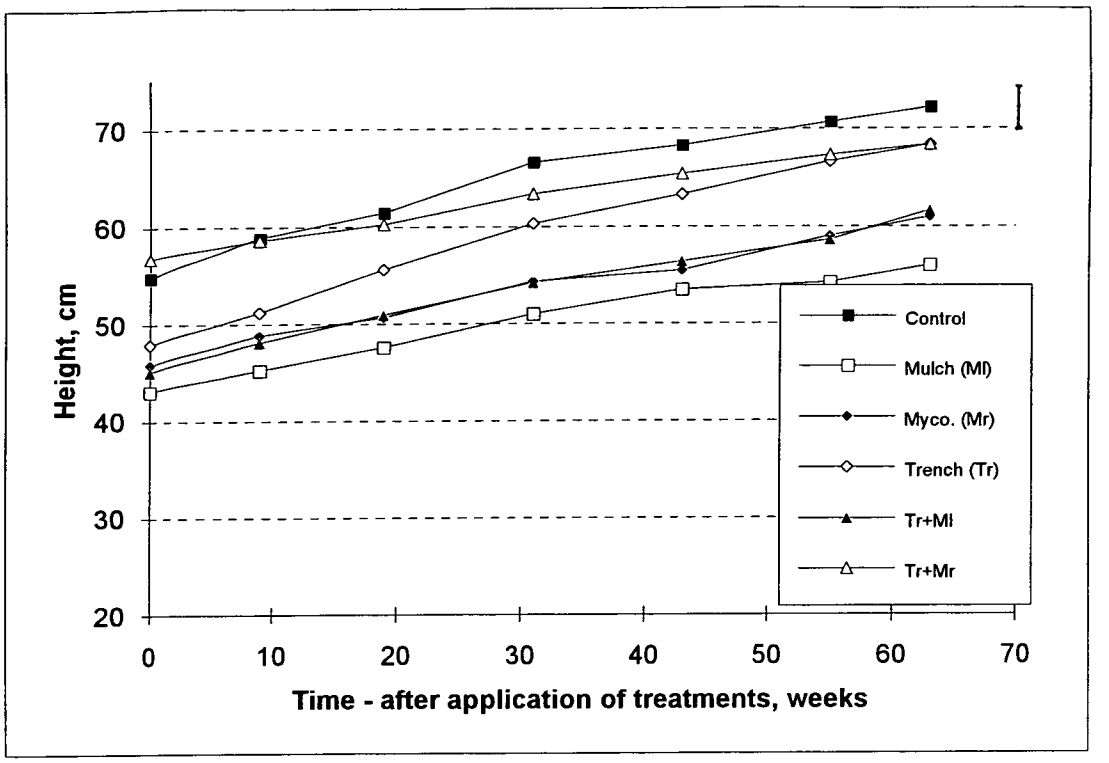
Table 4.6 : The mean effects of different treatments on growth of *Toona ciliata* at the age of about 2 years. (n = 60-75 trees per treatment)

Treatments	Survival %	Mean Height increment (cm)	Mean Diameter increment (cm)	Mean Notional volume increment (cu.cm)
Control	68.8	17.4	0.34	53.7 (1.896)#
Mulch	60.0	13.0	0.37	41.5 (1.771)
Mycorrhiza	70.9	15.2	0.39	46.0 (1.836)
Trench	57.1	20.4	0.42	59.3 (1.832)
Trench + Myco.	62.6	11.6	0.28	37.8 (1.803)
Trench + Mulch	69.5	16.5	0.30	39.9 (1.803)
Total treatment effect	ns	ns	ns	ns
Significance of Interactions				
a) Trench x mulch	-	*	ns	ns
b) Trench x myco.	-	ns	ns	ns
SE	$\pm$ 4.0	$\pm$ 2.2	$\pm$ 0.05	$\pm$ 9.0 ($\pm$ 0.054)
CV	$\pm$ 12.8	6.0 %	8.5 %	(22.6%) (5.1%)

= $\log_{10}$ transformed values

SE = Standard error for the whole treatments, CV = Coefficient of variation

investigate in the later stages of growth. Lack of improvement in survival by any of the treatments suggest that root competition effects from pine or too much soil moisture due to mulching was not further limiting the survival when compared to the control. Probably mulch had both favourable and unfavourable effects for these plants. Nevertheless, mulch could limit height and diameter growth of plants in some circumstances. It may be probable that mulch would have beneficial effects in later growth, once the plants are well established and achieved certain height growths rather than in the initial growth stages. Other reasons for poor growth might be poor conditions of plants at planting.



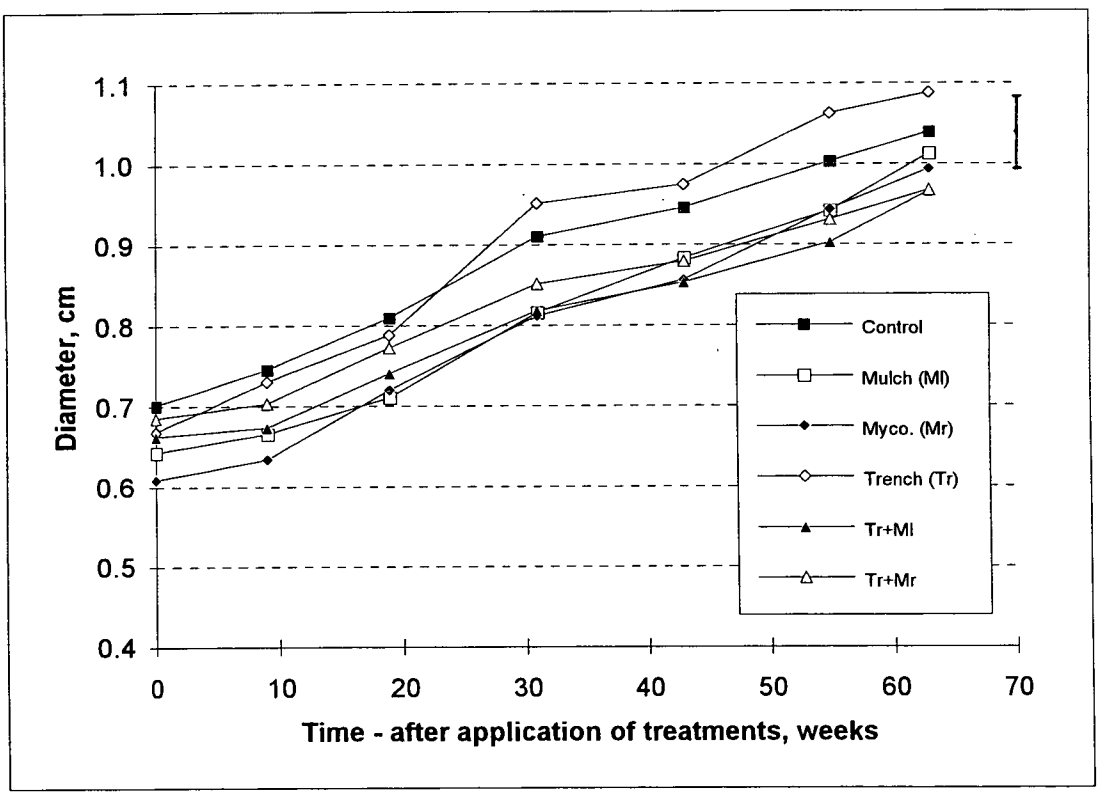


Figure 4.7 : Mean height and diameter growth of Toona ciliata under different treatments during the experimental period. (above - Height Growth, below - Diameter Growth)
The bar represents ± one overall standard error value for any treatment at the final measurement (n = 60-75 trees per treatment).

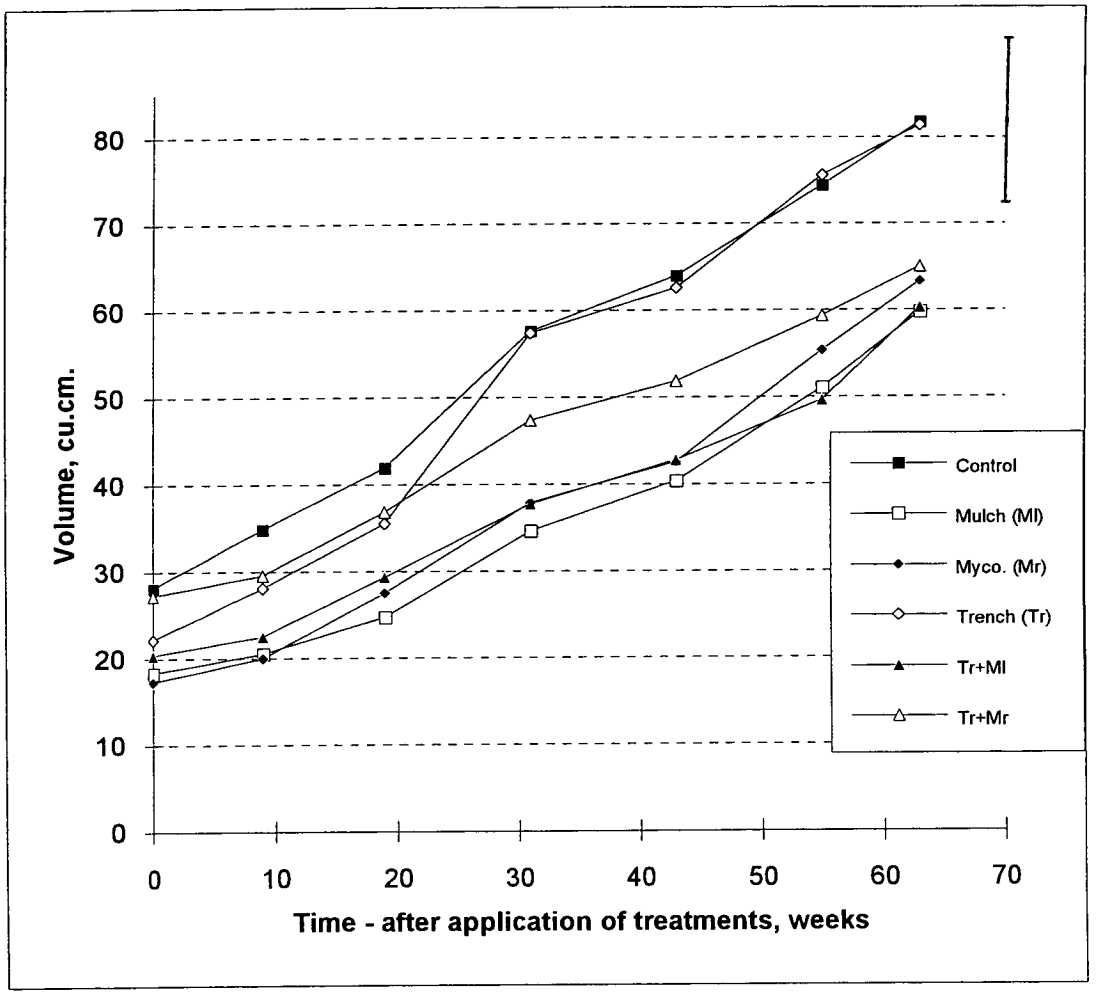


Figure 4.8 : Mean notional volume growth of Toona ciliata under different treatments during the experimental period.
The bar represents ± one overall standard error value for any treatment at the final measurement (n = 60-75 trees per treatment).

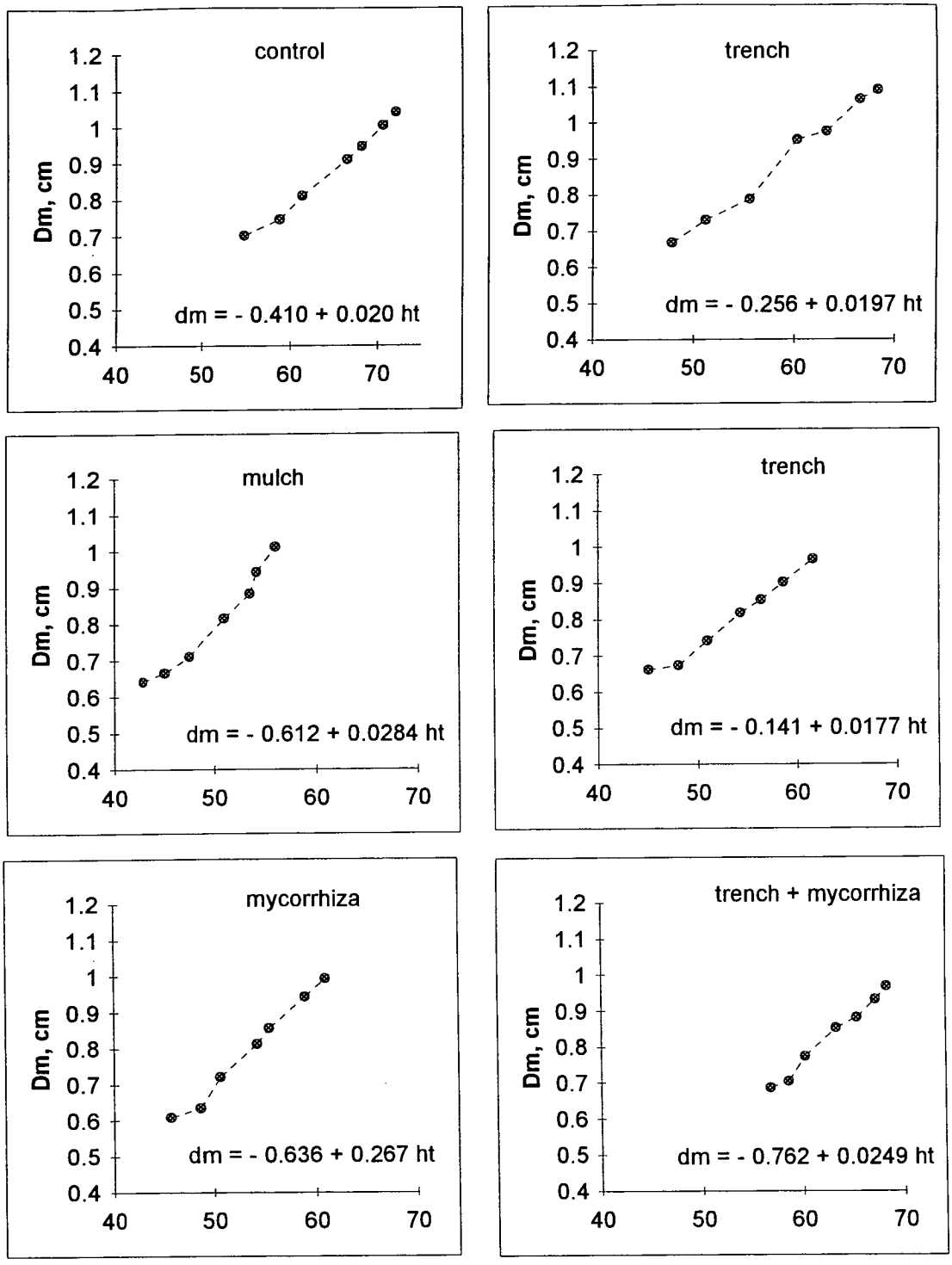


Figure 4.9 : Height (Ht) and Diameter (Dm) relationship of Toona ciliata showing changing relationships with different treatments.
(the equations assuming a linear relationship, n = 60-75 trees per treatment))

4.5 *SWIETENIA MACROPHYLLA*

4.5.1 General performance and observations

Swietenia grew well in the experimental period, as that of previously described species of *Alstonia* and *Khaya.* It established well and started initial growth by producing new flushes of leaves. Sufficient rainfall was received after planting which helped early establishment. Plenty of sunlight was available for plants with wide opening of pine canopy in this site. Overhead light with side protection from other trees is very favourable for early growth of this species. During its growth some termite attacks were observed for some plants and was treated with carbofuran insecticide and controlled well. No shoot borer attack was observed during the study.

4.5.2 Survival, Height, Diameter and Notional volume growth

Survival was very good recording values above 90% (Table 4.7). Due to these high values recorded under all treatments, as that of *Alstonia* and *Khaya,* no statistical analysis was required for this data. High survival indicates its ability to establish well under the present site conditions.

Average height growth was increasing continuously (but not the individual plant growth) and reached about 0.5 m within the first year of growth. The pattern of height increment is given in the Figure 4.10. It clearly shows that the combined treatment of mulch, trench and mycorrhiza had the greatest height increment as somewhat similarly experienced in the *Khaya* study. Overall treatment differences were significant at p=0.01 and the mulch and the combined treatment effects were highly significantly different from the control at p=0.01 (Table 4.7 and 4.8). The height increment was about 61% and 45% greater than the control for combined and mulch treatments respectively. Trench treatment was also significant at p=0.05 with an height increment of about 27%. However, the interaction between mulching and trenchig was found to be not significant (Table 4.7). Mycorrhiza treatment was statistically indistinguishable from the control, thought it showed about 22% height increment. It was clear from the Figure 4.10, that height growth of the combined treatment was showing increasing differences and would be likely to have shown increased effects in later stages.

Differences in diameter increment were not significant during the study period, probably it was too early for the plants to show differences. Combined treatment of Mulch+trench+mycorrhiza had about 8.4% more diameter increment than the control. Treatment interactions were not significant.

Notional volume growth was not significant at p=0.05% level though the average value recorded in the combined treatment showed an increment of 32.5% greater than compared to the control. The trend of volume increment suggests that it may be significant in later stages (Figure 4.11).

Height and diameter relationship was linear as shown in the Figure 4.12. A slight trend towards height increment compared to diameter increment can be observed in the combined treatment.

4.5.3. Discussion

The results of this study was somewhat limited due to the shorter period involved than in the other three trials. *Swietenia* has shown, in previously conducted pilot studies, that it is one of the promising species for underplanting in pine stands, showing quite fast growth rates and reaching the overstorey pine canopy level. In the present study highly significant height growth by mulching and combined treatments clearly show the effects of mulching in its own or in combination with others on the growth of *Swietenia*. Since trenching was also significant, probably combined treatment, including both mulching and trenching, tended to show better results than when these treatments were applied alone. This site was intermediate between Deltota and Panwila site in rainfall and therefore, probably trenching has been useful to reduce root competition effects from pine overstorey. The effects of mycorrhiza may be of less magnitude and whether it had any effect in the combined treatment was not evident since three treatments were involved there. However, the greatest height increment observed under the combined treatment than any of the other single treatments indicate that when all the treatments were applied together at the same time along with mycorrhiza, apparently plants would have received full benefits. It also tends to indicate that in combined treatment, it was trench rather than mycorrhiza which promoted growth in combination with mulch since in individual treatments trenching had always slightly better effects than mycorrhiza. However, the possibility of interactive effects of mycorrhiza cannot be ruled out. Mulching+trenching had a greater effect on height increment than any of the other treatments showing its

Table 4.7 : The mean effects of different treatments on growth of *Swietenia macrophylla* at the age of about 2 years using initial growth values and light as covariates. (n = 60-75 trees per treatment)

Treatments	Survival %	Height increment (cm)	Diameter increment (cm)	Notional volume increment (cu.cm)
Control	97.9	9.8	0.45	42.0 (1.780)#
Mulch	91.7	14.3	0.42	45.4 (1.735)
Mycorrhiza	96.3	12.0	0.41	39.6 (1.749)
Trench	97.6	12.5	0.46	50.0 (1.719)
Trench+Mulch + Mycorrhiza	95.8	15.8	0.49	56.0 (1.869)
Significance of treatments	-	**	ns	ns
Significance of interactions				
a) Trench x mulch	-	ns	ns	ns
b) Trench x myco.	-	ns	ns	ns
SE	-	$\pm$ 1.1	$\pm$ 0.04	$\pm$ 6.0 ($\pm$ 0.056)
CV	-	4.2 %	6.0 %	16.4 % (5.4 %)

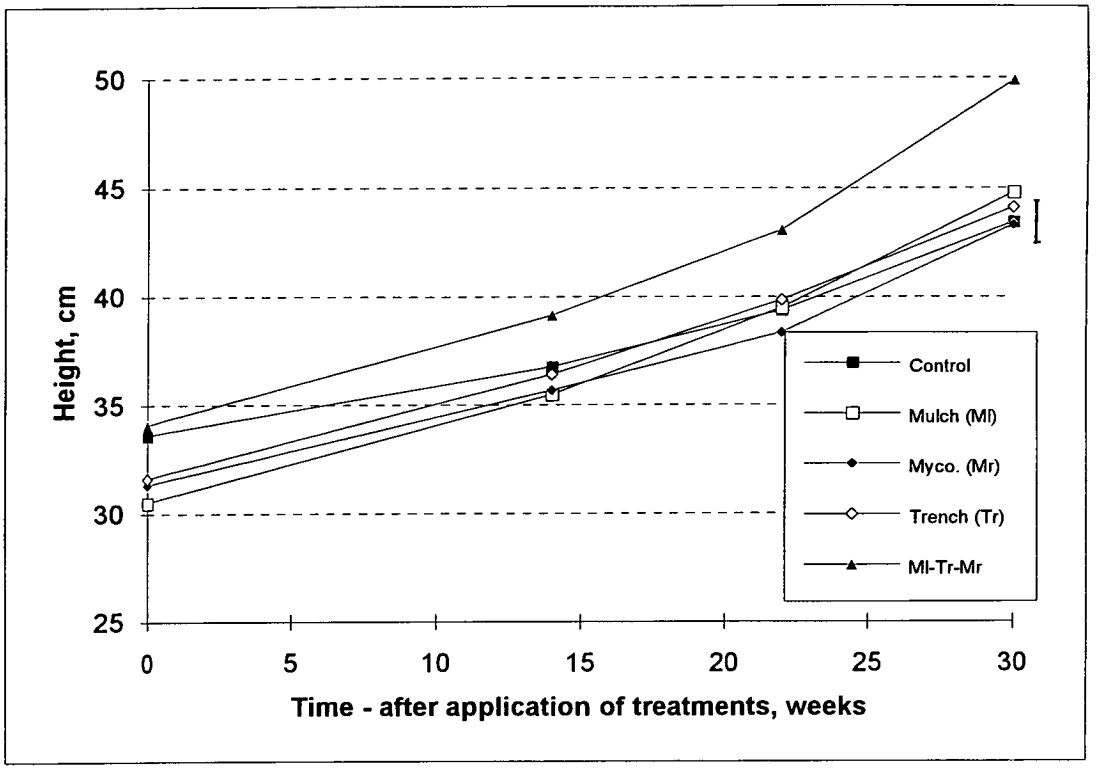
= Log_{10} transformed values

SE = Standard error for the overall treatments, CV = Coefficient of variation

Significance level : * = significant at 5% level

** = significant at 1% level

consistent effects. It is usually observed that *Swietenia* generally prefers moist conditions and therefore it may greatly be greatly benefited from sufficient soil moisture availability in the soil. In the present experimental area there were dry periods and soil moisture conservation by mulching or any other means will contribute to more shoot growth which may produce more leaves and this in turn may encourage faster establishment with sufficient root growth. In the early growth it was observed that during wet periods it increased height growth by producing flush of leaves whereas in the dry period this was temporarily stopped. Some surface feeder



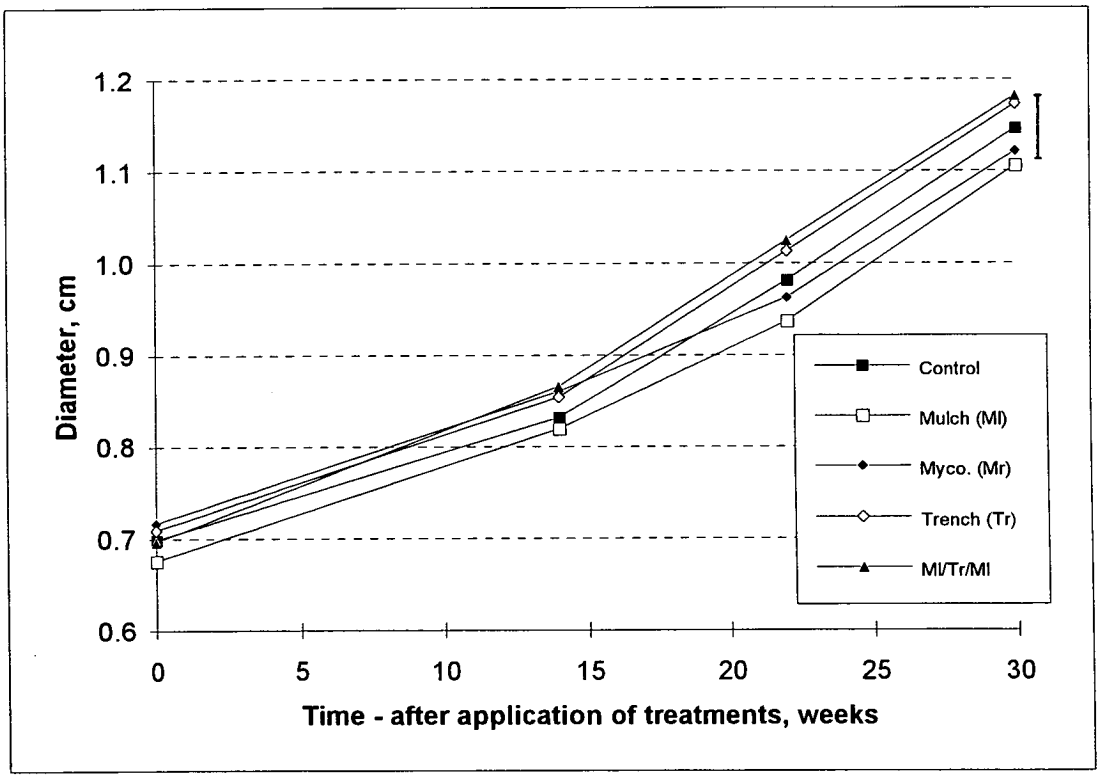


Figure 4.10 : Mean height and diameter growth of Swietenia macrophylla under different treatments during the experimental period. (above - Height growth, below - Diameter growth)
The bar represents ± one overall standard error value for any treatment at the final measurement (n = 60-75 trees per treatment).

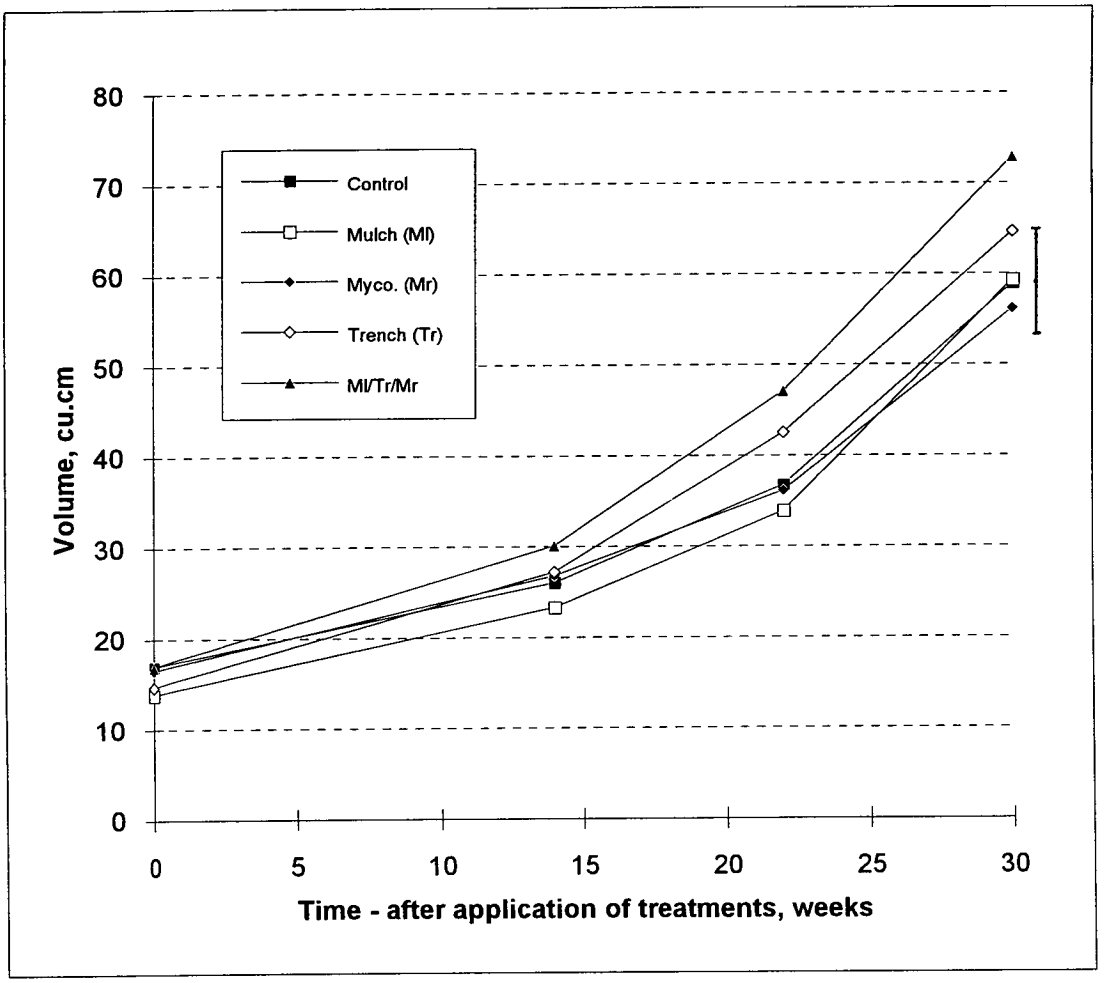


Figure 4.11 : Mean notional volume growth of Swietenia macrophylla under different treatments during the experimental period.
The bar represents ± one overall standard error value for any treatment at the final measurement (n = 60-75 trees per treatment).

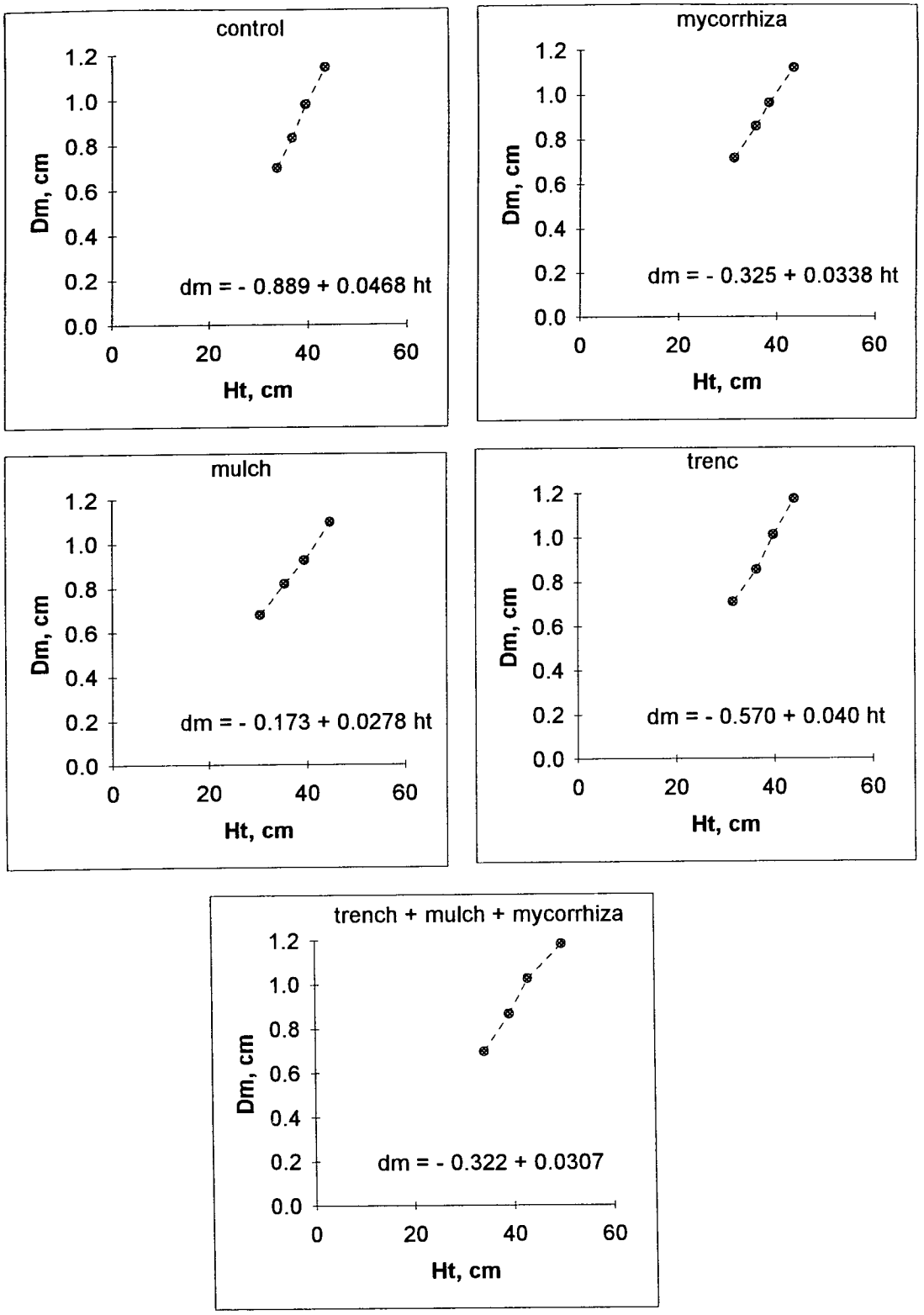


Figure 4. 12 : Height (Ht) and Diameter (Dm) relationships of Swietenia macrophylla showing changing relationships with different treatments. (the equations assuming a linear relationship, n = 60-75 trees per treatment).

Table 4.8 : The results of mean comparisons of *S. macrophylla* from the Tukey's test.

Treatments	Mean height
Control	41.3 (a)#
Mycorrhiza	42.8 (a)
Trench	45.3 (b)
Mulch	47.7 (c)
Mycorrhiza + Trench +Mulch	48.5 (c)

Means followed by the same letter are not statistically significant.
(values with 'b' and 'c' letters are significantly different from each other as well as from 'a')

roots were observed under mulch which may help in more absorption of water and nutrients from the mulched environment.

4.6 GENERAL DISCUSSION AND CONCLUSIONS

In the above mentioned trials, generally considerable improvements of shoot growth were observed with mulch application in the early growth development of underplanted broadleaved species. Mulching was always beneficial except in the very high rainfall area of Watawala where *Toona ciliata* was planted. Trenching alone was not significant in all cases though it showed some improvements in *Toona*. However, trenching was highly beneficial in combination with mulch in the comparatively dry site of Deltota where *Khaya* was planted, and probably in *Swietenia* at Galaha, where mycorrhizal treatment was also applied. Mycorrhizal treatment alone had no significant effects.

4.6.1 Mulching

The results of mulching are in general agreement with the findings in various other studies which showed beneficial effects of mulch application. Much of this research

is in agriculture, horticulture and agroforestry rather than in forestry. Different mulches including organic (e.g. Archbold et el, 1989) and artificial (e.g. Walter and McLaughlin, 1989) materials which have been used for different plant species under various climatic conditions. The results have been mostly in favour of mulching except in some limited situations where it was found to be unfavourable.

In some recent studies in Sri Lanka, Samarappuli (1995) reported that when tree seedlings of rubber (*Hevea*) are mulched with rice straw, better growth improvements and erosion control could be obtained in comparison to live mulch of cover crops or controls without mulch. Dharmasena (1994/1995) stressed the importance of using tree leaf mulches for agricultural crops in dry areas and also for soil erosion control.

In some other studies, various beneficial effects have been observed with various organic mulch types including pine needle mulch as in the present study. Comparatively greater height and diameters were observed in pine seedlings by Shamet et al (1994) when mulched with *Pinus gerardiana* needles in India. Better growth and survival was observed by Singh et al (1994) in*Pinus roxburghii* with the needle mulch of the same species and the results were even better when a broadleaved species leaf mulch was applied. The same authors found that mulch effect can be further improved when it was combined with fertilizer, where a lower plant mortality rate was attributed to conserved soil moisture and its use by plants in the dry periods while better growth was ascribed to N and P availability under the mulch. Testing various mulch material (rice husk, farmyard manure and pine needles) for the growth of *Eucalyptus* seedlings, Singh et al (1993a) found that all mulch materials gave higher biomass production over the control, and needle mulch was the best of all. Pine needles have been successfully used in southern USA for agriculture crops, forest nurseries and in landscape projects giving benefits of weed control, favourable plant root environment, regenerating soil structure, preventing soil crusting and reduced soil pH, but in one study were not suitable when adequate soil moisture was available (Makus et al, 1994). The use of pine needles for the growth of broadleaved tree species of *Acacia*, *Melia* and *Albizia* species has shown considerable growth improvements in a study by Singh et al (1991) in India. These findings show the potential of using pine needle mulches for the growth of young plants supporting the results obtained in the present underplanting study. Using other types of mulches Davies (1985) reported in a temperate climate that mulches concentrated soil moisture in the upper 7.5 cm of soil and also made nutrients available in this layer to

the plants and was therefore useful to growing plants compared to bare soils from which nutrients cannot be taken up when soil is dried up.

The beneficial effects obtained in the present study may generally be attributed to conserved soil moisture as clearly observed under mulch and possibly to improved nutrient status in the rooting zone of underplanted seedlings. Pine needles are particularly useful in soil moisture conservation since they break down slowly, compared to broadleaved species, which helps to retain it on the soil for a longer time. Easily decomposing mulches may be more useful for nutrient supply over a short period rather than soil moisture conservation unless they are repeatedly applied. Soil moisture conservation and its use during dry periods is one of the important benefits of mulching and it helps in better survival and early growth of tree seedlings. In the underplanted environment, it can generally be expected that overstorey trees will compete with understorey seedlings for soil moisture particularly when sufficient soil moisture is not available in the soil. In a similar way, overstorey trees may compete with the understorey when nutrients are in short supply such as in degraded lands. Mulching may be generally useful to overcome both of these problems, at least to some extent. Conservation of soil moisture under mulch was estimated by Singh et al (1988) reporting that under mulch, moisture was 25 % and 30-32 % more in surface and sub-surface layers respectively than without mulch. Significant improvements in N, P and K levels in the surface 10 cm was observed following mulching (Othieno and Ahn, 1980). Yobterik et al (1994) observed that ammonium N released from mulch material displaced base cations in the soil exchange complex, reduced ammonification and increased nitrification after 6 weeks of application of mulch. Rapid leaching of K can take place from mulch material within a month of its application (Christensen, 1985) and in some situations leaching of N, P and K can occur within about 11 days (Schroth et al 1992). In the present study, effects of mulch were beginning to appear within about 10-20 weeks after application of mulch. Some delay may be due to slow decomposition of nutrients. The effects were consistent throughout the experimental periods of about one and half years after application of treatments. In a temperate environment study, Truax and Gagnon (1993) observed that oak trees were still benefiting from mulching with plastic and straw materials even after 5 years of growth. These findings indicate that keeping leaf material around young tree seedlings can significantly improve the soil environment underneath it, enhancing their growth. This can be conveniently and more practically done under pine trees where large amounts of needle litter is available unless it is burnt.

In addition to the above mentioned benefits of mulching with reducing soil moisture evaporation from soil and improving nutrient status in the rooting zone of young plants various other benefits have also been reported. For example, Schroth et al (1992) reported better infiltration, higher porosity, higher biological activity, better root growth. Better infiltration rates are usually achieved by avoiding raindrop impact which can otherwise lead to soil surface sealing and reduced infiltration.

Reducing of soil temperature fluctuations is another important factor brought about by mulching (Singh, et al 1988) or any other type of soil cover. A mulch can absorb most of the incoming solar radiation and keeps soil cool in dry periods while in the wet period it can keep soil surface warmer and humid than the bare soil; warm moist soils are considered favourable for soil micro-organism and plant growth (Arnon, 1972). Soil temperatures are also reported to have the ability to affect the rate of production and quality of hormones (particularly cytokinins and gibberellin-like substances) produced by roots (Neilson and Humphries, 1966). The rate at which roots can take up water and nutrients from the soil is increased with soil temperature (Russell, 1973). Reduced soil temperature effects due to mulching were also observed in the present study which will be presented in Chapter 8.

No response or slightly unfavourable effects recorded in the study with *Toona* were attributed most probably to too much soil moisture, since rainfall was very high in this area as discussed in a previous section. Too much soil moisture can interfere with soil aeration causing anaerobic conditions. Some unfavourable effects of mulching can also occur due to the properties of mulch material used. Mulch with a high C:N ratio may temporarily immobilise N causing N deficiencies in plants (Wood, 1989). Some species like *Gliricidia* mulch is reported to have the possibility to cause Mn toxicity due to high Mn contents in the leaf (Yobterik et al, 1994).

The formation of a dense fine root mat by most of the species under the mulch treatment in the present study was found to be an interesting response by young understorey plants to favourably changed soil conditions under mulch (see Plate 4.2). This was quite marked under *Alstonia* and *Khaya* plants. These feeder roots may have been developed by the plants to explore the better soil micro-climatic conditions formed by mulching and utilize available resources. Similar results have been reported by some other authors. Gregoriou and Rajkumar (1984) reporting that active vigorous roots were developed near the soil surface below the mulch in avocado and

mango trees. Jackson et al (1990) presented evidence that large and rapid increases in the uptake kinetics of plant roots after creating nutrient-rich soil patches in the field showing rapid physiological plasticity of roots which can take place within days after the enrichment of soils. All these studies show that young tree root's ability to respond to improved soil conditions which well compares with the reporting of St John (1983) that tropical tree roots are known to grow in response to soil organic matter. There seems to be less research work done on physiological changes of roots to enriched soil patches in comparison to similar physiological changes in above-ground parts of plants.

4.6.2 Trenching

Lack of response to trenching was observed in some of these studies as described in previous relevant sections which indicates that pine tree roots were not in severe competition with underplanted seedlings in early stages of their growth under the conditions which existed in those studies, except in the comparatively dry site of Deltota where *Khaya* was planted and in an intermediate site where *Swietenia* was planted. This may be attributed to reduced root competition due to sufficient soil moisture in most of the sites as well as reduced tree density of pine trees followed by thinning. It should be noted that though soil moisture was generally sufficient, some soil moisture depletion can occur during dry spells which may be sufficient to check plant growth temporarily. Another possibility is regrowing of severed roots reducing the impact of trenching. In the *Toona* site, random thinning of pine might not have sufficiently reduced root competition compared to the row thinning in other studies which in turn would have had some effect on seedling growth. However, this could not be confirmed since trenching effect was still unable to show significant results in this case.

Similar results have been achieved by Denslow et al (1991) in a tropical rain forest where no effects of trenching were observed for the growth and survival of understorey seedlings for two years, suggesting root competition is not an important component in that environment. However, their research may not be strictly comparable with the present results since those seedlings were probably limited primarily by light. Verinumbe and Okali (1985) have also shown in an agroforestry study that root competition of trees did not affect annual crops interplanted but shade played an important role. However, these findings cannot be generalized to all

situations since various factors interact in different climates, soils and with different species.

When pine trees were thinned or when their roots in the seedling zone were severed by trenching there was a possibility that they can remain alive for some time as reported by some researchers. Ferrier and Alexander (1985) found that excised fine root material could persist under field conditions for at least 9 months and that associated mycorrhizal fungi could also remain metabolically active probably due to carbohydrate reserves in the tissues. Silver and Vogt (1993) found in a trenching study in a sub-tropical wet forest that, after felling the trees, root decay was slow and 48-65 % of the fine roots remained in trenched plots even after one year. However, such findings may vary depending on species and site conditions. Moreover, even if they are alive they may not be active in water and nutrient absorption since the above-ground parts of the trees have been removed. Another possibility would be that in tree communities root grafting can occur which may cause some roots to be active by attaching to other trees even after the felling of its own above-ground parts. Nevertheless, there appeared to be no evidence of such effects on the growth of underplanted seedlings in the present studies.

In contrast to these findings root competition effects have been observed in some trenching studies elsewhere. For example, in a root competition study of overstorey and understorey vegetation Putz (1992) found that *Pinus elliottii* benefited from overstorey coppiced broadleaves when tree seedlings were trenched around. Trenching resulted in increased foliar N and P concentrations, high soil moisture content and a doubling of above-ground growth in this study but there was no response to increase in light level showing that below-ground competition was more important than above-ground competition. Similar results were observed by Riegel et al (1992) showing that for the growth of understorey vegetation with an overstorey of pine, below-ground resources were more limiting than the above-ground. However, it is generally accepted that root competition effects can vary depending on the type of species, its density, climatic and soil conditions. Below-ground competition can be more intense when soil resources are limited (Putz and Canham, 1992).

4.6.3 Mycorrhiza application

When the experiments in this study were designed it was expected that the introduction of endomycorrhiza (now called arbuscular mycorrhiza - J. Wilson,

personal communication) from the infected soil under mature trees would be beneficial to the growth of underplanted broadleaved seedlings under pine where soil is generally degraded. It was also assumed that under pine plantations there may be hardly any endomycorrhizal inoculum potential due to the facts that pine trees are fully ectomycorrhizal, no endomycorrhizal host plants are available in the understorey and frequent occurrence of fire in the pine forest floor might have destroyed any fungal spores. Despite these points, underplanted trees were unable to show any response to mycorrhizal inoculation (except possibly in *Swietenia*) in comparison to uninoculated control failing to reject the null hypothesis that there are no effect of mycorrhiza on the growth of these seedlings as described in the preceding sections.

Virtually no studies have been reported on the effects of endomycorrhizal inoculation on tree seedling growth in Sri Lanka. However, ectomycorrhizal inoculation of pine seedlings with infected soils has been very successful in Sri Lanka for the establishment of pine plantations. Numerous studies in other countries have suggested that mycorrhizal inoculation potential declines when the tree cover is removed and the sites are disturbed in various ways (see Section 2.6). In degraded grasslands where pine has been established, growth of broadleaved tree seedlings is mostly poor which might be related to lack of mycorrhizal fungi and if so, sufficient and successful inoculation of seedlings should prove beneficial.

In the present study it is not known whether endomycorrhizal inoculation took place successfully since seedling roots were not investigated for infection which was beyond the scope of this study. Even if the inoculation occurred successfully, plants may perhaps take a longer time to show growth responses than the present experimental period of up to one and half years. Alternatively, at seedling stages mycorrhiza may just become a carbon drain on a plant. Also, under less stressful soil P conditions endomycorrhiza may not be effective in improving growth of plants (Allen, 1991). It was suggested by Anderson and Swift (1983) that P/N level is critical for mycorrhizal development; both a high P/N ratio and a low P/N ratio can reduce mycorrhizal activity. In the present study, soil P level was comparatively high (see Chapter 8) and N level was low and possibly this may have been responsible for lack of response. Studies of the inoculation of nursery plants would be useful and these effects should be investigated in further studies.

4.6.4 Conclusions

Lack of apparent responses to trenching at Panwila and Watawala sites indicated that the existing pine trees after their thinning were not imposing significant root competition for the early growth of underplanted broadleaved species under sufficient rainfall conditions experienced in those experimental areas. However, there was an indication that in a drier site root competition may exist and trenching was found to be useful in such situations at Deltota and Galaha sites. Mycorrhizal inoculation with top soil collected under the respective mature tree species proved to have no effect in terms of height, diameter and volume growth in the early stages of plant growth in present experimental areas.

It was clearly shown that mulching with pine needles was very beneficial for the significant growth improvements in the underplanted seedlings except in the very high rainfall area of Watawala. Application of pine needle mulch is practically feasible under pine since enough material can be easily collected under pine trees. Under drier situations mulching can be combined with trenching to achieve better growth rates. Growth improvements are very important for underplanted seedlings for rapid establishment under pine canopy. Early establishment and fast growth rates with mulching may enable those plants to successfully compete with pine trees for above- or below-ground resources.

CHAPTER 5

BIOMASS PRODUCTION AND GROWTH ANALYSIS OF DIFFERENT BROADLEAVES UNDER PINE

5.1 INTRODUCTION

This Chapter deals with dry mass production in leaves, stems and roots, leaf area development and related characteristics, and growth analysis of various species when they were growing under pine canopy. The experiments are same as in Chapter 4. Dry mass measurements of various parts of the plants were used to calculate parameters of growth analysis including Relative Growth Rate (RGR), Net Assimilation Rate (NAR), Specific Leaf Area (SLA), Leaf Area Ratio (LAR) and Leaf Weight Ratio (LWR). These parameters and dry mass measurements were compared for statistical significance using ANOVA under the different treatments of the experiments. Dry mass measurements were taken at the beginning and the end of the experiments. These two measurements were taken for the calculation of RGR and NAR. Initial dry weight measurements were pooled across the treatments within each replicate to get more representative values from limited number of plants sampled. For all the other measurements such as dry matter production in different plant parts, root:shoot ratio, SLA, LAR and LWR, the final biomass values were used. Results of ANOVA Tables are given in Appendix III.

5.2 *ALSTONIA MACROPHYLLA*

5.2.1 Dry mass yield and allocation

Mean dry matter production of plants is shown in Table 5.1 and Figure 5.1a. The mulch effect was highly significant ($p=0.01$) in comparison to unmulched treatments by factorial analysis of treatments (Table 5.3). Total dry mass was highest in the mulch alone treatment showing about 50% additional increment compared to the control. The mean value of mulch was about 1 kg per plant while the control had about 0.67 kg at the age of 2 years showing the effect of mulch for greater dry matter production. Mulch+trench treatment also recorded similarly higher values. Other treatments of trenching and mycorrhiza were not significant, which is similar to what

Table 5.1 Mean ± Standard Error values of leaf number, leaf area, root dry mass, stem dry mass, leaf dry mass and root:shoot ratio on per plant basis in *Alstonia macrophylla* at the age of about 2 years.

(n = 15-18 trees per treatment)

Treat-ments	Leaf Number	Leaf area (sq dcm)	Root dry mass (g)	Stem dry mass (g)	Leaf dry mass (g)	Total dry mass (g)	Root: shoot ratio
Control	170.0 ± 42.2	648.8 ± 170.3	161.7 ± 22.1	329.7 ± 39.4	183.0 ± 21.4	674.3 ± 81.1	0.31 ± 0.02
Mulch	219.7 ± 24.6	824.3 ± 98.7	205.3 ± 16.4	517.3 ± 16.2	289.3 ± 43.9	1012.0 ± 43.6	0.26 + 0.03
Mycor.	206.7 ± 41.9	791.5 ± 154.3	180.0 ± 45.1	385.7 ± 95.6	264.3 ± 125.5	830.0 ± 263.7	0.29 + 0.03
Trench	196.7 ± 29.8	758.9 ± 129.9	155.7 ± 17.2	337.7 ± 73.3	262.7 ± 54.2	756.0 ± 122.3	0.26 ± 0.03
Trench+ Mulch	228.3 ± 45.1	868.0 ± 166.7	219.3 ± 22.3	431.0 ± 69.1	316.3 ± 66.8	966.7 ± 157.1	0.30 ± 0.02
Trench+ Mycor.	182.0 ± 36.7	691.7 ± 138.5	140.0 ± 22.2	279.3 ± 43.9	150.7 ± 22.5	570.0 ± 86.1	0.33 ± 0.03
Average values	200.5 ± 40.5*	763.8 ± 156.0	177.0 ± 30.0	456.1 ± 63.6	244.4 ± 53.2	801.5 ± 135.7	0.29 ± 0.03

* Overall standard error values

was reported for the values in height, diameter and notional volume in the previous Chapter. Plots which received mycorrhizal treatment alone showed about 23% more of dry matter than the control though it was not significant. Although the total dry matter production was different in different treatments the proportion of dry matter allocation to different plant parts was very similar as shown in Figure 5.1a. Root, stem and leaf dry mass measurements showed that the highest biomass was in the stems (about half of the total biomass) followed by leaves and roots. *Alstonia* plants started branching for the first time at about 10 months followed by second branching at about 16 months after planting. This would have contributed to increased dry weights of stem and leaves. Two mulching treatments showed the highest mean values of leaf, stem and root dry mass separately. Mean root:shoot ratio varied from 0.26 to 0.33 in all treatments showing no statistical differences. This shows that

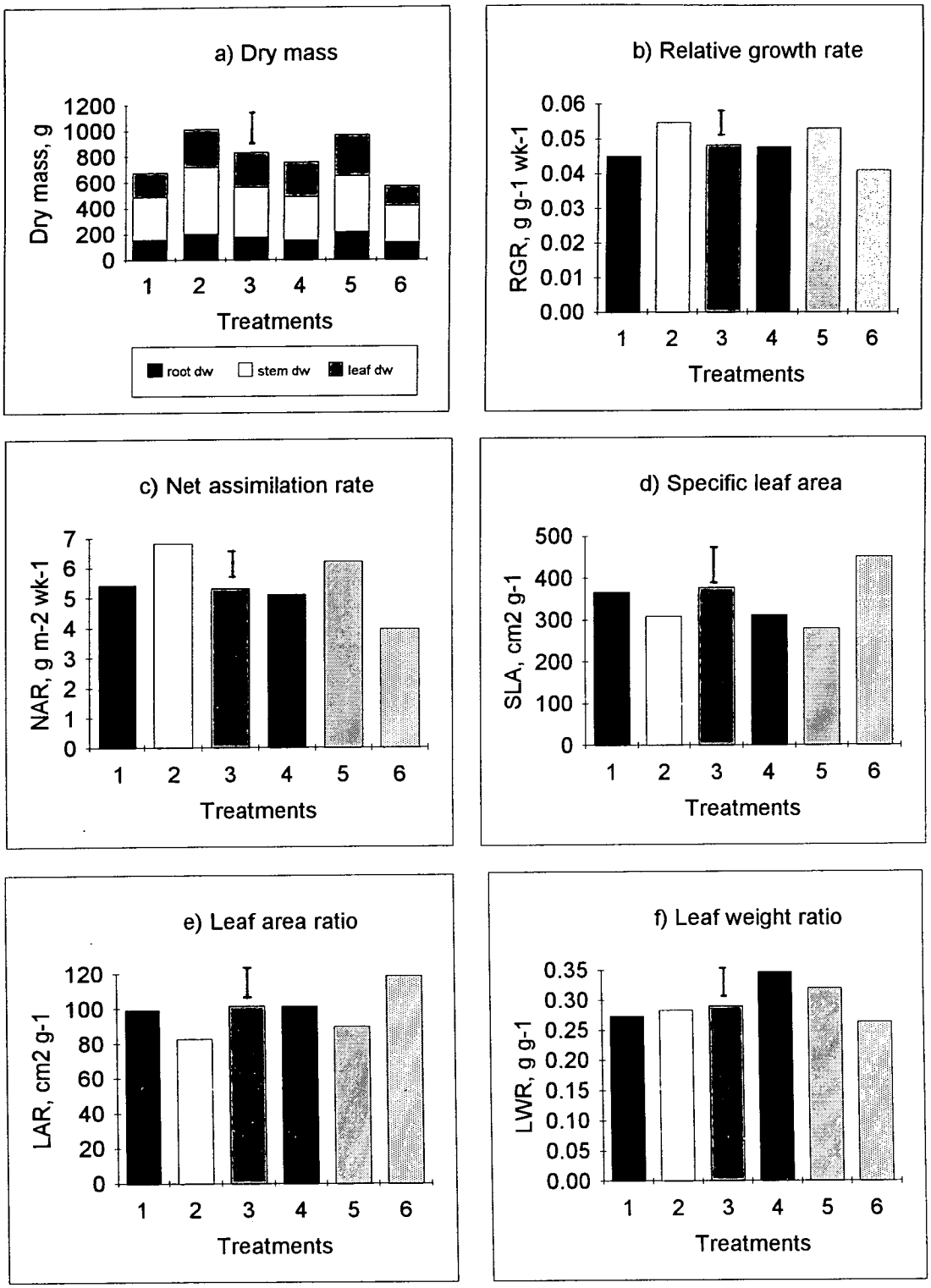


Figure 5.1 Different growth parameters of Alstonia macrophylla under different treatments at 2 years of age.

a) Treatments : 1 = control, 2 = Mulch, 3 = Mycorrhiza, 4 = Trench 5 = Trench+Mulch, 6 = Trench+ Mycorrhiza

b) The bar represents ± one overall standard error value for any treatment. (n = 15-18 plants per treatment)

Table 5.2 Mean ± Standard Error values of Relative Growth Rate (RGR), Net Assimilation Rate (NAR), Specific Leaf Area (SLA) and Leaf Weight Ratio (LWR) on per plant basis in *Alstonia macrophylla.*

(n = 15-18 trees per treatment)

Treatments	RGR ($g\ g^{-1}\ wk^{-1}$)	NAR ($g\ m^{-2}\ wk^{-1}$)	SLA ($cm^2\ g^{-1}$)	LAR ($cm^2\ g^{-1}$)	LWR ($g\ g^{-1}$)
Control	0.045 ± 0.001	5.4 ± 1.0	366.7 ± 79.4	99.2 ± 20.2	0.27 ± 0.01
Mulch	0.055 ± 0.002	6.8 ± 0.6	308.7 ± 65.8	82.5 ± 9.7	0.28 ± 0.03
Mycor.	0.048 ± 0.03	5.3 ± 3.1	377.7 ± 218.3	101.5 ± 58.7	0.29 ± 0.17
Trench	0.048 ± 0.028	5.1 ± 3.0	311.3 ± 180.0	101.3 ± 58.5	0.35 ± 0.20
Trench + Mulch	0.053 ± 0.031	6.2 ± 3.6	278.7 ± 161.1	89.7 ± 51.8	0.32 ± 0.18
Trench + Mycor.	0.041 ± 0.024	3.4 ± 2.3	450.7 ± 260.5	118.7 ± 68.6	0.26 ± 0.15
Average values	0.048 ± 0.004*	5.4 ± 0.6	348.9 ± 41.4	98.8 ± 9.8	0.29 ± 0.03

* Overall standard error values

Table 5.3 Results of analysis of variance for various growth parameters of *Alstonia macrophylla.*

Source	Leaf no.	Leaf area	Total dry mass	Root: shoot ratio	RGR	NAR	SLA	LAR	LWR
Mulch	ns	ns	**	ns	**	*	ns	ns	ns
Trench	ns	ns	ns	ns	ns	ns	ns	ns	ns
Mycor.	ns	ns	ns	ns	ns	ns	ns	ns	ns

* - significant at 5 % level ** - significant at 1 % level

ns - non significant

the growth improvements due to mulching was caused by improving the growth of both above- and below-ground plant parts proportionately.

Mean values of leaf number and leaf area under different treatments are given in Table 5.1. Mean leaf number was highest in the trench+mulch treatment closely followed by mulch alone treatment. Leaf area also had a similar pattern. The values for both leaf number and leaf area were lowest in the control. However, these differences were not statistically significant. The block effect was also not significant for these parameters.

All interaction effects of trenching vs mulching and trenching vs mycorrhiza were not significant and the details are given in Appendix III.

5.2.3 Growth analysis

Relative growth rate (RGR) was significantly greater ($p=0.01$) for mulch treatments. The values varied from 0.045 in the control to 0.055 g g^{-1} wk^{-1} in mulch treatments indicating increased dry matter production under favourable conditions with mulch (See Table 5.1 and Figure 5.1b). Trenching, mycorrhiza or their combinations were unable to show any significant differences. Net Assimilation Rate (NAR) was also significant at $p=0.05$ for mulch treatments in comparison to unmulched treatments. This indicates that dry matter production was more efficient per unit area of leaf under mulching when compared to the control and other treatments. The significance of both these parameters clearly indicates the beneficial effects of mulching experienced by the *Alstonia* plants. However, other parameters of growth analysis viz. Specific Leaf Area (SLA), Leaf Area Ratio (LAR) and Leaf Weight Ratio (LWR) were not significant for any treatments. However, they showed some clear differences between mean values of treatments as shown in Figures 5.1d, e, f. The results suggested that morphological changes of leaves in terms of leaf area or leaf weight development did not occur significantly with mulching or any other treatment effects.

5.3 *KHAYA SENEGALENSIS*

5.3.1 Dry mass yield and allocation

Dry matter production of *Khaya* was low compared to *Alstonia* during the experimental period since its growth rate was slow in these early stages of

Table 5.4 Mean ± Standard Error values of leaf number, leaf area, root dry mass, stem dry mass, leaf dry mass, total dry mass and root:shoot ratio on per plant basis in *Khaya senegalensis* at the age of about 2 years. (n = 15-18 trees per treatment)

Treat-ments	Leaf Number	Leaf area (sq cm)	Root dry mass (g)	Stem dry mass (g)	Leaf dry mass (g)	Total dry mass (g)	Root: shoot ratio
Control	15.5 ± 0.52	2477 ± 144.5	17.2 ± 1.14	22.9 ± 1.9	27.0 ± 1.2	67.1 ± 4.1	0.45 ± 0.02
Mulch	19.5 ± 1.9	3177 ± 342.7	22.5 ± 1.9	33.0 ± 3.4	36.1 ± 5.2	91.6 ± 8.9	0.38 ± 0.02
Mycor.	15.1 ± 0.52	2504 ± 139.5	16.7 ± 2.4	26.7 ± 2.1	31.2 ± 5.9	81.2 ± 5.2	0.34 ± 0.06
Trench	20.6 ± 3.1	2916 ± 183.2	19.1 ± 1.0	22.9 ± 1.0	28.1 ± 2.3	70.1 ± 3.1	0.44 ± 0.02
Trench+ Mulch	18.0 ± 0.87	3241 ± 133.4	23.7 ± 2.1	40.6 ± 5.1	46.9 ± 4.8	110.3 ± 12.4	0.34 ± 0.03
Trench+ Mycor.	18.1 ± 2.6	2633 ± 286.1	19.9 ± 3.9	30.3 ± 4.1	30.3 ± 3.6	80.4 ± 11.2	0.39 ± 0.02
Average values	17.8 ± 1.9*	2824.6 ± 216.5	19.8 ± 2.0	29.4 ± 2.8	33.3 ± 3.6	83.4 ± 7.1	0.39 + 0.03

* Overall standard error values

development. The mean values varied from about 67 g in the control to 110 g in the trench+mulch treatment as shown in Table 5.4. The overall treatment effect was highly significant for dry matter production (Table 5.6) and therefore individual treatment effects were compared using Tukey's test. The analysis showed that only trench+mulch treatment was significantly different from the control at p=0.05, recording about a 64% increase over the control. Mulch alone treatment had about 36% higher biomass production than the control although it was not significant (Table 5.8). Moreover, when the data were analysed in a factorial way to distinguish the effect of mulching, trenching and mycorrhiza separately it was found that plus-mulch treatments were highly significantly greater (p=0.01) compared to those without mulch including the control and the trench treatments (Table 5.6). The same analysis showed that trenching vs non trenching had no significant differences.

However, it should be noted that trenching had a significant effect when it was combined with mulch as shown in the individual treatment comparison by Tukey's test. This was also shown in the previous Chapter when growth parameters were compared in different treatments for the same species. This clearly shows that trenching was effective when it was combined with mulching for *Khaya* in this experimental site. It was also found that mycorrhiza treatments were significant for total dry matter production in factorial analysis in comparison to the treatments without it, as shown in Table 5.6. The block effect was non significant for dry matter production in this study.

Mean root:shoot ratios were significantly different at p=0.01 in this species; for mulch treatments the ratio was reduced (Table 5.6). This shows that mulch treatment increased total dry mass production in *Khaya* plants including both root and shoot dry mass (as shown above) while allocating more biomass to shoots in comparison to roots (see Figure 5.2 a) thereby reducing root:shoot ratio. Because of these changes noted in biomass allocation, root, stem and leaf dry mass productions were analysed separately. Separate ANOVA results of overall treatments on stem and leaf dry mass showed that both of these were significantly different within treatments at p=0.01 and 0.05 levels respectively, while root dry mass was not (Table 5.6). Further analysis with Tukey's test for mean comparisons, revealed that only trench+mulch treatment is significantly different from the control for both stem (p=0.01) and leaf dry mass (p=0.05) production (Table 5.8). Factorial analysis to compare the effects of mulched and unmulched treatments showed that mulch treatments produced significantly higher leaf (p=0.01), stem (p=0.001) and root (p=0.01) dry mass. In contrast, trenched plots in comparison to untrenched ones did not affect the dry mass production of any parameters studied. Higher total dry matter production by mycorrhiza treatments are notable since mycorrhiza treatments did not show any improvements in growth parameters of height, diameter and volume growth as described in the previous Chapter.

Mean values of leaf number and leaf area are given in Table 5.4. Leaf number produced by different treatments were not significantly different in this species (Tables 5.6). However, leaf area development was significantly (p=0.05) higher in mulched plots which would have increased the photosynthetic capacity of those plants.

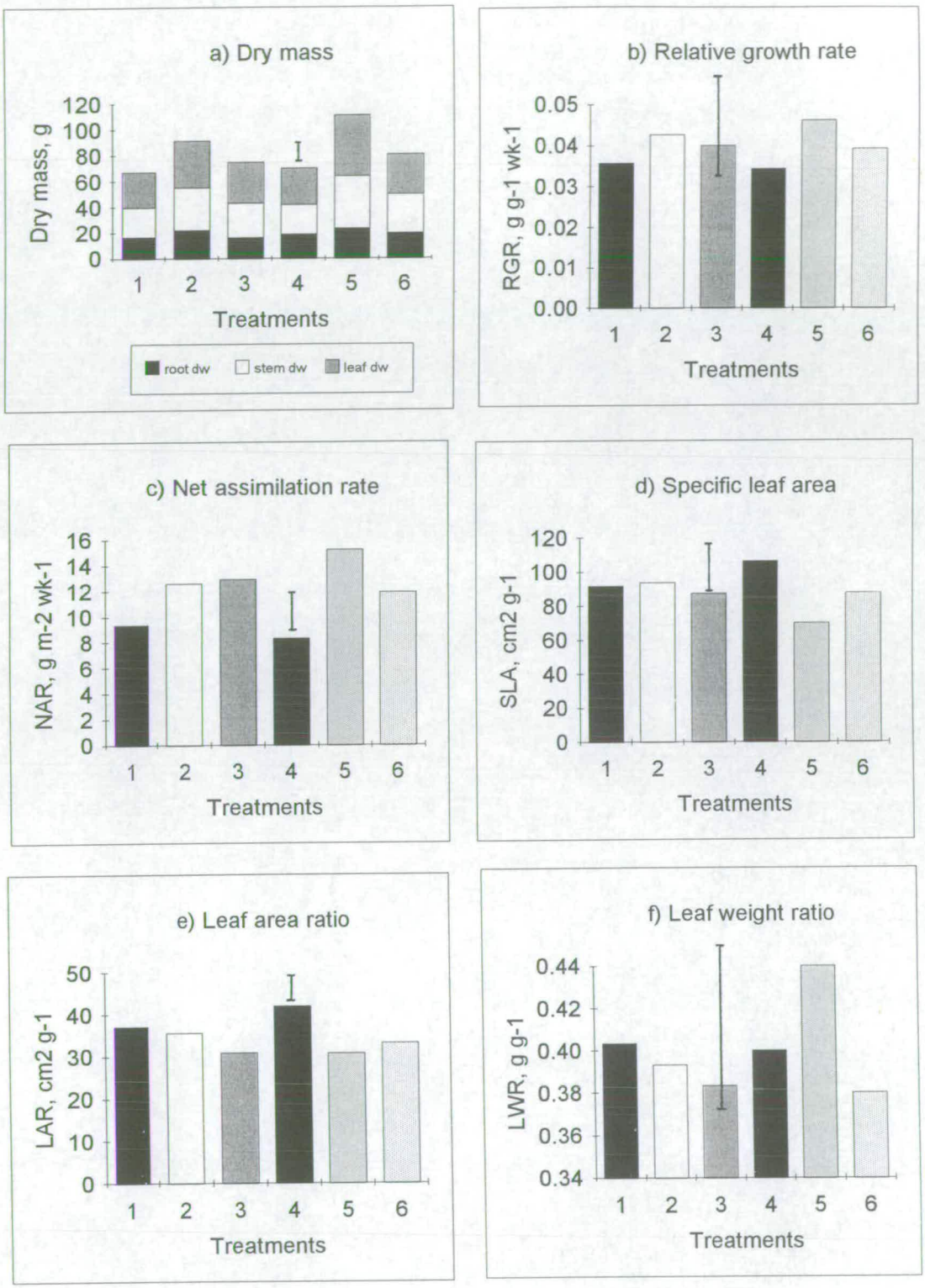


Figure 5.2 Different growth parameters of Khaya senegalensis under different treatments at the age of 2 years.

a) Treatments : 1 = Control, 2 = Mulch, 3 = Mycorrhiza, 4 = Trench 5 = Trench+Mulch, 6 = Trench+Mycorrhiza

b) The bar represents ± one overall standard error value for any treatment (n = 15-18 trees per treatment)

Table 5.5 Mean ± Standard Error values of Relative Growth Rate (RGR), Net Assimilation Rate (NAR), Specific Leaf Area (SLA) and Leaf Weight Ratio (LWR) on per plant basis in *Khaya senegalensis* at about 2 years of age. (n = 15-18 trees per treatment)

Treatments	RGR ($g\ g^{-1}\ wk^{-1}$)	NAR ($g\ m^{-2}\ wk^{-1}$)	SLA ($cm^2\ g^{-1}$)	LAR ($cm^2\ g^{-1}$)	LWR ($g\ g^{-1}$)
Control	0.036 ± 0.007	36.3 ± 3.5	91.7 ± 3.6	37.0 ± 2.2	0.40 ± 0.01
Mulch	0.043 ± 0.003	41.6 ± 6.8	93.8 ± 22.5	35.5 ± 5.6	0.39 ± 0.03
Mycor.	0.040 ± 0.008	45.3 ± 1.7	87.3 ± 19.4	30.9 ± 0.6	0.38 ± 0.07
Trench	0.034 ± 0.001	32.5 ± 3.2	106.1 ± 14.1	41.9 ± 4.1	0.40 ± 0.02
Trench + Mulch	0.046 ± 0.001	48.5 ± 4.7	70.0 ± 4.9	30.8 ± 3.0	0.44 ± 0.07
Trench + Mycor.	0.039 ± 0.006	42.5 ± 2.8	87.6 ± 4.9	33.1 ± 1.6	0.40 ± 0.03
Average values	0.040 ± 0.014*	41.1 ± 1.51	89.4 ± 13.5	34.9 ± 3.2	0.34 ± 0.04

* Overall standard error values

5.3.2 Growth analysis

Mean relative growth rate was significantly different at p=0.05 level for overall treatments. For mulching treatments also it had highly significant effect (p=0.001) over the unmulched treatments. The highest value of 0.046 $g\ g^{-1}\ wk^{-1}$was recorded in the trench+mulch treatments (Table 5.5 and figure 5.2b) showing clearly the effect of this combined treatment. Trenching had no effect on RGR values while mycorrhiza treatments showed significantly higher values (only marginally) compared to non-mycorrhiza treatments at p=0.05, possibly indicating some improvements of plant growth due to mycorrhiza treatments. Mean net assimilation rate was also significant for mulched over unmulched treatments and mycorrhiza over non-mycorrhizal treatments at p=0.01 level (Table 5.7 and Figure 5.2c).

Table 5.6 Results of analysis of variance for leaf number, leaf area, dry mass and root:shoot ratio of *Khaya senegalensis*.

Source	Leaf number	Leaf area	Root dry mass	Stem dry mass	Leaf dry mass	Total dry mass	Root: shoot ratio
Total treatments	ns	ns	ns	**	*	**	ns
Mulch	ns	*	**	***	**	**	**
Trench	ns	ns	ns	ns	ns	ns	ns
Mycor.	ns	ns	ns	ns	ns	*	ns

Table 5.7 Results of analysis of variance for various growth parameters of *Khaya senegalensis*.

Source	RGR	NAR	SLA	LAR	LWR
Total treatments	*	ns	ns	ns	ns
Mulch	***	**	ns	ns	ns
Trench	ns	ns	ns	ns	ns
Mycor.	*	**	ns	*(-)	ns

* - significant at 0.05 level ** - significant at 0.01 level

*** - significant at 0.001 level ns - non significant

(-) - negative effect

Table 5.8 The results of mean comparisons from Tukey's test for *Khaya senegalensis* at the age of about two years. (Values followed by the same letter are not statistically significant).

Treatments	Mean stem dry mass (g)	Mean leaf dry mass (g)	Mean total dry mass (g)	Mean RGR ($g\ g^{-1}\ wk^{-1}$)
Control	22.8 (a)	27.0 (a)	67.0 (a)	0.036 (a)
Mulch	32.9 (a)	36.1 (a)	91.5 (a)	0.043 (a)
Mycorrhiza	26.6 (a)	31.2 (a)	81.2 (a)	0.040 (a)
Trench	22.9 (a)	28.0 (a)	70.1 (a)	0.034 (a)
Trench + Mulch	40.6 (b) **	46.9 (b) *	111.2 (b) *	0.046 (b) *
Trench + Mycorrhiza	30.2 (a)	30.3 (a)	80.4 (a)	0.039 (a)

* - Significant at 5% level
** - Significant at 1% level

Significant improvements in both these parameters indicate some significant effects imposed by mulching and mycorrhiza treatments for growth of *Khaya* plants, as shown in Table 5.7.

Mean specific leaf area and leaf weight ratios were not significant for all the treatments tested in the experiment though they showed some differences as shown in the Figures 5.2d and 5.2f. However, a significant reduction in leaf area ratio was recorded in mycorrhiza treatments (Figure 5.2e) compared to other treatments which seems to be due to higher total dry matter production in comparison to leaf area development in those plants.

All interaction effects between treatments were not significant as shown in Appendix III.

5.4 *TOONA CILIATA*

5.4.1 Dry mass yield and allocation

As mentioned in the previous Chapter the growth of *Toona ciliata* was poor compared with the other species. The results of its mean dry matter production and leaf area development are presented in the Tables of 5.9, 5.11 and Figure 5.3a. Total dry mass production was not significantly different between any of the six treatments tested as similarly recorded for its growth parameters of height, diameter and volume growth in the previous Chapter. Factorial analysis of main treatments of mulch, trench and mycorrhiza showed that none of them were significantly different showing that these treatments have no considerable effect dry mass improvements of *Toona* in the early growth under the situation existing in the experimental site. However, some significant changes in the root:shoot ratio were noted in the mycorrhiza treatments (Table 5.11). It was significantly lowered ($p=0.05$) by this treatments possibly indicating that it induced shoot growth in comparison to root growth in the plants while total biomass production was unaffected. The mean values of this parameter changed from 0.17 in trench+mycorrhiza treatment to 0.26 in control and trench alone treatments. The block effect was non significant for this parameter.

Leaf development as shown by leaf number and leaf area parameters in Table 5.9 showed some differences between treatments. The mulch treatment had significantly ($p=0.01$) increased both leaf number and leaf area in the plants while trench and mycorrhiza treatments did not make any significant changes in these parameters. Leaf area was increased by about 36% by mulching. Mulching was not generally beneficial for growth of *Toona* plants but induced surface feeder root development in some plants (see section 4.4.5) which would have had some effect on the plant growth. Increased leaf number and leaf area development recorded under mulch would be beneficial for later growth of plants. The block effect was significant for leaf area but not for leaf number.

5.4.2 Growth analysis

Mean values of growth analysis parameters are given in Table 5.10 and the pattern of changes across the treatments are given in Figures 5.3 b,c,d,e and f. The mean relative growth rate was around 0.02 g g^{-1} wk^{-1} for all treatments and was not significantly different between treatments. Mean net assimilation rate values ranged

Table 5.9 Mean ± Standard Error values of leaf number, leaf area, root dry mass, stem dry mass, leaf dry mass, total dry mass and root:shoot ratio on per plant basis in *Toona ciliata* at the age of about 2 years. (n = 15-18 trees per treatment)

Treat-ments	Leaf Number	Leaf area (sq cm)	Root dry mass (g)	Stem dry mass (g)	Leaf dry mass (g)	Total dry mass (g)	Root: shoot ratio
Control	5.3 ± 1.0	416.3 ± 126.5	3.7 ± 1.3	6.4 ± 1.6	6.6 ± 3.2	17.4 ± 5.5	0.26 ± 0.05
Mulch	8.1 ± 0.6	581.0 ± 79.5	3.5 ± 0.9	6.2 ± 0.9	8.0 ± 0.7	17.7 ± 2.1	0.24 ± 0.05
Mycor.	8.5 ± 2.4	565.7 ± 181.0	3.6 ± 1.1	6.5 ± 1.7	9.2 ± 2.7	19.3 ± 5.5	0.23 ± 0.02
Trench	5.6 ± 0.5	410.0 ± 45.9	3.6 ± 0.7	8.0 ± 1.6	7.3 ± 1.3	18.9 ± 3.5	0.26 ± 0.03
Trench+ Mulch	8.4 ± 0.6	569.7 ± 88.1	3.9 ± 1.0	7.2 ± 1.4	8.7 ± 0.63	20.9 ± 2.3	0.23 ± 0.05
Trench+ Mycor.	6.4 ± 0.8	435.3 ± 11.8	2.3 ± 0.4	5.5 ± 1.3	8.3 ± 1.3	16.0 ± 2.5	0.17 ± 0.01
Average values	7.0 ± 1.1*	496.2 ± 70.1	3.4 ± 0.6	6.6 ± 1.2	8.0 ± 1.8	18.4 ± 3.3	0.23 ± 0.03

* Overall standard error values

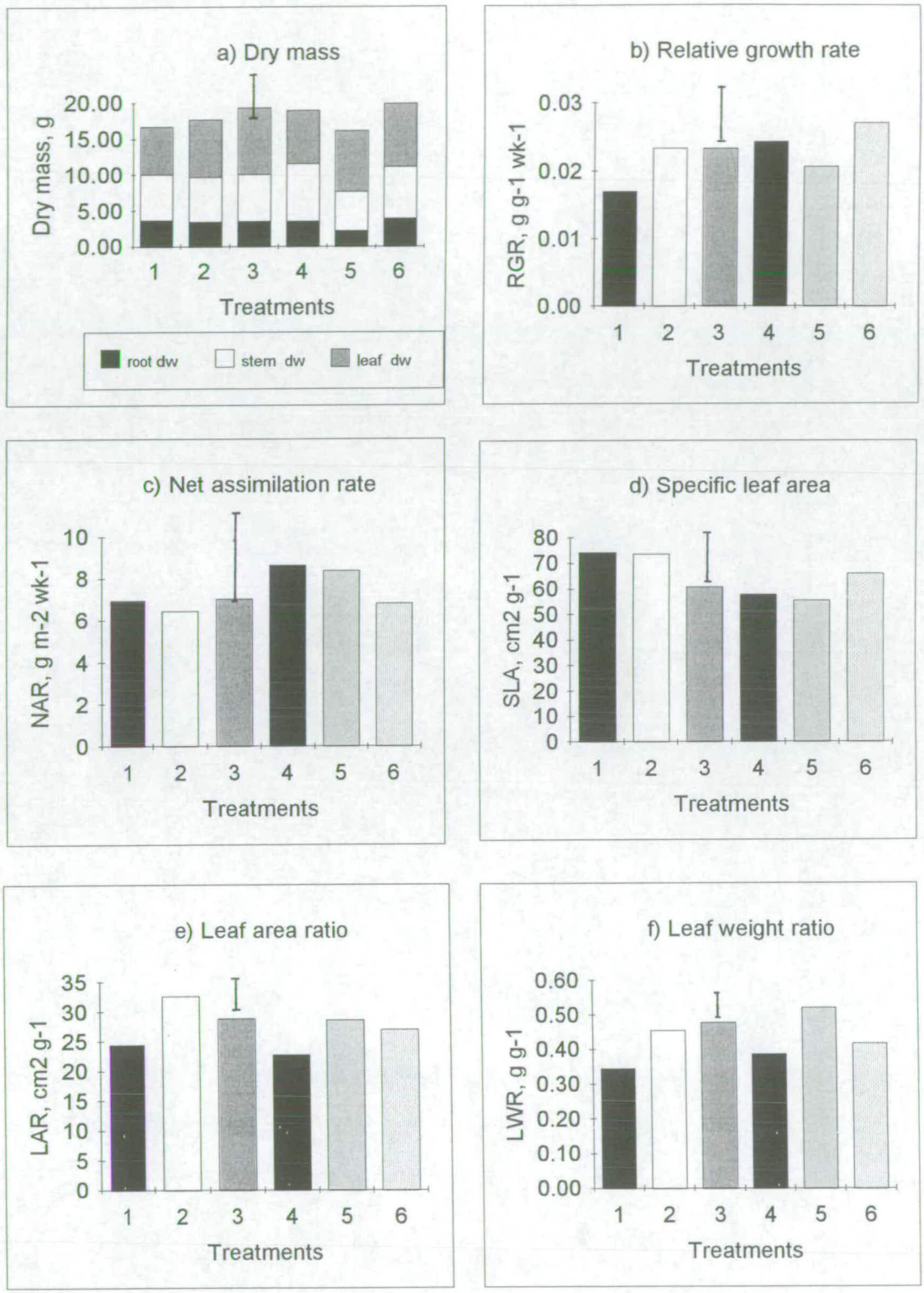


Figure 5.3 Different growth parameters of Toona ciliata under different treatments at the age of 2 years.

a) Treatments : 1 = control, 2 = Mulch, 3 = Mycorrhiza, 4 = Trench 5 = Trench+Mycorrhiza, 6 = Trench+Mulch

b) The bar represents ± one overall standard error value for any treatment (n = 15-18 trees per treatment)

Table 5.10 Mean ± Standard Error values of Relative Growth Rate (RGR), Net Assimilation Rate (NAR), Specific Leaf Area (SLA) and Leaf Weight Ratio (LWR) on per plant basis in *Toona ciliata* at the age of about 2 years. (n = 15-18 trees per treatment)

Treatments	RGR ($g\ g^{-1}wk^{-1}$)	NAR ($g\ m^{-2}\ wk^{-1}$)	SLA ($cm^2\ g^{-1}$)	LAR ($cm^2\ g^{-1}$)	LWR ($g\ g^{-1}$)
Control	0.02 ± 0.0015	6.9 ± 1.6	74.2 ± 11.8	24.4 ± 2.3	0.34 ± 0.06
Mulch	0.02 ± 0.0009	6.4 ± 0.3	73.63 ± 10.6	32.6 ± 1.8	0.45 ± 0.04
Mycor.	0.02 ± 0.06	7.0 ± 1.6	60.8 ± 4.5	28.9 ± 1.6	0.48 ± 0.01
Trench	0.02 ± 0.006	8.6 ± 2.3	57.8 ± 7.4	22.7 ± 3.6	0.39 ± 0.01
Trench + Mulch	0.03 ± 0.001	6.8 ± 2.5	66.0 ± 8.5	27.0 ± 1.6	0.42 ± 0.04
Trench + Mycor.	0.02 ± 0.005	8.4 ± 0.2	55.4 ± 10.6	28.5 ± 4.9	0.52 ± 0.05
Average values	0.02 ± 0.004*	7.4 ± 1.6	64.6 ± 9.5	27.3 ± 2.9	0.43 ± 0.04

* Overall standard error values

Table 5.11 Results of analysis of variance for various growth parameters of *Toona ciliata.*

Source	Leaf no.	Leaf area	Total dry mass	Root: shoot ratio	RGR	NAR	SLA	LAR	LWR
Mulch	**	**	ns	ns	ns	ns	ns	ns	*
Trench	ns	ns	ns	ns	ns	ns	ns	ns	ns
Mycor.	ns	ns	ns	*	ns	ns	ns	ns	ns

* - significant at 5 % level ** - significant at 1 % level

ns - non significant

from 6.4 to 8.6 g m^{-2} wk^{-1} between treatments and was also not significant. Specific leaf area and leaf area ratios were statistically similar in all treatments but the leaf weight ratio was significantly higher (p=0.05) in mulch treatments. The mean values of the control was 0.34 while mulch treatments had higher values around 0.43 g g-1 for this parameter. The significant results of leaf parameters indicate that the mulch treatments had some favourable effects on leaf production in *Toona*.

No interaction effects were found between treatments for any of the growth parameter studied (see Appendix III).

5.5 *SWIETENIA MACROPHYLLA*

5.4.1 Dry mass yield and allocation

Mean total dry matter production of *Swietenia* at about one year after planting varied from 19.0 g in the control to 25.3 g in the trench+mulch+mycorrhiza treatment which was an increase of about 33%. All the treatments showed higher values in varying degrees compared to the control (Table 5.12). However these differences were not distinguishable statistically (Table 5.14) as similarly reported for its notional volume growth. Root:shoot ratio was also not significant while showing changes between 0.18 in the combined treatment to 0.25 in the control. This indicates that the treatments applied might have increased shoot growth in comparison to root growth (See Figure 5.4 a). This may be beneficial for the establishment phase of the plants to achieve faster growth rates. Both leaf number and leaf area showed increases over the control in all treatments. The mean values of leaf area ranged from about 595 sq cm to 848 sq cm showing about 42% increase in combined treatment plots compared to the control plots. This was also not statistically significant apparently due to interaction between blocks and treatments which would have made the results more variable within the blocks. Leaflet number was also higher in all treatments than the control but was not significant. Although firm conclusions cannot be drawn from these results due to statistical non significance it indicates that some changes may have taken place in plants in all the treatments applied compared to the control. Increased leaf area, leaf number, shoot dry weight etc. may be expected to provide better results in terms of growth in these plants in later stages. The period over which the experiment was conducted possibly would have been not sufficient to show

Table 5.12 Mean ± Standard Error values of leaf number, leaf area, root dry mass, stem dry mass, leaf dry mass, total dry mass and root:shoot ratio on per plant basis in *Swietenia macrophylla* at about 1 year after planting. (n = 15-18 plants per treatment)

Treat-ments	Leaflet Number	Leaf area (sq cm)	Root dry mass (g)	Stem dry mass (g)	Leaf dry mass (g)	Total dry mass (g)	Root: shoot ratio
Control	27.3 ± 3.8	594.7 ± 89.0	3.7 ± 0.35	7.0 ± 0.12	8.2 ± 0.82	19.0 ± 0.59	0.25 ± 0.03
Mulch	35.3 ± 4.8	798.0 ± 123.1	3.8 ± 0.31	9.1 ± 1.67	10.8 ± 1.61	23.7 ± 3.57	0.20 ± 0.02
Mycor.	35.7 ± 3.9	800.3 ± 60.2	4.2 ± 0.31	10.4 ± 0.79	10.0 ± 0.93	24.6 ± 1.59	0.21 ± 0.01
Trench	35.3 ± 4.7	802.7 ± 115.9	4.3 ± 0.38	9.6 ± 2.11	11.0 ± 2.55	24.9 ± 4.8	0.23 ± 0.03
Trench+ Mulch+ Mycor.	38.0 ± 4.0	848.0 ± 105.9	3.9 ± 0.13	9.8 ± 0.60	11.6 ± 0.08	25.3 ± 0.55	0.18 ± 0.01
Average values	34.3 ± 4.1	768.7 ± 86.2	4.0 ± 0.3	9.2 ± 0.9	10.3 ± 1.3	23.5 ± 1.8	0.21 ± 0.02

changes due to treatments. The block effect was found to be non-significant for total dry matter production, leaf area and leaf number.

5.4.2 Growth analysis

None of the growth parameters studied showed significant results (Table 5.14). Mean relative growth rate and net assimilation rates were about 25% higher in combined treatment plots showing some possible improvements of growth due to the treatments during the experimental period (Table 5.13 ; Figures 5.4 b,c). Further improvements might be expected in later stages of growth. This could have happened due to increases in leaf number and leaf area and resulting efficiency of photosynthetic capacity of plants. Other parameters such as specific leaf area, leaf area ratio and leaf weight ratio were not affected much due to various treatments (Table 5.13 ; Figures d,e,f) and they were not significant statistically. The results indicate that any possible

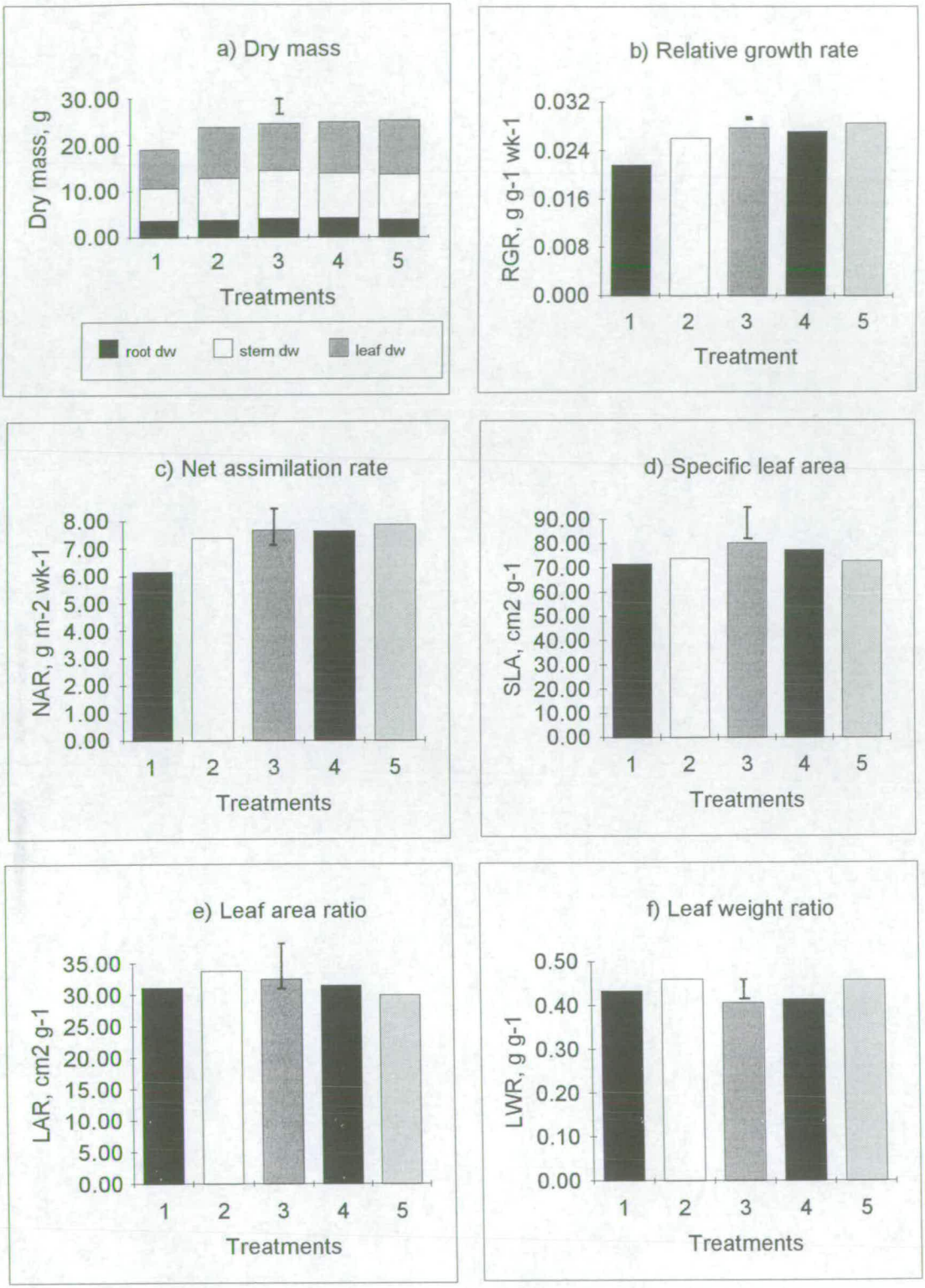


Figure 5.4 Different growth parameters of Swietenia macrophylla under different treatments at the age of 2 years.

a) Treatments : 1 = Control, 2 = Mulch, 3 = Mycorrhiza, 4 = Trench 5 = Trench+Mulch, 6 = Trench+Mycorrhiza

b) The bar represents ± one overall standard error value for any treatment. (n = 15-18 trees per treatment).

Table 5.13 Mean ± Standard Error values of Relative Growth Rate (RGR), Net Assimilation Rate (NAR), Specific Leaf Area (SLA) and Leaf Weight Ratio (LWR) on per plant basis in *Swietenia macrophylla* at about 1 year after planting.

Treatments	RGR ($g\ g^{-1}\ wk^{-1}$)	NAR ($g\ m^{-2}\ wk^{-1}$)	SLA ($cm^2\ g^{-1}$)	LAR ($cm^2\ g^{-1}$)	LWR ($g\ g^{-1}$)
Control	0.022 ± 0.002	6.2 ± 0.71	71.5 ± 4.3	31.1 ± 3.9	0.43 ± 0.03
Mulch	0.026 ± 0.003	7.4 ± 0.77	73.8 ± 2.1	33.7 ± 1.3	0.46 ± 0.01
Mycor.	0.028 ± 0.002	7.7 ± 0.45	80.1 ± 3.0	32.5 ± 0.8	0.41 ± 0.03
Trench	0.027 ± 0.003	7.6 ± 1.07	77.3 ± 9.3	31.4 ± 2.1	0.41 ± 0.02
Trench + Mulch+ Mycor.	0.028 ± 0.001	7.9 ± 0.69	72.7 ± 9.1	30.0 ± 6.0	0.46 ± 0.01
Average values	0.026 ± 0.003*	7.4 ± 0.83	75.1 ± 7.1	31.7 ± 3.8	0.43 ± 0.02

* Overall standard error values

Table 5.14 Results of analysis of variance for various growth parameters of *Swietenia macrophylla.*

Source	Leaf no.	Leaf area	Total dry mass	Root: shoot ratio	RGR	NAR	SLA	LAR	LWR
Total treatments	ns	ns	ns	ns	ns	ns	ns	ns	ns

ns = non significant

growth improvements at this stage is apparently due to improved shoot growth including increases in leaf number and leaf area.

Treatment interactions were not significant for this species as similarly observed for other species.

5.6 DISCUSSION

Growth characteristics and growth analysis in the previous sections discussed the individual performance of different species under pine canopy at different sites. Of the species discussed the highest growth rates were clearly achieved by *Alstonia* trees. The other species were performing satisfactorily in terms of early growth and survival except *Toona*, but their growth rates were much less than *Alstonia*. Considerable growth differences were shown in different growth parameters by different species with different treatments. A comparison of various growth parameters in different species is presented below.

The mean total biomass production at the end of the second year was highest in *Alstonia*, which was about ten times greater than that of *Khaya* plants. *Toona* plants had only about one fifth of total biomass than *Khaya* which indicates its poor performance under the present trials (see average values of Tables 5.1, 5.4 and 5.8). *Swietenia* dry matter values cannot be directly compared with these values since they are based on only one year results. However, the mean values of *Swietenia* at one year after planting were higher than those obtained for *Toona* at two years after planting indicating that *Swietenia* has much faster dry matter production than *Toona* under pine canopy in the present sites.

Mulching increased total dry matter production particularly in *Alstonia* and *Khaya* plants. In *Khaya*, as described earlier in section 5.3.1, trenching in combination with mulching increased total dry matter production, but not when applied alone. Moreover, it also increased mean stem and leaf dry mass of the same species significantly. Mulching also increased leaf area and leaf number in *Toona* plants thus showing some benefits of this treatment even under higher rainfall conditions which may contribute for later development of these plants. Mycorrhiza treatments did not contribute for improved dry mass production in *Alstonia*, nevertheless, it had some effects on total dry mass production in *Khaya* plants only at $p=0.05$.

Root:shoot ratios at final biomass measurement varied between species; the highest average of 0.39 was in *Khaya* while *Alstonia* and *Toona* recorded 0.29 and 0.23

respectively. These values may change with the age of plants. This shows that *Khaya* allocates more biomass to root growth than the other species in its early growth. Initial biomass measurements of root:shoot ratios of this species had even higher values (data not shown) showing a higher proportion of roots compared to shoots in terms of weight in the earliest growth. The proportion of biomass allocation is apparently changing over time allocating more biomass to shoots. This indicates that *Khaya* plants tend to develop a better root system in the early stages and therefore its shoot growth is comparatively lowered during this period, but it may be expected to be faster in later stages of growth due to already well established root system. Plate 5.1 shows general root system of *Khaya* and additional feeder root development under mulch treatments. This type of growth habit has been generally observed under normal plantation conditions. In contrast, *Alstonia* was allocating more biomass to shoot growth thereby achieving faster growth rates. Ericsson (1995) showed that increased allocation of dry matter to below-ground parts is associated with an increased amount of starch in tissues and a change in the internal balance between C and N in roots and shoots. This gives some indication about how dry matter is partitioned in plants. Root:shoot ratio was somewhat lowered by mycorrhizal treatments in *Toona* inducing shoot growth which was in contrast with the finding of Chakravarty and Chatarpaul (1990) where they reported that higher root:shoot ratios can be developed by mycorrhizal infection in *Larix* species. In addition to these factors which affect biomass allocation to different parts of plants McMillin and Wagner (1995) reported that the processes involved are partially under genetic control.

Mulch treatments significantly decreased root:shoot ratio indicating shoot growth improvement was higher than root growth improvement in *Khaya*. This may be due to improved moisture and nutrient status in the rooting zone. It also developed a better tap root than any of the other species which is a better adaptation to cope with stressful conditions during the dry periods. Shoot growth is generally more inhibited by moisture stress than root growth in plants (Ledig et al, 1970) and high root:shoot is generally a characteristic of shade tolerabt species (Kitajima, 1996). The highest biomass in *Alstonia* was in stems while in all the other species it was in leaves. Nevertheless, leaf area was very high in *Alstonia* compared to all other species since it produced larger leaves particularly at later stages of the experiment, while *Khaya* had the second largest leaf area. *Alstonia* in these experiments had comparatively lower root:shoot ratio and was growing fast probably indicating sufficient nutrient supply for its growth. *Swietenia* had an average root:shoot ratio of 0.21 which varied

between 0.18 to 0.25. Studying biomass allocation in *Swietenia*, Gerhardt (1995) reported that root:shoot ratio is not changed by light levels in a secondary forest but it tended to increase with age. Trenching did not affect biomass growth or related parameters in most of the cases in the present experiments except coupled with mulching in *Khaya*. In somewhat similar fashion, Gerhardt (1995) also reported that in a secondary forest, *Swietenia* did not respond to trenching. Generally, root competition for soil resources changes root:shoot ratio by increasing biomass partitioning to roots at the expense of the shoots (Kolb and Steiner, 1990). Lack of change in root:shoot ratios except in *Khaya* may possibly indicate that there was not much root competition from pine for broadleaves except for *Khaya* or it may be a general characteristic of those species. When nutrient supply is limited pioneer species in tropical areas are also reported to have higher phenotypic plasticity and are able to allocate higher biomass to roots increasing the root:shoot ratio (Rincon and Huante, 1995) but this type of change was not observed in *Alstonia*.

Average values of mean relative growth rates showed that the highest RGR is in *Alstonia* (0.048 g g^{-1} wk^{-1}) closely followed by *Khaya* (0.040 g $g^{-1}wk^{-1}$). *Swietenia* and *Toona* had lower values of 0.026 g g^{-1} $wk^{-1}$and 0.023 g g^{-1} wk^{-1} respectively. However, it should be noted that different species were growing in different sites which limits direct comparison. RGR values in *Swietenia* may be expected to improve further in later stages since plants usually show faster growth rates once they are well established (See Plate 5.2 for early and late growth of*Swietenia* trees under pine canopy). The above values show the higher efficiency of dry matter production in *Alstonia* and *Khaya* plants in comparison particularly to *Toona*. However, RGR values recorded here during a period of 11 months between 11 and 22 months of age seems to be much lower than that recorded by Konuche (1994) for African species of *Cordia* and *Vitex* species which were between 0.2 to 0.4 g g^{-1} $wk^{-1}$for a period of one month and he reported the values are decreased with decreasing light levels. However, the present values are comparable with what is reported by Pathak et al (1983) in *Leucaena leucocephala* recording 0.056 g g^{-1} wk^{-1} under full sunlight to 0.037 under 20% of full sunlight. Walters et al (1993) also reported that RGR values decrease continuously with increasing plant mass and age and reported lower values up to about 0.020 g $g^{-1}wk^{-1}$.

Relative growth rate of plants is affected by various factors and it is inherently low in shade tolerant species (Kitajima, 1996). Various nutrients are reported to increase RGR in plants. Ericsson and Kahr (1995) reported that plant magnesium content was

linearly correlated to RGR in birch seedlings grown under solution culture and under Mg limiting conditions, carbohydrate production was decreased, partially affecting root growth. Stadenberg et al (1994) showed in *Salix viminalis* plants grown in sand pots, that added nitrogen increases RGR, dry weight and total leaf area while decreasing root:shoot ratio. Generally, RGR is increased by nutrient status and light in plants as reported by McKee (1995). Mycorrhizal inoculation can also improve nutrient status and in turn RGR (Hogberg, 1989). On the other hand moisture stress can reduce RGR, NAR and LAR as demonstrated in tropical species *Gmelina arborea* by Ogbonnaya et al (1992). RGR is also dependant on age of plants; it usually increases with exponential growth of shoots and then decreases (Lord et al, 1993). Reduction in RGR is also reported by Singh et al (1993b) with age in tropical species. In temperate broadleaves it has been found that RGR is positively related to canopy net photosynthesis, LWR, LAR and rates of respiration in leaf, stem and roots. In contrast, under low light levels RGR was not correlated with net photosynthesis, but was positively correlated with LAR, LWR and rates of stem and root respiration.

Average mean net assimilation rate values were highest in *Khaya* recording 11.6 g m^{2-} wk^{-1} while *Alstonia* recorded the lowest average value of 5.4 g m-2 wk^{-1}. Both *Toona* and *Swietenia* recorded the same intermediate value of 7.4 g m-2 wk^{-1}. These indicates that dry matter production per unit leaf area is more efficient in*Khaya* than in *Alstonia*, although the leaf area was lesser in it. *Toona* is apparently inferior to *Swietenia* in this respect as its NAR up to about two years of age was similar to the value of *Swietenia* up to the age of one year. These values are somewhat below the values reported by Coombe (1960) for a fast growing tropical pioneer species *Trema guineensis* where the values were 14-15 g m^2 wk^{-1}. Significant improvements in NAR due to mulch treatments in all species except *Toona* shows that mulch can cause physiological changes in those plants which contribute to improved growth rates. Mycorrhizal inoculation also increased NAR in *Khaya*, though this was partly offset by reduction in LAR (see sections below) but still increasing RGR values.

Average specific leaf area was highest in *Alstonia* (348 cm^2 g^{-1}) while in other species it was much lower, with somewhat similar values between 65-90 cm^2 g^{-1}. This suggests that leaf morphology is different in *Alstonia* in comparison to all the other species. Dry matter in leaves of *Alstonia* seems to be thinly distributed increasing the leaf surface area which may be an adaptation to utilize a larger amount of sunlight. However, this may increase water loss from leaves and possibly due to this reason this species is generally growing better in wet areas. In *Eucalyptus*

species, SLA increases with shade as reported by Stoneman and Dell (1993), suggesting that leaf dry weight may be a better predictor of biomass production than leaf area in forest stands where shade is likely to affect growth specifically. Under drought stress conditions SLA is reported to be decreased in order to improve water use efficiency in plants (Philipps and Riha, 1993). In tropical rain forest species Reich and Walters (1994) found that SLA is highly correlated to net photosynthetic rate per unit leaf weight but not with unit area basis.

Average LAR was also fairly high in *Alstonia* (99.0 cm^2 g^{-1}) compared to other species showing that it has a higher photosynthetic area per unit weight of the tree while other species had only about 1/3 of this value. In contrast, average mean LWR was lowest in *Alstonia* (0.29 g g^{-1}) while other species had values between 0.34 to 0.43 g g^{-1}. Lower LWR in *Alstonia* was due to higher biomass allocation to stems which helped it to grow taller, also producing branches in early stages increasing the photosynthetic area considerably in comparison to other species. The fast growing ability under favourable conditions seems to make it grow more competitively under an overhead canopy of another species. In *Khaya*, LAR was significantly reduced in mycorrhizal treatments as described earlier which seems to be due to increase in leaf biomass or total biomass in relation to leaf area rather than a decrease in leaf area. *Toona* had the lowest LAR due to its shedding of leaves during some periods which reduces the leaf area per plant. *Swietenia* recorded higher values than *Toona* at half its age. Leaf development in *Swietenia* was faster during wet periods as observed by developing new flushes of leaves.

The differences in growth analysis parameters in different species was also affected by some of the treatments applied in the experiments. Mulching particularly improved RGR and NAR values of *Alstonia* and *Khaya* plants and this suggests that mulching treatment had a considerable ability to improve the dry matter production and its efficiency in this two species which may be highly valuable in silviculture of underplanting in pine stands. Trenching seems to be useful only under certain conditions as similarly reported for other growth parameters in the previous Chapter. Mycorrhiza inoculation improved RGR and NAR values only in *Khaya* probably through improved nutrition levels. In *Pinus sylvestris* Wallander et al (1994) showed that N, P, K concentration of shoots and RGR were negatively correlated with mycorrhizal development while Ca, Mg and starch concentrations in the shoots positively correlated. They also showed that high N supply can reduce concentrations of Ca, Mg and starch. Berta et al (1995) reported that arbuscular mycorrhizal

colonization increased root, stem and leaf weights, leaf area, SLA, and root length in *Prunus* species.

Specific Leaf Area was not affected by any of the treatments in any of the species in the present study. However, SLA has been reported in other studies to undergo plastic adjustments with respect to environmental changes in tropical pioneer species (Rincon and Huante, 1993). Leaf area ratio was affected (significantly lowered) only by mycorrhiza treatment and only in *Khaya* plants which seems to have been due to increase in leaf weight in this treatment without much effects on leaf area or leaf number. Leaf weight ratio was increased only by mulch treatment and only in *Toona*, which also seems to be due to increased leaf weights as a result of increased leaf number in contrast to what was experienced in *Khaya* plants. These findings indicate that mulch treatment had some favourable effects on only leaf development of *Toona* during the period of the experiments, but not for the overall growth of plants. However, this gives a valuable indication that improved leaf growth may result in later growth improvements of these plants. *Alstonia* showed no effect at all of mycorrhiza treatments as similarly reported in the previous Chapter. This might suggest an infection already of those plants as some mature trees of the same species were present in surrounding areas of the experimental site. Further research is necessary to monitor the growth in relation to mycorrhizal infection of broadleaved species under pine and if proven, could be used as an important silvicultural practice to improve growth of broadleaved species under pine or in other plantation conditions.

Growth analysis can be used to study growth responses as well as the changes in the tree structure and function caused by various factors. This can be done by separating RGR into its physiological component of NAR and morphological component of LAR. LAR is the product of SLA and LWR. It has been shown by Osunkoya and Ash (1991) that acclimatization potential in non-pioneer species may be more related to physiological than to morphological plasticity in rain forest species. The shade tolerant plants are reported to be distinct in their phenoplasticity in that they are able to maintain a constant relative growth rate over a range of light intensity from full sunlight to moderate shade due to the inverse relationship between dry matter gained per unit of leaf area (NAR) and the leaf area per unit dry weight of leaf (LAR), thus the productivity of leaf is maintained in low light intensities by changing the leaf area (Crawford, 1989). However, under the present experiments LAR was not changed

except in mycorrhizal treatments in *Khaya*. Lack of change in LAR was possibly due to the fact that light level was not changed across the treatments.

5.7 CONCLUSIONS

Out of the four species tested in these experiments, *Alstonia* is generally a species showing the characteristics of a pioneer. It is a colonizing species and grows well in fairly degraded lands although the growth is usually much better in fertile lands. The results of the biomass study showed that it can accumulate large amounts of biomass within a short period, with large leaves with rapidly expanding leaf areas. It showed the highest average RGR of all species which was further improved by mulching treatments which is clearly an advantage in the silviculture of underplanting. It seems to be well suited for planting under pine with additional growth improvements if mulching is done. Although *Khaya* is capable of growing in full sunlight it also has the ability to grow under shade (see section 2.3.3). It survived well under pine showing marked improvements in biomass production particularly due to combination of mulch and trench treatments. In another study Dalton and Messina (1995) showed that under shelterwood systems trenching is effective to improve water potential of understorey trees when overstorey basal area is high, and also overstorey could reduce transpiration in understorey plants. Similarly, as shown in the present studies trenching may be beneficial under certain conditions particularly when overstorey tree density is high or in low rainfall areas where root competition between species is likely. Mulch treatments produced improvements in some leaf characteristics. Accordingly, mulch and trench treatments seems to be beneficial for *Khaya* when it is planted under pine. Biomass production of *Toona* was not generally improved due to the treatments but found increased leaf weight ratios due to mulch application which may be beneficial for its later growth developments. *Swietenia* biomass production was not significantly improved with treatments apparently due to too short time period of growth monitoring. However, some improvements were shown due to the treatments particularly with the combined treatment of mulch, mycorrhiza and trenching.

CHAPTER 6

THE EFFECTS OF DIFFERENT THINNING REGIMES OF PINE ON GROWTH OF UNDERSTOREY BROADLEAVED SPECIES

6.1 INTRODUCTION

In this experiment different broadleaves including *Alstonia macrophylla*, *Toona ciliata*, *Swietenia macrophylla* and *Michelia champaca* were grown in the same pine stand under four different thinning regimes. The objectives of this experiment were to assess the growth and survival of these species under varying degrees of competition from pine overstorey for above and below ground resources as a result of different stocking densities, to compare the performance of different species and to find out interactions between species and thinning. In the previously explained trials in Chapter 4 and 5 three of these species were tested separately at different sites. In the present study, all the species were tested at the same site so that growth of different species could be compared under similar environmental conditions. The trial site was at a higher elevation than in the trials described in the last two Chapters and therefore climatic conditions were somewhat different from previously mentioned experiments. The site was in a slopy land and had been subjected to annual fires before the present trials were established. Thinnings were carried out in order to reduce the density of pine trees to specified levels of basal area. Unthinned controls showed a basal area of about 30 m^2 per ha while the other treatments had 20, 15 and 10 m^2 per ha. The respective tree densities for these basal areas were 793, 465, 316 and 208 trees per ha. Different species were planted in separate plots under each thinning treatment. Details of experimental design is given in section 3.3.4 in Chapter 3. Plant height and diameter were recorded 3 times for a period of about one year after planting in the field. Notional volume was calculated by multiplying height with squared diameter.

Data were analyzed using ANCOVA in Randomised Complete Block design. Treatments were arranged in a factorial way, considering thinning levels and species as two factors for the statistical analysis. Final measurements of treatments were adjusted by the analysis of covariance depending on the initial height. Initial measurements of height, diameter and volume were taken as the covariates for each analysis. Volume measurements were $\log_{10}$ transformed before analysis to make

variances homogenous. Survival percentage data were arc-sine transformed and analysed.

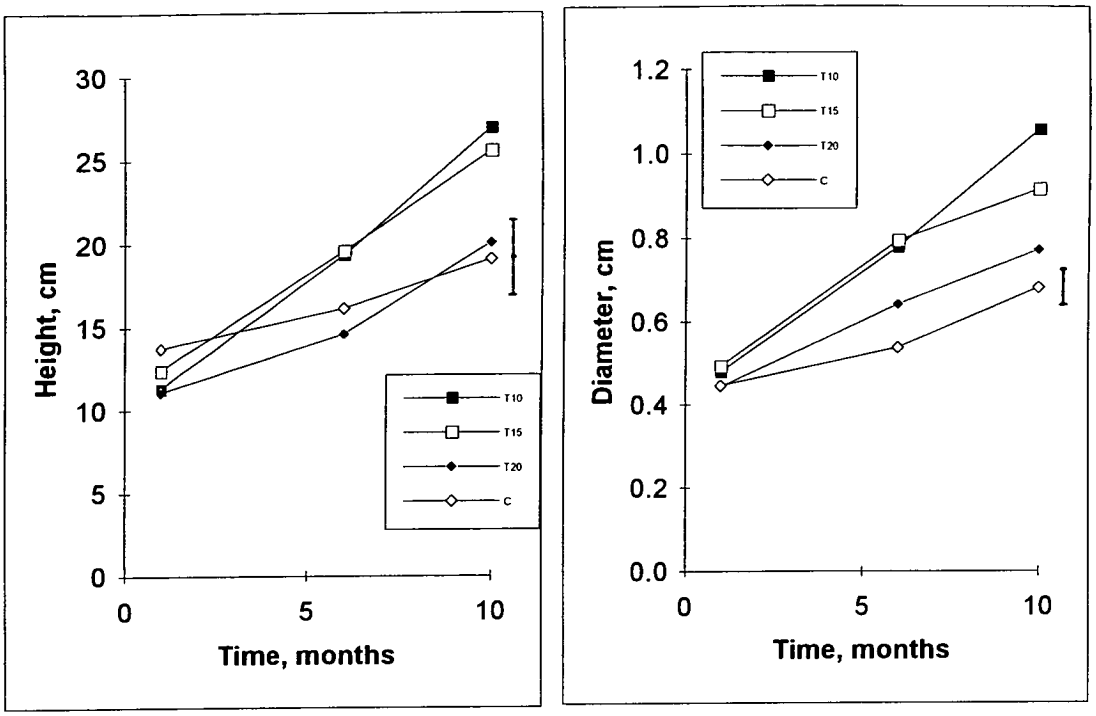
6.2 GROWTH OF DIFFERENT SPECIES UNDER DIFFERENT THINNING REGIMES

6.2.1 Survival and general performance

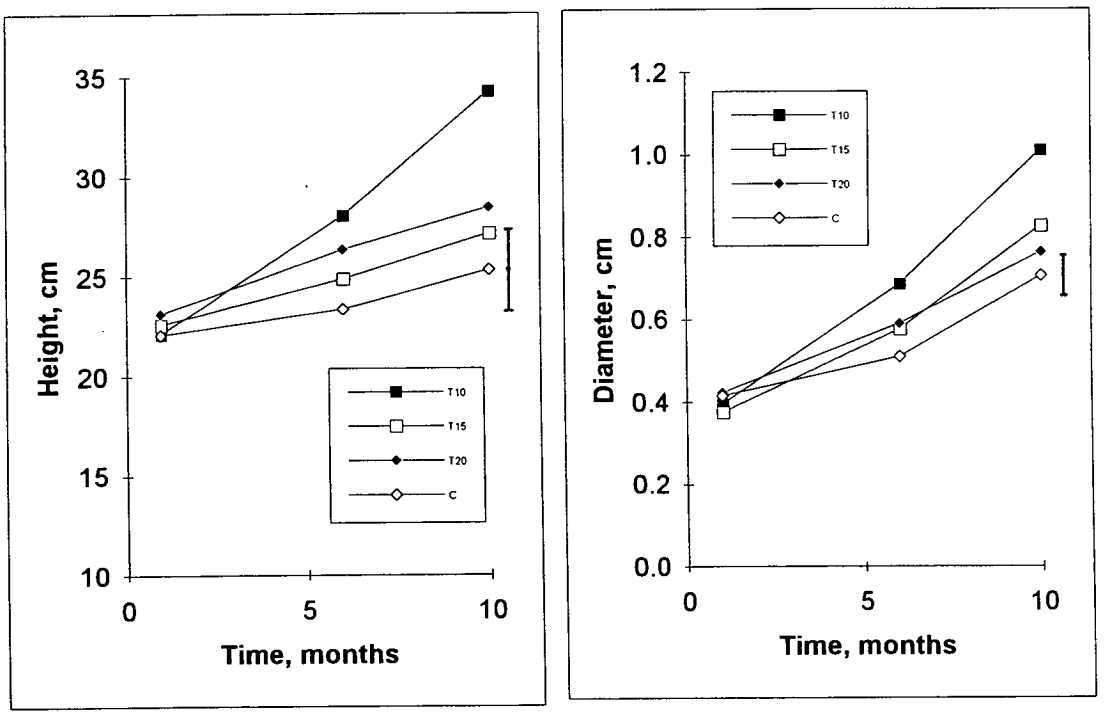
Survival was generally satisfactory, with all the species studied recording mean percentage values above 80. Survival percentage was highly significant between species but was non significant between thinning levels. (Table 6.1) suggesting that thinning level did not affect survival. The interaction between species and thinning intensities were also non significant. This may indicate that all these species can tolerate fairly high shade in terms of survival, even in the unthinned control. Mean values for *Toona* and *Michelia* were significantly lower than those of S*wietenia* and *Alstonia* (Table 6.2). Survival appeared to be mainly affected by dry weather experienced within the first year of planting. During this period the growth of all species was affected to some extent, often showing stunted growth. *Michelia* was seemed to be more susceptible to dry conditions than other species in early growth which reduced its survival percentage to some extent. All species recovered later from these effects when sufficient rains were received. Survival was not affected in the three different blocks in this experiment as indicated by non significant block effect.

6.2.3 Height growth

Mean height growth of different species over the period at different thinning treatments are presented in the Figures 6.1 and 6.2. This shows that height growth was much increased in all species under the highest thinning intensity (lowest basal area). In *Michelia,* height growth increased markedly at 10 and 15 m^2 basal area in comparison to the other thinning treatments. Within them, the growth patterns were generally similar throughout the experimental period. *Swietenia* height growth at the highest thinning intensity had a similar pattern and showed greater increases over time compared to the three other thinning treatments. Lower intensity thinning regimes showed lesser differences between them although having lowest values at the highest density (control) of pine trees. In *Alstonia,* mean height growth was also



Michelia champaca



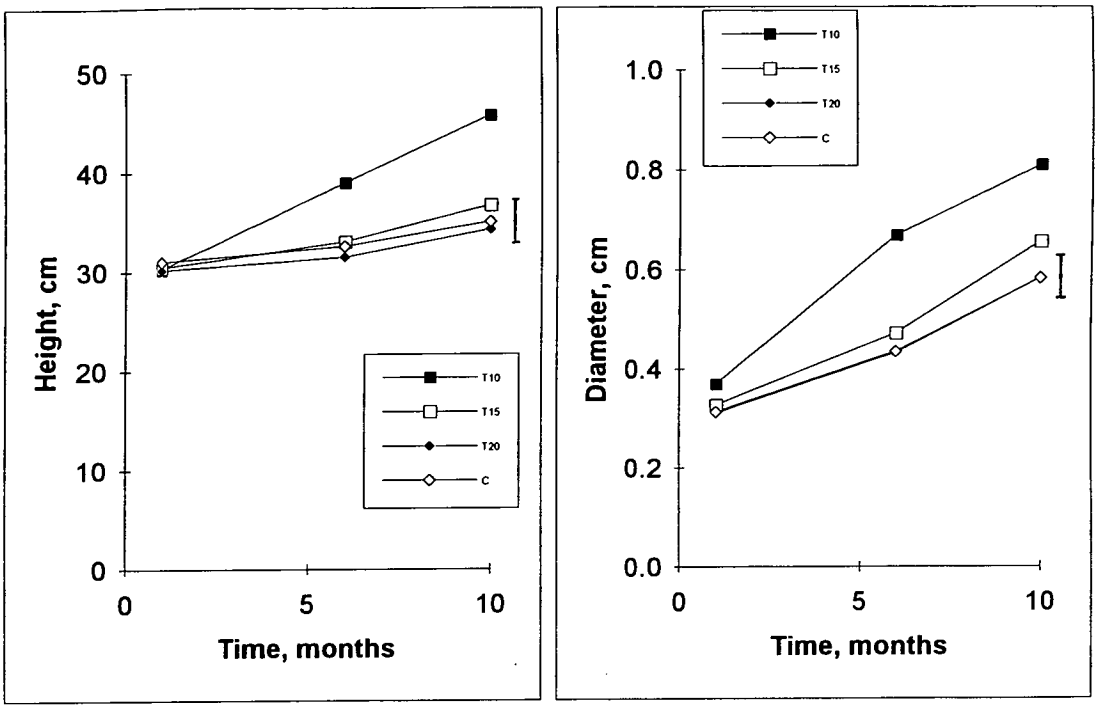
Swietenia macrophylla

Figure 6.1 Height and diameter growth of Michelia and Swietenia trees at different thinning levels of pine overstorey.

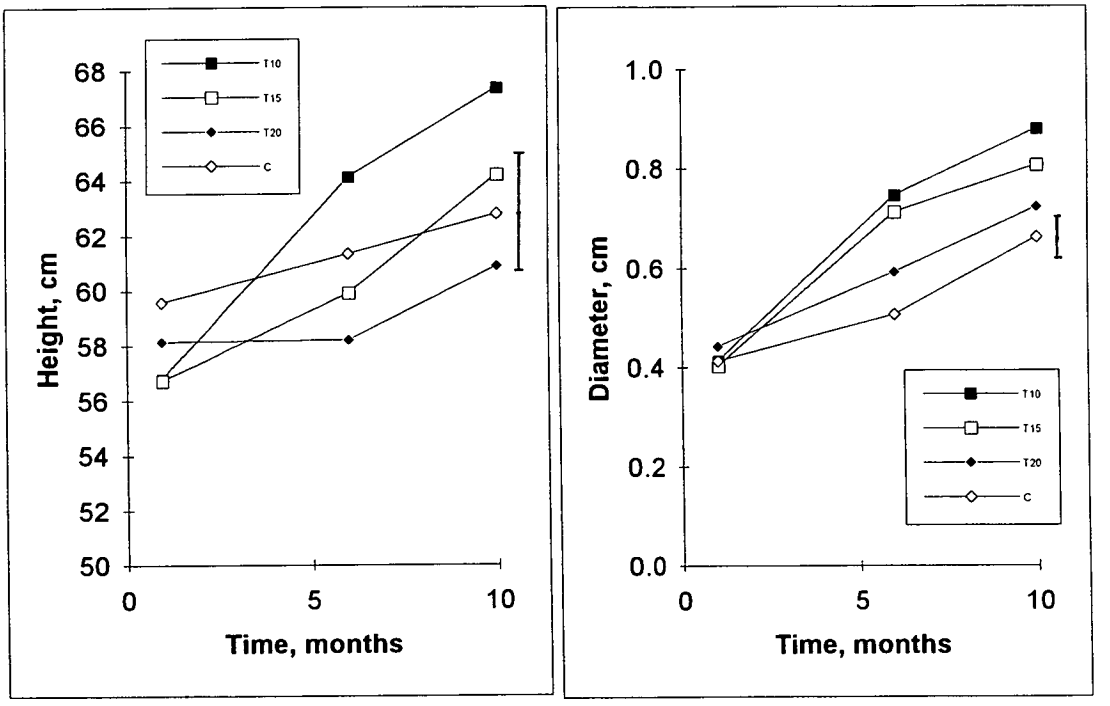
a) (T10, T15, T20 and C = 10,15,20 and 30 sq. m. per ha of basal area respectively)

b) The bar represents ± one overall standard error value for any treatment.

(n = 72 trees for each treatment)



Alstonia macrophylla



Toona ciliata

Figure 6.2 Height and diameter growth of Alstonia and Toona trees at different thinning levels of pine overstorey.

a) (T10, T15, T20 and C = 10,15,20 and 30 sq. m. per ha of basal area respectively)

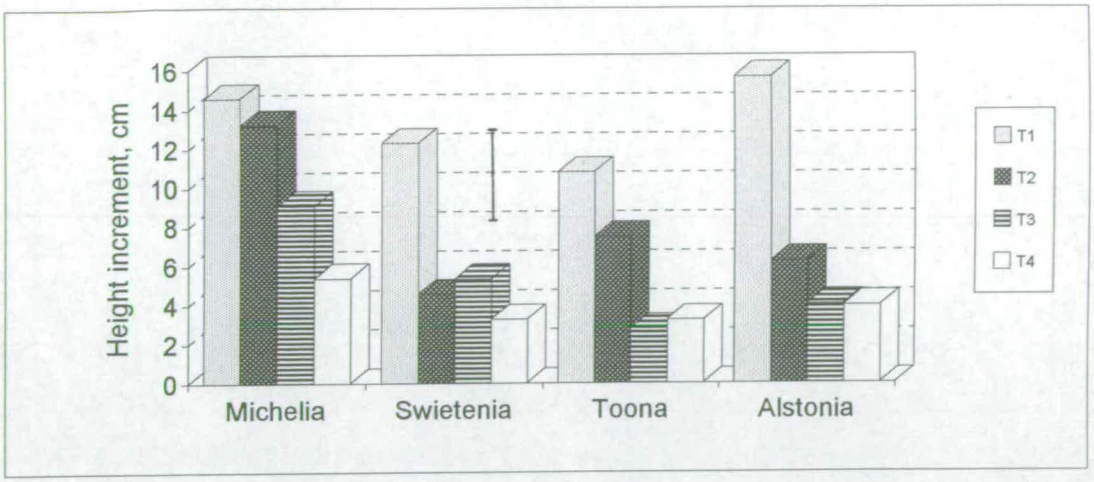
b) The bar represents ± one overall standard error value for any treatment.

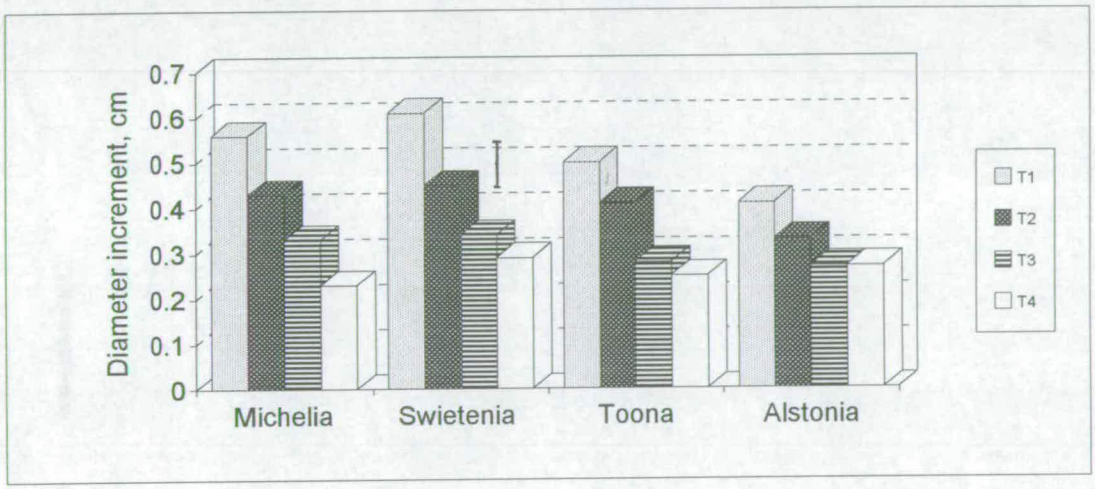
(n = 72 trees for each treatment)

greatly improved by the highest thinning level, while in all other thinning levels it did not differ greatly. Mean height growth of *Toona* was increasing with time in both thinning treatments of 10 and 15 m^2 basal area but not much in the control and in 20 m^2 levels. Initial height at the time of first measurement was somewhat variable in this species since the plants started showing differential growth rates apparently due to genetical variations. This was not much evident at the time of planting. These results show a general effect in all species of a strong reduction in height growth at tree densities of 20 m^2 basal area or more. Mean height increment of different species under different thinning regimes between first and final measurements is given in Figure 6.3. These results show that *Michelia* responded proportionately to increasing thinning intensities. Response of *Swietenia* and *Alstonia* height growth indicated that they were much affected at the basal area intensities of more than 15 m^2 while *Toona* growth was much lowered at 20 m^2 or more basal area.

Analysis of height data for species and thinning levels and their interactions showed that species and thinning levels were significantly different at p=0.01 and 0.001 levels respectively while the interaction between species and thinning was not significant at p=0.05 (Table 6.1). Lack of interaction between species and thinning levels suggests all the species show somewhat similar growth response to changes in overstorey tree densities. Further analysis with Tukey's test for mean comparisons showed that all the species were significantly different from each other across the thinning intensities (Table 6.2). The greatest height growth was achieved in *Swietenia* while lowest was in *Toona* when all the thinning intensities were considered. However, under the highest thinning intensity the greatest height growth was in *Alstonia* closely followed by *Michelia* as shown in Figure 6.4. This might suggest that under the existing conditions in this experimental site *Alstonia*, *Michelia* and possibly *Swietenia* have the potential to show greater height growths than *Toona* under more open conditions. On the other hand at second highest thinning level of 15 m^2 per ha *Michelia* surpassed the growth of all other species showing its ability to increase height growth under more shady conditions which was consistent under all thinning levels (See Figure 6.4).

Analysis of mean values by mean comparison test showed that the highest thinning level (10 m^2 per ha) was significantly different from the second highest thinning level (15 m^2 per ha) for height growth of all species. Moreover, the second highest thinning level was also significantly different from the other two lowest thinning





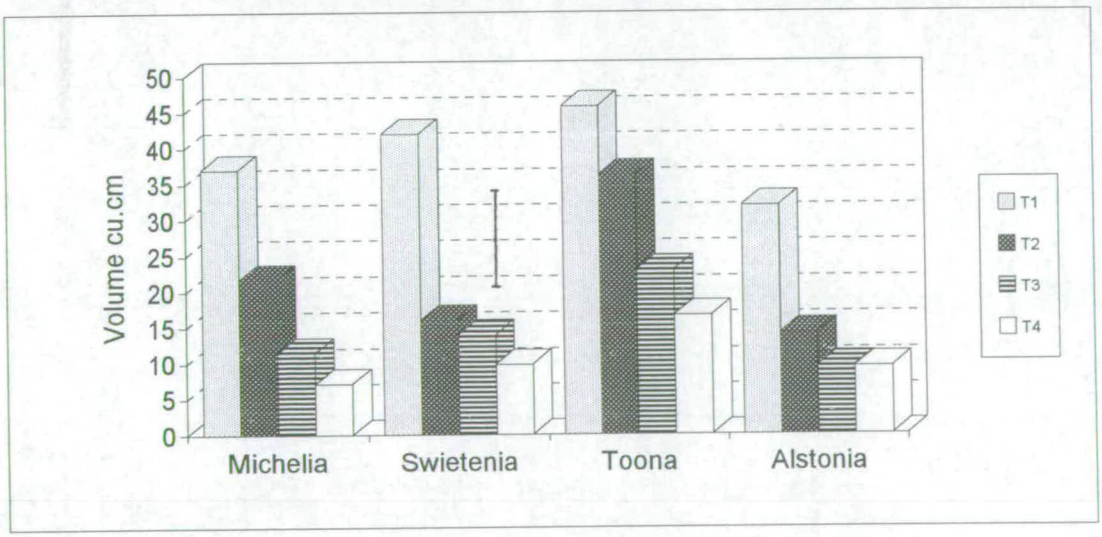


Figure 6.3 The effects of diffrent thinning regimes of pine on height, diameter and volume growth of the broad leaved species of Michelia, Swietenia, Toona and Alstonia.

a) T1=10, T2=15, T3=20, T4=30 m2/ha of basal area.

b) The bar represents ± one overall standard error value for any treatment. (n = 72 trees for each treatment)

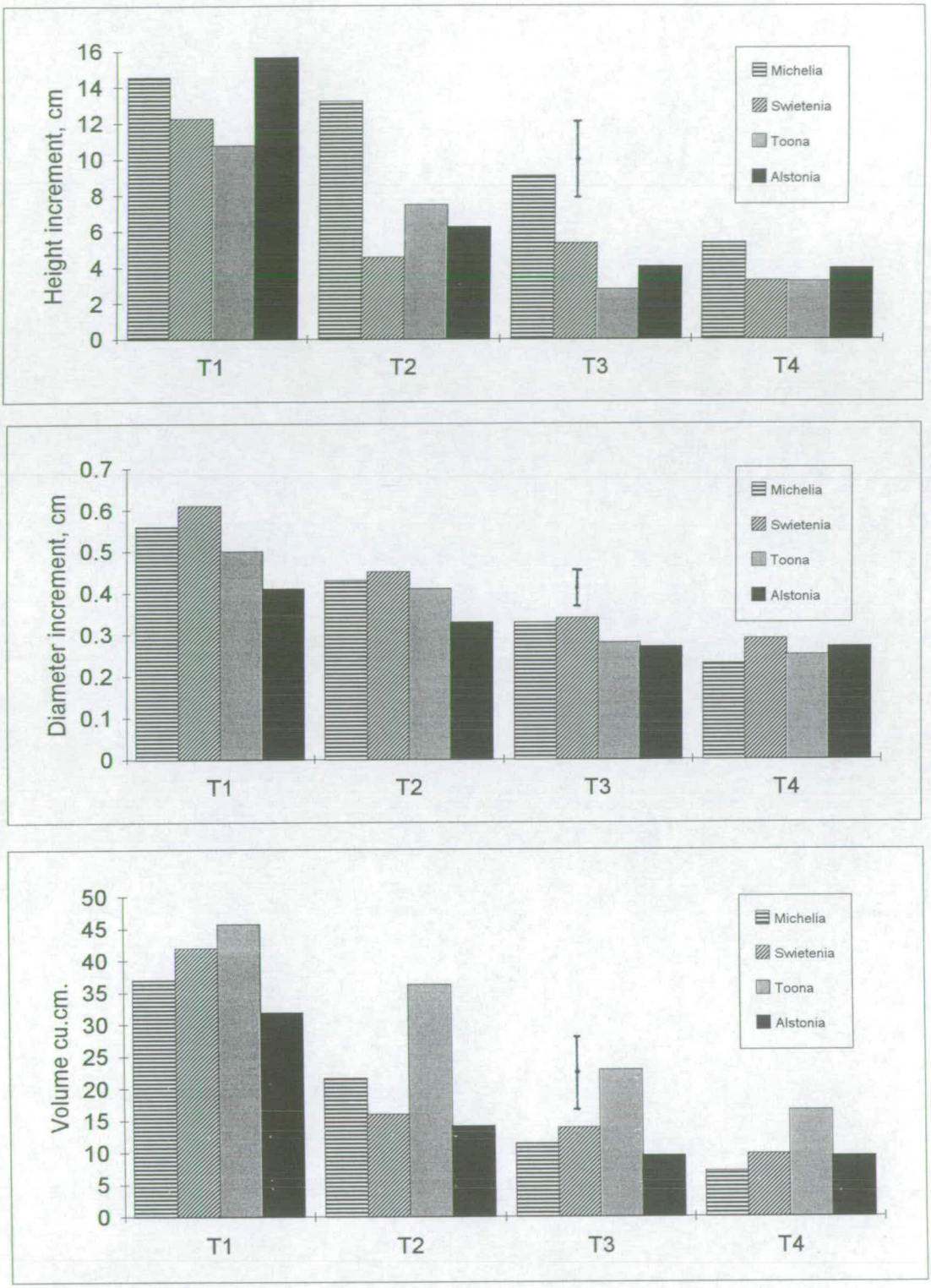


Figure 6.4 Performance of different broadleaved species under different thinning regimes of pine (For comparison with Fig. 6.3).
(T1=10 , T2=15, T3=20, T4=30 m2/ha of basal area)
The bar represents ± one overall standard error value for any treatment.
(n = 72 trees for each treatment)

levels while the lowest two including the control were not statistically different. This demonstrates that for height growth improvements in this species more open conditions are favoured in comparison to higher density overstorey conditions which not only reduce light level but also may increase root competition from pine trees for the growth of understorey plants. Block effect was highly significant for the treatments possibly due to slopy land where the trials were conducted.

6.2.4 Diameter growth

In all species diameter growth was reduced with increasing density of overstorey trees. Mean diameter growth patterns in different species under different thinning regimes during the experimental period are given in Figures 6.1 and 6.2. It is clear from these that they show somewhat similar pattern to height growth improvements. In all species diameter growth improved markedly in more open conditions with high thinning intensity beginning from a few months after field planting. The second highest thinning intensity of 15 m^2 per ha basal area was also better compared to other lower thinning intensities in all species. With increasing basal area, diameter increment gradually declined except in *Alstonia* where both lowest thinning intensities were similar (Figure 6.3). Under more open conditions the greatest diameter improvement was in *Swietenia*.

Statistical analysis of mean diameter growth showed that diameter was significantly different between species at the p=0.05 level (Table 6.1). Mean comparison tests showed that *Michelia* and *Swietenia* had greater diameter increments than *Toona* and *Alstonia* (Table 6.2). Diameter growth varied significantly between thinning treatments. Thinning levels were highly significant for diameter growth at p=0.001. Both higher thinning intensities were significantly different from the lower thinning intensities. The highest thinning intensity was also significantly different from the second highest thinning level which was similar to what was found for height growth. These findings show that diameter growth is much retarded under high overstorey pine tree densities of 20 and 30 m^2 basal area levels. The Species x thinning interaction was non-significant as for height growth and the block effect was significant.

Table 6.1 The results of analysis of variance for different treatments and their interactions in the thinning experiments.

Source	Survival %	Height	Diameter	Notional volume
Species	***	**	*	ns
Thinning	ns	***	***	***
Species x Thinning	ns	ns	ns	ns
Covariate	-	***	ns	***
CV	12.3	10.2	11.0	8.7

ns = non significant

* = significant at p=0.05

** = significant at p=0.01

*** = significant at p=0.001

CV = Co-efficient of variation

Table 6.2 The results of mean comparisons in the thinning experiments from the Tukey's test. (n = 72 trees per treatment)

Treatments	Mean survival %	Mean height (cm)	Mean diameter (cm)	Mean volume (cu. cm)
Swietenia	98.5 (b)	43.5 (c)	0.83 (b)	22.9 (a)≠
Toona	82.8 (a)	15.4 (a)	0.76 (a)	21.2 (a)
Alstonia	95.0 (b)	38.3 (b)	0.70 (a)	20.2 (a)
Michelia	83.3 (a)	56.1 (d)	0.82 (b)	24.0 (a)
T1 - 10 m^2/ha	92.8 (A)	44.5 (C)	0.93 (C)	37.2 (C)
T2 - 15 m^2/ha	90.2 (A)	38.7 (B)	0.80 (B)	24.2 (B)
T3 - 20 m^2/ha	93.5 (A)	36.1 (A)	0.71 (A)	17.8 (A)
T4 - 30 m^2/ha	88.5 (A)	34.0 (A)	0.66 (A)	14.7 (A)
SE*	5.21	2.25	0.049	6.60

* Overall standard error for all treatment means

≠ Values followed by same letter are not statistically different from each other.

6.2.5 Volume growth

Mean notional volume growth increment as shown in the Figure 6.3 was markedly decreased with increasing overstorey tree density. Volume growth increment of*Alstonia* and *Swietenia* was favoured only in the highest thinning level and in all other three thinning intensities it was considerably reduced possibly indicating their volume growth is affected under high overstorey density and prefer much open conditions. In contrast *Michelia* and *Toona* showed gradual decline of volume growth with decreasing thinning intensity probably indicating that they are consistently better able to tolerate shade in volume growth. In general, volume growth of all broad leaved species was much decreased at higher overstorey tree densities particularly at basal area levels of 20 and 30 m^2 per ha (Figure 6.4).

Statistical analysis of volume growth revealed that volume growth was not significantly different between species (Table 6.1 and 6.2) which was different from height and diameter growth analysis as explained earlier. However, similarly to height and diameter growth analysis, thinning levels were highly significant for mean volume growth across all the species. The highest thinning intensity of 10 m^2per ha basal area was significantly different from 15 m^2 basal area. The other two lower thinning intensities were statistically same but was different from both of the higher levels of thinning which is similar to what explained for height and diameter growth. The reduction of mean volume growth from the highest to lowest thinning levels in all species was about 60% which shows that the control plots with 30 m^2 were very unfavourable for the growth of all underplanted broadleaved species. Block effect for volume growth was highly significant.

6.3 DISCUSSION

As described in the preceding sections, all species performed in a somewhat similar pattern under different thinning intensities. Compared with the almost unthinned control plots of 30 m^2 per ha, about 40%, 60% and 74% of trees had to be removed to bring down the basal areas up to 20, 15 and 10 m^2 per ha respectively. This shows that the most open plots had heavy thinning bringing the final number of trees down to 208 per ha from 793 in the control, while the intermediate basal areas had 465 and 316 trees per ha. Direct light transmission as a percentage of full sunlight was 58%, 52%, 35% and 18% for the basal areas of 10, 15, 20 and 30 m^2 per ha respectively. This shows that light levels were somewhat closer in the lowest basal area levels. The

relationships between light and understorey tree growth will be discussed in detail in Chapter 7.

All parameters of height, diameter and volume generally decreased at higher tree densities of pine, indicating constraints for their development under increasing basal area of overstorey trees. It was also clear that basal area of 20 m^2 per ha or more reduced growth considerably in almost all species. The basal area levels of 20 and 30 m^2 were statistically similar for all growth parameters studied, though there were some differences in mean values as shown in Figures 6.3 and 6.4. All species preferred more open conditions showing better height, diameter and volume growth. *Swietenia* and *Alstonia* tended to show much reduced growth above 10 m^2 basal area (below 54% light level) particularly for height and volume indicating their greater preference for reduction in overhead canopy. This seems to be in agreement with the findings of Ramos et al (1992) which showed that 68% light transmission is more favourable for the growth of *Swietenia macrophylla* compared to a 37% light level. In the other two species of the present study, these parameters were much affected only beyond 15 m^2 basal area possibly indicating apparently their higher shade tolerance comparatively. It should be noted in this site that variation in canopy openness may be confounded with variation in other factors such as root competition. Regeneration of commercial shade-tolerant species is not affected much by increasing basal area while regeneration of intolerant species increased with decreasing basal area as reported by Negreros-Castillo and Mize (1993). Good survival (above 83%) in all species in the present study under all levels of shade shows their adaptability to remain even under heavy shade conditions although their growth may be affected. Very little site specific information relating establishment, survival and initial growth of tree species to varying levels of light is available as mentioned by Carter and Klinka (1992).

It has been generally observed under field conditions in Sri Lanka and other tropical countries that *Swietenia* is shade intolerant except in the nursery stages and early growth after field planting. It has been planted under the overhead shade of secondary natural forests successfully for a long time in the country which clearly shows its capacity to adapt to shade conditions. The field experience on growing *Swietenia* further shows that direct overhead sunlight with side protection from other trees is very beneficial for its growth. However, the experience of its growth under plantation species such as pine is generally lacking in the country, except for some recent attempts to introduce it into pine plantations in a pilot project. In these attempts, it

was grown under pine stands where only pre-commercial thinning had been done at the time of planting of *Swietenia* and this was followed by a subsequent thinning. Under these conditions *Swietenia* grew up to 8-9 m under more open conditions and 5-6 m under more shady conditions at about 8 years after planting. This shows the ability of *Swietenia* to grow under pine, especially if sufficient thinning is carried out to facilitate its growth. Stevenson (1927) reported a long time ago in Central America that *Pinus caribaea* lands are naturally colonized by other species including *Swietenia macrophylla*. However, apparently no investigations have been reported of any attempts to grow *Swietenia* under *Pinus caribaea* in other countries.

In *Alstonia*, full sunlight is preferred directly from field planting, however it also has the capacity to grow under overhead shade conditions as can be observed in most of the areas where it is growing in the country. *Alstonia* which like *Swietenia* is naturally regenerating once it is established, is probably adapted to shade conditions for its seed germination and early seedling growth, probably a pre-requisite for natural establishment. *Alstonia* can also be observed spreading naturally into pine plantations (in some cases up to pole stage saplings) which gives some supportive evidence for the possibilities of introducing it to pine plantations. *Toona* and *Michelia* have also not been tested under plantation conditions in the country, although they are planted widely and also naturally regenerating to some extent in private lands. Under these conditions, these species can be observed to grow in mixtures with other species, and also naturally growing seedlings can be observed to thrive under shade. The conditions under such intimate mixtures are vary variable and experimental evidence with respect to the growth requirements are generally lacking.

Thinning of a stand normally reduces the number of trees competing for light, soil moisture and nutrients. After thinning, more light reaches beneath the canopy which can be made available for any understorey plants. The light level beneath the canopy can be controlled by timing and changing of the intensity of thinning of trees and also by pruning of crown. Thus, monitoring and balancing of light distribution between different storey components can increase the total productive potential of stands. The degree of shade can be used as a silvicultural tool to encourage upward growth and straight stems in the understorey. Individual trees in thinned stands have deeper crowns thereby intercepting more sunlight with the greater photosynthetic area. However, in species such as *Swietenia macrophylla*, which is less strongly light demanding, reduction of crown depth due to shading is reported to be lower (Evans, 1992).

Thinning of a tree stand not only increases light level on the forest floor but also reduces root competition from the overstorey trees for soil moisture and nutrients and also possibly changes micro-climatic conditions beneath the overstorey canopy. There seems to be a relationship between shade tolerance and soil moisture as has been investigated by some researchers. Carter and Klinka (1992) reported that shade tolerance in some species decreases with increasing soil moisture. Therefore increasing levels of light is required with increasing available soil moisture. In a similar investigation Oosting and Kramer (1946) suggested that forest seedlings are more drought resistant in the open than in the shade and therefore such species grow better in the margin of forests where more sunlight is received. In the present study, increasing levels of light due to increased thinning levels would have been associated with less root competition from pine for soil moisture making more soil moisture available to growing seedlings and therefore possibly would have reduced shade tolerance of plants in more open conditions. However, on the other hand more open conditions may increase soil moisture evaporation from soil and evapo-transpiration from understorey trees balancing the effect of reduced root competition for soil moisture. Nevertheless, these effects may be site specific and therefore more studies are needed to confirm this. In the present study, increased height, diameter and volume growth were reported in all species and this may be attributed to increased light as well as possible reduction in root competition for soil moisture and nutrients. It may also be expected that tree seedlings and overstorey may not compete much with one another in the initial stages of understorey growth with respect to root competition. These findings are in agreement with Tryon et al (1992) who reported that percentage light was directly related to percentage radial growth improvements in sugar maple plants under oak overstorey. They also postulated that heredity of species may be of considerable importance in addition to silvicultural characteristics and environmental factors.

In addition to the factors discussed above, thinning of tree stands will increase solar and thermal radiation on the forest floor and also probably reduce air humidity depending on the level of intensity. Increased solar radiation may increase soil temperature and in turn nutrient mineralization rates in the litter layers. Vesterdal et al (1995) reported that accumulated C and P were negatively linearly correlated with thinning intensity under temperate climates. They also reported that C:P and C:N ratios tended to decrease in the heaviest thinning plots and suggested that more favourable micro-climate and substrate is created for saprophytic organisms under

heavily thinned conditions which may enhance mineralization. Apart from these possible benefits, reduction of pine litter accumulation by reduction of tree stocking would be beneficial in the present study area since slow litter breakdown is associated with high fire risk which is extremely harmful for early growth of understorey species. However, the effects of thinning may gradually disappear with tree root growth and canopy closure in remaining trees unless repeated thinnings are carried out subsequently. Successful establishment and growth of understorey species in initial stages is very important in underplanting since this may enable them to successfully compete with overstorey trees for available soil resources and light.

6.4 CONCLUSIONS

The results of this part of the study shows the adaptability of different species to varying levels of pine overstorey thinning. In general, all species performed better under the heaviest thinning regime of 10 m^2 basal area. *Michelia* and *Toona* was comparatively better at 15 m^2/m. However, sudden heavy thinning of overstorey pine trees may encourage weed growth on the forest floor and also may render the pine trees susceptible to wind damage in addition to creating unfavourable and harsh environmental conditions under the existing degraded site conditions. Shading effect will usually improve these conditions. Moreover, light level seems to be much improved when basal area is reduced from 20 to 15 m^2 per ha with considerable growth improvements in underplanted species. Therefore it seems to be more appropriate and practical to thin stands down to 15 m^2 without much affecting the growth of the species, and this involves about 60% removal of trees from the existing density of about 800 trees per ha. With the same thinning intensity, possibly light level can be further improved by row thinning rather than uniform thinning if rows are oriented towards east to west direction or nearly so. Very low intensity thinning or unthinned situations will interfere with understorey growth, markedly affecting the growth as revealed in this study, and it also poses a risk of damage for understorey seedling when subsequent thinning is done in the overstorey. Therefore, manipulation of pine canopy before planting understorey species and subsequent opening to facilitate their later growth seems to be essential for maximizing the growth and in turn for the success of underplanting. The continuation of this study for a longer period may be particularly important since it can result more valuable information on the effects of thinning levels on later growth of these species. Moreover, the effects of silvicultural practices such as mulching in addition to thinning and probably their combined effects can be tested in later studies.

CHAPTER 7

GROWTH RESPONSES OF BROADLEAVES TO LIGHT ENVIRONMENT UNDER PINE CANOPY

7.1 INTRODUCTION

Previous chapters have dealt with soil micro-climatic changes imposed by various experimental treatments and their influences on broadleaved seedling growth under pine. This chapter focuses on the effects of light environment on the growth of underplanted seedlings. The investigations are based on the same experimental sites discussed in the previous chapters. A quantification of the light environment where the different experiments were conducted and possible effects of existing light regimes on growth of broadleaved species are discussed. Whether the effects of light influenced the experimental treatments described in previous Chapters were investigated by taking light as a covariate in the ANOVA. Possible relationships between light levels and sapling growth in different experiments are also discussed in this Chapter.

Light level in the understorey was measured using hemispherical photographs (see section 3.5). Hemispherical photography using fish eye lenses has been used to measure light conditions under tree canopies for a long time (e.g. Anderson, 1964). In contrast to sensor measurements which directly measure photon flux density, hemispherical photos provide a means of assessing light conditions over a relatively longer period of time. They also have the advantage of estimating diffuse and direct components of the light environment separately. Although the technique gives reasonable estimates of understorey light environment, it has been realized that the technique is unable to detect small differences in understorey light environments. Other disadvantages are lack of consideration for penumbral effects of sunflecks, differences in light transmission due to atmospheric changes and reflections of transmittance from leaves which may introduce some errors into the light measurement. Also, the indirect light factor is calculated assuming sky is uniformly bright which is not the case in most field situations (Chazdon, 1988). Nevertheless, various researchers (eg. Chazdon and Field, 1987) have found good correlations between photographic estimates and measured values of photosynthetically active

photon flux density (PPFD) in various studies, indicating general assumptions are often sufficient for reasonable accuracy.

Light is one of the most important factors controlling plant growth and is particularly important in underplanted environments. The availability of light is usually greatly limited though depending on the opening of the overhead canopy. The major factors that influence light in the understorey depend on the nature of the forest canopy, position of the sun, atmospheric conditions of the region, cloudiness etc. The forest canopy is the main factor influencing the quality, quantity and duration of photosynthetically active radiation (PAR) at ground level (Boardman, 1977). Movement of the sun and atmospheric changes cause large diurnal and seasonal changes in the quality and quantity, and duration of day light. Solar radiation consists of direct and indirect (diffuse) components which are received at varying levels on understorey plants depending on the changes of the factors mentioned above, complicating its influences on plant growth beneath the forest canopies. As both forms of radiation passes through vegetation, spectral quality is altered by selective absorption, transmission, and reflection of wavelengths by foliage, branches and boles (Chazdon, 1988). In cloudy climates, much of the light can be diffuse. The diffuse light on the floor shows a high proportion of far-red and near infrared radiation also with an increase in green light relative to the blue and red wavelengths (Boardman, 1977). Direct sunlight creates sunflecks when it passes through holes in the canopy bringing direct radiation to the forest floor, which is important for photosynthesis of understorey plants. In understorey conditions, sunflecks have sometimes been estimated to contribute over two-thirds of all PAR (Pearcy, 1987) while Chazdon (1986) reported that it may contribute 10-78% of the daily PAR on clear days. In contrast, diffuse radiation penetrates all canopy openings which may also be important for plant growth.

Different species are adapted to different light environments and those species with at least some shade tolerance are important for underplanting. However, early successional species which are light demanding are reported to be more plastic than shade tolerant late successional species (Carpenter and Smith, 1981; Boardman, 1977). Bazzaz and Carlson (1982) reported that these early successional species are capable of changing patterns of photosynthetic response to light intensities in such a way that they become more like shade plants when grown in shade and also they have higher physiological flexibility relative to that of late successional species (Bazzaz, 1979). In contrast, late successional species are generally unable to adapt to high light

environment. Early successional species may often be also plastic in their response to moisture conditions (Pickett and Bazzaz, 1978) and temperature (Chabot and Chabot 1977). Though these species in different categories of shade tolerance can grow differently in some cases, early successional species generally grow better in the high light environment and late successional species grow well in the shade environment while the mid successional species grow well in both environments (Bazzaz and Carlson, 1982). In shade adapted species, long life spans have been suggested as a means of conserving nutrients (Chabot and Hicks, 1982) and as enduring shade (Coley et al, 1985). When plant species are raised in 'sun' conditions, their leaves contain more nitrogen and this is associated with an increased mesophyll conductance (Ramos and Grace, 1990). However, the differences between shade-adapted and sun-adapted species are not clear in some tropical species since morphological, physiological and biochemical properties of leaves may change during tree development (Bazzaz and Pickett, 1980). Most shade tolerant plants have a lower light saturation point (Bazzaz and Carlson, 1982). Light saturation can occur in these plants at about 10-15% of full sunlight and the photosynthetic rate can remain unchanged if they are exposed to intensities above saturation (Bazzaz, 1979). In some cases too much exposure of shade adapted leaves to high light intensities may cause photoinhibition (Boardman, 1977).

Leaves of plants grown at low light intensities may have more chlorophyll per unit weight or unit volume of leaf, but the chlorophyll content per unit area is often lower than that of leaves grown at higher light intensities. Proportion of chlorophyll b relative to chlorophyll a increases as the light intensity is lowered. (Boardman, 1977). The higher capacity for C fixation per unit area of leaf is associated with greater amounts of the carboxylating enzyme, ribulose biphosphate carboxylase (RUBISCO), but the capacity for C fixation per unit volume of leaf is directly related to leaf thickness. Dark respiration is reported to be lower in shade tolerant plants (Bazzaz and Carlson, 1982) thus conserving photosynthates. Higher dark respiration in intolerant species can cause lower assimilation rates under shade. (Loach, 1970).

Thus, different light intensities can change the physiological and morphological characteristics of leaves and other parts of the plants. High light intensities cause stronger development of palisade and spongy mesophyll cells resulting in thicker leaves (Boardman,1977). The development of leaf thickness depends on energy supply and not directly on the light intensity as shown by Hughes and Evans (1963) where specific leaf area (SLA) was more closely related to net assimilation rate

(NAR) rather than light intensity. Corr (1983) found that a major adaptation to a lower light intensity is the formation of thinner leaves with a higher water content resulting in a higher SLA in species such as *Galinsoga parviflora* and *Stachys silvatica.* Another important adaptation is the decrease of the root weight ratio in low light. This may have not much unfavourable effects due to lower transpiration rates under low light conditions. Dry matter not used for root growth may benefit the stems and leaf area development. Light demanding species that grow in areas where soil moisture is not limiting, generally produce larger leaves as shown in the present study in *Alstonia* and in another Sri Lankan study of *Shorea* species by Ashton (1995). However, under conditions where soil moisture is limiting pioneers often produce smaller leaves (Ashton, 1995). Internodal elongation and thereby stem elongation occurs in plants in response to inadequate light intensity in light-demanding species but generally not in shade tolerant species (Kimmins, 1987).

Popma and Bongers (1988) reported that plants grown under more open conditions in large gaps have a high root:shoot ratio, a high Specific Leaf Weight (SLW) and a low Leaf Area Ratio (LAR), while plants grown under shade had the opposite. Shade tolerant species were able to grow in the shade because of a high NAR values. However, it was also noted that all species do not simply show shade or sun plant characteristics, but may instead exhibit complex growth responses in which they show characteristics of both tolerant and intolerant species in response to different light. Whitmore and Gong (1983) compared NAR of tropical species and found that it is higher in shade tolerant ones. Okali (1972) also found that NAR increases in fast growing rain forest species from 54% to 100% full sun.

When light passes through the canopy red and blue light regimes are selectively absorbed while most of the far-red light is transmitted through the vegetation (Smith, 1981). Plants growing below overstorey canopies are therefore subjected to both low photon flux density of light and direct sunlight, and low R:FR ratios (Longman and Jenik, 1987; Whitmore, 1975). Tropical pioneer species are reported to respond strongly to R:FR in terms of greater height growth and a shift in allocation to stem growth over leaf growth in low R:FR as compared to high R:FR under open conditions (Tinoco-Ojanguren and Pearcy, 1995; Smith, 1981).

Species are categorised as pioneer (also called light demanders, secondary species or early successional species) or climax (shade demanders, primary species or late successional species) mainly based on their requirement for sunlight for the seed

germination, establishment and growth, in addition to various other characteristics. This terminology is somewhat confusing and there is no general agreement (Whitmore, 1990), and it also lacks a precise definition (Swaine and Whitmore, 1988). The confusion is increased because some species show intermediate characteristics with the features of both pioneer and climax species. It is now generally considered that tree species are best seen as lying in a continuum between the extreme ends of pioneers and climax species.

Swaine and Whitmore (1988) reported that species whose seeds only germinate in gaps in the forest canopy are pioneers and those that germinate under shade (very rarely under full sun as well) are non-pioneers or climax species. Climax species are sub-divided according to varying degrees of seedling shade tolerance. Strongly shade tolerant species grow slowly and form dark, dense and hard timber while less shade tolerant species grow fast and have pale, light and soft timber. Pioneer species, with their strong demand for light, also generally show the characteristics of inability to survive below canopy shade, production of small seeds, shorter life cycle etc. Another important characteristics of these two groups are that pioneers maintain a soil seed bank while climax species have a seedling bank on the forest floor. The least shade-tolerant climax species are very similar to pioneer species except for the property of the capacity to germinate and establish below a canopy. Within climax species there is variation in the amount of solar radiation needed for seedling growth. At one extreme there are species which need solar radiation for fast growth, such as for example those called light hardwoods in Malaysia. Apart from the essential character of germination and seedling establishment below a canopy they resemble pioneers. At the other end, via the continuum of response, are other climax species which require very little or no increase in solar radiation for release and are considered heavy hardwoods (Swaine and Whitmore, 1988). Species which become dominant in late secondary forests later than pioneers but earlier than climax species are identified as late secondary species by some authors, though Swaine and Whitmore (1988) prefer to call them as large pioneers which live longer than small ones or as a light-demanding sub-group of climax species (Whitmore, 1990).

Some other important features of pioneer and climax species are reported by Kitajima (1996): pioneers have higher rates of phenotypic plasticity, acclimation potential and inherent relative growth rate while having low root:shoot ratio and initial seedlig size; while the opposite is observed in climax species. Generally, light saturated rates of photosynthesis and light compensation point are considerably higher in light

demanding species than in shade bearing species (Boardman, 1977). Light saturation in late successional species occurs at much lower light intensities of around 10-15% of full sunlight (Bazzaz, 1979). In early successional species the environmental conditions are varying and the species adapted to such habitats may show physiological and morphological plasticity to adapt to the existing environment (Bazzaz and Carlson, 1982).

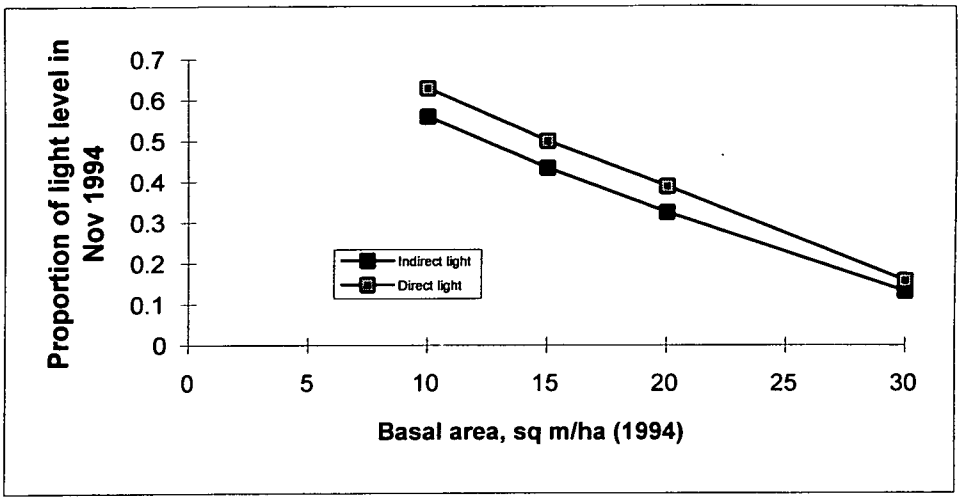
7.2 RESPONSES OF DIFFERENT SPECIES TO LIGHT LEVELS

7.2.1 Estimation of light levels found in the different pine stands in relation to thinning levels

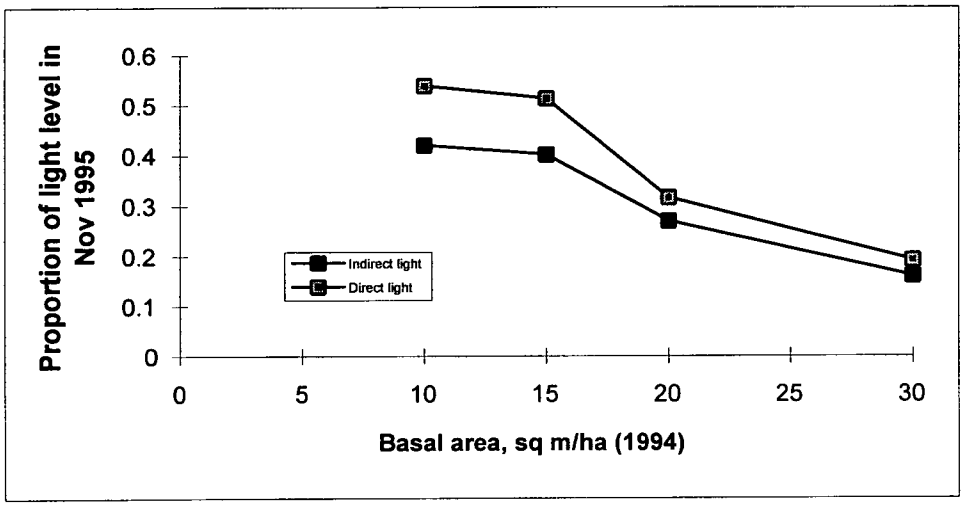
The light environment under different pine stands was characterized using hemispherical photographs (see Plate 7.1). Direct and indirect light levels (direct and indirect site factors respectively) as a percentage of full sunligh were calculated separately from the photographs (see section 3.5). These showed that mean values of both parameters were closely related and the indirect factor was always somewhat lower than the direct factor (Figures 7.1a and 7.1b). This is in accordance with the findings by Turner (1990) who reported a good correlation between the two components. Mean basal area of pine at different thinning intensities was linearly related to tree stocking (Figure 7.1c). The canopy opening in unthinned, row thinned and uniformly thinned stands photographed by fish eye lens are shown in Figures 7.2, 7.3 and 7.4. This gives an indication of the amount of canopy opened in comparison to the unthinned control.

All the light levels described hereafter in this section refer to direct light unless otherwise stated. In the thinning experiment at the Kinigama site where different species were planted at the same site, the results showed that thinning (in this case uniform thinning throughout the stand) increased light level on the forest floor considerably as expected. About 8 measurements were done per each thinning treatment. The almost unthinned stand had a light level of 16% of full sunlight which increased up to a maximum of 63% at the highest thinning intensity with intermediate values of 39% and 50% at medium thinning intensities (see Figure 7.1a). These values were obtained in a few months after the thinning operation. A second light measurement one year after the first one showed that light transmission has reduced at certain thinning intensities. In the highly thinned plots, light levels decreased from 63% to 54% possibly due to canopy expansion in response to thinning of the stand

a)



b)



c)

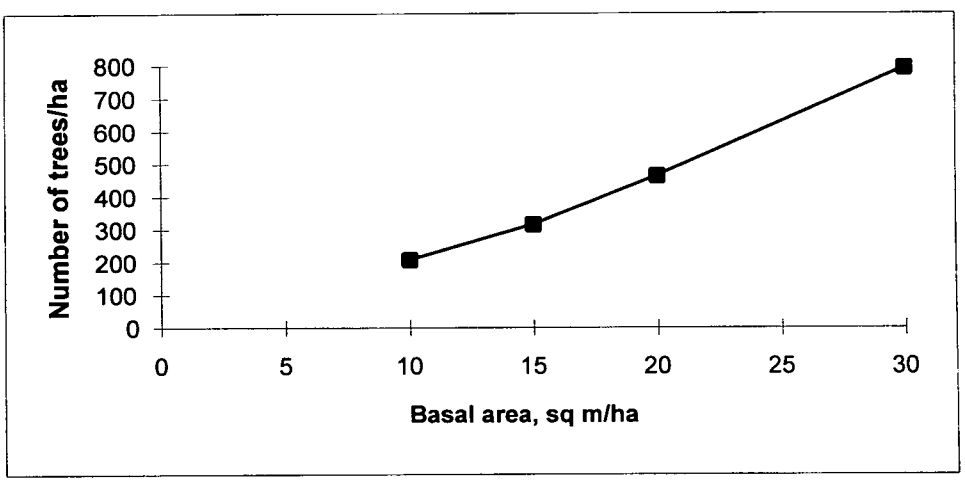


Figure 7.1 Relationships between light level, basal area and tree stocking density at different thinning intensities at Kinigama site.
a) and b) Proportion of light level at different basal areas in 1994 and 1995 respectively. Note basal area is for 1994 in both cases.
c) Relationship between tree stocking density and basal area. (Basal area on x axis for comparison). d) The bar represesnts + one standard error for light levels at 10 sq m/ha basal area.

Plate 7.1 a) Photographing the canopy using the fish-eye lens.
b) A close-up of fish-eye lens fitted to the camera.

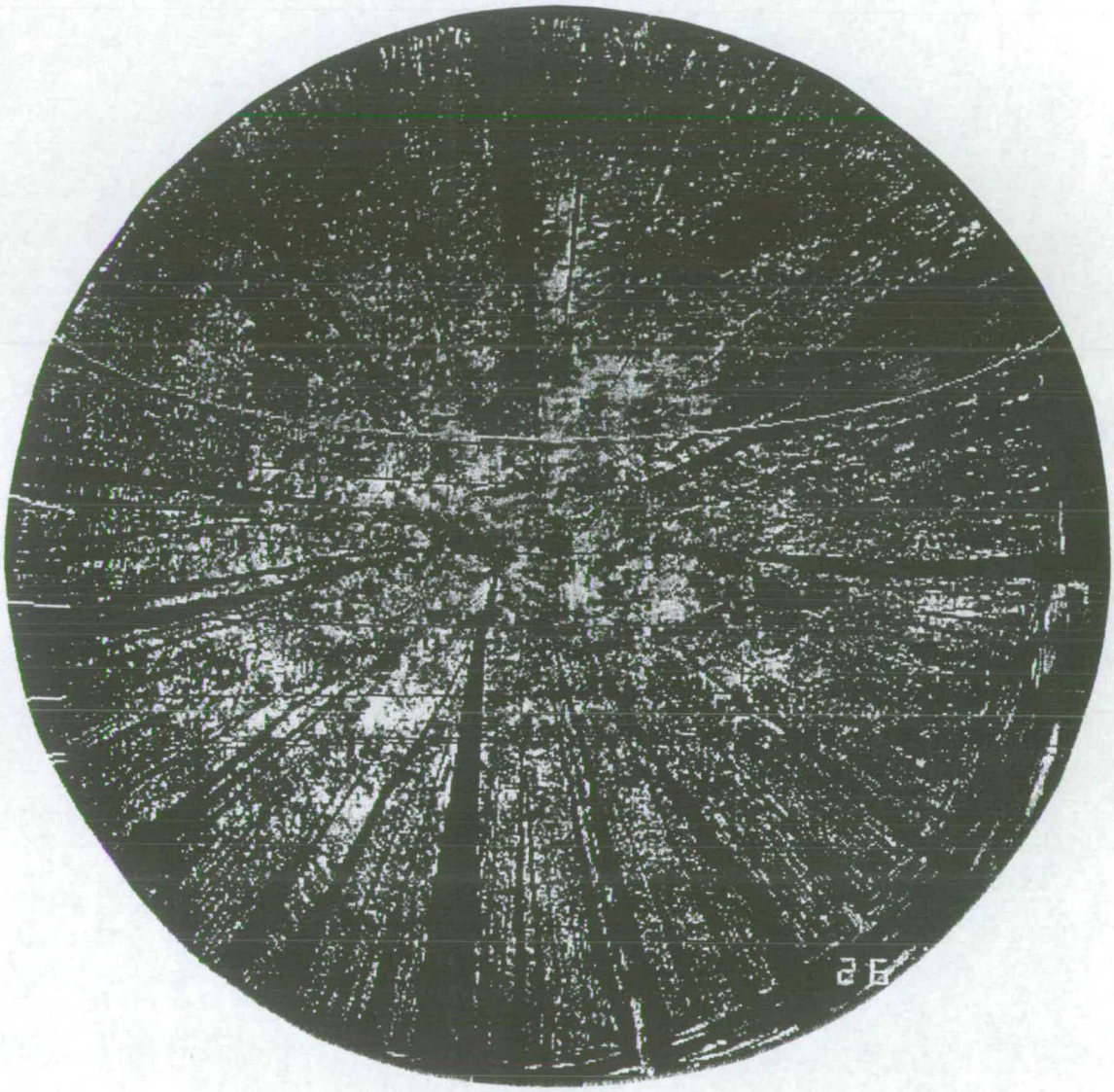


Figure 7.2 A hemispherical photograph of the canopy of an unthinned pine stand. Horizontal lines represent solar tracks at different times of the year.

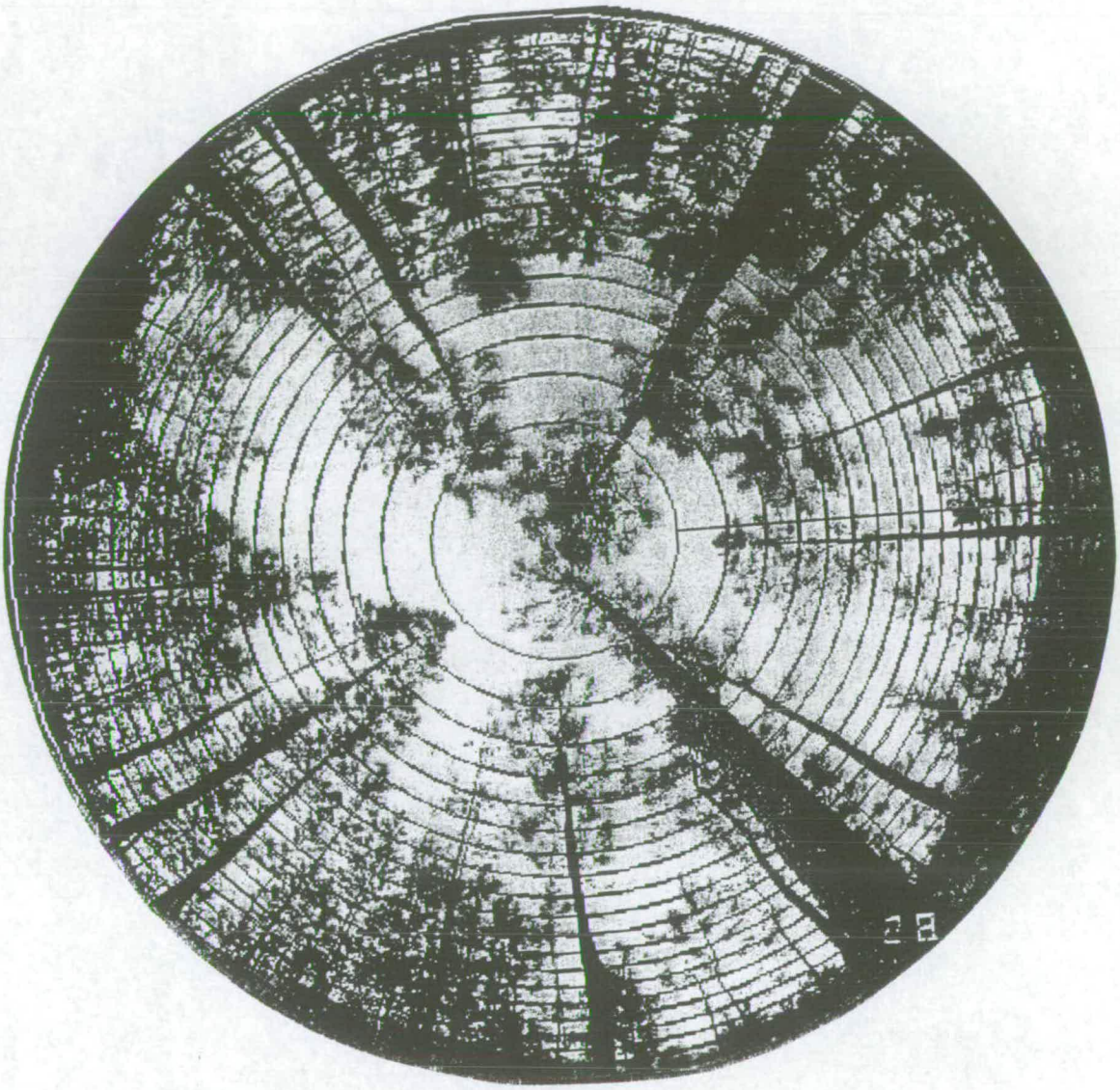


Figure 7.3 A hemispherical photograph of the canopy of a uniformly thinned pine stand. Concentric circles were those used for indirect light measurements.

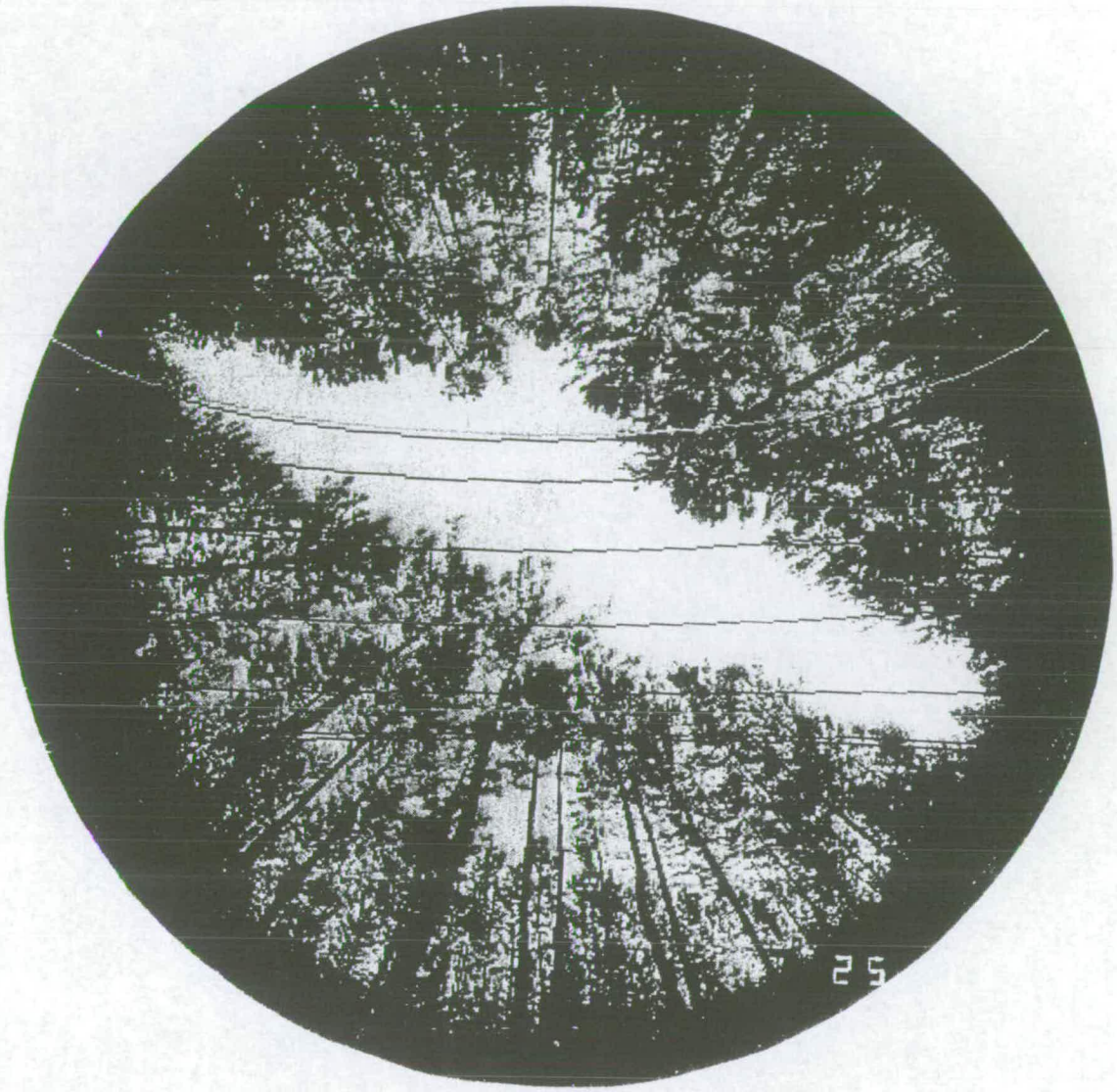


Figure 7.4 A hemispherical photograph of the canopy of a row thinned pine stand.

during a one year period. Light intensity in second highest thinning level was not much changed. However, in the third thinning level it decreased up to 32% from the initial value of 39% while in the unthinned stand again light levels remained almost the same (Figure 7.1b). With these changes, average light levels at different thinning intensities over a one year period was calculated to be 58%, 52%, 35% and 18% of full sunlight at the different thinning levels having basal areas of 10, 15, 20 and 30 m^2 respectively. These light levels and basal areas were achieved by removing 74%, 60%, 40% and 0% of trees respectively from the unthinned stand which had a tree density of about 800 trees per ha.

In the *Alstonia* site, where row thinning was done, the underplanted trees received an average light level of about 60% in about one year after thinning which reduced to 45% in another one year later averaging a light level of about 52% during the experimental period. Thinning intensity in this stand was about 50% of trees removed, which was achieved by removing 2 adjacent rows out of each 4 rows as described in Chapter 3. These values show that light level at one year after thinning in this row-thinned stand was even higher than the values obtained for the heaviest thinning with uniform method in the previously mentioned site at the same time interval (Table 7.1). However, average light level beneath the canopy between first and second years was much comparable with the plots with highest thinning intensity at the Kinigama site. This clearly shows that much higher light intensities can be obtained with row thinning compared to uniform thinning at the same thinning intensity. It can also be noted that in row thinned stands the light levels in the understorey are further affected by the row orientation; maximum with East-West and minimum with North-South directions. In this site, row orientation was nearly at a North-South direction which indicates that the light level would have been further improved if rows were in an East-West direction. Another factor which contributed to higher light levels in this stand was the comparatively narrow crown width compared to a normal plantation. Therefore, getting a higher light level by narrower crown was offset by the North-South orientation of the tree rows.

In the site where *Khaya* was planted, row thinning was done with the same thinning intensity of 50% tree removal, in a similar way to the above mentioned*Alstonia* site. In this site, the pine canopy was well grown and pine tree orientation was nearly East-west direction which allowed the forest floor to receive maximum sunlight available at this thinning intensity. The light level was measured to be about 49% at about one year after thinning which reduced to about 40%, averaging 44% of full sunlight

during the experimental period. Therefore, light levels for understorey plants in this site were comparatively lower than the *Alstonia* site and somewhat comparable to the second heaviest thinning intensity of thinning trial at Kinigama for the experimental period.

In the *Swietenia* site, row thinning was done with the same thinning intensity of 50% tree removal but with a different method, as described in Chapter 3, where three adjacent rows were removed out of each 6 rows making the open strip wider than the *Alstonia* and *Khaya* sites. Tree orientation was at a nearly East-West direction. Average light levels recorded in this site were about 50% of full sun while the values at one year after thinning about 53% which was closer (a little lower) to the light level at the highest thinning intensity of the Kinigama thinning trial at the same time period after thinning.

The *Toona* site was thinned uniformly throughout the stand, in contrast to row thinning at most of the other sites. Thinning intensity was a 50% removal of trees as that of other trial sites. Light intensity on the forest floor at one year after thinning was about 46% which reduced to 40% one year later, averaging approximately 43% of full sun during the experimental period. Light level one year after thinning (during the experimental period) was in between the second and third thinning levels (15 and 20 m^2 per ha basal area levels) of thinning experiment at Kinigama. At the Kinigama site also, 50% reduction of tree density gave a similar light intensity of around 41%. This further shows that uniform thinning method gives lower light levels to understorey vegetation compared to row thinning at the same intensity.

These measurements show that row thinning is preferable when higher light intensities are required for underplanted species. Row thinning also gives various other advantages which will be discussed elsewhere.

7.2.2 Relationship between light environment and broadleaved sapling growth under pine canopy

The influence of light factors on tree sapling growth is important in underplanted environments both because light may be a limiting factor under these conditions, and also since different broadleaved species may respond differently under particular conditions. Direct and indirect site factors (DSF and ISF respectively) which are photographic estimations of direct and indirect light components respectively,

measured in individual plant positions selected randomly in each experimental site varied within a considerable range. The growth of individual plants and their corresponding direct and indirect light environments were studied to find out possible relationships. The two site factors were not combined to develop total site factors (TSF) since fractions of incident radiation were not known. Whitmore et al (1993) recommended that for sites where TSF cannot be obtained then DSF should be used in predominantly sunny climates and ISF in predominantly cloudy ones. They also reported that different forests cannot be compared by photo-estimation unless the radiation is similar in different sites, since what is estimated are the ratios of radiation in the open to that within the forest. Direct site factor in this study represents the annual average of direct light calculated depending on the position of solar tracks in different parts of the year. Results generally indicated that individual light environments were not well correlated with the height or diameter growth. Comparable light levels of the different study sites are given in Table 7.1.

Mean light levels and mean height growth increments at the Kinigama site are given in Figure 7.5a. This shows that about 50% of direct light or above is linked with much greater height increments particularly in *Alstonia* and *Swietenia* indicating their stronger light preference. A rather contrasting difference was found in *Michelia* which responded very uniformly showing possibly much of its adaptability to shade environment without abrupt changes in growth. *Toona* was intermediate in response compared to those species and showed gradual increases in height when light levels increased approximately above 30% of full sun. Some of these aspects were discussed in the previous Chapter.

Alstonia macrophylla at the Panwila site under row-thinning grew successfully under the existing conditions of pine understorey environment as described in detail in previous Chapters. As shown in Table 7.1, light level was fairly high in this site mainly because of row thinning and comparatively smaller pine crowns in this stand which allowed plenty of sunlight to fall on the ground. Analysis of covariance was performed for height and growth relationship of this species taking light as the second covariant and it was found that the light covariate was not significant. Spot measurement of sunlight by hemispherical photos showed that direct and indirect light levels varied between 24% to 62% and 21 to 62% respectively averaging about 52% at the end of about two years after thinning. Individual plant growth and respective light levels were plotted against each other and regression coefficients (R^2) were calculated to investigate the possible relationships. Results indicated no

Table 7.1: Different experimental sites with respective basal areas of pine trees and % light levels in about one year after thinning of pine.

Site	Species	Thinning method	Basal area (sq.m/ha)	Direct Light level %
1) Kinigama				
Plot type (a)	Mixed species	Uniform	10*	54
(b)	do	do	15	51
(c)	do	do	20	32
(d)	do	do	30	19
2) Panwila	*A. macrophylla*	Row	13	59
3) Deltota	*K. senegalensis*	do	28	49
4) Galaha	*S. macrophylla*	do	23	53
5) Watawala	*T. ciliata*	Uniform	18	46

* Basal areas from 10 to 30 sq m. per ha down the column were obtained just after thinning while those from 13 to 18 sq m. per ha were one year after thinning.

apparent relationship between the two parameters. However, some extreme values (outliers) seemed to affect the relationship in each case and therefore, they were excluded as identified by the MINITAB regression analysis method and remaining data points were re-plotted. This procedure include calculation of standardized residual of each data point which is (residual)/(standard deviation of the residual). A standardized residual greater than 2, in absolute value, is usually considered large and they were treated as unusual observations or extreme values. No relationship was found even after excluding outliers (however, this was not the case in other species), further confirming that the existing average light levels around 52% (ranging between 21% to 62%) had little influence on growth of this species (Figures 7.5 b and c). This seems to be due to light saturation of these plants at lower values than these levels. Light saturation at a low level possibly shows shade tolerant capacity of this species. *Alstonia* growth in Figure 7.5 a could not be directly compared with figures 7.5 b and c since they were in different ages. Neither height nor diameter growth showed any response within the light levels found. Increasing light levels had no relationship with growth improvements, and growth differences in individual plants would presumably have occured through the influence of other factors (see Figure 7.5 b and c). The R^2 values for all the relationships between height and diameter with

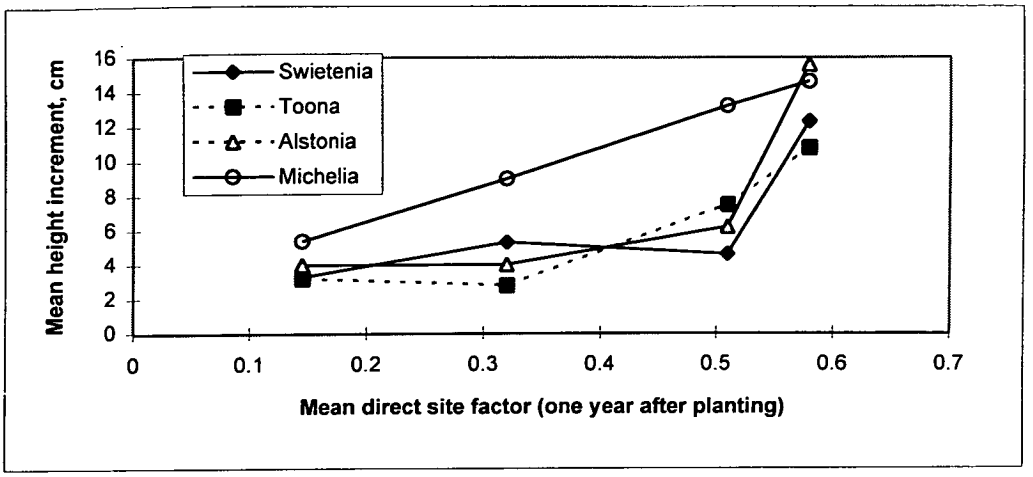
direct and indirect light were very low and are not presented. This can possibly be attributed to higher level of average light received in this site which would have been sufficient not to limit the growth of *Alstonia*. Being a species showing some attributes of a pioneer species, this type of response can probably be expected from this species since pioneers are capable of adapting to changing light conditions (Bazzaz and carlson, 1982; Swaine and Whitmore, 1988).

In *Khaya*, the analysis of covariance taking light factor as a second covariant showed that existing range of light is not significantly affecting height, diameter and volume increment of this species (see section 4.5.2). Also, the individual plant growth and respective light levels were not related well when individual data were considered. However, when the extreme values were identified and removed as described in *Alstonia*, the relationships between light and growth parameters were strengthened between some parameters as shown in Table 7.2.

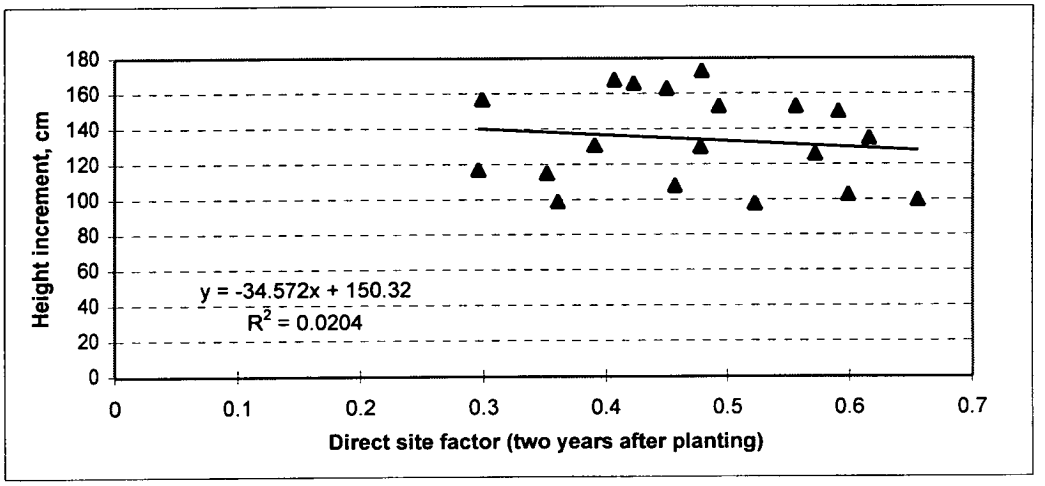
According to Table 7.2, some positive relationships could be identified between height increase and direct site factor. Final height was more closely related to direct light than the height increase, however, both were significant by regression analysis. Final height would have been a better indicator of the response to light since height increase here was recorded during a period between 8 to 24 months of age whilst final height represented a period between 0 to 24 months of age. Diameter increase could not be predicted from any of the light parameters since R^2 values were very low. Indirect light factor was not related to either height or diameter parameters. These findings might suggest that *Khaya* is responding to some extent for the increase of 20 to 55% of full sunlight (see Figures 7.6 a and 7.7 a for relationships with and without removing outliers).

No significant effect of the light regime was found on the growth of *Toona* at Watawala site by the covariant analysis. However, in a similar manner to *Khaya*some relationship could be found after excluding outliers, but was not with all data points, as evidenced by very low R^2 values (Figure 7.6 b and 7.7 b). The relationship between growth and light was slightly negative which is in contrast to*Khaya* plants and might perhaps indicate that lower light levels than the present average of 46% of full sunlight would have been beneficial in terms of height and diameter growth of this species. Regression coefficients between different parameters are given in the Table 7.4 and this shows that both height and diameter were having negative relationship with increasing light.

a)



b)



c)

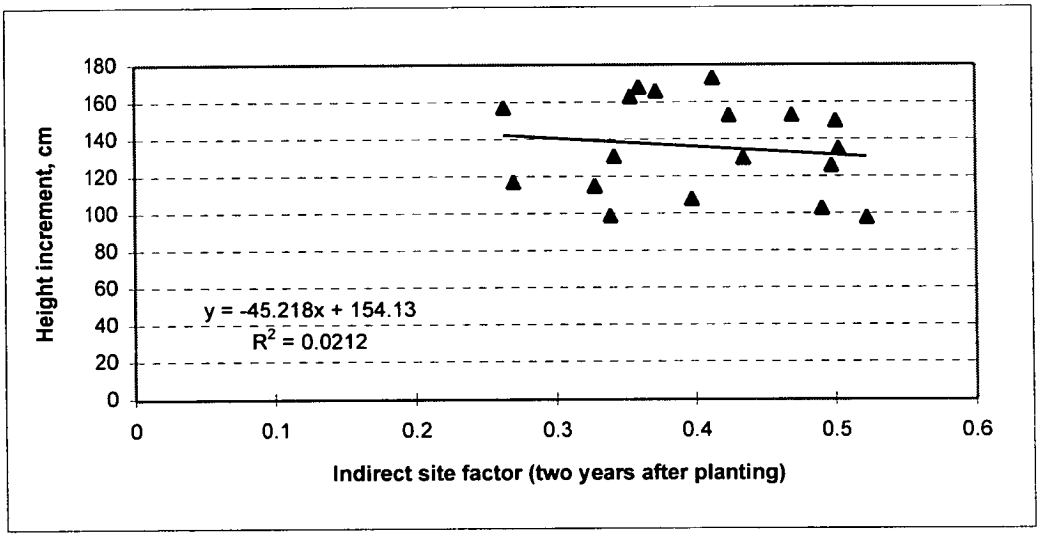


Figure 7.5 Relationships between light level and height growth.

a) Mean height vs mean direct site factor for different broadleaves planted under pine at Kinigama site.

(The bar represents ± one overall standard error for any species, n = 72).

b) and c) Height increments vs direct and indirect site factors of Alstonia macrophylla at Panwila site.

Table 7.2 Coefficient of determination of height and diameter increments of *Khaya senegalensis* at Deltota site as affected by direct and indirect light components. (n = 15 trees)

Growth parameter	Light parameter	Coefficient of determination (R^2)
Height increment	Direct	0.22 *
Final height	-do-	0.40 **
Diameter increment	-do-	0.16
Final diameter	-do-	0.05
Height increment	Indirect	0.003
Final height	-do-	0.005
Diameter increment	-do-	0.05
Final diameter	-do-	0.008

* significant at p=0.05

** significant at p=0.01

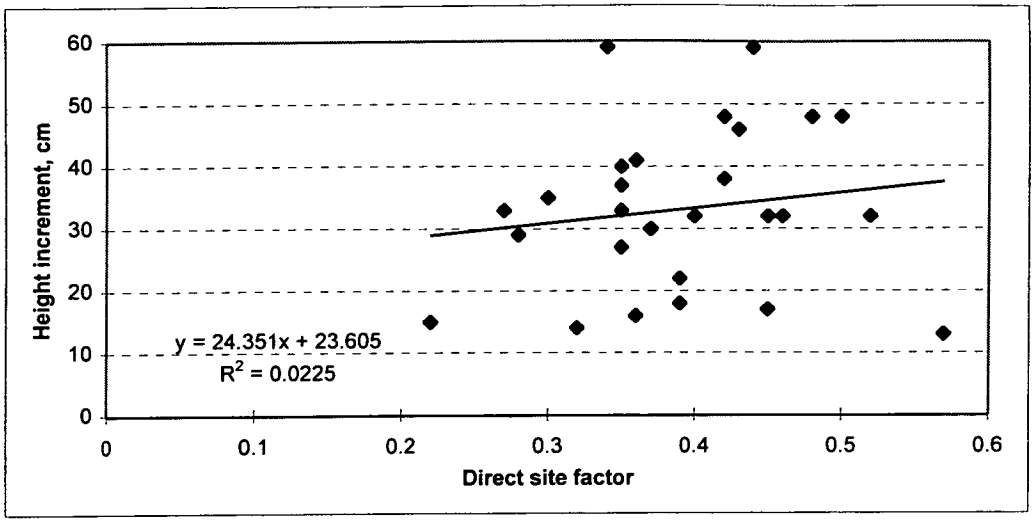
Table 7.3 Coefficient of determination of height and diameter increments of *Toona ciliata* at Watawala site as affected by direct and indirect light components. (n = 17 trees)

Growth parameter	Light parameter	Regression coefficient (R^2)
Height increment	Direct	0.27
Final height	-do-	0.66 **
Diameter increment	-do-	0.005
Final diameter	-do-	0.44 *
Height increment	Indirect	0.23
Final height	-do-	0.25
Diameter increment	-do-	0.03
Final diameter	-do-	0.40 *

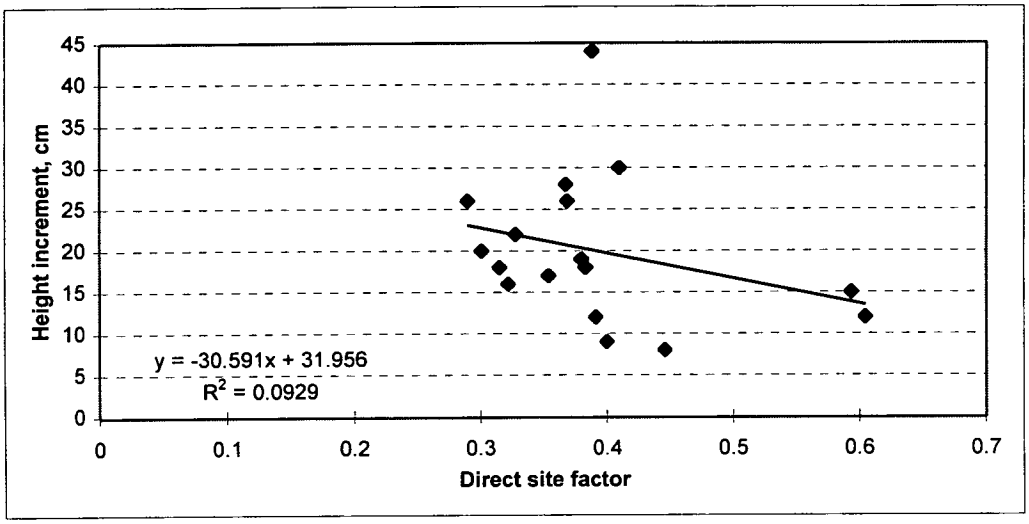
* significant at p=0.05

** significant at p=0.01

a)



b)



c)

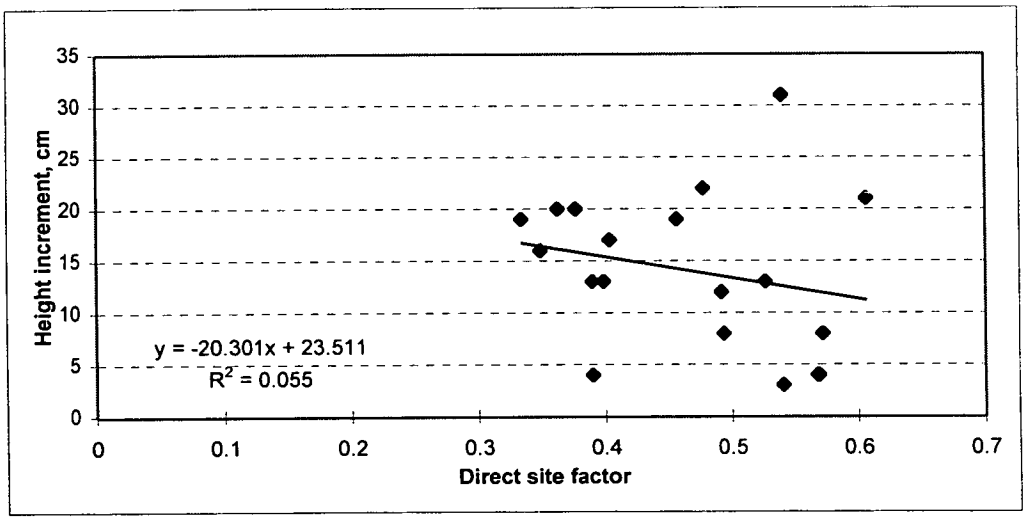
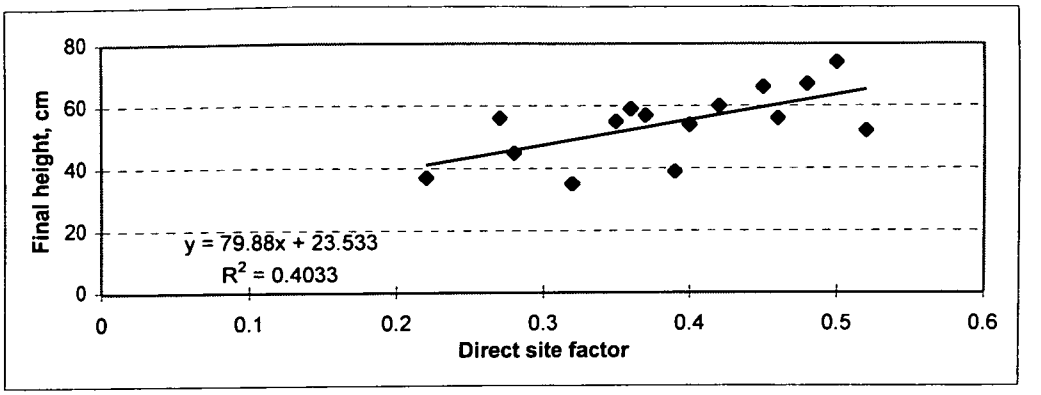
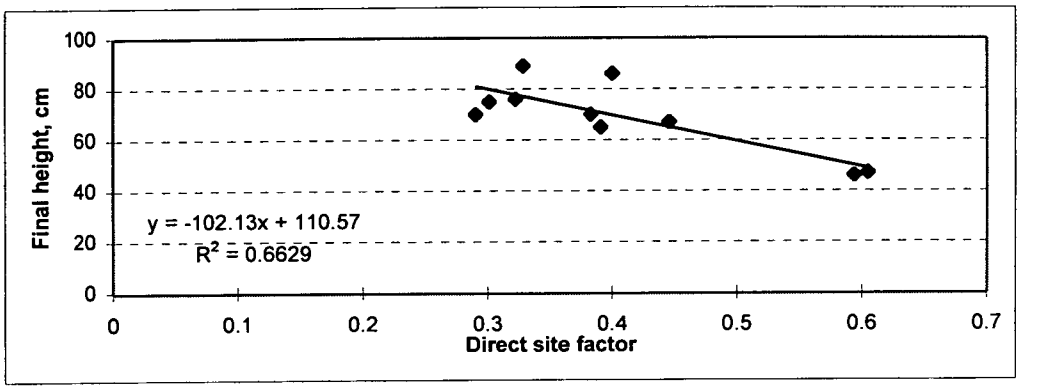


Figure 7.6 Relationships between light and height growth of different broadleaves planted under pine; a) Khaya senegalensis, b) Toona ciliata c) Swietenia macrophylla
(Note very low regression coefficients with extreme values).

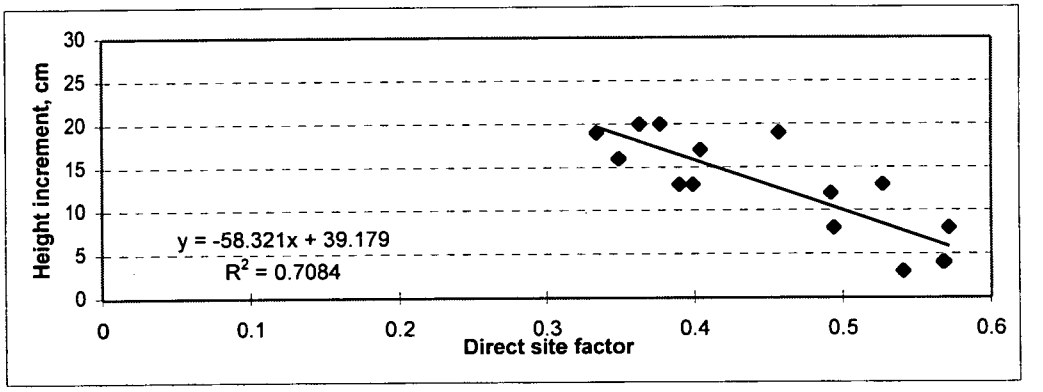
a)



b)



c)



d)

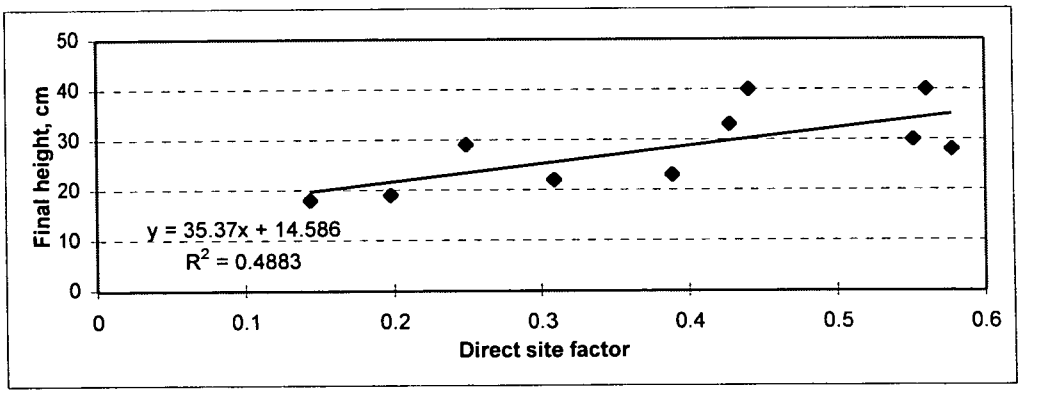


Figure 7.7 Relationships between light and height growth of different broadleaves
a) Khaya senegalensis, b) Toona ciliata, c) Swietenia macrophylla
d) Michelia champaca
(The relationships are after excluding extreme values)

In contrast to these 3 species, *Swietenia* growth in the Galaha site had a significant effect (p=0.05) to changing light levels by the covariant analysis (see Apendix II). This was shown only in height growth and not for diameter and volume growth. This indicated that light factor also has affected the height growth of this species in addition to other treatments described in Chapter 4. Regression analysis greatly improved R^2 values in height increase but not in increase of diameter growth when outliers were removed. R^2 values between height increase and direct light was 0.71, while height increase and indirect light was 0.79 showing both are highly significant at P=0.001. Relationships of other parameters had very low R^2 valus (Data not presented). Final height or diameter growth was not considered here since the increase in height or diameter growth represented the period from planting to final measurements. Height and diameter growth here decreased with increasing light as shown in Figure 7.7 c indicating its shade requirements in early stages of growth (see also Figure 7.6 c for the relationship without excluding outliers).

Table 7.4 Coefficients of determination of height and diameter increments of *Michelia champaca* at Kinigama site as affected by direct and indirect light components. (n = 10 trees)

Growth parameter	Light parameter	Regression coefficient (R^2)
Height increment	Direct	0.22
Final height	-do-	0.49 *
Diameter increment	-do-	0.20
Final diameter	-do-	0.22 *
Height increment	Indirect	0.17
Final height	-do-	0.44
Diameter increment	-do-	0.17
Final diameter	-do-	0.18

* significant at p=0.05

Michelia champaca at Kinigama site had consistent growth improvements at a greater range of increasing light levels as shown in Figure 7.7 d. It can be noted that the growth continuously improved with increasing light levels. This was also demonstrated in Figure 7.5 a, where plot mean values were used for both light and growth parameters. This was possible at Kinigama site since different plots had

different thinning regimes, as explained in the previous Chapter. As shown in Table 7.4, direct light with final height and diameters had a significant regression coeffients while all the other relationships were not significant.

Plot mean values would possibly give better reflection of the relationship between light and growth parameters rather than the values of individual plants. Individual plant growth may be affected by other external factors which could obscure the actual relationship between light effects and plant growth. There were no apparent relationships (with all data points) even when individual treatments were considered. However, this was not done since this will considerably reduce the data available for individual analysis which may reduce the accuracy of the results.

7.3 DISCUSSION

The quantification of the light environment in which broadleaved species were grown under pine canopy was useful to assess the growth performance in relation to different levels of solar radiation. The main aim of the light study was to find out whether existing light levels were adequate for the growth of broadleaved species and how different light levels affect their growth. This may be helpful to develop appropriate silvicultural practices for underplanting where light factor in the understorey plays a major role. However, it is clear from the experimental designs that a wide range of light levels could not be achieved in different experiments, except in the thinning study. Row (strip) thinning generally allows relatively uniform light conditions along a same strip, nevertheless it may vary in different positions of the strip such as in the middle or edge of the strip. Therefore, though light levels may be roughly same between different plots within a same strip, light level within a plot may vary to some extent.

It can be generally observed that strip thinning of pine trees in a uniform stand generally allows plenty of solar radiation to penetrate to the forest floor though this may vary depending on tree crown width, tree height, number of tree rows removed within a strip and orientation of open strips. The situation is different in uniformly thinned stands where lower light intensities are generally obtained compared to row-thinned stand with the same thinning intensity. In an uneven aged tree stand, the light levels on the forest floor may be even lower due to the structure of canopies. Moreover, an even aged coniferous overstorey canopy possibly allows more light to pass through the canopy, particularly diffuse light rather than a similar broadleaved

canopy since broadleaves directly intercept a greater amount of direct solar radiation. Majority of the research findings on the effects of light environment on understorey plants in the tropics seems to have been concentrated on natural forest environment with uneven aged mixed species and information on understorey light environment under plantation conditions are largely lacking.

In understorey environment, mostly it is too little solar radiation which limits the growth of plants as supported by most of the relevant studies. On the other hand, too much radiation can also limit plant growth in some situations, particularly in the species which are not obligately sun plants or pioneer species. It has been experienced under field conditions of tree planting that some light shade is beneficial even for open grown tree species, if site conditions are very unfavourable such as with low soil fertility and long dry periods with drought stress conditions. This may usually be linked with ameliorating effects of overstorey shade under harsh environmental conditions.

The species selected for the present study are able to tolerate some shade at least in some periods of their life. Therefore, it was expected in the design of the experiments that a light overstorey shade will not severely limit the growth of these species. *Swietenia*, *Toona* and *Michelia* species used in the present study are shade demanding species in their early growth as experienced in field conditions in Sri Lanka and other tropical countries. However, they are mostly light demanding in later stages of growth but also can well tolerate light shades. In fact, light shades improve their tree form considerably, encouraging faster height growth producing quality timber. Full sunlight generally limits the early growth of these species. Shade requiring plants such as those may experience photoinhibition, if light intensity exceeds light saturation for a longer period (Chazdon, 1988) since they have low light-saturated photosynthetic capacities (Boardman, 1977; Bjorkman, 1981). *Alstonia* and *Khaya*, on the other hand, are not demanding of shade for their growth but can tolerate some shade without much affecting the growth as can be generally observed in the countryside. In this respect, they seem to be facultatively sun species.

The species investigated in the present studies appear to be having characteristics of both pioneers and climax species in the tropics. It is now recognised that the species cannot be grouped into distinct classes of shade tolerance, rather they are in a continuum between the two extremes of light-demanding and shade tolerant. In such classification of different species between these two extremes, the soil fertility

aspects can also be taken into consideration since early successional species (species capable of colonizing highly disturbed sites) can grow not only in full open sunlight but also under degraded soil conditions with low soil fertility and low soil moisture. Such species are generally used in current reforestation programmes such as *Acacia* and *Eucalyptus* species in most tropical countries. A certain group of other species are somewhat different from these in that they are not so tolerant of harsh environmental conditions but can grow in less fertile soil conditions under some shade and in more fertile conditions under full sunlight. *Alstonia* and *Khaya* can probably be included in this category. The other three species used in this study *Swietenia*, *Toona* and *Michelia* species are obligately shade demanding in early stages as mentioned earlier, and also demanding some soil fertility and if these conditions are not met, their growth will be affected showing poor growth rates. Therefore, they are more towards shade tolerant species than *Alstonia* and *Khaya* on this continuum of shade tolerance capacity. When soil is degraded, some shade levels are generally beneficial even for sun plants, and on the other hand, when soil is reasonably fertile full sunlight seems to be not so favourable even for this shade tolerant species. These interpretations are based on field observations only and therefore have to be further investigated by field experiments.

Whitmore (1990) identifies *Swietenia* as a large pioneer species in contrast to smaller and medium pioneer species such as *Trema*, *Macaranga* and *Acacia* species. He also reported that pioneer species often have smaller seeds than climax species. However, it seems that *Swietenia* with somewhat larger seeds, shade preferance characteristics in early growth indicates some deviations from real pioneers. The same argument applies to *Khaya* as well. *Alstonia*, however, with smaller seeds, more light preference and more ability to grow in degraded sites than *Swietenia* shows the signs more of a pioneer species. Swaine and Whitmore (1988) reported that some light demanding climax species are considered as light hardwoods in Malaysia while shade demanding climax species are known as heavy hardwood species. *Alstonia* fits in as a light hardwood in this respect. They also identified *Toona* and *Swietenia* species as late secondary or large pioneer species. *Khaya senegalensis* is typically found in tree savannas and deciduous dry forests, and tolerates light shade when young (Lamprecht, 1989). Kwesiga (1984) reported that it is a climax species which grows slowly from large seeds, produces dense wood and is tolerant of some shade, and these characteristics are mostly similar to *Swietenia*. He also demonstrated that *Khaya senegalensis* can maintain a positive carbon balance at very low photon flux density, indicating its shade tolerance capacity.

In Sri Lanka, it is grown in the Wet and Intermediate Zone climatic areas where rainfall is above 1750 mm, nevertheless not in the Dry Zone where rainfall is less than this with a long dry period of about 4-5 months. It is planted only under the partial shade in secondary forests as an enrichment planting along the opened strips and successful plantations have been established by this method. In various other countries too, it is generally planted under partial shade and this also helps to protect it from shoot borer attack. Partial shade is also beneficial to protect the plants from desiccation under dry conditions as seedlings do not tolerate extended dry periods. Authors elsewhere also describe that it tolerates shade in young stages (Webb et al, 1984; Lamprecht, 1986) although it is said to be also growing under full sunlight from the field planting in some other countries (J. Mayhew, personal communication). It is generally experienced that full overhead light with some lateral shade encourages its height growth. It has also been observed in Sri Lanka that its growth is not satisfactory under degraded land conditions. This is supported by another study where it was demonstrated that seedlings planted in degraded land responded well to fertilizer application and top soil replacement (Nussbaum et al, 1995). Soil fertility, soil moisture and light might possibly interact for the growth of this species. Thus perhaps it can grow under full sunlight when soil moisture and nutrients are not limiting the growth.

In the present study, it was shown that different species performed in a somewhat different manner. *Alstonia* with some attributes of a pioneer species did not respond to a limited range of light levels on individual plant basis with an average light value of about 52% of full sun. *Khaya* and *Michelia* showed slightly positive response while *Toona* and *Swietenia* had slightly negative response obtained with limited data after excluding extreme values. It may be possible that even though the individual plant light measurements varied a great deal, majority of the understorey plants would have received sufficiently high light levels. Therefore, average light values of different experimental plots would have been more representative of respective light environments.

When a thinned tree strip lies in an East/West direction a large proportion of direct solar radiation will be received by understorey plants but still hemispherical photos may record lower values since the full sky is not exposed to understorey plants due to side covers by overstorey tree stems, canopies in adjacent tree rows etc. Another possible error which can be introduced to the relationship between plant growth and

light measurements in individual plants is residual variations introduced by unmeasured variations such as soil fertility changes in micro-site conditions, genetic variation in individual plants, closeness of the position of decaying pine stumps to broadleaved species etc.

It was found from the present results, that in some cases the direct site factor was related to growth parameters while in others it was indirect site factor as shown in the regression analysis (Tables 7.2 to 7.4). In *Khaya* and *Michelia*, only direct light showed a relationship with some growth parameters while in *Toona* and *Swietenia* both direct and indirect site factors were related. In *Alstonia*, neither factor was significant. Sasaki and Mori (1981) found that growth of tropical dipterocarp seedlings was more closely related to indirect (diffuse) light levels in a range below 20% of full sunlight than to sunfleck activity. Similar results were reported by Pukkala et al (1993) mentioning that the correlation between seedling growth and radiation was best for the diffuse radiation component rather than total or direct radiation and suggested that this may be due to the fact that trees can utilize diffuse radiation more effciently than direct radiation, and diffuse radiation may correlate better than direct radiation with the availability of the other site resources such as water and nutrients.

In the regression analysis of light values and plant growth, poor predictive values showed by *Alstonia macrophylla* indicate that its growth was not influenced by the available light range possibly due to sufficient light intensity received by it under the pine canopy where row thinning was done. Also, it is probable to assume that its fast height growth along with branching would have allowed its upper leaves to access more and more sunlight when it grew taller and taller since light intensity increases when height from the ground level increases. Nakashizaka, (1985) found that indirect site factor increases with increases in height from the ground and also towards the centre of the canopy opening. Similar results can be expected for direct site factor as well. However, in other species some indications were shown as to whether the existing solar radiation is sufficient for the growth of underplanted broadleaved species.

In the case of *Swietenia* and *Toona*, the present level of light might be sufficient or too much as indicted by some negative response to increasing light levels. However, continuously increasing growth shown at Kinigama thinning experiment (Figure 7.5a) may be attributed to much reduced basal area of pine overstorey as compared to

other experimental sites. In other study sites, particularly in the case of row-thinned sites, light levels similar to what was received in the highest thinning intensities at Kinigama site was achieved with removing fewer trees. In other words, under similar light levels Kinigama plots had a very low basal area (10 m^2 per ha) while *Swietenia* plots at Galaha had a higher basal area (23 m^2 per ha). Higher basal area of overstorey trees may also lead to higher root competition from pine trees. Therefore, it may be possible that higher basal area of pine trees with a higher number of trees under the same light level would have created some root competion for understory *Swietenia* and *Toona* plants. This can be further confirmed in the case of *Swietenia* at Galaha, where row thinning was done, revealed that the effect of trenching was significant (see Chapter 4) indicating some root competition from pine trees for those plants. These findings indicate that under the influence of root competition from overstorey pine trees, probably light levels in the row-thinned stand in *Swietenia* experiment was sufficient or too much, but under conditions of reduced root competition more light could be utilized by those species, particularly *Swietenia*.

Khaya and *Michelia* probably need more sunlight than they experienced in the sites, as indicated by some positive response to increasing light levels. With *Khaya*, being a species capable of growing in the full sun, this type of response can be expected, and might be beneficial with more light. However, *Michelia* had a peculiar response to light levels as opposed to all other species showing very uniform response to increasing or decreasing light levels as described in a preceding section. Lack of response to individual plant growth without excluding extreme data, can be attributed to factors such as genetical differences in individual plants, micro-site variations including soil physical and chemical properties which would have been confounded with the effects of light. However, when plot average values are considered the influence of those factors can be generally excluded since it can be assumed that these variations are fairly uniformly distributed within an experimental block.

Greater height growth of plants in shade is sometimes attributed to stem elongation as a result of increased internodal elongation, in comparison to those grown under full light. This occurs, especially if the dim light is rich in far-red radiation (low red:far red ratio) as usually happens in forest understorey environments. However, under these situations, internodal elongation usually occurs at the expense of diameter growth and therefore, diameter increment will be minimal. On the other hand, height growth can also be negatively affected by low light levels in some species due to inadequate dry matter production. In the present experiments, diameter growth was

continuously increasing with increasing height growth as shown in Chapter 4 and this would probably imply that height growth increases were not due to internodal elongation associated with dim light conditions, but rather due to continuous accumulation of dry matter. It should also be noted that light levels in the present experimental sites were comparatively high as mentioned elsewhere. Diameter growth improvement is a better indicator of growth of trees since carbon allocation to stem wood has low priority in comparison to the growth of foliage and roots, and storage of foods in the stem and roots, and therefore, continuous stem growth indicate a reasonable balance in the distribution of carbohydrates (Waring and Schlesinger, 1985). In can also be noted that internodal elongation usually occurs in light demanding species and not in shade tolerant species (Kimmins, 1987).

Seedlings of most species attain maximum height growth under partial shade while light demanding species, such as pines, may attain maximum height growth in full sunlight. These light levels can be reduced as much as 50% with little loss in height growth, although involving significant diameter loss (Kimmins, 1987). This author also mentioned that shade tolerant seedlings such as sugar maple and sycamore attain maximum height growth at light intensities as low as 20% of full sun, and there is a significant growth reduction in full sunlight. The above results are in accordance, to some extent, with present findings.

The average light values varied in the present study ranging between 19% and 59%. When light levels experienced in the present experiments are compared to those observed in other studies, mainly in natural forest environments, the present values are generally much higher. In an Indonesian tropical forest, understorey light as a percentage of the full sun has been reported as between 0.6-0.8 % (Torquebiau, 1986) and 1-2% in Costa Rica (Chazdon and Fetcher, 1984). In a small gap of natural forest, it was around 9% and in a larger gap 15-35% (Chazdon and Fetcher, 1984) while for a seasonal climate in north India it has been reported to be between 10-54% of full sun (Lee, 1987). Chazdon (1986) reported that optimum light level for saplings of shade tolerant species were between 1-26% of full sun where the highest value was comparable to a large gap in a natural forest. Photosynthetic rate of most of the tropical species are reported to increase above the 1-2% of low light under the forest canopy (Clark, 1990). The light levels measured in the present experiments may be in the range where light vs growth function curve flattens off after sharp increases in very low light levels.

7.4 CONCLUSIONS

This study revealed some different responses of broadleaved species to pine understorey light environment. Increased thinning levels associated with decreased basal area leads to increase in light levels for understorey plants while reducing root competition which improved the growth of all species studied. However, under double-row thinning conditions of pine overstorey with 50% removal of trees, allowing about 59% full sunlight to fall on the understorey, *Alstonia* seems to grow well showing signs of adequate sunlight. Both *Swietenia* and *Toona* responded well to increased sunlight with considerable reduction in overstorey basal area. However, under triple-row thinned conditions of pine with removing 50% of pine trees, *Swietenia* showed signs of slightly negative effects of increasing light. *Toona* with uniform thinning also, showed some negative signs with increasing light levels. On the other hand, *Khaya* and *Michelia* showed better responses to increasing light level and therefore possibly even higher thinning intensities may be useful for them particularly for *Khaya* sapling growth.

CHAPTER 8

SOME SOIL ENVIRONMENTAL ASPECTS OF THE PINE UNDERSTOREY

8.1 INTRODUCTION

The sites used for forest plantation establishment in the tropics are often degraded lands and largely unsuitable for most agricultural purposes. Land degradation usually occurs as a result of gradual removal of natural forest cover which has protected the soil for a long period and subsequent agricultural activities mainly in the form of shifting cultivation which involves land clearing and burning. Many of the tropical soils available for reforestation are intensely weathered, inherently infertile and are easily degraded. They can easily be leached of nutrients particularly on sites subject to high rainfall (Wormald, 1992). Strong soil acidity in some areas can also adversely affect the capacity of the top soil to hold nutrients in a form available for plant use. The Cation Exchange Capacity (CEC) of degraded soils are generally low and C:N ratio tends to be high. Nevertheless, under undisturbed forest vegetation these soils are capable of carrying a large volume of vegetation on the higher rainfall sites because the nutrient supply available in the top soil is maintained by the rapid decomposition and mineralization of the litter layer on the soil surface, and nutrients are efficiently recycled.

Nitrogen is generally limiting in the tropics and most soil N is derived from the mineralization of organic matter. However, Vitousek (1984) reported that in tropical forest soils, more N is available than those in temperate forests. In the organic form it is not generally available to plants and must be converted by fungi and bacteria to the mineral form. Phosphorus is also deficient in highly weathered tropical soils (Dabin, 1980) and is present in much smaller quantities than nitrogen. It is reported that many tropical forest soils have little phosphorus return compared to most temperate forests (Vitousek, 1984). Most of the P in the soil is held in a form unavailable to plants but is converted to available form at a slow rate. A problem in many soils, especially acid soils, is the fixation of P to clay particles which makes the availability of P very low, though this may be seen as an advantage in that the P is available over a long period. But organic matter P is less readily fixed than inorganic P and therefore, it is important to maintain the organic content of the soil. Potassium is present in the soil

in larger quantities and is less frequently deficient. However, it is easily leached under high rainfall conditions and also due to intensive weathering the supply can become lower in soils (Kemmler, 1980). Calcium and Magnesium can also be deficient in strongly leached soils. Sulphur can be lost by leaching and by volatilization during burning (Wormald, 1992).

With warmer temperatures and higher rainfall, the humid tropics are subjected to strong weathering of the soil which leads to continual leaching of minerals from the upper layers and often the formation of deeper soils. Leaching depletes mineral resources particularly sodium, potassium, calcium and magnesium. The rapid rate of decomposition of organic matter in the upper layers leads to a thin litter layer and low level of organic matter in the soil (Mabberley, 1994). Only about 18 per cent of tropical soils are reported to have high base status and about half of soils have low base status due to long and intensive weathering, consisting mainly of sesquioxides, kaolinitic clays, and resistant rock-forming materials (Evans, 1992). Kaolinitic clay has low cation exchange capacity, so its nutrient-holding capacity is mainly a function of humus content, which is the case in both top and subsoils. As a result, plant fine roots generally tend to be concentrated in the surface soils and few are found below (Mabberley, 1994). In many tropical countries including Sri Lanka, soil erosion is a serious environmental hazard, particularly in slopy lands which depletes nutrient resources. Protection of these soils by maintaining an appropriate vegetation cover is one of the important consideration to overcome this problem. It seems that this cannot be fulfilled with just establishing any type of tree cover in degraded sites, as experienced in case of monoculture pine plantations in the present study (see Chapter 1 for details).

The main soil types occurring in the experimental sites are, as mentioned in Chapter 3, Red Yellow Podzolic soil, Reddish brown latasolic soils, Reddish Brown Earths and Immature Brown loams. Red Yellow Podzolic soils are well drained reddish to yellowish, medium to moderately fine textured soils occurring in a wide range of topography in the Wet and Intermediate Zones of Sri Lanka. It is the dominant great soil group found in pine planted upland areas (Alwis and Panabokke, 1972). These soils in the undisturbed state are very deep extending up to 3 meters. They have moderate available water holding capacity and are one of the most stable soils. They are strongly acid in reaction and have moderate CEC and low base saturation capacity. Reddish Brown Latasolic soils are well drained reddish brown, moderately fine textured soils occurring on upper and mid parts of rolling and hilly terrain. These

soils are very deep in the undisturbed state, the depth reaching up to 3 meters or over. They are medium acid soils and have a moderate CEC and low base saturation. Reddish Brown Earths are well to imperfectly drained moderately fine textured soils that occupy upper and mid slopes of the landscape. They are highly susceptible to erosion. The normal depth is 1-1.2 m. They have a low available water, slightly acid to neutral in reaction and have moderate CEC and high base saturation. Immature Brown Loams are well drained to yellowish brown, medium to moderately fine textured soil occurring on upper and mid aspects of steeper slopes on rolling and hilly landscapes. They are highly erodible and moderately shallow (about 30 to 70 cm deep). They have moderate available water holding capacity. Slightly acid to neutral in reaction, they have moderate CEC and moderate base saturation (Ranaweera, et al. 1991).

In deforested areas, which are usually covered with grasses and subject to frequent burning, the A horizon may be particularly absent due to its vulnerability to erosion, particularly during the monsoonal rainy periods. The *Pinus caribaea* plantations have been raised on such degraded soils, and grown successfully there despite these conditions. Weil (1982) reported that P appeared to be the growth limiting nutrient in the hilly areas where pine has been grown. He also reported after analysing soil samples that soil erosion, possibly associated with fire, has decreased organic matter by 37%, total N 29%, available P (Olsen) by 36% and exchangeable bases by 20%, and increased acidity levels. These examples show the magnitude of the soil erosion problem experienced in these highland areas particularly due to removing of ground cover litter and vegetation due to fire. Gunatilleke (1989) reported that low levels of N in these lands may be a growth limiting factor in the long term for *Pinus* as well as for any other broadleaved species that may be interplanted with pine.

Having the tree cover with pine plantations for about 15 years would have changed the soil conditions to some extent and this may affect the growth of underplanted broadleaved trees. However, these conditions may vary in different areas. One of the aims of the present studies was to quantify the soil environment under pine trees where broadleaved tree species were grown which may give some background information in relation to their performances described in the previous Chapters and also to identify possible limiting nutrients and physical properties for the growth of broadleaved underplanted species.

8.2 RESULTS AND DISCUSSION

8.2.1 Soil properties under pine overstorey

8.2.1.1 Soil chemical properties

The results of soil analysis are given in Tables 8.1, 8.2, and 8.3. The analyses were done mainly in the Panwila, Deltota and Watawala sites. The results in the Deltota site can be applied roughly to the Galaha site as well, since the two sites were in the same region. Some additional analyses were done in the soils under the pine mulch used in the present experiments and also in some grassland sites adjacent to the experimental sites for comparisons.

In this section, nutrient levels in different sites are compared based on some standard values depicted by Landon (1984) for tropical soils. Tables 8.1, 8.2 and 8.3 present values obtained from normal soils at different experimental sites, soils under the mulch at the experimental sites and grassland sites adjacent to pine sites used in the present experiments. Some other results obtained in another study in grassland sites and in natural forest sites are also presented for comparisons (Weil, 1982). Nutrient levels in the mulched soils give an estimation of the effects of mulching on soil fertility aspects of those micro-sites, and grassland nutrient levels allow comparison of soil fertility in respective soils after supporting pine trees for a period of about 15 years.

According to the results in the Table 8.1, total N% was low in all trial sites recording the values around 0.1%. This can be rated as low to very low N levels; low values in Panwila and Deltota sites while a very low value in Watawala. When comparing these values with mulch treated soils there was no apparent improvement in N level due to mulching effect. In grassland sites also, the N level was more or less similar to those values. However, values in the natural forest (Table 8.3) was about four times higher than those. Low N in these sites may be partly due to volatilization losses of N from the litter during fires.

Phosphorus levels somewhat varied in different sites ranging from about 11 to 15 ppm, the highest recorded in Watawala site. These values indicate moderate available P levels. However, under mulch, these levels were much improved in Watawala site, while decreased in Panwila and slightly improved in Deltota sites. By contrast,

Table 8.1 Soil chemical properties in normal topsoil (0-20 cm) at the different experimental sites (Values represent mean ± one standard error of three composite samples).

Nutrient/soil property	Experimental site		
	Watawala	Panwila	Deltota
Total N % (titration 0.02 N HCL)	0.07 ± 0.003	0.10 ± 0.006	0.11 ± 0.009
Available P (Olsen, ppm)	15.1± 0.70	11.0± 1.07	13.1 ± 0.09
Exchangeable K (meq/100 g soil)	0.07 ± 0.005	0.15 ± 0.020	0.10 ± 0.012
Exchangeable Ca (meq/100 g soil)	0.16 ± 0.03	0.46 ± 0.14	0.40 ± 0.04
Exchangeable Mg (meq/100 g soil)	0.12 ± 0.01	0.44 ± 0.14	0.28 ± 0.03
Exchangeable Na (meq/100 g soil)	0.04 ± 0.003	0.03 ± 0.0	0.03 ± 0.0
Total Exchangeable Bases (meq/100 g soil)	0.39 ± 0.03	1.09 ± 0.30	0.81 ± 0.05
Organic C (titration 0.02 N HCL)	1.31 ± 0.06	1.65 ± 0.24	1.66 ± 0.18
C:N ratio	18.7	16.4	14.6
Soil pH	5.1	5.1	4.9

Table 8.2 Soil chemical properties in topsoil (0-20 cm) under mulch at the different experimental sites (mean values of 3 composite samples).

Nutrient	Experimental site		
	Watawala	Panwila	Deltota
Total N % (titration 0.02 N HCL)	0.07	0.12	0.11
Available P (Olsen, ppm)	21.6	7.07	15.2
Exchangeable K (meq/100 g soil)	0.03	0.21	0.08
Exchangeable Ca (meq/100 g soil)	0.82	1.54	1.27
Exchangeable Mg (meq/100 g soil)	0.37	1.09	0.53
Exchangeable Na (meq/100 g soil)	0.03	0.12	0.16
Total exchangeable bases (meq/100 g soil)	1.25	2.96	2.04
Cation Exchange Capacity (meq/100 g soil)	3.95	6.41	8.75
Organic C (titration 0.02 N HCL)	1.20	1.88	1.70
C:N ratio	17.1	15.7	15.5
Soil pH	5.1	4.9	5.1

Table 8.3 Soil chemical properties in normal topsoil (0-20 cm) in grasslands adjacent to the different experimental sites (outside the pine plantations) also including a natural forest site for comparison (mean values ± standard error of three composite samples).

Nutrient/soil property	Site			
	Watawala	Panwila	unspecified site (Weil,1982)	Natural forest (Weil, 1982)
Total N % (titration 0.02 N HCL)	0.10 ± 0.01	0.12 ± 0.006	0.11	0.48
Available P (Olsen, ppm)	2.94 ± 0.39	5.32 ± 0.58	3.00	4.00
Exchangeable K (meq/100 g soil)	0.06 ± 0.01	0.12 ± 0.006	0.10	0.25
Exchangeable Ca (meq/100 g soil)	0.34 ± 0.05	0.55 ± 0.04	0.54	3.81
Exchangeable Mg (meq/100 g soil)	0.24 ± 0.05	0.40 ± 0.11	0.11	1.22
Exchangeable Na (meq/100 g soil)	0.05 ± 0.018	0.03 ± 0.003	-	-
Cation Exchange Capacity (meq/100 g soil)	5.73	7.72	-	-
Total Exchangeable basea (meq/100 g soil)	0.69	1.1		
Organic C (titration 0.02 N HCL)	1.19 ± 0.14	1.18 ± 0.14	1.67	6.77
C:N ratio	11.9	9.8	15.2	14.1
Soil pH	4.8	4.8	4.05	4.4

grassland site and natural forest site had very low P levels about one third of pine soils. This indicate that low P levels in grasslands have been considerably improved under pine trees which may be useful for understorey growth. This is in accordance with the finding of Weil (1982) who reported that P levels in grassland sites before pine establishment was very low and attributed this to poor availability rather than low total supply. He further mentioned that many of the soils in those areas contain iron in the soil which can bind P, however, significant amounts of P may be available with oxidation of organic matter. Under conditions of low P availability mycorrhiza is particularly useful for tree growth and therefore, at the time of establishment of pine trees ectomycorrhiza might have greatly contributed to the growth of this species under the existing conditions. At later stages of growth, some litter breakdown and ash from the burnt material would have improved P levels in these soils.

Potassium levels in the experimental sites were generally low, recording values lower than 0.2 meq per 100 g of soil. In Watawala site, it was particularly low most probably due to leaching as a result of higher rainfall. Mulching improved K levels only in Panwila site, whereas in the Watawala site K levels were even lower. In grassland site, the values were similar to those under pine indicating that K levels have not been improved by pine tree cover. This can be due to leaching and also soil erosion which removes top layer with nutrients. Weil (1982) reported that K levels are satisfactory in the upper soil layers in grasslands but low in lower layers and therefore erosion and tree harvesting can easily deplete K reserves in those sites.

All the experimental sites had generally low values of calcium, moderate values of magnesium, sodium and total exchangeable bases. Grassland sites had somewhat higher values of those nutrients while natural forest site had comparatively even higher values. Ca, Mg and total exchangeable bases were lowest at the Watawala site (about half of that at the other two sites) apparently due to heavy leaching of those nutrients. However, with mulch application, Ca, Mg and total exchangeable bases were improved by about three times in this site, though not Na. In other two sites also, Ca, Mg levels and total exchangeable bases were increased about two fold and Na four fold with mulch application. One of the reason for this may be concentration of nutrients under mulched conditions. Thus, mulching may well have the potential to increase Ca, Mg, Na and total exchangeable bases in these sites.

Organic carbon (C) was very low in all sites when compared to natural forest sites, as can be generally expected. Levels were a little lower in grassland than in pine sites.

Therefore, it seems pine tree cover has not improved C level in the soil, probably due to frequent burning of litter layer under pine and also in grasslands which would have hindered litter build up and breakdown. Much slower decomposition of pine needles may also partly contribute for lower organic matter build up in the top soils. Low organic matter levels may considerably influence soil fertility, physical properties such as bulk density and biological activities in these soils. Mulching slightly increased organic C only in Panwila and Deltota sites and may be expected to further improve the situation slowly since the decomposition rates are comparatively slow.

C:N ratios recorded in the experimental sites were high mainly due to low N levels. They were not much affected by mulching, although in Watawala and Panwila sites it decreased slightly. Higher C:N values generally represent low microorganism activities and possible N deficiencies.

pH values were around 5.0 indicating somewhat acidic properties of these soils. This was not affected by mulching treatments and was more or less similar in all sites. In grasslands it was lower still which shows pine plantations has somewhat increased the pH values. This might be partly due to regular burning of pine sites which could neutralize acidity levels to some extent.

CEC values were available only for mulched plots and grassland sites and which indicated that grasslands have somewhat higher values. Weil (1982) reported that high humus and clay contents in some of these sites may increase CEC.

In a soil study conducted by Dharmawardane (1987) in a pine plantation at a higher elevation (around 1300 m) than the above mentioned sites but closer to the Kinigama site in the present study, reported that the soil pH, Ca, Mg and K were higher in grassland conditions than pine sites. Nevertheless, organic matter, CEC, extractable P and total N were lower under grasslands in comparison to pine plantations. Higher P level and lower Ca, Mg levels in pine soils in comparison to grasslands are in accordance with what was recorded in the above mentioned trials at Watawala, Panwila and Deltota, and therefore can probably be considered as a general situation under pine tree cover. Other aspects of nutrient status are somewhat different to the findings in the present experimental sites discussed above. These variations can be attributed to different site conditions, elevation and rainfall (higher elevation and lower rainfall). Dharmawardane (1987) further reported that some soil improvements

can be expected in pine sites within 10-16 years and then introduction of other species may be feasible.

A somewhat similar study was reported by Turner and Lambert (1988) in temperate pine forests in New Zealand, where they found that in low fertility sites, soils under pine were lower in N, Mg and pH and higher in organic matter and aluminium, while in high fertility sites N and organic matter were lower while other factors were not significantly different, in comparison to native forest sites. Apparent deficit in total N was attributed to the thinning levels. In forest soils with limited rooting depths due to shallow soils, the A horizon may be more subject to depletion than that in a profile with a greater depth available for rooting as reported by Turner and Kelly (1985).

In wetter areas in comparison to drier sites (in this case Watawala is particularly wet, Panwila is wet and Deltota is comparatively dry) the soil generally becomes more acid and lower in available bases, K, Ca and Mg due to leaching of those bases when water percolates through the soil profile. Low levels of nutrients due to leaching may be a reason for poor performance of *Toona* in the Watawala site with some plants showing die back. Lamb (1968) reported that root systems of *Toona* species are sensitive to impeded drainage and rapid reduction of nutrients due to leaching by the heavy rains. Moreover, under wet conditions P levels generally become less available and the content of organic matter and its constituent N in the surface soil increases due to more vegetation promoted by year-round soil moisture. This was not experienced in the present sites probably due to destruction of organic matter by fires. More highly weathered clay minerals in the wetter zones also have the ability to tightly bind P in unavailable form. At the same time organic matter decomposition can also be reduced by the relatively cooler temperature (Weil, 1982) as experienced in Watawala. It was noted in the present study that under wetter conditions, pine litter breakdown is promoted as observed under the mulch.

Mulching appeared to increase bases including Ca and Mg, and also K and P only in some sites. This may be one of the reasons which promoted fine feeder root development in upper soil layers under the mulch as described in Chapter 4. It can also be noted that litter decomposition can create temporary N deficiencies due to microbial utilization of this nutrient in some circumstances which might be a reason that N was not improved with mulch though total N would not be affected. If this is the case N improvements can be expected later on. Also, continuous breakdown of

mulched litter which is accelerated under mulched conditions, as observed in the field (see section 8.2.1.4) can be expected to release more nutrients in later stages.

8.2.1.2 Soil physical properties

Soil texture was compared in different sites and with adjacent grassland sites (Table 8.4). Watawala site had more sand while Panwila site had more clay in upper layers of soil. Textural classes were sandy clay loam in Watawala and Deltota sites, and clay loam in Panwila site. Some soil profile studies were also done to study physical properties of different layers of soil in two extreme sites Watawala and Deltota (see Appendix V for details). These indicated that in the lower layers between 42-75 cm (B1 layer) of the Watawala site had poor pore distribution with many fine and few medium pores with compared to the upper layer of 10-42 cm with which had a few fine and many medium pores. This indicates that lower layers of soil without sufficient large or medium size pores may tend to cause saturation of water with poor drainage conditions under heavy rainfall conditions. This may be one of the reason for the poor growth of *Toona ciliata* in the Watawala site. In contrast, Deltota both upper layers up to about 85 cm consisted many medium and fine pores probably indicating better drainage conditions than the Watawala site.

The soil structure was weak (Table 8.4) in upper A layer of 10-42 cm at Watawala site compared to Deltota site which may also likely to cause poor drainage conditions. However, these conditions may vary from place to place within the same site. Shape of the soil aggregates were sub angular blocky in all the cases (Appendix V). Iron stones were present in the B1 layer of Watawala soils indicating the leaching of iron in high rainfall and then oxidation in this layer.

Soil bulk density and porosity values obtained in the experimental sites are given in Table 8.4. Bulk density values gives some indications of soil compaction, and porosity gives aeration and root penetration. In soils even with similar texture, bulk density may vary depending on organic matter levels, root penetration and soil structure. Bulk density values were highest in Watawala and lowest in Deltota. Mulching usually reduced bulk density in the surface layers which is very useful for plant growth and probably another reason (in addition to nutrient release and soil moisture improvements) for stimulating fine root growth noted in all species studied in the present experiments. The level of decrease of bulk density with mulching was 3%, 7.6% and 10.4% and level of increase of porosity was 4.8%, 8.9% and 12.5% for

Watawala, Panwila and Galaha sites respectively. Bulk density and therefore porosity was not improved with mulch in the site of Deltota where lowest bulk density was recorded. This may probably be due to comparatively less wet conditions experienced in this site which apparently did not much promote litter breakdown as in the more wetter sites.

Table 8.4 Physical properties of soils at the different experimental sites.

Physical property	Watawala	Panwila	Deltota	Galaha
Soil texture				
a) sand %	50.9 (56.6)*	35.0 (46.6)	44.9	-
b) silt %	28.2 (15.6)	22.6 (14.6)	24.1	
c) clay %	19.5 (26.6)	41.5 (38.1)	31.0	
Soil structure aggregate -				
a) stability	weak	moderate	mod. to fine	moderate
b) size	medium	coarse-fine	medium	coarse-med.
c) shape	s.a.b.**	s.a.b	s.a.b.	s.a.b.
Bulk density	1.62 (1.57)***	1.43 (1.32)	1.38 (1.38)	1.44 (1.29)
Total Porosity	38.8 (40.7)***	46.0 (50.1)	47.9 (47.9)	45.6 (51.3)
Water holding capacity (wt/wt %)	24.7 (22.5)*	28.0	35.8 (26.3)	-

* - Values within the bracket in the row are for grassland sites.

** - s.a.b. = sub angular blocky

*** - Values within the bracket in the row are for mulched soils.

Water holding capacity was considerably higher in Deltota and lowest in the Watawala site and intermediate in the Panwila site which may be related to respective bulk densities. Low water holding capacity in the Watawala soil may indicate that it can be saturated easily, particularly under higher rainfall conditions, which might limit plant growth. This could also have partly contributed to the poor growth of *Toona* in these site. Grassland values were lower by about 9% and 26% for Watawala and Deltota sites respectively which may indicate probably improved soil physical

properties in the upper layers of soil under pine tree cover. However, these values may change from site to site depending on soil properties.

8.2.1.3 Soil temperature

Soil temperature was measured using a hand-held infrared thermometer as described in the section 3.6. This was done mainly to assess the effects of mulching on soil temperature reduction. Results showed that at the Panwila site, average soil temperature in an open land was 38.4°C which reduced to 32.4°C under the pine trees. This was further reduced to an average of 29.7°C under mulch. Under cloudy conditions, temperature underneath the mulch was 26.3°C when outside the mulch it was 30.2°C. At Deltota site soil temperatures with and without mulch was 23.5°C and 25.5°C respectively. More marked temperature reductions were recorded at Watawala site with 22.8°C under mulch and 29.0°C without mulch. Thus, temperature reductions in surface soils from mulching varied from 2.0°C to 6.2°C at different sites. In addition to this, temperature below the surface level is also usually reduced by mulching during day time while increase during night time thereby reducing the fluctuations (Longman and Jenik, 1987) although these were not measured in the present study. Reduced soil temperature during the hotter parts of the day may be useful in tropical environments to favour root growth partcularly in early stages and also to improve soil faunal activities. It can also reduce soil moisture evaporation thereby improving soil fungal activities. Truax and Gagnon (1993) reported that organic mulch reduces soil temperature while artificial black plastic mulch increases soil temperature which may be useful in temperate environments. They also reported that increased heat transmission by plastic mulch may be useful to increase nitrogen mineralization while organic mulch also can increase nitrogen levels by the improved microbial decomposition.

8.2.2 Soil fauna and the mulched soil environment

Various soil insects were observed underneath the pine mulch which was a marked difference in comparison to the unmulched soils where day-time insect activities were minimal, at least on the upper soil layers. The biggest insects observed were wood lice (*Isopoda* species) which are one of the common animals found among rotting wood. Their presence indicate increased humidity conditions under the mulch. Centipedes (*Chilopoda* spp), millipedes (*Diplopoda* spp), small spiders, beetles, ants, bristle-tails (*Diplura* spp), spring tails (*Collembola* spp) and in some cases

earthworms and termites were other soil animals found. They may be playing an important role in the initial breakdown of litter.

The effects of soil fauna on nutrient dynamics of soils and in turn for plant growth have been well researched. Various groups of macrofauna are reported to increase in N levels markedly (Anderson et al, 1983). Wensem et al (1993) reported that isopods had a positive effect on N mineralization in aged litter and the influence of litter-feeding soil animals were strongest in relatively low quality litter with a low C:N ratio in which carbon content and composition may be limiting for microbial growth. In a controlled environment, Huhta et al (1988) demonstrated that soil animals contribute to N release and the humification process of humus. It is generally believed that fragmentation of organic matter, channelling and mixing of soil components are major roles by which soil fauna stimulates microbial activity. When these activities are inadequate, additional mineralization by microbial grazers can increase plant growth during critical periods although these effects may be short term (Ingham et al, 1985).

However, Visser (1985) reported that mesofauna in the soil environment may reduce fungal species richness and divert fungal successional patterns on decaying plant residues. Nevertheless, Klironomos and Kendrick (1995) suggested that endomycorrhiza may have adapted for a long time to be less palatable to soil arthropods than are non-mycorrhizal fungi and this would help to protect the plants against pathogens and parasites. Klironomos et al (1992) also reported that grazing of litter inhabiting fungi by the soil fauna may suppress the effects of phytoxicity and root infection by litter fungi, in addition to their effects of liberating N.

In an investigation of forest fire on beneficial soil animals, Collet et al (1993) found that *Collembola* and earthworm activities were decreased up to one and three years respectively in eucalypt forests and suggested therefore, two consecutive fires may interrupt the decomposer cycle for up to three years as they are major decomposers of forest litter. In a study in conditions similar to those of the present study, Setala and Huhta (1991) investigated the effects of soil fauna on birch (*Betula pendula*) seedlings on a coniferous forest floor in a controlled environment. They reported that seedling leaf, stem and root biomasses were increased by 70%, 53% and 38% respectively and nitrogen and phosphorus contents of leaves by 3 and 1.5 times respectively while water content of the soil remained significantly higher in the presence of fauna, clearly indicating their effects on plant growth through enhanced

nutrient mobilization and favourable changes in the structural soil properties. Based on these and other findings it can be expected in the present study too, that soil fauna, which was markedly increased under mulch, would have had some favourable effects on the growth of broadleaved species.

8.2.3 Pine litter decomposition under mulch

Pine litter is slowly decomposing when compared to most of the broadleaved species. Very slow decomposition tends to make it accumulate on the forest floor attracting fire and disturbing nutrient cycles. However, in this study, it was noted that when pine needles were used as a mulch by piling needles in a thick compacted layer around understorey tree saplings, decomposition was enhanced in comparison to loosely packed thin litter layers naturally found on the forest floor. It was also observed that the lower litter layers of the mulch started decomposition earlier and faster than the upper layers. This seems to be linked with more moisture retained for a longer period in the lower layers. Higher moisture level for a longer period due to reduced evaporation of moisture within the mulch and in the soil keeps the mulch damp, which tends to encourage fungal growth and litter breakdown as observed clearly under the mulch (see Plate 8.1). White fungal mycelium could be clearly observed only under the moist mulch. This is in accordance with the finding of Kowal (1969) who reported that leaching *Pinus echinata* needles with water increased decomposition under laboratory conditions. Also, King and Heath (1967) showed that the leaching of newly fallen leaves of deciduous trees had greater effect in accelerating litter breakdown through increased microbial decomposition and increased palatability to soil animals possibly due to removal of polyphenols by the leaching.

Under natural conditions of the pine forest floor this usually does not take place due to the loose accumulation of stiff needles which dry up quickly during the dry periods reducing any fungal growth and also attracting fire thereby destroying even partly decomposed material. This tends to leave a fresh undecomposed needle litter layer on the forest floor which will be ready for burning in the next dry season.

It was further observed that the litter which was in contact with the soil in the lowest layer of mulch are even more decomposed than the needles just above it which are also wet. It seems that litter in contact with soil may be wetter and soil fungi can easily get into these and starts decomposition easily. The microclimate created under

the mulch with high soil moisture and high humidity seems to favour the functions of soil inhabiting micro-organisms and fungi. Further, soil insect activities are also favoured under the mulch as mentioned in the previous section which also helps in the initial breakdown of litter. It was observed that litter decomposition starts under mulched conditions in about 5-6 months while under unmulched conditions it takes a much longer time.

8.3 CONCLUSIONS

The studies on the soil environment of broadleaves under pine overstorey elucidated some of the underlying differences in soils in different sites and some of the changes brought about by mulching. There were some differences in soil chemical characteristics between sites and it seems that this is partly due to leaching of nutrients associated with rainfall. In general, all the sites seemed to have low soil fertility conditions. Phosphorus levels have been increased under pine trees in comparison to grasslands without pine tree cover. Mulching appears to have contributed to increases in calcium, magnesium, sodium and total exchangeable bases in addition to the improvement in soil physical properties such as bulk density, total porosity and water holding capacity. Mulching also affected soil fauna favourably which may also have contributed to nutrient dynamics and physical property improvements in soil. These improvements in the soil environment may be important for the growth of broadleaves under pine.

Plate 8.1 a) Decomposing pine needles with fungal mycelium under the wetter mulch conditions.

b) Development of ground vegetation including creepers after thinning the pine overstorey, which may help to protect the soil from erosion.

CHAPTER 9

GENERAL DISCUSSION AND CONCLUSION

9.1 INTRODUCTION

The present study was carried out to investigate the growth responses of broadleaved tree species under the environment of a pine monoculture overstorey. Various experimental treatments and management practices were designed and applied to improve the growing environment in order to reduce the effects of possible growth limiting factors. These included reduction of potential root competition from overstorey trees for nutrients and soil moisture by trenching and particularly soil moisture conservation by mulching treatments, improvement of plant nutrient uptake levels by mycorrhizal inoculation, improvements of light levels by various thinning intensities and thinning methods. The effects of these treatments were estimated by monitoring various growth parameters of the understorey trees and also by quantifying the light and soil environment in which they grew. The results were discussed in detail in previous chapters and conclusions were drawn. This chapter draws together the results and discusses them in general. Some silvicultural implications of the findings with possible management guide-lines for underplanting, and suggestions for future studies are also considered.

9.2 EFFECTS OF SOIL ENVIRONMENT

Soil environmental factors such as soil fertility, moisture and physical properties play major roles in the growth of tree species. One of the major challenges nowadays in reforestation programmes is the establishment of forest plantations particularly in the often degraded lands available for this purpose. Soil fertility is one of the important factors which affects the growth and survival of forest seedlings in such lands. It is generally observed that once the original tree cover is removed and cultivated with agricultural crops without proper soil conservation measures and fertiliser inputs they become gradually denuded, rendering them unsuitable for the growth of most of the valuable local and exotic tree species.

As mentioned in Chapter 1, pine plantations in Sri Lanka have been established mainly in degraded soils in grasslands where *P.caribaea* and *P.patula* have proved

themselves capable of growing successfully. Apart from pine, only a few species can sustain growth in these degraded lands. It was generally expected that after establishing the pine tree cover, conditions would have improved and would create better micro-climates for planting other broadleaves under its canopy, when compared to planting directly in open grasslands with degraded soils. An overstorey tree cover can provide shelter for growing understorey trees by reducing direct solar radiation and thereby lowering evapotranspiration from understorey trees and evaporation from the soil, by maintaining higher humidity, and by increasing soil fertility through the decomposing litter. In addition to these, appropriate silvicultural practices can be adopted to minimize possible root competition between overstorey and understorey trees, and also to increase solar radiation to sufficient levels for understorey trees. In contrast, if the pine tree cover were completely removed at the end of its rotation period, most of the broadleaves could not then be planted in these lands except for a few species such as eucalypts and acacias some of which are highly adapted to harsh environmental conditions.

Besides these advantages generally experienced under an overhead canopy, competition for above- and below-ground resources can be limiting factors for understorey growth. However, it would be possible to deal with this situation with proper management of the existing tree cover, as done in the present studies. For example, felling trees in rows can reduce root competition while maximizing available sunlight to understorey growth. Once growth limiting factors are overcome at least to some extent it would be possible to establish broadleaved tree species under pine overstorey while enhancing ecological stability of the existing environment. This method of forest establishment which is similar to a shelterwood system is more appropriate for species which are unable to grow in exposed harsh environmental conditions, but not for species which are tolerant of such conditions and highly light demanding. The success of this method of establishment of forest trees depends mainly on the ameliorative effects of the existing tree cover on the understorey environment. Additionally, selection of appropriate species is also important.

Root competition for water and nutrients may be very important in an understorey environment and if it cannot be properly controlled may lead to poor growth and high mortalities of understorey plants. Root competition effects between overstorey and understorey trees in the soil environment were not shown to be important in wetter sites in the present experiments, apparently due to adequate availability of soil moisture for both understorey and overstorey trees. This was experienced with

Alstonia and *Toona* species. However, there were signs of root competition effects in the case of *Swietenia* and *Khaya* species which were growing in sites having comparatively lower rainfall, particularly at the *Khaya* site. This was evidenced by the significant growth effects following trenching. Trenching in combination with mulching increased height, diameter and volume growth of *Khaya* and trenching alone had some effects in *Swietenia*. Thus it was found that root competition from pine overstorey trees may set in for the growth of understorey broadleaves if sufficient soil moisture is not available. A similar finding was reported by Rutnum (1959) indicating that root competition and consequent loss of soil moisture during the dry periods may be limiting factors in shelterwood planting in the Dry Zone of Sri Lanka. Nevertheless, in the wetter areas, controlling root competition by measures such as trenching seems to be unnecessary, if sufficient spacing between pine trees and broadleaves is provided, preferably with the row thinning method as in the present study. However, these findings cannot be extrapolated to later stages of growth of broadleaves since their extending root system may interact with pine trees and growth could then be affected. Nevertheless, once broadleaves have grown sufficiently and established well, they will be in a strong position to compete with pine, if necessary. Also, in wetter sites since there may not be much competition for soil moisture; root competition effects might be mainly for soil nutrients. Since half of the pine trees had been removed in the present experimental sites, it can be expected that the active pine root mass in the soil was also halved, at least for some time. However, existing tree roots may extend laterally in response to thinning, diminishing these effects. At a later stage it might be necessary to further reduce root competition by another thinning of the pine.

The importance of trenching for reducing root competition has been shown by various other researchers for a long time. For example, Kimmins (1987) reported that elimination of root competition for moisture and nutrients by digging a trench around an area of shaded forest floor rapidly increased invasion of seedlings of various species. Also, trenching experiments by Vitousek et al (1979) demonstrated increased mineralization of organic matter and great improvements in nutrient availability. In the case of pine, Gadgil and Gadgil (1971, 1975) have shown that exclusion of ectomycorrhizal fungi by trenching can increase the availability of nutrients.

In addition to reduction of possible root competition effects, improvements in the soil micro-environment around the rooting zone of tree seedlings by mulching is also important as shown in detail in Chapter 4 and 5. Mulching helps in soil moisture

conservation during dry periods and available moisture can be utilized by plants to continue growth during these periods. Usually it is the upper horizon of soil which easily dries up due to surface evaporation during dry periods. Young plants, particularly depend on soil moisture and nutrients from these upper layers of soil and therefore are constrained, when the upper soil layers have dried out. However, if mulching increases the availability of soil moisture (also possibly with some extra nutrient supply) for a longer period than unmulched soil, plants could continue growth even during the dry periods until soil moisture level is considerably depleted. This advantage for the growth of mulched plants may be the reason why mulching had noticeable and significant impacts on growth of underplanted broadleaves in the present experiments. This advantage is particularly useful in an understorey environment where the understorey plants can be under pressure from overstorey trees for moisture and nutrient resources.

Alstonia responded well to mulching with significant height, diameter and notional volume increases of 20%, 28% and 63% over the control respectively. In *Khaya*, mulch alone increased these three growth parameters by 47%, 20% and 50% respectively, and this was almost doubled when mulch was combined with trenching. However, trenching did not show growth improvements when applied alone. This might be attributed to the possibility that the mulch effect was fully realized only when pine root competition was eliminated by trenching, while in the presence of root competition (without trench treatment) the growth improvement due to mulching was only half of that. Lack of response to trenching alone was possibly due to lack of root competition from pine roots when soil micro-climate was not improved with mulching. Another possibility would be that trenching increased the availability of nutrients to the understorey plants but this could be utilized only when soil moisture level was improved with mulching. Therefore, trenching alone had no effect and in combination with mulching improved the situation greatly with the interaction between the two treatments. However, this type of response was not observed in *Alstonia* where one reason might be less vigorous root competition as the pine tree size was comparatively smaller. In *Swietenia*, somewhat similar results were experienced to *Khaya* where trenching and mulching when applied alone increased height by 27% and 45% respectively more than the control, while their combination improved the height growth by 61%. Only in this case could a significant response to the 'trenching alone' treatment be observed. *Toona* also showed some response to trenching (17% and 23% more growth than the control for height and diameter respectively), however, these effects were not significant.

Mulching was found to be increasing base cations such as Ca, Mg and Na in all experiments, while other nutrients did so only in some sites. In addition, it also changed soil physical properties increasing bulk density, total porosity and water holding capacity. In addition to the above advantages of mulching it was observed that mulch reduced soil surface temperature and also harboured insect detrivores thus helping soil physical improvements and litter breakdown. Pieces of needles and fungal hyphae were observed under the moister mulched conditions which is also a sign of starting litter breakdown. All these were obviously beneficial for improving micro-site conditions of the rooting zone of broadleaves as evidenced by the development of fine feeder root system in the surface layers of soil underneath the mulch, particularly by *Khaya* and *Alstonia*. This was observed in all species including even some of the *Toona* plants at the much wetter Watawala site. Fine root biomass is reported to increase with increased water and/or nutrient availability in the top soil (Kessler, 1995). Better developed root-mats may increase the uptake of water and nutrients, and encourage tree growth. The environment under mulch was like a 'real' forest floor which was a contrast to a normal pine forest floor. If mulch was made by brushing or putting the needles around the underplanted seedlings, it could also check the spread of fire. Thus, mulching treatment gave encouraging results in the present study and it may be possible to further improve the practice.

The benefits provided by mulch may vary depending on the type of mulch material used and prevailing climatic conditions. In the present experiments, organic mulches were used for all experiments but other artificial mulch materials such as black plastic have also been tested particularly under temperate conditions. However, in tropical countries it is usually impractical to use artificial mulches in forest environments and also could be disadvantageous if they raise soil temperatures. Within organic mulch types, some materials are easily decomposed of which life time is shorter while others decompose slowly and last longer. Usually, mulches with low C:N ratios are easily decomposed and release nutrients faster than those with high C:N ratios. Nevertheless, this can be disadvantageous for perennial trees since they need nutrients and soil moisture for a longer period with longer lasting mulch material such as pine needle and wood chip mulches. Hence, those which slowly decompose may be more useful in this case. It should also be noted that this type of mulch may cause temporary nitrogen deficiencies in the early stages of decomposition due to low C:N ratios of the substrate which apparently constrains the microorganisms to utilize available soil nitrogen for litter decomposition. Easily decomposing mulch gives

rapid turn-over by soil dwelling insects that use the mulch as a source of food and by microorganisms that also break down the organic matter (Budelman, 1989). In later stages of the growth of broadleaves under the pine overstorey environment, it can be expected that their own litter may also provide a comparatively fast decomposing mulch and in combination with slowly decomposing pine mulch may provide a valuable mixture of both types of mulch material.

Environmental factors may also influence the effectiveness of mulch. Particularly, high rainfall conditions without sufficient sunny spells may tend to cause anaerobic conditions in soils under the mulch. However, it seems that even in high rainfall areas if sufficient sunny intervals are developed, these conditions can be avoided as experienced in the present study. It was observed in the Watawala site where *Toona* was grown that mulching might have created unfavourable effects or lack of response due to the very high rainfall conditions (around 5000 mm) with less sunny intervals during the rainy periods. However, in the other sites, mulching generally improved growth. In forest plantation establishment, use of mulch is not generally practised due to unavailability of sufficient mulch material in reforestation sites and also due to lack of knowledge and experience about the benefits of mulching.

In *Alstonia* mulch had increased rates of both RGR and NAR. Increase in NAR shows that it could increase the photosynthetic area and photosynthetic capacity of the plants which is important for continual growth increases. Lack of significant changes in morphological growth parameters in leaves such as SLA due to mulch and other treatments in this species indicated that improved growth is not associated with morphological changes but due to physiological changes. In *Khaya*, also mulch increased both RGR and NAR significantly. These two growth parameters were increased in *Swietenia* in the combined treatment of mulch, trench and mycorrhiza, but this was not statistically significant during the experimental period. Further increase in these parameters with later stages of growth are likely. Low RGR rates may be an indication of shortage of major resources of light, water and nutrients. Higher RGR in mulch treatments indicated that it could have improved the soil micro-climate in understorey broadleaves, probably reducing any stress situations likely to develop. Root:shoot ratio was not affected by mulch in *Alstonia* since both root and shoot dry weights were improved by this treatment. By contrast, in *Khaya* root:shoot ratio was significantly reduced by mulching due to improved shoot growth. High root:shoot ratios are characteristic of stress situations although absolute root biomass may be reduced by stress (Kessler, 1995). Stress situations may have

developed under the present conditions in unmulched plants due to shortage of soil moisture, deficiencies in nutrients and root competition from the overstorey trees.

When little water is available, all soluble ions could become less mobile in the soil because air spaces replace water in the pores between the soil particles. Under acidic conditions of soil, plant growth can be severely affected since cations are displaced by hydrogen ions on clay particles and soil organic matter and also P availability can decrease substantially (Black, 1968). Leaching of nutrients including N, P, K, Ca and Mg can also be a serious problem in high rainfall areas unless they are replenished by recycling. K is most susceptible to leaching followed by Ca and N, and P is similar to N. The entire K content of litter can potentially be leached. Accordingly, it would be important to know about the existing nutrient status in the soil and possible changes due to environmental factors on the forest floor in order to ensure success of underplanting.

When the trees have developed roots to deeper layers of soil they can tap soil moisture from those layers, and also when roots spread horizontally, they can take up more nutrients by exploring a larger surface area and therefore the effects of mulch may not be so evident in later stages of tree growth. This is true not only for mulching but also for any other silvicultural treatments like thinning. However, the initial boost of growth due to mulching may help plants to grow faster and get access to available resources both above- and below-ground more efficiently. Moreover, if mulch material persist on the soil for a longer period it may provide a continuous source of nutrients with its gradual decomposition. It was observed in *Alstonia* trees in the present experiment that even at the age of about 2 years, with their height reaching about 2 m, they had a mass of fine feeder roots under the pine needle mulch showing that they are still benefiting from the mulch. Observations showed that the root system of *Alstonia*, which was the largest and fastest growing species among the species studied, was well within the mulched zone of about 50-75 cm away from the base of the plant. Therefore it can be expected that they will be benefiting from the mulch applied for probably at least another two years. Other species with their comparatively slow growth can be expected to benefit from mulching for a period of at least 5 years altogether, according to their probable horizontal root expansion rates. Even if some roots exceed the mulched area, roots directly under the mulch and thereby the whole plant may be benefitted. However, it is important to replenish the mulch from time to time since it can be displaced due to heavy rains and winds. With the progress of the growth of broadleaved trees, they will also add leaf litter by

themselves naturally, enabling them to capture the site resources more effectively. Thus, initial growth encouragements from mulching (and also from trenching in drier sites) as observed in the present experiments, may be expected to enhance the competitive ability of the understorey trees in their later growth.

Mycorrhizal inoculation of soil was used as another measure of improving soil micro-climate, although the results were not encouraging due to limited response observed in the plants studied. Height, diameter and volume growth were not improved by mycorrhizal treatments significantly, but instead that it affected dry weight development in some cases. In *Khaya*, mycorrhizal inoculation increased total dry weights and as a result, leaf area ratio (LAR) was decreased due to lack of corresponding leaf area development. RGR and NAR were also improved with this treatment. In *Toona* mycorrhiza could change only root:shoot ratio at a marginally significant level. Therefore it was shown that these two species responded to mycorrhizal inoculations with increases in some growth parameters. In *Swietenia* also, mycorrhiza alone treatment increased plant height by 22% but this was not statistically significant. Improved leaf growth might be due to better nitrogen and/or phosphate uptake of those plants due to mycorrhizal associations. Mycorrhiza also increased RGR and NAR in *Khaya* plants which was a contrasting difference and worthwhile to further explore. Fine feeder root development under mulch as mentioned elsewhere may possibly encourage infection of mycorrhizal fungi as well.

Some mycorrhizal surveys were done as an addition to the present experimental studies and some of the results were summarized in Appendix VI. This shows that there were some endomycorrhizal spores present in the topsoils of pine plantations. This may have occurred associated with weed growth within or adjacent to these plantations and also due to insects and animal movements. Spore numbers were somewhat similar to what was found under the mature broadleaved trees. It can also be noted that in both cases a large number of these spores were dead. However, the effectiveness as an inoculum could have been higher in the mature tree soils since they contained fungal hyphae, infected root parts etc, in addition to spores. Using a trap culture (planting short term agriculture crops in a pot containing soils from the experimental sites) a massive increase in spore numbers was observed showing the high potential of using this practice as a method of producing inoculum for infecting plants. Various endomycorrhizal species identified by spore type and some ecto- and ectendo mycorrhiza present in pine roots are also listed in the same Appendix.

The significance of mycorrhiza in plant growth has been extensively studied and a large amount of related research support their role and importance in maintaining forest ecosystems. Various researches have shown that the external hyphal network of mycorrhizal fungi plays an important role in nutrient uptake, especially the nutrients that are not very mobile in soil solution, thereby often improving growth of the tree. The occurrence of hyphal networks between plants has also been identified and mineral nutrients can be passed between plants through these links (Newman, 1988). The same study also suggested that mycorrhizal hyphal links promote direct nutrient cycling by avoiding the mineralization process. Nutrient accumulation and retention by mycorrhiza are also reported to be beneficial to reduce erosion and leaching losses of nutrients (Miller and Jastrow, 1994). These are some of the important features among many others, which can be brought about by mycorrhizal fungi in a plant community. Abbot and Gazey (1994) reported that it may be an advantage to maintain high level of diversity of VA mycorrhizal fungi within soil, irrespective of their individual contribution to mycorrhiza formation since this would ensure maximum opportunity for suitable fungi to dominate when soils conditions are changed with forest practices. Thus, proper introduction and harnessing of these associations in the introduced broadleaves as in the present study could be very beneficial and should be encouraged for the establishment of viable and sustainable forest ecosystems in these lands.

Mycorrhizal effects suggested in the present study may influence plant growth to a greater extent at later stages of growth and this should be further explored in future studies. Present findings indicated some potentials. Possible interactions between ecto- and endomycorrhizal associations would also be worthwhile to investigate since both mycorrhiza will have to exist in the same environment in the present case. Also, it may be important to retain some conifer trees in the mixture since ectomycorrhiza are particularly important for efficient nutrient cycling in this mixed species environment (P.A. Mason, personal communications). There is increasing evidence that ectomycorrhizas may utilize organic sources of nitrogen and phosphorus. Mycorrhizal infection might be an important factor determining the survival and growth of tropical tree seedlings.

9.3 RESPONSES TO LIGHT ENVIRONMENT

The importance of the light environment and tree growth was discussed in detail in Chapter 7. Regulation of light level is clearly very important in underplanted environments and its effects were investigated under different thinning regimes and examined in two different thinning methods. A large area of unthinned pine plantations exists in Sri Lanka due to the delay in scheduled thinnings as mentioned in Chapter 1. These stands are over-crowded and unsuitable not only for underplanting but also for the growth of pine itself since competition for limited resources is reducing the growth of individual trees. Therefore, sufficient thinning is required particularly to facilitate broadleaved growth in the pine understorey.

Uniform thinning in the pine stands with selective removal of suppressed trees accrues benefits to the remaining pine trees themselves when compared to row thinning. However, in this method, there seem to be some disadvantages for the understorey trees with respect to light levels and root competition as it allows a lower light level to penetrate to the forest floor when compared to row thinning at the same thinning intensity, as found in the present study. Light level received in the row thinning method can be altered by changing the orientation of the rows. Adjers et al (1995) reported that *Shorea* species should not be planted directly under the overhead canopy, instead they should be planted in a 2 m wide line or otherwise growth will be retarded. They also reported that southeast-northwest as the best planting direction for some of these species. These findings are somewhat similar to the present finding where row thinning was found to be more beneficial. Root competition may be comparatively high in uniform method since pine roots can invade the rooting zone of broadleaves from any side, whereas with the row thinning method it may be mainly from one side which is closest to the pine row. However, in real practical situations perhaps this may not be the case under certain situations. In the management of understorey trees it is much easier to carry out maintenance operations (including weeding, fertilizing, fire protection etc) in the row thinning method where broadleaves are also planted in rows. Another main advantage of row thinning is, that it can considerably reduce the possible damage to understorey plants when subsequent thinning is done in the pine overstorey. Therefore, in terms of managing limited resources, row thinning may prove beneficial in comparison to uniform thinning.

It was also noted in the present study that very heavy thinning, as in the heaviest thinning treatment at the Kinigama site (reducing overstorey basal area to 10 m^2/ha) can lead to some unfavourable situations, though the understorey trees showed better growth rates at this intensity during the experimental period. Two main consequences are the susceptibility of remaining pine trees to wind damage in some situations and over-exposure of the forest floor which reduces the nursing effects of the overstorey. Excessive solar radiation may dry up surface soils easily which may cause water deficits in understorey plants reducing their growth and survival rates. This may be the reason that most of the valuable tree species are generally found to be difficult to grow under fully exposed and less fertile conditions. Therefore, these two extremes of too low and too high solar radiation should preferably be avoided when sensitive tree species are planted as an understorey in pine lands.

There seems to be a high potential for underplanting in wet pine areas (but may be not in very wet areas) as shown by the present studies. If uniform thinning is done, reduction of basal area up to about 15 m^2 per ha would be the most appropriate to avoid excessive opening of the overstorey canopy. This level of basal area may be further adjusted to some extent by increasing or decreasing the levels depending on the species selected for underplanting. This thinning intensity involves removing about 60% of trees from the existing density of 800 trees per ha. All species tested in the Kinigama site responded reasonably well to this thinning intensity and the results obtained could be further enhanced probably with trenching and mulching, more likely with heavy thinning. One of the best species at this high elevation site would be *Michelia champaca* which had a contrasting growth pattern in response to light when compared to other species. Its growth response was very uniform in response to light levels or thinning levels but this was not the case with other species. *Toona ciliata* also seemed to grow better under the conditions at the Kinigama site where rainfall was not excessive.

Row thinning with its comparative advantages seems to work well for most of the species studied. *Alstonia* was the best species in the whole study in terms of performance, showing excellent growth rates. Light levels received in this stand was about 59% of the full sun with only 50% removal of trees, which was higher than what was achieved at the heaviest thinning intensity (with 74% tree removal) treatment at the Kinigama site. The conditions were further improved in *Alstonia* when trees were mulched indicating that sufficient light levels combined with enough soil moisture favours its growth considerably in the present site.

In other sites, double row thinning with about 50% tree removal for *Khaya* plants appeared insufficient as indicated by a trend of somewhat improved growth with increasing light. Therefore, a higher level of light with increased thinning intensity (probably triple row thinning) may be useful for the growth of this species.

For *Swietenia macrophylla* growth, triple row thinning was not found to be unfavourable which allowed plenty of light to fall on the plants. However, there was a slight trend of growth decline with increasing light, probably indicating too much light is unfavourable. However, light level will be gradually reduced with time due to expansion of pine tree foliage and therefore light levels may be optimal at later stages of growth.

Site conditions were not very favourable for the growth of *Toona ciliata* at the Watawala site and light measurements indicated that it was too high for its growth although it was low compared to other row thinned sites. This was attributed to other factors such as too heavy rainfall which would have limited its root expansion probably reducing its capacity to respond to higher light intensities. However, under more favourable conditions, as experienced at Kinigama site, this species seems to be responding well to increasing light.

Alstonia showed signs of light saturation between about 21% and 62% light of full sunlight indicating its ability to grow under some shade although it can grow under full sunlight conditions. The fact that it produces small wind dispersed seeds may indicate a position towards the pioneer end of the continuum. *Khaya* has been described as a shade tolerant species (Kwesiga, 1984) at early stages but light demanding later. In the present experiments it indicated some response to increasing light levels when these were increased from 20% to 55%. *Swietenia*, however, showed signs of slightly decreasing growth with increasing light level from about 30% to 60% probably indicating some shade requirements in early stages although it is reported to have the capacity to grow under full sunlight elsewhere. *Toona* followed the same trend as that of *Swietenia* between the light levels of about 35% to 55%. *Michelia*, in contrast, showed a clear response to increasing light conditions overa a wide range of light conditions of 15% to 60%. In the thinning trial, however, all species showed positive responses to increasing light levels plus reduced root competition from overstorey associated with increased thinning. The results from

thinning trial cannot be directly compared with other trials since they were in different sites under somewhat different climates.

The survival percentage of the species studied were high except at Watawala site where site conditions were somewhat unfavourable. The plants in the control treatment also showed high survival in most species indicating existing soil and light factors are not much affecting the survivorship, however, growth rate may be affected. Improving the soil and light environment is therefore important for the success of underplanting broadleaves under pine.

Spatial variation in light availability leads to variation in other physical and biotic environmental factors, including temperature, soil moisture, herbivore abundance etc. Thus plant establishment in the understorey is influenced by species-specific responses to these multiple factors confounded with the light environment and not merely upon the light intensity, spectral quality, or sunfleck frequency as reported by Kitajima (1996).

An increasing number of investigations on underplanting in natural forests in the tropics are becoming available. Nevertheless, experimental evidence on underplanting in forest plantations is generally lacking in the tropics in comparison with temperate areas. Some of the information being obtained from natural forest environments or controlled environment conditions can be applied to plantation conditions as well, for example response of understorey species to different light levels. Even more important, however, will be the results of field experiments such as those in the present study.

The hypotheses tested in the present study were given in Chapter 1, some of them being rejected and and some accepted, based on the findings of the study as follows;

1) It was evident that all broadleaved species tested in the present study had the potential to grow under pine provided the general climatic conditions were favourable for the reqirement of the individual species.

2) Root competition effects were observed only in comparatively dry sites as evidenced from the trenching studies. Mulching was found to be highly beneficial for the growth of broadleaves except in very wet areas, while mycorrhiza application were proved to be having some benefits in species except *Alstonia*.

3) Of the different thinning methods used, row thinning was apparently beneficial in comparison to uniform thinning. In case of uniform thinning, higher thinning intensities proved to be useful generally for most of the species studied.

4) Solar radiation levels were found to be generally sufficient in row thinned stands for the growth of understorey broadleaved species, while in the case of uniform thinning lower tree densities of the overstorey showed beneficial effects on the understorey with higher solar radiation and possibly reduced root competition. Little correlation was found between the growth of individual plants and the light levels they received.

9.4 SOME ECOLOGICAL CONSIDERATIONS

In the present study areas, low soil fertility, soil erosion and frequent burning of forest floor have created suboptimal conditions for most of the broadleaved species growth. Under these conditions developing seedlings or saplings may face stress situations, particularly if the overstorey and understorey are not properly manipulated. When plants respond to stress there can be changes in assimilation of carbon and other resources within the plant. Dickson and Isebrands (1991) reported that environmental changes are sensed primarily by leaves and a decrease in leaf sink strength shifts carbon allocation from developing leaves to the lower stem and roots, thus providing more assimilate for roots. Possible stresses due to lack of sufficient solar radiation may be reduced by having mixtures with stratified canopies of sun-adapted species in the high-light environment in the overstorey and shade-adapted species in the low light of the understorey. It was reported by Vandermeer (1989) in agricultural ecosystems that a monoculture cannot utilize all the niche space available, and a second crop type can fit in without disturbing the first crop too much and this is similar to the coexisting of two or more species in natural ecosystems. This can be well applied to forest ecosystems where underplanting is done, particularly if the overstorey is sufficiently thinned.

In the present study a series of field trials were carried out to study the gradual conversion of even-aged pine monocultures to uneven-aged pine-broadleaf mixture. This is the first phase of the conversion programme and it is planned subsequently to convert these stands to uneven-aged broadleaved monoculture or uneven-aged mixed broadleaved forest (see Plate 9.1). Thus, the final aim of this conversion programme

is to eliminate the identified unfavourable effects of pine monocultures, associated mainly with insufficient thinning and fire, and establish a forest cover which would be relatively self-perpetuating with a continuous forest cover maintained by continuous underplanting or encouraging natural regeneration. If successful, this can avoid clearfelling method of forest harvesting which is unfavourable particularly for highland areas where soil is susceptible to erosion and also for nutrient cycling in impoverished sites. Furthermore, broadleaved forests will minimize fire hazard which does much harm to these stands at present. Common pest attack of the shoot borer in Meliaceae species such as *Swietenia* and *Toona* may also be reduced by underplanting, through mixing them with other non-susceptible species. Enrichment planting or mixed species plantations were suggested as an appropriate silvicultural management systems for reducing such pest attacks by Newton et al (1993).

It is important to note that, as mentioned in Chapter 1, in environmentally sensitive areas protection forests are more important than production forests. In fact, a well established broadleaved forest with one or more suitable species, as those studied in the present study, can play a major role not only to protect the soil environment in these areas but also to give better economic returns than even-aged pine monocultures, as they presently stand. It was indicated from the present study that pine tree cover may be successfully used for the establishment of broadleaved forests, provided soil and light environmental factors are properly manipulated. If the method is found to be successful with further studies, indeed, more degraded grasslands can be planted with pine in order to capture the site resources successfully and to convert them into broadleaved forests subsequently, since most broadleaves cannot establish themselves in these lands. Perhaps, underplanting may be easier if it is done at earlier growth stages of pine than was done in the present study since younger pine trees may be more manageable in terms of controlling competition to broadleaves.

Forest management and utilization can have a considerable influence on the stability and sustainability of forest ecosystems. Larsen (1995) identified that resistance and resilience (resistance to external stress and recoverability from a perturbation respectively) are important in forest ecosystems to increase the stability of the system ensuring sustainability. He also suggested that by mixing different species it is possible to avoid temporal decoupling of biomass production and mineralization, and also that avoiding clearcutting in the regeneration of a forest may cause minimum damage to the ecosystem and the micro-climate already established by the forest cover. Thus new scientific approaches are required in silviculture to understand

Plate 9.1 a) Growing dipterocarp saplings under pine in a pilot study, showin the pine monoculture becoming an uneven aged mixture.

b) A well established mixed forest including introduced *Swietenia* a indegenous species with naturally regenerating seedlings in the understorey.

ecological interactions in forest ecosystems and develop sustainable forest plantations.

9.5 CONCLUSION

As mentioned in Chapter 1, the main objective of this study was to assess the effects of soil and canopy treatments on the early performance of broadleaved species introduced under pine overstorey. Survival was high in all species except at the very high rainfall site. Out of the soil treatments, mulching around understorey plants was highly beneficial with evidence of soil micro-climatic and growth improvements in all species studied except *Toona*. Dry matter production, relative growth rate and net assimilation rates were also improved by this treatment, particularly in *Alstonia* and *Khaya* species. Reduction of root competition from the overstorey trees by means of trenching appeared to be useful only in comparatively drier sites. Improvement of the rooting zone by application of mycorrhizal inocula did not show marked results during the experimental period, though there were slight growth improvements in some species. Light levels at the individual tree level were found to be not well correlated with the growth of trees. Light intensity achieved by present thinning methods with about half of the tree removal from the existing stand seemed to be generally adequate, particularly with the row thinning method. However, further adjustments on the thinning intensity may be required depending on the species. Site-species matching was found to be important because of the clearly different responses shown by the five broadleaves in this study.

9.6 IMPLICATIONS FOR FOREST MANAGEMENT

9.6.1 Thinning method of the overstorey

The forestation method of underplanting attempted in the present study has some resemblance to the shelterwood silvicultural system described by Matthews (1989). Shelterwood systems are normally employed to establish a new forest crop by encouraging natural regeneration through manipulating the overhead canopy. In contrast, underplanting involves deliberately planting an understorey beneath an overstorey rather than depending on natural regeneration. This system usually leads to a mixed stand consisting of two or more species. Thinning of the overstorey trees or some opening of the canopy is one of the important requirements in both systems to encourage growth of the understorey seedlings.

As in the present studies, underplanting can be done by uniform thinning or row thinning of the overstorey. Out of these two methods, row thinning seems to be more useful for underplanting because of its advantages. In addition to the increased light levels usually obtained in the understorey by this method, it makes planting of understorey, subsequent cultural practices and overstorey thinning much easier than the uniform method. Control of fire can also be somewhat easier since opened strips of the overstorey will receive a lower amount of pine needles and hence low fuel accumulation particularly in early years of thinning. However, uniform thinning may be useful where pine trees have grown to a great height and diameter and therefore, selectively thinning of poor trees may be more appropriate rather than premature felling of larger trees. Trees remaining after thinning can provide shelter for seedlings in the understorey.

In case of row thinning, thinning intensity and method can be controlled relatively easily. For example 50% tree removal can be achieved by thinning trees in the order of 1:1 (thinning one row out of each 2 rows), 2:2 or 3:3 and so on. The thinning method can be adapted to do thinning to a pre-determined level such as 40%, by 2:3 (thinning two out of each 5 rows), 60% by 3:2 etc. It is also possible in this method to leave a wider strip unthinned so that after planting broadleaves in the open strip, further thinning of the overstorey would be much easier since trees can be felled to this wider unthinned strip thereby minimizing the damage to the understorey trees. Light level can also be changed in this method by changing the orientation of open strips. In the uniform method, it is relatively difficult to thin a stand down to a pre-determined level while maintaining the uniformity of the overstorey canopy. However, if there are low light levels even after thinning, it may be possible to do some pruning of pine tree branches which can increase light level on that part of the understorey, although it may be expensive.

9.6.2 Suitable sites

In selecting suitable pine sites for underplanting, it was clear from the present study and also from other general observations that wetter areas (Wet Zone) are more suitable rather than drier areas. However, too wet areas are also generally unsuitable, unless site species matching is properly worked out. In drier pine areas, understorey seedling mortality could be high, particularly in the case of unusual dry periods. Moreover, fire risk is also higher in those areas and severe losses can be experienced

unless intensive fire control measures are adopted. Establishment of a broadleaved understorey may be still possible in the drier parts of the highland areas (Intermediate Zone) provided careful attention is given for correct timing of planting, trenching around seedlings to reduce root competition, application of mulch possibly in combination with some fertilizer application etc and also with fire control measures.

It would be better to select younger pine plantations rather than mature ones, since if pine trees are bigger in size, root competition may be severe under such situations. Also, taller trees with wider crowns may reduce the light level available for understory considerably, unless heavy thinning is carried out. In such cases it would be more suitable to do uniform thinning without felling full grown pine trees.

9.6.3 Management of understorey trees

Once the overstorey trees are thinned and broadleaves are underplanted the crowns of the overstorey may gradually expand to fill the unoccupied space reducing the understorey light levels. Similarly root competition can also set in and may interfere with the growth of understorey trees. In order to cope with this situation, it may be necessary to do another thinning in the overstorey during the course of time. This might be done generally in about 8-10 years after planting broadleaves, depending on the growth of understorey trees. At this thinning all the sub-dominant pine trees can be removed retaining the best pine trees for final felling. Alternatively, further row thinning can be carried out in the unthinned strip in order to widen the existing open strip where broadleaves were planted. A thinning of understorey trees can also be done at this stage as required.

At the rotation age of pine which is about 25-30 years for timber production, all remaining pine trees can be clear felled and the newly opened area can then be used for planting the second understorey with the same broadleaved species planted earlier or with some other broadleaved species. Thus the older understorey becomes a new overstorey for newly planted seedlings. At this stage, it may also be possible to leave some pine trees uncut and keep them for a further long period (may be until broadleaved species are felled) so as to minimize damage to broadleaved trees during thinning. Also, this would help to keep ectomycorrhizal associations for a longer time in this environment and otherwise they may gradually disappear from the ecosystem, possibly losing their potential benefits as mentioned elsewhere. It may also be possible to grow naturally regenerated pine seedlings to allow under pine or

broadleaved overhead canopy so that mixed state of species can be maintained. It was suggested by Fenger (1975) that when pine seedlings are suppressed in their early growth up to about 10 years by means of such as shade from an overstorey that formation of low quality juvenile core can be reduced and thus would help to improve timber properties. All the species tested in this study have self regenerating capacity which is extremely useful in environmentally sensitive areas to avoid clear-felling of the plantations. Clear-felling is generally less desirable in environmentally sensitive areas due to accelerated soil erosion in steep lands, nutrient depletion of the site etc as described earlier also, although it may well be the economically best method for harvesting a plantation. It is also expected that broadleaved plantations will reduce the fire risk considerably, in comparison to conifers, minimizing the possible damage to the forest floor.

Understorey seedlings should be provided with a better environment by applying a mulch such as pine needles which can give considerable growth advantages as demonstrated in the present experiments. This practice can be done easily and cheaply under pine overstorey due to plentiful availability of needles. Mulching should be done preferably immediately after planting in the field since this will ensure soil moisture availability for a longer period than unmulched plants. It is also important to replenish the mulch whenever necessary as it can be displaced by run-off water and winds. Trenching is generally required only in the areas where longer dry periods are expected (in Intermediate, and Intermediate and Wet Zone boundary areas). However, trenching is time consuming and laborious work to do, particularly if a large number of plants are involved, whereas mulching is easy and quick.

It is important to give due consideration for environmental aspects in forest plantations established in the central hilly areas of the country, rather than concentrating on pure economic aspects, for, if not, plantations in the area may not be sustainable in the long run. In fact, the broadleaves tested in this study are not only ecologically more acceptable than pine but also economically more attractive, if grown successfully. It is reported that trees which are adapted to water and nutrient stress conditions (but not to low light conditions) such as pine and eucalypt trees, generally produce low quality litter. On the other hand species adapted to shade conditions (but not to water and nutrient stresses) produce high quality litter. (Chapin, 1991). Mixing broadleaf litter with those of conifers can enhance litter breakdown in conifers, if broadleaves contain higher nutrient contents in their litter to decrease the C:N ratio of the litter mixture (Kelty, 1992). Mixed plantations can provide increased

structural and biological diversity of forests and once established, silvicultural systems of uneven-aged plantation management can be adopted.

9.7 EXPERIMENTAL LIMITATIONS

This study was undertaken to investigate the possibilities of planting broadleaved species under pine overstorey canopy. The early growth of some potential species have been evaluated in a series of experiments in relation to soil and light environmental aspects. The experiments were carried out under field conditions and some of their limitations are discussed below.

Lack of arranging all experiments within the same environment can cause a problem for directly comparing the results of different experiments since the species performance may vary in different environments, so one experiment was arranged to have various species in one site. However, this particular site where different species were compared was not very representative of the other sites of the study. Nevertheless, conducting the experiments in different environments gave the advantage of application of results to a wider geographical area.

Mulching, which was one of the main treatment of the experiments was done with only one mulch material, pine needles, and since it is somewhat different from other organic mulch material such as grass and broad leaves, the results of mulching may not be directly applicable to other available mulch material. Mycorrhizal treatments were applied only at a later stage of field planting and this would have relatively reduced its capacity to infect and influence growth of broadleaves planted under pine. Rather, it would have been better if inoculation could be done at the nursery stage of growth.

The effectiveness of trenching might have been limited to some extent by the re-growth of pine roots. Although trenching was repeated once during the experimental period, pine root growth below the bottom of the trench could have occurred, competing with broadleaves. Inserting plastic or metal barriers into the trench to prevent pine root penetration would have been useful, however this may interfere with soil moisture movements in the soil and may cause more soil moisture depletion in the rooting zone of broadleaves or excessive soil moisture in the wet periods. Moreover, it is largely impractical to do this practice in the field. Digging trenches

deeper than what was done in the present experiments may prove beneficial, nevertheless it is extremely difficult with large number of trees.

In the light studies, although the light environment was quantified with hemispherical photographs, red:far red ratio of the solar radiation in the pine understorey environment could not be measured and this necessarily limited the knowledge gained with respect to understorey illumination.

One of the main species in this series of experiments, *Toona ciliata* was planted in a site with very high rainfall (Watawala) and this was later found to be unfavourable for its growth. It was also tried in another site (Kinigama) which was drier than a normal wet area but its growth potential could not be evaluated in average wet zone conditions where *Alstonia macrophylla* grew very well. *Khaya senegalensis* was tried in a site which was a little higher in elevation than it is usually grown and this would have somewhat affected its growth rates.

Information derived from the present study is directly applicable only for establishment and early growth stages of broadleaved species. These results may not be sufficient to predict the performance of these species in their later stages of growth.

There were some limitations of the experimental design and analysis adopted. Selection of a limited number of treatment combinations out of the all possible combinations limits the information generated by these experiments. Some of the two factor combinations and the three factor combination except in one experiment could not be used, due to practical difficulties in accommodating and handling a large number of treatments as mentioned in section 3.3.4. This limited the information gained in some of the interaction effects. A fully factorial design would have given such information. Another limitation in the design of experiments was that each species had been planted at a different site, confounding the effects of species with site. It was partly why the Kinigama site was chosen, where the species were all present together, in order to make comparisons with information of performance of species under different site conditions.

9.8 SUGGESTIONS FOR FUTURE WORK

All the experiments were conducted in the present study under field conditions. Although, this would give better applicability under practical situations, it is important to conduct experiments also under controlled environmental conditions by which the effects of individual environmental factors such as light and their effects on the growth of broadleaved species can be more closely studied. This would also enable the disentangling of the effects of other factors, for example, root competition which otherwise may obscure the effects of light factor due to interaction effects. The effects of lower light levels than what was experienced in the present study may also be tested on the growth of the suitable broadleaved species so as to determine the critical light levels of individual species which may be very useful in practical situations of understorey tree planting.

Mixing of two or more broadleaves under pine canopy can be studied in future. Although this may complicate the situation due to various interactions, it may generate useful information on ability of coexistence of different species and their possible interactions both positive and negative. This type of situation, if practically viable, can lead to formation of more complex mixtures which may be even more advantageous in protecting sites and also for the sustainability of the protection sites. One of the initial possibilities is mixing *Alstonia macrophylla* with *Swietenia macrophylla* since both species can grow fast under suitable environments. Both species have the capacity of tolerating shade in early stages, better response to incoming radiation in later growth and also with high natural regeneration capacities.

Testing of other potential species for underplanting in pine would be worthwile. One of the potential candidates is *Dipterocarpus* species, mainly due to their shade tolerance capacity and value in the reforestation activities in the country. It would also be interesting to study the compatibility of *Dipterocarpus* with pine since both species are ectomycorrhizal in contrast to what was experienced in the present study where two different mycorrhizal types were involved. Planting leguminous trees with known N-fixing nodules may be another possibility to improve site fertility conditions.

Mulching was the best experimental treatment tested in this study for the growth of broadleaves. Further investigations are required to test the effects when pine needles are combined with other materials or artificial fertilizers. Encouraging results have

been experienced in other studies with this combination as described in the section 4.6.1.

Mycorrhizal inoculation of broadleaves to be underplanted with pine at nursery stage and monitoring the resulting growth performances in comparison with uninoculated controls will be important. It will also be important to study the level of infection and fungal strains, and their relatedness to growth parameters. Identification of mycorrhizal species in different tree species and to find out whether same mycorrhizal species can infect different broadleaved tree species will be useful in mixing different species in an understorey.

Studies in effects of light levels on photosynthesis of different species will be useful and this type of information can be used to plan different strategies in underplanting practices. The effects of red:far red ratio on understorey growth should also preferably be studied. In certain cases interactions between light and nutrient levels exist and these may be studied in future work since both light and nutrients are important limiting factors in the understorey environments.

The present study gave reasonably sufficient information on the thinning level of the pine overstorey. Moreover, it is further needed to study the effects of second thinning which was suggested to be done in 8-10 years after the establishment of broadleaves. It is also important to study the practical difficulties which will be experienced in second thinning and work out the possible ways to overcome those.

REFERENCES

Abbott, D.T. and Crossley, D.A. Jr (1982). Woody litter decomposition following clear-cutting. *Ecology* **63**(1), 35-42.

Abbott, L.K. and Gazey, C. (1994). An ecological view of the formation of VA mycorrhizas. In: *Management of Mycorrhizas in Agriculture, Horticulture and Forestry*. Proceedings of an international symposium, Sept/Oct, 1992, Perth, WA, Australia (Ed. Robson, A.D., Abbott, L.K. and Malajczuk, N.), pp 69-78, Kluwer Academic Publishers, London.

Adjers, G., Hadengganan, S., Kuusipalo, J., Nuryanto, K. and Vesa, L. (1995). Enrichment planting of dipterocarps in logged-over secondary forests: effects of width, direction and maintenance methods of planting line on selected *Shorea* species. *For. Ecol.Manage.* **73**, 259- 270.

Ahmed, D.H., Ghani, A.B., Ab-Ghani, A.R. and Darus, H.A. (1989). Flowering and fruiting in Calamus manana. *RIC Bulletin* **8**(1-4), 2.

Allen, E.B. and Allen, M.F. (1986). Water relations of xeric grasses in the field: interaction of mycorrhizae and competition. *New Phytol.* **104**, 559-571.

Allen, M.F. (1991). *The Ecology of Mycorrhizae*. Cambridge University Press, Cambridge, UK.

Allen, M.F., Moore, T.S. Jr and Christensen, M. (1982). Phytohormone changes in *Bouteloua gracilis* infected by vesicular mycorrhizae. II. Altered levels of gibberellin-like substances and abscisic acid in the host plant. *Can. J. Bot.* **60**, 468-471.

Alwis, de, K.A. and Panabokke, C.R.(1972). Handbook of the soils of Sri Lanka,*J. Soil Sci. Soc. Ceylon* **2**.

Amaranthus, M.P. and Perry, D.A. (1987). Effects of soil transfer on ectomycorrhiza formation and, the survival and growth of conifer seedlings in disturbed forest sites. *Can J. For. Res.* **17**, 944-950.

Amaranthus, M.P. and Perry, D.A. (1994). The functioning of ectomycorrhizal fungi in the field: linkages in space and time. *Plant and Soil* **159,** 133-140.

Anderson, J.M., Ineson and P. Huish, S.A. (1983). *Soil Bio. Biochem.* **15**(4), 463-467.

Anderson, J.M. and Swift, M.J. (1983). Decomposition in tropical forests. In: *Tropical Rain Forest: Ecology and Management* (Eds. Sutton, S.L., Whitmore, T.C. and Chadwick, A.C.), pp 287-309. Special Publication of British Ecological Society 2, Blackwell Scientific Publications, Oxford.

Anderson, M.C. (1964). Studies of the woodland light climate: the photographic computation of light conditions. *J. Ecol.* **52**, 27-41.

Ang, L.H. (1991). Effects of open and underplanting on early survival and growth of *Endospermum malaccense* (sesendok), *Alstonia angustiloba* (pulai) and *Shorea parvifolia* (meranti sarang punai). *J. Trop. For. Sci.* **3**(4), 380-384.

Anonymous, (1945). Silvicultural Research Administration - 1943, Ceylon. p 14.

Anonymous, (1963). Silviculture: Rehabilitation of logged indigenous forests. *Extr. Rep. For. Res. Inst. NZ. For. Ser.* 1963/1964. 387-340. (CAB Forestry Abstracts).

Applegate, G.B. and Nicholson, D.I. (1988). Carribaean pine in an agroforestry system on the Atherton/Tableland in north east Australia. *Agrof. Sys.* 7(1), 3-15.

Archbold, D.D., Strang, J.G. and Hines, D.M. (1989). Yield component responses of Hull thornless blackberry to nitrogen and mulch. *Hortic. Sci.* **24**(4), 604-607.

Arnon, I. (1972). *Crop production in dry regions*, Vol. 1. Background and principles., Leonard Hill, London.

Ashton, M.S. (1995). Seedling growth of co-ocurring*Shorea* species in the simulated light environments of a rain forest. *For. Ecol. Manage.* **72**, 1-12.

Attiwil, P. M. and Adams, M.A. (1993). Nutrient cycling in forests*New Phytol.* **124**, 561-582.

Bahuguna, V.K., Negi, J.D.S., Joshi, S.R. and Naithani, K.C. (1990). Leaf litter decomposition and nutrient release in *Shorea robusta* and *Eucalyptus camaldulensis* plantations. *The Indian Forester* **116**(2), 103-114.

Baldwin, M.F. (1991). *Natural resources of Sri Lanka* - conditions and trends. A report prepared for the NARESA, Sri Lanka. 1991.

Ball, J.B., Wormald, T.J. and Russo, L. (1995). Experience with mixed and single species plantations. *Commonw. For. Rev.* **74**(4), 303-305.

Bandaratillake, H.M. (1988). Watershed afforestation for controlling soil erosion and landslides. *The Sri Lanka Forester* **xviii** (3 & 4). 131-136.

Bandaratillake, H.M. (1994). *Administrative report of the Conservator of Forests Sri Lanka for the year 1994*. Forest Department, Colombo, Sri Lanka.

Barnes, R.D. (1988). Tropical Genetics at the Oxford Forestry Institute,*Commonw. For. Rev.* **67** (3), 231-241.

Basu, P.K. and Aparajita-Mandi (1987). Effect of Eucalyptus monoculture on the soils of south West Bengal, Midnapore District. *J. Trop. For.* **3**(3), 228-234.

Bazzaz, F.A. (1979). The physiological ecology of plant succession.*Ann. Rev. Ecol. Sys.* **10**, 351-371.

Bazzaz, F.A. and Carlson, R.W. (1982). Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia (Berlin)* **54**, 313-316.

Bazzaz, F.A. and Pickett, S.T.A. (1980). Physiological ecology of tropical succession: a comparative review. *Ann. Rev. Ecol. Syst.* **11**, 287-310.

Bell, T.I.W. (1973). Erosion in the Trinidad Teak Plantations.*Commonw. For. Rev.* **52**(153), 223-233.

Bernadzki, E., Kowalski, M. and Szujeck, A.(1984). Use of broadleaved understorey for the protection of Scots pine stands. III *Sympozjum Ochromy Ekosystemow Lesmych.* Vol 1, 193-204. (CAB Foretry Abstracts).

Berta, G., Trotta, A., Fusconi, A. Hooker, J.E., Munro, M., Atkinson, D., Giovannetti, M., Morini, S., Fortuna, P., Tisserant, B., Gianinazzi-Pearson, V. and Gianinazzis, S. (1995). Arbuscular mycorrhizal induced changes to plant growth and root system morphology in *Prunus cerasifera. Tree Physiol.* **15**(5), 281-293.

Bevage, D.I. and Richards, B.N. (1970). Nitrogen in the growth of *Araucaria cunninghamii* Ait. underplanted in *Pinus* stands. *Ecology* **51**(1), 134-142.

Binkley, D. (1984). Importance of size-density relationship in mixed stands of Douglas-fir and red alder. *For. Ecol. Manage.* **9**(2), 80-85.

Binkley, D. Dunkin, K.A., DeBell, D. and Ryan, M.G. (1992). Production and nutrient cycling in mixed plantations of *Eucalyptus* and *Albizia* in Hawaii. *For. Sci.* **38**, 393-408.

Bjorkman, O. (1981). Responses to different quantum flux densities. In: *Encyclopaedia of Plant Physiology* (Ed. Lange, O.L., Nobel, P.S., Osmond, C.B. and Ziegler, H.), pp 57-107. Springer-Verlag, Berlin.

Black, C.A. (1968). *Soil Plant Relationships* (second edition). John Wiley and Sons, New York.

Boardman, N.K. (1977). Comparative photosynthesis of sun and shade plants.*Ann. Rev. Plant Physiol.* **28**, 355-377.

Bolan, N.S. (1991). A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. *Plant and Soil* **159**, 89-102.

Boot, R.G.A. and Gullison, R.E. (1995). Approaches to developing sustainable extraction system for tropical forest products. *Ecol. Appl.* **5**(4), 896-903.

Bowan, G.D. (1994). The ecology of ectomycorrhiza formation and functioning. *Plant and Soil* **159**, 61-67.

Bowen, G.D. (1980). Misconceptions, concepts and approaches in rhizosphere biology. In: *Contemporary Microbiol Ecology* (Ed. Ellwood, D.G.). pp 28, Academic Press, London.

Brown, J.M.B. (1955). Shelter and early growth of beech.*Quart. J. For.* **49**(3), 175-180.

Budelman, A. (1989). The performance of selected leaf mulches in temperature reduction and moisture conservation in the upper soil strata.*Agrof. Sys.* **8**, 53-66.

Burkhart, H.E. and Tham, A. (1992). Predictions from growth and yield models of the performance of mixed-species stands. In: *The Ecology of Mixed-Species Stands of Trees* (Ed. Cannell, M.G.R., Malcolm, D.C. and Robertson, P.A.), pp 21-34. Blackwell Scientific Publications, London.

Carlyle, J.C. and Malcolm, D.C. (1986). Larch litter and nitrogen availability in mixed larch-spruce stands. I. Nutrient withdrawal, redistribution and leaching loss from larch foliage at senescence. *Can. J. For. Res.* **16**(2), 321-326.

Carpenter, S.B. and Smith, N.D. (1981). A comparative study of leaf thickness among southern Appalachian hardwoods. *Can. J. Bot.* **59**, 1393-1396.

Carter, R.E. and Klinka, K. (1992). Variation in Shade tolerance of Douglas fir, western hemlock, western red cedar in coastal British Columbia. *For. Ecol. Manage.* **55**, 87-105.

Chabot, B.F. and Chabot, J.F. (1977). Effects of light and temperature on leaf anatomy and photosynthesis in *Fragaria uesca*. *Oecologia* **26**, 367-377.

Chabot, B.F. and Hicks, D.J. (1982). The ecology of leaf life spans.*Ann. Rev. Ecol Sys.* **13**, 229-259.

Chakravarty, P. and Chatarpaul, L. (1990). Effects of fertilization on seedling growth, ectomycorrizal symbiosis and nutrient uptake in *Larix laricina*. *Can. J For.* Res. **20**(2), 245-248.

Chapin, F.S. III (1991). Effects of multiple environmental stresses on nutrient availability and use. In: *Responses of Plants to Multiple stresses* (Ed. Mooney, H.A., Winner, W.E. and Pell, E.J.), pp 67-88. Academic Press, San Diego.

Chapin, F.S. and Kedrowski, R.A. (1983). Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology* **64**, 376-391.

Chazdon, R.C. and Fetcher, N., (1984). Light environment of tropical forests. In: *Physiological Ecology of Plants in the Wet Tropics* (Ed. Medina, E., Mooney, H.A. and Vazquez-Yanes, C.), pp 27-36. Dr. W. Junk, The Hague.

Chazdon, R.C. and Field, C.B.(1987). Photographic estimates of photosynthetically active radiation: evaluation of a computerized technique. *Oecologia* **73**, 525-532.

Chazdon, R.L. (1986). Light variation and carbon gain in rain forest understorey palms. *J. Ecol.* **74**, 995-1012.

Chazdon, R.L. (1988). Sunflecks and their importance to forest understorey plants. *Adv. Eco. Res.*. **18**, 2-52.

Chilvers, G.A., Lapeyrie, F.F. and Horan, D.P. (1987). Ectomycorrhizal vs endomycorrhizal fungi within the same root system. *New Phytol.* **107**. 441-448.

Chmyr, A.F. and Skiba, A.A. (1979). Effect of stand composition and structure on the moisture supply of Norway spruce in plantations below the forest canopy. *Lesnoi-Zhurnal* No 1, 10-14. (CAB Forestry abstracts).

Chowdhary, R.L., Abdul Bari, P.A. and Prasad, K.G. (1987). Performance of tropical pine and their provenances in Tamil Nadu. *The Indian Forester* **113**(2), 101-111.

Christensen, B.T. (1985). Wheat and barley straw decomposition under field conditions: effects of soil type and plant cover on weight loss, nitrogen and potassium content. *Soil Bio. Biochem.* **17**, 691-697.

Christensen, N.L. (1973). Fire and the nitrogen cycle in *Adenostroma* chaparral. *Science* **181**, 66-68.

Clark, D.B. (1990). The role of disturbance in the regeneration of neotropical moist forests. In: *Reproductive Ecology of Tropical Forest Plants* (Eds. Bawa, K.S. and Handley, M.), pp 291-315. Man and Biosphere Series, Vol. 7, UNESCO, Paris./ Parthenon press, Casnforth, England.

Coley, P.D., Bryant, J.P. and Chapin III, F.S. (1985). Resource availability and anti-herbivore defense. *Science* **230**, 895-899.

Collett, N.G., Neuman, F.G., Tolhurst, K.G. (1993). Effects of two short rotation prescribed fires in spring on surface-active arthropods and earthworms in dry sclerophyll eucalypt forest of west-central Victoria. *Aust. For.* **56**(1), 49-60.

Coninck, J.G.C. de (1987). *Soil and Plant Analysis*: a laboratory guide. Internal Report, Institute of Fundamental Studies, Kandy, Sri Lanka.

Coombe, D.E. (1960). An analysis of the growth of*Trema guinensis*. *J. Ecol.* **48**(1), 219-230.

Corner, E.J.H. (1940). *Wayside Trees of Malaysia*. Vol. 2. The Malayan Nature Society, Kuala Lampur.

Corr, W.J. (1983). Growth and morphogenesis of sun and shade plants I. The influence of light intensity. *Acta. Bot. Neerl.* **32**, 1-2, 49-62.

Cown, D.J. (1992). Corewood (Juvenile wood) in *Pinus radiata*. *NZ. J. For.* Sci. **22**(1), 87-95.

Cown, D.J., McConchie, D.L. and Kimberley, M.O. (1989). A sowing study of Fijian plantation grown large-leaf mahogany. *Commonw. For. Rev.* **68**, 4.

Crawford, R. (1989). *Studies in Plant Survival* - Ecological case histories of plant adaptations to adversity. Studies in Ecology, Vol. II. Blackwell Scientific Publications, Oxford.

Cuevas, E., Brown, S. and Lugo, A.E. (1991). Above- and below-ground organic matter storage and production in a tropical pine plantation and a paired broadleaf secondary forest. *Plant and Soil* **135** (2), 257-268.

Dabin, B. 1980. Phosphorus deficiency in tropical soils as a constraint on agricultural output. In *Priorities for Alleviating Soil Related Constraints to Food Production in the Tropics*, pp 217-232. International Rice Research Institute, Philippines.

Dalton, C.T. and Messina, M.G. (1995). Water relations and growth of loblolly pine seedlings planted under a shelterwood and in a clearcut. *Tree Physiol.* **15**(1), 19-26.

Dano, A.M. (1990). Effects of burning and reforestation in grassland watersheds in the Philippines. *Research needs and applications to reduce erosion and sedimentation in tropical steep lands*. Proceedings of the Fiji Symposium, June, 1990 (Ed. Ziemar, R.R. and O'-Loughlin, L.L.), pp 53-61. IAHS-Asia Publication No. 192.

Dassanayake, M.D. and Fosberg, F.R. (1983). *A revised handbook to the Flora of Ceylon* Vol IV. Amerind Publishing Co., New Delhi, India.

Dassanayake, M.D. and Fosberg, F.R. (1987). *A revised handbook to the Flora of Ceylon* Vol VI. Amerind Publishing Co., New Delhi, India.

Dassanayake, M.D. and Fosberg, F.R. and Clayton, W.D. (1995) *A revised handbook to the Flora of Ceylon* Vol IX. Amerind Publishing Co., New Delhi, India.

Davidenko, M.V. and Nevzorov, I.M. (1978). The resistence of pine/Caragna plantations to *Heterobasidion annosum*. *Lesnoe-Khozyaistvo* **6**, 78-79. (CAB Forestry Abstracts).

Davies, E.J.M. (1966). Dappled shade work with Sitka Spruce. *Scott. For.* **20**(1), 52-55.

Davies, R.J. (1985). The importance of weed control and the use of tree shelters for establishing broadleaved trees on grass-dominated sites in England. *Forestry* **58**(2), 167-180.

DeBano, L.F. and Conrad, C.E. (1978). The effects of fire on nutrients in a chaparral ecosystem. *Ecology* **59**, 489-497.

DeBell, D.S., Whitesell, C.D. and Schubert, T.H. (1989). Using N_2 - fixing*Albizia* to increase growth of *Eucalyptus* plantations in Hawaii. *For. Sci.* **35**(1), 64-75.

Dembner, S. (1991). Provisional data from the forest resources assessment, 1990 project, *Unasylva* **42** (164), 40-44.

Denslow, J.S., Newell, E. and Ellison, A.M. (1991). The effects of understorey palms and cyclanths on the growth and survival of*Inga* seedlings. *Biotropica* **23**(3), 225-234.

Dickson, R.E. and Isebrands, J.G. (1991). Leaves as regulators of stress response. In: *Response of Plants to Multiple Stresses* (Ed. Mooney, H.A., Winner, W.E. and Pell, E.J.), pp 4-29. Academic Press, San Diego, USA.

Dittmar, O. and Knapp, E. (1986). The increment performance of underplanted beech after removal of the Scots pine overstorey. *Sozialistische-Forstwirtschaft* **36**(7), 210-215. (CAB Forestry Abstracts).

Dharmasena, P.B. (1994/1995). A conservation farming practice for small reservoir watersheds: a case study from Sri Lanka. *Agrof. Sys.* **28**(3), 203-212.

Dharmawardena, H.S. (1987). *The influence of Pinus caribaea on soil characteristics in the Erabedda plantations of lower montane zone of Sri Lanka.* M.Sc. Thesis, University of Sri Jayawardanepura, Sri Lanka.

Eguiluz-Piedra, T. (1986). Taxonomic relatioships of *Pinus tecunumanii* from Guatemala. *Commonw. For. Rev.* **65**(4), 303-313.

Emmingham, W.H., Bondi, M. and Hibbs, D.E. (1989). Underplanting western hemlock in a red alder thinning: early survival, growth and damage. *New Forests* **3**(1), 31-43.

Ericsson, T. (1995). Growth and shoot:root ratio of seedlings in relation to nutrient availability. Nutrient uptake and cycling in forest ecosystems. *Plant and Soil* **168/169**, 205-214.

Ericsson, T. and Kahr, M. (1995). Growth and nutrition of birch seedlings at varied relative addition rates of magnesium. *Tree Physiol.* **15**(2), 85-93.

Ermolenko, P.M. (1990). Effect of the tree and herbaceous layers on advance growth of *Pinus sibirica. Lesnoe-Khozyaistro* No. **9**, 25-28. (CAB Forestry Abstracts).

Evans, G.C. (1972). *The Quantitative Analysis of Plant Growth - Studies in Ecology* Vol. 1. Blackwell Scientific Publications, Oxford.

Evans, J. (1992). *Plantation Forestry in the Tropics.* (Second edition), Oxford Scientific Publications, Oxford.

Eyre, L.A. (1987). Pinus caribaea on Melville Island, Northern Territory.*Aust. For.* **50,**(3), 179-183.

FAO (1956). *Tree Planting Pracices in Tropical Africa.* FAO, Rome.

FAO (1986). Data book on endangered tree and shrub species and provinences.*FAO Forestry Paper 77*, pp 178-183. FAO, Rome.

Fenger, S. (1975). Two generations of pine in the same stand.*S. Afri. For. J.* **93**, 21-24.

Ferguson, E.R. (1963). Overstorey density key to pine seedling survival and growth in east Texas. *J. For.* **61**(8), 597-598.

Ferrier, R.C. and Alexander, I.J. (1985). Persistence under field conditions of excised fine roots and mycorrhizas of spruce. *Ecological interactions in soil, plant, microbes and animals* (Ed. Fitter, A.H., Atkinson, D., Read, D.J., Usher, M.B), pp 175-179. Blackwell Scientific Publications, Oxford, UK.

Finlay, R.D. and Read, D. J. (1986a). The structure and function of the vegetative mycelium of ectomycorrhizal plants. I Translocation of ^{14}C - labelled carbon between plants interconnected by a common mycelium. *New Phytol.* **103**, 143-156.

Finlay, R.D. and Read, D.J. (1986b). The structure and function of the vegetative mycelium of ectomycorrhizal plants. II. The uptake and distribution of phosphorous by mycelial strands interconnecting host plants. *New Phytol.* **103**, 157-165.

Fischer, E. (1993). The conversion of Scots pine stands with oak sown by jays and planted oak. *Forst-und Holz* **48**(18), 525-528. (CAB Forestry Abstracts).

Flanagen, P.W. and Van Cleve, K. (1983). Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. *Can. J. For. Res.* **13**, 795-817.

Fogal, R., and Cromack, K. Jr (1977). Effect of habitat and substrate quality on Douglas-fir litter decomposition in Oregon. *Can. J. Bot.* **55**, 1632-1640.

Forestry Master Plan, (1995). Forest Department, Colombo, Sri Lanka (draft report).

Fuller, W.H.S., Sannon, S. and Burgess, P.S. (1955). Effects of burning on certain forest soils of northern Arizona. *For. Sci.* **1**, 44-50.

Gadgil, R.L. and Gadgil, P.D. (1971). Mycorrhiza and litter decomposition.*Nature* **233**, 133.

Gadgil, R.L. and Gadgil, P.D. (1975). Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata*. *NZ. J. For. Sci.* **5**(1), 33-41.

Gerhardt, K. (1995). Biomass allocation by broad-leaf mahogany seedlings, *Swietenia macrophylla* (King), in abandoned pasture and secondary dry forest in Guanacaste, Costa Rica. *Biotropica* **27**(2), 174-182.

Gerold, D. (1987). Scots pine plant spacing trial at Markersbach - a stand history and growth evaluation of one of the oldest trial plots in the world. *Sozialistische-Forstwirtschaft* **37**(9), 274-278. (CAB Forstry Abstracts).

Ghosh, R.L. and Singh, S.P. (1981). Trends in rotation. *The Indian Forester* **107**(6), 336-347.

Gibson, G.L., Barnes, R.D. and Berrington, J. (1983). Provenance productivity in *Pinus caribaea* and its interaction with environment. *Commonw. For. Rev.* **62**(2), 93-106.

Goldammer, J.G. (1988). Rural land-use and wildland fires in the tropics. *Agrof. Sys.* **6**, 235-252.

Goldammer, J.G. (1993). Fire Management. In: *Tropical Forestry Handbook* Vol 2. (Ed. Pancel, L.), pp 1221-1265. Springer-Verlag, Berlin.

Golkin, S.L. and Cassels, P.K. (1989). An appraisal of Sabah Softwood Sdn. Bhd. 12 years after establishment. *Planter* **65** (760), 301-310.

Gomez, K.A. and Gomez, A.A. (1984). *Statistical Procedures for Agricultural Research* (second edition), John Wiley and Sons, New York.

Greaves, A. (1981). Progress in the *Pinus caribaea* Morelet and *Pinus oocarpa* Schiede, International Provenance trial. *Commonw. For. Rev.* **60** (1), 35-43.

Gregoriou, C. and Rajkumar, D. (1984). Effects of irrigation and mulching on shoot and root growth of avocado (*Persea americana* Mill.) and mango (*Mangifera indica* L.). *J. Hortc. Sci.* **59**(1), 109-117.

Grier, C.C (1975). Wildlife effects on nutrient distribution and leaching in a coniferous ecosystem. *Can. J. For. Res.* **5**, 599-607.

Gryazev, E.N. (1975). Spruce plantations under (hardwood) forest canopy. *Lesnoe-Khozyaistvo* No **12**, 58-60. (CAB Forestry Abstracts).

Gullison, R.E., Panfil, S.N., Strouse, J.J and Hubbell, S.P. (1996). Ecology and management of mahogany (*Swietenia macrophylla* King) in the Chimanes forest, Beni, Bolivia. *Bot. J. Linn. Soc.* **122**, 9-34.

Gunatilleke, I.A.U.N. (1989). Soils and nutrient under pines in Sri Lanka. In: *Reforestation with Pinus in Sri Lanka* (Ed. Gunasena, H.P.M., Gunatilleke, S. and Perera, A.H.), pp 38-45. Proceedings of a symposium organized by University of Peradeniya, Sri Lanka.

Gurth, P. and Kruse, R. (1988). Historical studies on high-quality oak stands in the Markgraflerland (southwestern Germany). *Allgemeine-Forst und Jagdzeitung* **159**(3-4), 49-56. (CAB Forestry Abstracts).

Hall, F.C., Hedrick, D.W. and Keniston, R.F. (1959). Grazing and Douglas-fir establishment in the Oreong White Oak type. *J. For.* **57**(2), 98-103.

Handley, W.R.C. (1954). Mull and Mor formation in relation to forest soils. *Bull. For. Comm.* No. **23**. London.

Harley, J.L. and Smith, S.E. (1983). *Mycorrhizal symbioses.* Academic Press, London.

Harvey, A.E., Larson, M.J. and Jurgenson, M.F. (1976). Distribution of ectomycorrhizae in a mature Douglas-fir/Larch forest system in Western Montana. *For.Sci* **22**, 393-398.

Heap, A.J. and Newman, E.I. (1980). Links between roots by hyphae of vesicular-arbuscular mycorrhizas. *New Phytol.* **85**, 169-171.

Heath, D. (1995). *An Introduction to Experimental Designs and Statistics for Biology.* VCI Press, London.

Henriksen, H.A. and Sanojca, K. (1983). Influence of an understorey of beech on the development of epicormic branches of *Quercus robur*. *Forstlige-Forsogsvaesen-i- Denmark* **39**(1), 93-119. (CAB Forestry Abstracts).

Hiley, W.E. (1956). Underplanting of Japanese Larch. *Quart. J. For.* **50**(3), 189-196.

Hogberg, P (1989). Growth and nitrogen inflow rates in mycorrhizal and non-mycorrhizal seedlings of *Pinus sylvestris. For. Ecol. Manage.* **28**(1), 7-17.

Holmes, C.H. (1946). Grasslands and their afforestation in Ceylon. *The Indian Forester* **72**, 6-11.

Hughes, A.P. and Evans, G.C. (1963). Plant growth and the aerial environment. IV. Effects of daylength on *Impatiens parviflora. New Phytol.* **62**, 367-388.

Hughes, J.F. (1971). The wood structure of Pinus caribaea in relation to use characteristics, growth conditions and tree improvement. Symposium on selection and breeding to improve some tropical conifers. 15th IUFRO Congress, Gainesville, Florida.

Huhta, V., Setata, H. and Haimi, J. (1988). Leaching of N and C from birch leaf litter and raw humus with special emphasis on the influence of fauna. *Soil Biol. Biochem.* **20**(6), 875-878.

Hunt, R. (1978). *Plant growth analysis.* Edward Arnold, London.

Ineson, P. and Mctiernan, K. (1992). Decomposition of foliar litter mixtures: A microcosm experiment. In: *Responses of Forest Ecosystems* (Ed. Teller, A.,

Mathy, P., and Jeffers, J.N.R.), pp 703-706. Elsievier Applied Science, London.

Ingham, R., Trofymow, J.A., Ingham, E.R. and Coleman, D.C. (1985). Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. *Ecol. Monogr.* **55**(1), 119-140.

Irvine, F.R. (1967). *Woody Plants of Ghana*. Oxford University Press, London.

Jackson, R.B. Mainwaring, J.H. and Caldwell, M.M. (1990). Rapid physiological adjustment of roots to localized soil enrichment. *Nature* **344**, 58-60.

Janos, D.P. (1980). Mycorrhizae influence tropical succession. *Biotropica (suppl.)* **12**(2), 56-64.

Kallio, M., Dykstra, D.P. and Binkley, C.S. (1987). *The Global Forest Sector: an analytical perspective*. John Wiley and Sons, New York.

Keay, R.W.J. (1989). *Trees of Nigeria*. Clarendon press, Oxford, UK.

Kellman, M. (1984). Synergistic relationships between fire and low soil fertility in neotropical savannas: a hypothesis. *Biotropica* **16**(2), 158-160.

Kelty, M.J. (1992). Comparative productivity of monocultures and mixed-species stands. In: *The Ecology and Silviculture of Mixed-Species Forests* - Forestry Sciences, Vol 40. (Ed. Kelty, M.J., Larson, B.C. Oliver, L.D.), pp 125-144. Kluwer Academic Publishers, Dordrecht.

Kelty, M.J. and Cameroon, I.R.(1995). Plot designs for the analysis of species interactions in mixed stands. *Commonw. For. Rev.* **74**(4), 322-332.

Kemmler, G. (1980). Potassium deficiency in soils of the tropics as a constraint to food production In: *Priorities for Alleviating Soil-Related Constraints to Food Production in the Tropics* (Ed. anonymous). International Rice Research Institute, Philippines.

Kerr, G., Nixon, C.J., Mathews (1992). Silviculture and yield of mixed-species stands: the UK experience. In: *The Ecology of Mixed Species Stands of Trees.* (Ed. Cannel, M.G.R., Malcolm, D.C. and Robertson, P.A.), pp 35-51, Blackwell Scientific Publishers, London.

Kessler, J.H.B. (1995). *Woody Plants in Agro-Ecosystems of Semi-arid Regions.* Springer-Verlag, Berlin.

Kimmins, J.P. (1987). *Forest Ecology*. Macmillan Publishing Company, New York.

King, H.G.C. and Heath, C.W. (1967). The chemical analysis of small samples of leaf material and the relationship between disappearances and composition of leaves. *Pedobiologia* **7**, 192-197.

Kitajima, K. (1996). Ecophysiology of tropical tree seedlings. In: *Tropical Forest Plant Ecophysiology* (Ed. Mulkey, S.S., Chazdon, R.L. and Smith, A.P.), pp 559-565. Chapman and Hall, New York.

Klironomos, J.N. and Kendrick, W.B. (1995). Stimulative effects of arthropods on endomycorrhizas of sugar maple in the presence of decaying litter.*Functional Ecol.* **9**(3), 528-536.

Klironomos, J.N. and Widden, P and Deslandes, I. (1992). Feeding performance of the collembolan *Folsomia candida* in relation to microfungal successions on decaying litter. *Soil Bio. and Biochem.* **24**, 685-692.

Klock, G.O. and Grier, C.C. (1981). Effect of fire on the long-term maintenance of forest productivity. In: *Proceedings, Forest Fertilization Conference* (Ed. Gessel, S.P., Kenady, R.M. and Atkinson, W.A), pp 247-250. Washington, USA.

Kolb, T.E. and Steiner, K.C. (1990). Growth and biomass partitioning of northern red oak and yellow-poplar seedlings: effects of shading and grass root competition. *For. Sci.* **36**(1), 34-44.

Konuche, P.K.A. (1994). *The influence of light environment on indigenous tree seedlings in Kenya.* Ph.D. Thesis, University of Edinburgh.

Kowal, N.E. (1966). Shifting cultivation, fire and pine forests in the Cordillera, Central Luzon, Philippines. *Ecol. Monogr.* **36**, 389-419.

Kowal, N.E. (1969). Effects of leaching on pine litter decomposition rate.*Ecology* **50**(4), 739-740.

Kraemer, J.F. and Herman, R.K. (1979). Broadcast burning: 25 years effects on forest soils in the Western flanks of the Cascade Mountains. *For. Sci.* **25**, 427-439.

Kriek, W. (1968). Preliminary report on underplanting trials in tropical high forests. *Department of Uganda, Technical Note.* No. **158/168**. (CAB Forestry Abstracts).

Kushalapa, K.A. and Kushalappa, K.A. (1987). Nutrient status under Mysore gum plantations for ten years near Bangalore. *J. Trop. For.* **3**(2), 142-147.

Kwesiga, F.R. (1984). *Aspects of the growth and physiology of tropical tree seedlings in shade.* Ph.D. Thesis, University of Edinburgh.

Lamb, A.F.A. (1968). *Cedrela odorata.* Commonwealth Forestry Institute, *Fast growing timber trees of the lowland tropics.* No. **2**, Oxford.

Lamb, A.F.A. (1973). *Pinus caribaea* Vol. I. Commonwealth Forestry Institute, *Tropical Forestry Paper No.* **6**. Oxford.

Lamb, D. and Lawrence, P. (1993). Mixed species plantations using high value rainforest trees in Australia. In: *Restoration of tropical forest ecosystems*. (Ed. Lieth, H. and Lohmann, M), pp 101-108. Kluwer, Netherlands.

Lamb, F.B. (1966). *Mahogany of Tropical America: Its Ecology and Management*. University of Michigan Press, Ann Arbor, MI.

Lamprecht, H. (1989). *Silviculture in the Tropics*, Technical Cooperation-Federal Republc of Germany (GTZ), Eschborn, Germany.

Landon, J.R. (1984). *Booker Tropical Soil Manual*. A handbook for soil survey and agricultural land evaluation in the tropics and sub-tropics. Booker Agriculture International Ltd. London.

Larsen, J.B. (1995). Ecological stability of forests and sustainable silviculture. *For. Ecol. Manage.* **73**, 85-96.

Ledig, F.T., Bormann, F.H., Wenger, K.F. (1970). The distribution of dry matter growth between shoot and roots in Loblolly Pine. *Bot. Gaz.* **131**(4), 349-359.

Lee, D.W. (1987). The spectral distribution of radiation in two neotropical rainforests. *Biotropica* **19**, 161-166.

Lisanework, N. and Michelsen, A. (1994). Litterfall and nutrient release by decomposition in three plantations compared with a natural forest in the Ethiopian highland. *For. Ecol. Manage.* **65**(2-3), 149-164.

Likens, G.E. (1992). Some applications of the ecosystem approach to environmental problems and resource management. In: *Response of Forest Ecosystems to Environmental Changes* (Ed. Teller, A., Mathy, P. and Jeffers, J.N.R.), pp 16-30. Elsevier Applied Science, London.

Little, T.M. and Hills, F.J. (1978). *Agricultural Experimentation - Design and Analysis*. John Wiley, New York.

Liyanage, M. de S., Tejwani, K.G. and Nair, P.K.R. (1984). Intercropping under coconuts in Sri Lanka. *Agrof. Sys.* 2, 215-228.

Loach, L. (1970). Shade tolerance in tree seedlings II. Growth analysis of plants raised under artificial shade. *New Phytol.* **69**, 273-286.

Longman, K.A. and Jenik, J. (1987). *Tropical Forest and its Environment*. Longman Scientific and Technical, Harlow, Essex, UK.

Lord, D., Morissette, S. and Allaire, J (1993). Influence of light intensity, night air temperature and CO_2 concentration on the growth of containerized black spruce seedlings grown in the greenhouse. *Can. J. For. Res.* **23**(1), 101-110.

Mabberley, D.J. (1994). *Tropical Rain Forest Ecology* (second edition). Blackie Academic and Professional, UK.

MacLean, D.A., Woodley, S.J., Weber, M.G. and Wein, R.W. (1983). Fire and nutrient cycling. In: The Role of Fire in Northern circumpolar ecosystem (Ed. Wein, R.W. and MacLean, D.A.), pp 111-127. John Wiley and Sons, New York.

Magmuski, K. (1987). Conversion trials in medium-aged Scots pine stands. *Sylwan.* **131**(1), 47-52.

Makus, D.J., Tiwari, S.C., Pearson, H.A., Haywood, J.D. and Tiarks, A.E. (1994). Okra production with pine straw mulch. *Agrof. Sys.* **27**(2), 121-127.

Malcolm, D.C. (1957). The replacement of unhealthy larch stands in South Shropshire and North Herefordshire. *Sylva*, Edinburgh No. **38**, 15-17.

Marschner, H. and Dell, B. (1994). Nutrient uptake in mycorrhizal synbiosis. *Plant and Soil* **159**, 89-102.

Mason, P.A., Wilson, J., Last, F.T. and Walker, C. (1983). The concept of succession in relation to the spread of sheathing mycorrhizal fungi on inoculated tree seedlings growing in unsterile soils. *Plant and Soil* **71**, 247-286.

Mather, A.S. (1990). *Global Forest Resources.* Belhaven Press, London.

Matthews, J.D. (1989). *Silvicultural Systems.* Clarendon Press, Oxford.

McKee, K.L.(1995). Interspecific variation in growth, biomass partitioning and defensive characteristics of neotropical mangrove seedlings: response to light and nutrient availability. *Am. J. Bot.* **82**(3), 299-307.

McMillin, J.D. and Wagner, M.R.(1995). Effects of water stress on biomass partitioning of ponderosa pine seedlings during primary root growth and shoot growth periods. *For. Sci.* **41** (3), 594-610.

Millar, C.S. (1974). Decomposition of coniferous leaf litter. In: *Biology of Plant Litter Decomposition* Vol. I (Ed. Dickinson, C.H. and Pugh, G.J.F.), pp 105-128. Academic Press, London.

Miller, R.M. and Jastrow, J.D. (1992). The application of VA mycorrhizae to ecosystem restoration and reclamation. In: *Mycorrhizal functioning* (Ed. Allen, M.F.), pp 438-457. Chapman and Hall, New York.

Miller, R. M. and Jastrow, J.D. (1994). Vesicular-arbuscular mycorrhizae and biogeochemical cycling. In: *Mycorrhizae and Plant Health* (Ed. Pfleger, F.L. and Linderman, R.G.), pp 189-212. American Phytopathological Society, Minnesota, USA.

Mo, J., Brown, S. and Lenart, M. (1995). Nutrient dynamics of a human-impacted pine forest in a MAB Reserve of subtropical China. *Biotropica* **27**(3), 290-304.

Montaginini, F., Gonzalez, E., Porras, C. and Rheingans, R. (1995). Mixed and pure plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. *Commonw. For. Rev.* **74**(4),

Nakashizaka, T. (1985). Diffuse light conditions in canopy gaps in a beech (*Fagus crenata*. Blume) forest. *Oecologia* (Berlin) **66**, 472-474.

Negreros-Castillo, P. and Mize, C. (1993). Effects of partial overstorey removal on the natural regeneration of tropical forest in Quintana Roo, Mexico.*For. Ecol. Manage.* **58**(3-4), 259-272.

Neilson, K.E. and Humphries, E.C. (1966). Effects of root temperature on plant growth. *Soils and Fertilizer* **29**(1), 1-7.

Newman, E.I. (1988). Mycorrhizal links between plants: their functioning and ecological significance. *Adv. Ecol. Res.* **18**, 243-270.

Newton, A.C., Baker, P., Ramnarine, S., Mesen, J.F. and Leakey, R.R.B. (1993). The mahogany shoot borer: prospects for control. *For. Ecol. Manage.* **57**, 301-328.

Niefnecker, W. (1992). Results of trial plantings of exotic conifers species with long-term shelter. *Forst und Holz* **41**(14), 419-421. (CAB Forestry Abstracts).

Northup, R.R., Zengshou, Y., Dahlgren, R.A. and Vogt, K.A. (1995). Polyphenol control of nitrogen release from pine litter. *Nature*. **377**, 227-229.

Ogbonnaya, C.I., Nwalozie, M.C. and Nwaigbo, L.C. (1992). Growth and wood properties of *Gmelina arborea* (verbanaceae) seedlings grown under five soil moisture regimes. *Am. J. Bot.* **79**(2), 128-132.

Oglesby, K.A. and Fowness, J.H. (1992). Effects of chemical composition on nitrogen mineralization from green manures of seven tropical leguminous trees. *Plant and Soil* **143**, 127-132.

Okali, D.U.U. (1972). Growth-rates of some West African forest-tree seedlings in shade. *Annals. Bot.* **36**, 953-959.

Okali, D.U.U. and Dodoo, G. (1973). Seedling growth and transpiration of two west African mahogany species in relation to water stress in the root medium.*J. Ecol.* **61**(2), 421-438.

Onis'kiv, N.I. (1977). Improving the productivity of pine stands in the Poles'e. *Lesnoe-Khozyaistvo* No. **12**, 49-52. (CAB Forestry Abstracts).

Oosting, H.J. and Kramer, P.J. (1946). Water and light in relation to pine reproduction. *Ecology* **27**, 47-53.

Osunokoya, O.O. and Ash, J.E. (1991). Acclimation to a change in light regime in seedlings of six Australian rainforest species. *Aus. J. Bot.* **39**(6), 591-605.

Othieno, C.D. and Ahn, P.M. (1980). Effects of mulches on soil temperature and growth of tea plants in Kenya. *Exp. Agric.* **16**, 287-294.

Oya, K. and Tokashiki, Y. (1984). Soil fertility in a shifting cultivation on Iriomote island of Okinawa. I. Nutrient stored in the forest and their impact to the soil. *Japanese J. Trop. Agri.* **28**(4), 218-222.

Palm, C.A. and Sanchez, P.A. (1990). Decomposition and nutrient release pattern of the leaves of three tropical legumes. *Biotropica* **22**(4), 330-338.

Panayotou, T. and Ashton, P.S. (1992). *Not by Timber Alone - Economics and Ecology for Sustaining Tropical Forests*, Island Press, Washington, DC.

Pancel, L. (1993). Species selection. In: *Tropical Forestry Handbook*, Vol. 1 (Ed. Pancel, L), pp 569-643. Springer-Verlag, Berlin.

Parke, J.L., Linderman, R.G. and Trappe, J.M. (1983). Effect of root zone temperature on ectomycorrhizal and vesicular-arbuscular mycorrhiza formation in disturbed and undisturbed forest soils of southwest Oregon and nothern California. *For. Sci.* **30**, 300-304.

Parker, R.E. (1973). *Introductory Statistics for Biology.* The Institute of Biology's Studies in Biology No. 43, Edward Arnold, London.

Pathak, P.S., Rai, M.P. and Roy, R.D. (1983). Seedling growth of *Leucaena leucocephala* (LAM.) de Witt. I. Effects of Shading. *Indian J. For.* **6**(1), 28-31.

Pearcy, R.W. (1987). Photosynthetic gas exchange response of Australian tropical forest trees in canopy, gap and understorey micro-environments. *Functional Ecol.* **1**, 169-178.

Penafiel, S.R., Nobbe, B.F. and Ngales, L. (1980). Juvenile growth of Benguet pine (*Pinus kesiya* Royle ex Gordon) seedlings planted under *Alnus* stands. *The Sri Lanka Forester* **14**(3 & 4), 197-203.

Perera, A.H. (1989a). Growth and performance of pines in Sri Lanka. In: *Reforestation with Pinus in Sri Lanka* (Ed. Gunasena, H.P.M., Gunatilleke, S. and Perera, A.H.), pp 29-37. Proceedings of a symposium organized by University of Peradeniya, Sri Lanka.

Perera, A.H. (1989b). Ecological issues on pines in Sri Lanka. In: *Reforestation with Pinus in Sri Lanka* (Ed. Gunasena, H.P.M., Gunatilleke, S. and Perera, A.H.), pp 56-60. Proceedings of a symposium organized by University of Peradeniya, Sri Lanka.

Perry, D.A. and Maghembe, J. (1989). Ecosystem concepts and current trends in forest management: time for reappraisal. *For. Ecol. Manage.* **26**, 123-140.

Perry, D.A., Molina, R. and Amaranthus, M.P. (1987). Mycorrhizae, mycorrhizospheres and reforestation: current knowledge and research needs. *Can. J. For. Res.* **17**, 929-940.

Philipps, J.G. and Riha, S.J. (1993). Canopy development and solar conversion efficiency in *Acacia auriculiformis* under drought stress. *Tree Physiol.* **12**(2), 137-149.

Pickett, S.T.A. and Bazzaz, F.A. (1978). Organization of an assemblage of early successional species on a soil moisture gradient. *Ecology* **59**, 1248-1258.

Plumptre, R.A. (1979). Pruning of fast growing*Pinus* for wood uniformity: Can you have your cake and eat it? *Commonw. For. Rev.* **58**(3), 181-189.

Polglase, P. J., Comeford, N.B. and Jokela, E.J. (1992). Leaching of inorganic P from litter in southern pines. *Soil Sci. Soc. Am. J.* **56**, 573-577.

Poore, D., Burgess, P., Palmer, J., Rietbergen, S. and Synnott, T. (1989). *No Timber without Trees - Sustainability in Tropical Forests*, Earthscan Publications, London.

Popma, J. and Bongers, F. (1988). The effects of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia (Berlin)* **75**, 625-632.

Preuhsler, T., Kuhnel, S. and Bock, K. (1994). The growth of direct-sown oak under Scots pine shelter in Nurnberg Forest. *Forst und Holz.* **49**(5), 123-128. (CAB Forestry Abstracts).

Preuhsler, T. and Rehfuess, K.E. (1982). The improvement of degraded Sots pine (Pinus sylvestris) sites in the Oberpfalz. *Forstwissenschaftliches-Centralblatt.* **101**(6), 388-407. (CAB Forestry Abstracts).

Proctor, J. (1967). A nutritional disorder of pines. *Commonw. For. Rev.* **46**, 145-152.

Pukkala, T., Kuuluvainen, T. and Stenberg, P. (1993). Below-canopy distribution of photosynthetically active radiation and its relation to seedling growth in a boreal *Pinus sylvestris* stand. *Scand. J. For. Res.* **8**, 313-325.

Putz, F.E. (1992). Reduction of root competition increases growth of slash pine seedlings on a cutover site in Florida. *S. J. Appl. For.* **16**(4), 729-738.

Putz, F.E. and Canham, C.D. (1992). Mechanisms of arrested succession in shrublands: root and shoot competition between shrubs and tree seedlings. *For. Ecol. Manage.* **49** (3-4), 267-275.

Rai, S.N. (1990). Restoration of degraded tropical rain forests of western Ghats. *The Indian Forester* **116**(3), 179-188.

Raison, R.J. (1979). Modification of the soil environment by vegetation fires with particular referance to nitrogen transformations: a review. *Plant and Soil* **51**, 73-108.

Raison, R.J. (1980). Possible forest site deterioration associated with slash-burning. *Search* 11(3), 68-72.

Raison, R.J., Khanna, P.K. and Woods, P.V. (1985 a). Mechanism of element transfer to the atmosphere during vegetation fires. *Can. J. For. Res.* **15**, 132-140.

Raison, R.J., Khanna, P.K. and Woods, P.V. (1985b) Transfer of elements to the atmosphere during low-intensity prescribed fire in three Australian subalpine eucalypt forests. *Can. J. For. Res.* **15**, 132-140.

Ramos, J. and Grace, J. (1990). The effects of shade on the gas exchange of seedlings of four tropical trees from Mexico. *Functional Ecol.* **4**, 667-677.

Ramos, J.M., and Amo, S del (1992). Enrichment planting in a tropical secondary forest in Veracruz, Mexico. *For. Ecol. Manage.* **54**(1-4), 289-304.

Ranasinghe, D.M.S.H.K. and Newman, S.M. (1993). Agroforestry research and practices in Sri Lanka. *Agrof. Sys.* **22**, 119-130.

Ranaweera, K.A.H., Seneviratne, L.K. Arudpragasm, K.D. and Hewawasam, H.T. (1991). *The Causes and Consequences of Natural Disasters and the Protection and Preservation of the Environment.* SAARC. Country Report of Sri Lanka.

Ratnayake, C.K., Arambewela, L.S.R., Silva, K.T.D. de, Atta-ur-Rahman, Alvis, K.A. (1987). Alkaloids of *Alstonia macrophylla. Phytochemistry* **26**(3), 868-870.

Rauf, A.F. (1982). A financial appraisal of rotan manan (*Calamus manan*) cultivation at the Bukit Belata Forest Reserve. *The Malaysian Forester* **45**(4), 576-582.

Ray, G.J. and Brown, B.J. (1995). Restoring Caribbean dry forests: evaluation of tree propagation techniques. *Restor. Ecol.* **3**(2), 86-94.

Reeves, F.B., Wagner, D.W., Moorman, T. and Kiel, J. (1979). The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs natural environments. *Am. J. Bot.* **66**, 1-13.

Reich, P.B. and Walters, M.B. (1994). Photosynthesis-nitrogen relations in Amazonian tree species. II. Variation in nitrogen vis-a-vis specific leaf area influences mass- and area-based expressions. *Oecologia* **97**(1), 73-81.

Reid, W.V. and Miller, K. R. (1989).*Keeping Options Alive: The Scientific Basis for Conserving Biodiversity*, World Resources Institute, Washington, D.C.

Richards, B.N. (1962). Increased supply of nitrogen brought about by*Pinus. Ecology* **43**(3), 538-541.

Riegal, G.M., Miller, R.F. and Krueger, W.C. (1992). Competition for resources between understorey vegetation and overstorey *Pinus ponderosa* in north eastern Oregon. *Ecol. Appl.* **2**(1), 71-85.

Rietbergen, S. (1993). *The Earthscan Reader in Tropical Forestry.* Earthscan Publication, London.

Rincon, E. and Huante, P. (1993). Growth responses of tropical deciduous tree seedlings to contrasting light conditions. *Trees: Struc. and Funct.* 7(4), 202-207.

Rincon, E. and Huante, P. (1995). Influence of mineral nutrient availability on growth of tree seedlings from the tropical deciduous forest. *Trees: Struc. Funct.* **9**(2), 93-97.

Risch, S.J. (1981). Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. *Ecology* **6**, 85-98.

Robinson, G.O. (1975). *The Forest Service*. Johns Hopkins University Press, London.

Robinson, R.K. (1973). Mycorrhiza and "Second rotation decline" in*Pinus patula* in Swaziland. *S. Afri. For. J.* **84**. 16-19.

Rowan, S.J., McNab, W.H. and Brender, E.V. (1975). Pine overstorey reduces fusiform rust in underplanted loblolly pine. USDA Forest-Service, *Southern Forest Experimental Station, Research Note*. No. SE **212**, 6.

Russell, E.W. (1973). *Soil Condition and Plant Growth.* (10th edition), Macmillan, London.

Russell, J.S., Cameron, D.M., Whan, I.F., Beech, D.F., Prestwidge, D.B. and Rance, S.J. (1993). Rainforest trees as a new crop for Australia.*For. Ecol. Manage.* **60**(1-2), 41-58.

Rutnam, P.W. (1959). Growth of plants under the shelter of natural forest in the dry zone. *The Ceylon Forester* **4**(2), 224-226.

Samarappuli, L. (1995). Mulching with paddy straw to reduce immaturity and improve yields. *Bull. Rubber Research Institute of Sri Lanka* **32**, 53-60.

Sasaki, S. and Mori, T. (1981). Growth responses of dipterocarp seedlings to light. *The Malaysian Forester* **44**, 319-345.

Savage, S.M. (1974). Mechanism of fire induced water repellancy in soil. *Soil Sci.Soc. Am. Proc.* **38**, 737-744.

Schenk, S. (1994). Experience with advance planting for conversion. *Allgemeine-Forst-Zeitschriff* **49**(10), 519-520. (CAB Forestry Abstracts).

Schroth, G., Zech, W., Heimann, G. (1992). Mulch decomposition under agroforestry conditions in a sub-humid tropical savanna: processes and influences of perennial plants. *Plant and Soil* **147**(1), 1-11.

Sen, N.N. (1965). Trend of development of forestry in Halwani, Ramnagar and T and B divisions of Uttar Pradesh during the last 50 years. *The Indian Forester* **91**(3), 158-169.

Setala, H. and Huhta, V. (1991). Soil fauna increase *Betula pendula* growth: Laboratory experiments with coniferous forest floor. *Ecology* **72**(2), 665-671.

Shamet, G.S., Chauhan, P.S., and Sood, R. (1994). Nursery studies on potting mixture, mulching and fertilizer requirements of chilgosa pine (*Pinus gerardiana* Wall.) *Indian Journal of Forestry* **17**(3), 225-229.

Siagurua, P. and Taurereko, R. (1988). Line planting with striplings of *Cedrela odorata* in logged over natural forest. *Klinkii* **3**(4), 10-16. (CAB Forestry Abstracts).

Siagurua, P., Taurereko, R. and Tisseverasinghe, K. (1987). Line planting with striplings of *Cedrela odorata*. *Klinkii* 3(3), 76-80. (CAB Forestry Abstracts).

Siapino, I.B. (1983). *Alstonia macrophylla*. *The Sri Lanka Forester* **16**(1-2), 37.

Siddiqi, N.A., Khan, M.A.S., Islam, M.R. and Hoque, A.K.F. (1992). Underplanting - a means to ensure sustainable mangrove plantations in Bangladesh. *Bangladesh J. For. Sci.* **21**(1/2), 1-6.

Silver, W.L. and Vogt, K.A. (1993). Fine root dynamics following single and multiple disturbances in a sub-tropical wet forest eco-system. *J. Ecol.* **81**(4), 729-738.

Singh, R.P., Rana, B.S. and Garkoti, S.C. (1993b). Biomass and production patterns of three dominant tree species along a given series in a natural troipical forest at Chakia, Varnasi (India). *The Indian Forester* **119**(6), 472-480.

Singh, S.B., Gupta, G.N., Prasad, K.G., Mohan, S (1988). Use of mulch in establishment of tree species in dry lands. *The Indian Forester* **114**(6), 307-316.

Singh, S.B., Promod-Kumar, Prasad, K.G., Kumar, P.(1991). Response of various tree species to irrigation regimes and leaf residue management. *J. Indian Soc. Soil Sci.* **39**(2), 229-232.

Singh, S.B., Promod-Kumar, Prasad, K.G., Kumar, P.(1993a). Potential water requirement of *Eucalyptus* - a preliminary study. *The Indian Forester* **119**(7), 549-552.

Singh, S.B., Promod-Kumar, Prasad, K.G., Singh, R.K., Malik, N. and Kumar, P. Effects of nitrogen and Phosphorus and mulch on growth and establishment of *Pinus roxburghii*. *The Indian Forester* **120**(3), 242-247.

Schoenberger, N.M. and Perry, D.A. (1982). The effect of soil disturbance on growth and ectmycorrhizae of Douglas-fir and western hemlock seedlings: a greenhouse bioassay. *Can. J. For. Res.* **12**, 343-353.

Smith, D.W. (1970). Concentrations of soil nutrients before and after fires. *Can. J. Soil Sci.* **50**, 17-29.

Smith, D.M. (1986). *The Practice of Silviculture*. John Wiley and Sons, New York.

Smith, D.W. and Sparling, J.H. (1966). The temperatures of surface fires in jack pine barrens. I. The variation in temperature with time. *Can. J. Bot.* **44**, 1285-1292.

Smith, H. (1981). Light quality as an ecological factor. In: *Plants and their Atmospheric Environment* (Ed. Grace, J., Ford, E.D. and Jarvis, P.G.), pp 93-110. Blackwell Scientific Publishers, Oxford.

Snook, L. K. (1993). *Stand dynamics of mahogany (Swietenia macrophylla King) and associated species after fire and hurricane in the tropical forests of the Yucatan Peninsula, Mexico.* Ph.D. Dissertation, University of Yale, Michigan, USA.

Sony, P., Sanjay, S. and Mathur, H.N. (1985). Infiltration studies under different vegetation cover. *Indian J. For.* **8** (3), 170-173.

Speight, M.R. and Speechly, H.T. (1992). Pine shoot moth in South-east Asia I: Distribution, Biology and Impact. *Commonw. For. Rev.* **61** (2), 121-134.

Staaf, H. and Berg, B. (1982). Accumulation and release of plant nutrients in decomposing Scots pine needle litter. II. Long term decomposition in a Scots pine forest. *Can. J. Bot.* **60**, 1561-1568.

Stadenberg, I., McDonald, A.J.S. and Palmer, S. (1994). Diurnal variation in leaf extension of *Salix viminalis* at two nitrogen supply rates. *Tree Physiol.* **14**(10), 1131-1138.

Stadtmueller, T. (1990). Soil erosion in east Kalimantan, Indonesia. In: *Research needs and applications to reduce erosion and sedimentation in tropical steep lands.* Proceedings of the Fiji Symposium, June, 1990 (Ed. Ziemar, R.R. and O'-Loughlin, L.L), pp 221-230. *IAHS-Asia Publication* No. **192**.

Steel, R.G.R. and Torrie, J.H. (1980). *Principles and Procedures of Statistics.* a *biometrical approach* (second edition), McGraw Hill, London.

Stevenson, N.S. (1927). Silvicultural treatment of mahogany forests in British Honduras. *Emp. For. J.* **6**(1), 219-227.

St John, T.V. (1983). Response of tree roots to decomposing organic matter in two Amazonian rain forests. *Can. J. For Res.* **13**. 346-349.

Stoneman, G.L. and Dell, B. (1993). Growth of *Eucalyptus marginata* (Jarrah) seedlings in a green house in response to shade and soil temperature. *Tree Physiol.* **13**(3), 239-252.

Suratomo, F.G. (1977). Infestation of the leading shoot of mahogany (*Swietenia macrophylla* King) by *Hypsipyla robusta* (Moore) in West Java, Indonesia. *Proceedings, Symposium on Forest Pests and Diseases in Southeast Asia* April 20-23, 1976, Bogor, Indonesia, pp 121-132. Indonesia, BIOTROP.

Swaine, M.D. and Whitmore, T.C., (1988). On the definition of ecological species groups in tropical rain forests. *Vegetatio* **75**, 81-86.

Tang, H.T. and Chew, T.K. (1980). Preliminary results of two six-year old underplanting trials at Tapaha Hills Forest Reserve, Perak. *The Malaysian Forester* **43**(2), 193-211.

Tarrant, R.F. (1961). Stand development and soil fertility in a Douglas Fir-Red Alder plantation. *For. Sci.* 7(3), 238-246.

Taylor, B.R., Parkinson, D. and Parsons, W.F.J. (1989). Nitrogen and lignin content as predictors of litter decay: a microcosm test. *Ecology* **70**(1). 97-104.

Tharper, H.S., Vijayan, A.K. Vniyal, K. (1992). Vesicular-arbuscular mycorrhizal associations and root colonization in some important tree species. *The Indian Forester* **118**(3), 207-217.

Thattil, R.O. and Nadesalingam, P. (1991). Pitfalls in mean separation procedure. In: *Multipurpose Tree Species in Sri Lanka - Research and Development* (Ed. Gunasena, H.P.M.), pp 74-81. Proceedings of the regional workshop on Multi-purpose Tree Species, Kandy, Sri Lanka, 5-7, April, 1991.

Tinoco-Ojanguren, C. and Pearcy, R.W. (1995). A comparison of light quality and quantity effects on the growth and steady-state and dynamic photosynthetic characteristics of three tropical tree species. *Functional Ecol.* **9**(2), 222-230.

Tisdall, J.M. (1994). Possible role of soil microorganisms in aggregation in soil. *Plant and Soil* **159**, 115-121.

Torquebiau, E.F.(1986). Mosaic patterns in dipterocarp rain forest in Indonesia and their implications for practical forestry. *J. Trop. Ecol.* **2**, 301-325.

Trabaud, L. (1994). The effects of fire on nutrient losses and cycling in a*Quercus coccifera* in Garrigne (Southern France). *Oecologia* **99**, 379-386.

Truax, B., Gagnon, D. (1993). Effects of straw and black plastic mulching on the initial growth and nutrition of butternut, white ash and bur oak. *For. Ecol. Manage.* **57**(1-4), 17-27.

Tryon, E.H., Lanasa, M. and Townsend, E.C. (1992). Radial growth responses of understorey sugar maple (*Acer saccharum* Marsh.) surrounding openings. *For. Ecol. Manage.* **55**, 249-257.

Turlyuk, V.D.(1983). Quality changes in needle foliage and the biological productivity of Norway spruce underplantings. *Lesovedenie-i-Lesnoe-Khozyaistvo* **18**, 57-61. (CAB Forestry Abstracts).

Turlyuk, V.D. (1984). Phytoclimatic regime under the canopy of poplar stands underplanted with Norway spruce. *Lesovedenie-i-Lesnoe-Khozyaistvo* **19**, 63-66. (CAB Forestry Abstracts).

Turner, I.M. (1990). Tree seedling growth and survival in a Malaysian Rain Forest. *Biotropica* **22**(2), 146-154.

Turner, J. and Kelly, J. (1985). Effects of radiata pine on soil chemical characteristics. *For. Ecol. Manage.* **11**, 257-270.

Turner, J. and Lambert M.J.(1988). Soil properties as affected by *Pinus radiata* plantations. *NZ. J. For.* **18**(1), 77-91.

Tworkoski, T.J., Smith, D.W. and Parrish, D.J. (1986). Regeneration of red oak, white oak and white pine by underplanting prior to canopy removal in the Virginia Piedmont. *S. J. App. For.* **16**(5), 206-210.

Unsworth, M.H. (1992). Climate and air pollution as determinants of forest ecosystem processes. In: *Responses of Forest Ecosystems To Environmental Changes* (Ed. Teller, A., Mathey, P. and Jeffers, J.N.R.), pp 63-75. Elsevier Applied Science, London.

Vandermeer, J. (1989). *The Ecology of Intercropping.* Cambridge University Press, Cambridge, UK.

Venkataramany, P. (1956). Underplanting in teak plantations in Madras State. *The Indian Forester* **82**(5), 225-236.

Verinumbe, I., and Okali, D.U.U. (1985). The influence of coppiced teak (*Tectona grandis* L.F) regrowth and roots on intercropped maize (*Zea mays* L.).*Agrof. Sys.* **3**, 381-386.

Vesterdal, C. and Dalsgaard, M., Felby, C., Raulund-Rasmussen, K. and Jorgenson, B.B. (1995). Effects of thinning and soil properties on accumulation of carbon, nitrogen and phosphorus in the forest floor of Norway spruce stands. *For. Ecol. Manage.* 77, 1-10.

Visser, S. (1985). Role of the soil invertebrates in determining the composition of soil microbial communities. In: *Ecological Interactions in Soil*, Special Publication, No. 4 of the British Ecological Society (Ed. Fitter, A.H., Atkinson, D., Read, D.J., Usher, M.B.), pp.297-317. Blackwell Scientific Publishers, Oxford.

Vitousek, P.M. (1984). Litterfall, nutrient cycling and nutrient limitation in tropical forests. *Ecology* **65**(1), 285-298.

Vitousek, Jr G., Grier, C.C., Melillo, J.M., Reiners, W.A. and Todd, R.L. (1979). Nitrate losses from disturbed ecosystems. *Science* **204**, 469-473.

Vivekanandan, K. (1988). Provenance research on *Pinus caribaea*. In : *Reforestation with Pinus in Sri Lanka* (Ed. Gunasena, H.P.M., Gunatilleke, S. and Perera, A.H.), pp19-28. Proceedings of a symposium organized by University of Peradeniya, Sri Lanka.

Wagner, S.(1994). Introduction of broadleaved trees into Scots pine stands on poor sands in northeastern Lower Saxony. *Forstarchir* **65**(1), 3-9. (CAB Forestry Abstracts).

Wallander, H., Nylundi, J.E. and Sundberg, B (1994). The influence of IAA, carbohydrate and mineral concentration in host tissue on ectomycorrhizal development on *Pinus sylvestris* L. in relation to nutrient supply.*New Phytol.* **127**(3), 521-528.

Walters, M.B., Kruger, E.L. and Reich, L.P.B.(1993). Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: species, light environment and ontogenetic considerations. *Oecologia* **96**(2), 219-231.

Walter, R.F. and McLaughlin, S.B. (1989). Black polythene mulch improves growth of plantation-grown loblolly pine and yellow-poplar. *New Forest* **3**(3), 265-274.

Waring, R.H. and Schlesinger, W.H. (1985). *Forest Ecosystems - Concepts and Management.* Academic Press, London.

Webb, D.B., Wood, P.J., Smith, J.P., and Henman, G.S. (1984). A guide to species selection for tropical and subtropical plantations. *Tropical Forestry Paper* No. **15** (second edition). Commonwealth Forestry Institute, Oxford.

Weil, R.R. (1982). *Soils of the Upper Mahaweli Reforestation and Watershed Management Project, Sri Lanka.* USAID Project 383-0055, Forest Department, Sri Lanka.

Wenban-Smith, M.G. (1993). Survival and Growth Rates of Line-Planted Mahogany (*Swietenia macrophylla.* King) in the Wet Zone Galle and Matara Districts of Sri Lanka. Unpublished report. Oxford University-University of Peradeniya.

Wendel, G.W. (1971). Converting hardwoods on poor sites to White Pine by underplanting and direct seeding. *US For. Ser. Res. Paper.* Northeast Forest Experimental Station. No. NE **188**, 18.

Wensem, J. van., Verhoef, H.A., Straalen, N.M. van., Van-Wensem, J. (1993). Litter degradation stage as a prime factor for isopod interaction with mineralization processes. *Soil Biol.Biochem.* **25**(9), 1175-1183.

Wessemael, B. van (1993). Litter decomposition and nutrient distribution in humus profiles in some mediterranean forests in southern Tuscany. *For. Ecol. Manage.* **57**(1-4), 95-114.

Whitmore, T.C. (1975). *Tropical Rain Forests of the Far East* (first edition). Clarendon Press, Oxford.

Whitmore, T.C. (1981). *Tropical Rain Forests of the Far East* (second edition). Clarendon Press, Oxford.

Whitmore, T.C. (1990). *An Introduction to Tropical Rain Forests.* Clarendon Press, Oxford.

Whitmore, T.C., Brown, N.D., Swaine, M.D., Kennedy,D., Goodwin-Bailey, C.I. and Gong, W.K. (1993). Use of hemispherical photographs in a forest ecology: Measurement of gap size and radiation totals in a Bornean tropical rain forest. *J. Trop. Ecol.* **9**, 131-151.

Whitmore, T.C. and Gong, W.K. (1983). Growth analysis of the seedlings of Balsa, *Ochroma lagopus. New Phytol.* **95**, 305-311.

Williston, H.C. and Huckenpahler, B.J. (1958). Responses in six conifers in North Mississippi underplantings. *J. For.* **56**(2), 135-137.

Wood, M. (1989). *Soil Biology,* Blackie and Son, London.

Wormald, T. J. (1975). *Pinus patula.* Commonwealth Forestry Institute, University of Oxford, *Tropical Forestry Paper*, No.**7.**

Wormald, T. J. (1992). Mixed and pure forest plantations in the tropics and subtropics. *FAO Forestry Paper **103***. FAO, Rome.

WRI (World Resources Institute), (1992). World Resources 1992-1993. Oxford University Press, London.

Yobterik, A.C., Timmer, V.R., Gordon, A.M. (1994). Screening agroforestry tree mulches for corn growth: a combined soil test, pot trial and plant analysis approach. *Agrof. Sys.* **25**(2), 153-166.

Young, A. (1990). *Agroforestry for Soil Conservation.* ICRAF, Nairobi, Kenya:CAB International, Wallingford, England.

Yurgenson, A.A. and Yurgenson, N.A. (1984). Effect of spacing on the increment of underplanted Norway spruce. *Lesovedenie-i-Lesnoe-Khozyaistvo* **19**, 66-70. (CAB Forestry Abstracts).

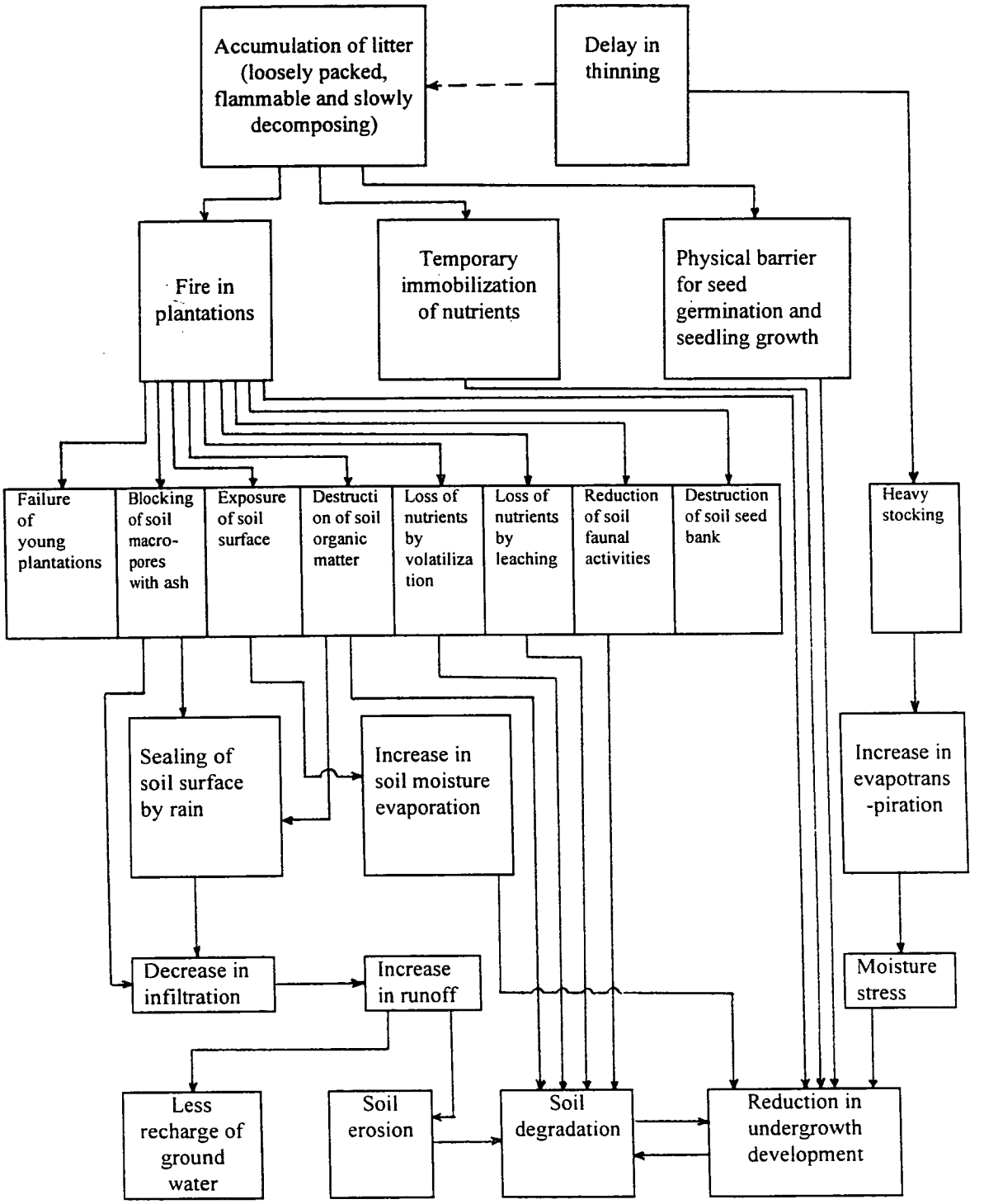
Zar, J.H. (1996). *Biostatistical Analysis* (Third edition). Prentice-Hall International, Upper Saddle River, NJ, USA.

Zobel, B.J. and Van Buijtenen, H. (1988). Wood variability: its Causes and Control, Springer-Verlag, Berlin.

Zobel, B.J., Wyk, G.V. and Stahl, P. (1987).*Growing Exotic Forests.* John Wiley and Sons, New York.

APPENDIX I

Theoretical model of ecological consequences of burnt pine plantations



APPENDIX II

ANOVA TABLES FOR RESULTS IN CHAPTER 4

Appendix II - 1 : Total treatment effect for final height of *Alstonia macrophylla.*

Source of variation	Degrees of freedom (df)	Sum of squares (ss)	Mean squares (ms)	F - value	Level of significance
Covariate	1	4600.3	4600.3	12.54	**
Treatments	5	4346.8	869.4	2.37	ns
Block	2	1079.3	539.6	1.47	ns
Error	9	3302.9	367.0		
Total	17	11428.8			

Covariate = initial value of the trees at the start of the experiment

Symbols : ns = not significant at p=0.05
* = significant at p=0.05
** = significant at p=0.01
*** = significant at p=0.001

Appendix II - 2 : Total treatment effect for final diameter of *Alstonia macrophylla.*

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.588	0.588	3.39	ns
Treatments	5	1.432	0.286	1.65	ns
Block	2	0.188	0.094	0.54	ns
Error	9	1.561	0.173		
Total	17	4.311			

Appendix II - 3 : Total treatment effect for final notional volume (log transformed values) of *Alstonia macrophylla.*

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.160	0.160	9.3	*
Treatments	5	0.152	0.030	1.76	ns
Block	2	0.017	0.008	0.49	ns
Error	9	0.155	0.017		
Total	17	0.514			

Appendix II - 4 : Mulch effect of *Alstonia macrophylla* for final height by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	2100.8	2100.8	6.14	*
Treatments	1	3173.3	3173.3	9.27	*
Block	2	460.7	230.4	0.67	ns
Error	7	2395.5	342.2		
Total	11	7674.0			

Appendix II - 5 : Trench effect of *Alstonia macrophylla* for final height by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	1804.5	1804.5	2.3	ns
Treatments	1	76.0	76.0	0.1	ns
Block	2	373.2	186.6	0.24	ns
Error	7	5492.8	784.7		
Total	11	7674.0			

Appendix II - 6 : Mycorrhiza effect of *Alstonia macrophylla* for final height by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	2281.3	2281.3	7.7	*
Treatments	1	0.5	0.5	0.0	ns
Block	2	1265.0	632.5	2.1	ns
Error	7	2079.8	297.1		
Total	11	4888.3			

Appendix II - 7 : Mulch and trench effects of *Alstonia macrophylla* for final height by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	2190.2	2190.2	4.76	ns
Mulch	1	3189.5	3189.5	6.9	*
Trench	1	91.8	91.8	0.2	ns
Mulch x Trench	1	1.2	1.2	0.00	ns
Block	2	512.2	256.1	0.56	ns
Error	5	2302.6	460.5		
Total	11	7674.0			

Appendix II - 8 : Mycorrhiza and trench effects of *Alstonia macrophylla* for final height by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	2261.5	2261.5	5.63	ns
Myco.	1	0.5	0.5	0.00	0.97
Trench	1	69.1	69.1	0.17	ns
Myco. x Trench	1	3.6	3.6	0.01	ns
Block	2	1271.8	630.9	1.56	ns
Error	5	2007.0	401.4		
Total	11	4888.3			

Appendix II - 9 : Mulch effect of *Alstonia macrophylla* for final diameter by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.033	0.033	0.16	ns
Treatments	1	1.095	1.095	5.23	*
Block	2	0.206	0.103	0.49	ns
Error	7	1.466	0.209		
Total	11	2.941			

Appendix II - 10 : Trench effect of *Alstonia macrophylla* for final diameter by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.039	0.039	0.11	ns
Treatments	1	0.006	0.006	0.02	ns
Block	2	0.200	0.100	0.27	ns
Error	7	2.555	0.365		
Total	11	2.941			

Appendix II - 11 : Mycorrhiza effect of *Alstonia macrophylla* for final diameter by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.738	0.738	16.18	**
Treatments	1	0.000	0.000	0.01	ns
Block	2	0.051	0.026	0.56	ns
Error	7	0.319	0.046		
Total	11	1.076			

Appendix II - 12 : Mulch and trench effects of *Alstonia macrophylla* for final diameter by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.014	0.014	0.05	ns
Mulch	1	1.100	1.100	3.78	ns
Trench	1	0.010	0.010	0.04	ns
Mulch x Trench	1	0.001	0.001	0.00	ns
Block	2	0.214	0.106	0.37	ns
Error	5	1.454	0.291		
Total	11	2.941			

Appendix II - 13 : Mycorrhiza and trench effects of *Alstonia macrophylla* for final diameter by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.667	0.667	11.21	*
Myco.	1	0.0008	0.0008	0.01	ns
Trench	1	0.0059	0.0059	0.1	ns
Myco. x Trench	1	0.0187	0.0187	0.32	ns
Block	2	0.060	0.030	0.50	ns
Error	5	0.297	0.0594		
Total	11	1.076			

Appendix II - 14 : Mulch effect of *Alstonia macrophylla* for final volume (log transformed values) by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.062	0.062	3.27	ns
Treatments	1	0.113	0.113	5.96	*
Block	2	0.015	0.007	0.40	ns
Error	7	0.133	0.019		
Total	11	0.332			

Appendix II - 15 : Trench effect of *Alstonia macrophylla* for final volume (log transformed values) by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.062	0.062	1.74	ns
Treatments	1	0.000	0.000	0.01	ns
Block	2	0.0157	0.007	0.22	ns
Error	7	0.247	0.035		
Total	11	0.332			

Appendix II - 16 : Mycorrhiza effect of *Alstonia macrophylla* for final volume (log transformed values) by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.123	0.123	14.2	**
Treatments	1	0.000	0.000	0.01	ns
Block	2	0.019	0.009	1.11	ns
Error	7	0.061	0.009		
Total	11	0.189			

Appendix II - 17 : Mulch and trench effects of *Alstonia macrophylla* for final volume (log values) by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.0632	0.0632	2.44	ns
Myco.	1	0.1136	0.1136	4.38	ns
Trench	1	0.0003	0.0003	0.01	ns
Mulch x Trench	1	0.0036	0.0036	0.14	ns
Block	2	0.0182	0.0091	0.35	ns
Error	5	0.1296	0.0259		
Total	11	0.3319			

Appendix II - 18 : Mycorrhiza and trench effects of *Alstonia macrophylla* for final volume (log values) by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.115	0.115	9.90	*
Myco.	1	0.00008	0.00008	0.01	ns
Trench	1	0.00041	0.00041	0.03	ns
Myco. x Trench	1	0.0022	0.0022	0.19	ns
Block	2	0.020	0.010	0.88	ns
Error	5	0.582	0.012		
Total	11	0.189			

Appendix II - 19 : Total treatment effect for final height of *Khaya senegalensis*.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	32.28	32.28	2.73	ns
Treatment	5	624.10	124.82	10.54	***
Block	2	13.13	6.57	0.55	0.59
Error	9	106.58	11.84		
Total	17	862.85			

Appendix II - 20 : Mulch and trench effects of *Khaya senegalensis* for final height by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	45.48	45.48	5.12	ns
Mulch	1	398.04	398.04	44.82	***
Trench	1	46.28	46.28	5.21	ns
Mulch x Trench	1	22.68	22.68	2.55	ns
Block	2	0.55	0.28	0.03	ns
Error	5	44.41	8.88		
Total	11	617.6			

Appendix II - 21 : Mycorrhiza and trench effects of *Khaya senegalensis* for final height by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.57	0.57	0.05	ns
Myco.	1	0.03	0.03	0.00	ns
Trench	1	19.1	19.1	1.82	ns
Myco. x Trench	1	24.9	24.9	2.39	ns
Block	2	8.95	4.48	0.43	ns
Error	5	52.34	10.47		
Total	11	107.9			

Appendix II - 22 : Total treatment effect for final diameter of *Khaya senegalensis*.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.076	0.076	4.92	*
Treatments	5	0.261	0.052	3.37	*
Block	2	0.078	0.039	2.54	ns
Error	9	0.139	0.015		
Total	17	0.765			

Appendix II - 23 : Mulch and trench effects of *Khaya senegalensis* for final diameter by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.072	0.072	4.03	ns
Mulch	1	0.117	0.117	6.51	*
Trench	1	0.058	0.058	3.25	ns
Mulch x Trench	1	0.006	0.006	0.35	ns
Block	2	0.019	0.009	0.53	ns
Error	5	0.090	0.018		
Total	11	0.482			

Appendix II - 24 : Myco. and trench effects of *Khaya senegalensis* for final diameter by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.0048	0.0048	0.21	ns
Myco.	1	0.0041	0.0041	0.18	ns
Trench	1	0.0340	0.0340	1.50	ns
Myco. x Trench	1	0.0030	0.0030	0.13	ns
Block	2	0.043	0.022	0.96	ns
Error	5	0.113	0.022		
Total	11	0.233			

Appendix II - 25 : Total treatment effect for final volume (log transformed values) of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.058	0.058	17.64	**
Treatment	5	0.233	0.046	14.22	***
Block	2	0.008	0.004	1.32	ns
Error	9	0.029	0.003		
Total	17	0.415			

Appendix II - 26 : Mulch and trench effects for final volume (log values) of *Khaya senegalensis* by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.0524	0.0524	33.40	**
Mulch	1	0.126	0.126	80.39	***
Trench	1	0.016	0.016	10.14	*
Mulch x trench	1	0.0008	0.0008	0.01	ns
Block	2	0.00002	0.000008	0.01	ns
Error	5	0.0078	0.0015		
Total	11	0.263			

Appendix II - 27 : Mycorrhiza and trench effects of *Khaya senegalensis* for final volume (log values) by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.0061	0.0061	1.31	ns
Myco.	1	0.002	0.002	0.50	ns
Trench	1	0.013	0.013	2.76	ns
Myco. x Trench	1	0.0016	0.0016	0.35	ns
Block	2	0.0078	0.0039	0.84	ns
Error	5	0.0235	0.0047		
Total	11	0.085			

Appendix II - 28 : Total treatment effect for final height of *Toona ciliata*.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	156.2	156.2	10.3	*
Treatments	5	165.0	33.0	2.2	ns
Block	2	144.7	72.3	4.8	*
Error	9	136.6	15.2		
Total	17	1091.4			

Appendix II - 29 : Mulch and trench effects of *Toona ciliata* for final height by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	29.02	29.02	3.07	ns
Mulch	1	62.87	62.87	4.65	ns
Trench	1	6.50	6.50	0.69	ns
Mulch x Trench	1	89.79	89.79	9.50	*
Block	2	119.3	59.7	6.31	*
Error	5	47.26	9.45		
Total	11	759.83			

Appendix II - 30 : Mycorrhiza and trench effects of *Toona ciliata* for final height by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	146.7	146.7	4.67	ns
Myco.	1	0.79	0.79	0.03	ns
Trench	1	90.34	90.34	2.87	ns
Myco. x Trench	1	20.3	20.3	0.65	ns
Block	2	44.1	44.1	1.4	ns
Error	5	188.6	31.44		
Total	11	534.3			

Appendix II - 31 : Total treatment effect for final diameter of *Cedrela toona*.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.0042	0.0042	0.57	ns
Treatments	5	0.0326	0.0065	0.87	ns
Block	2	0.0750	0.0375	5.02	*
Error	9	0.0672	0.0074		
Total	17	0.1795			

Appendix II - 32 : Mulch and trench effects of *Toona ciliata* for final diameter by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.0082	0.0082	1.83	ns
Mulch	1	0.0017	0.0017	0.38	ns
Trench	1	0.0001	0.0001	0.02	ns
Mulch x Trench	1	0.004	0.004	1.06	ns
Block	2	0.104	0.052	11.5	*
Error	5	0.022	0.004		
Total	11	0.135			

Appendix II - 33 : Mycorrhiza and trench effects of *Toona ciliata* for final diameter by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.005	0.005	0.47	ns
Myco.	1	0.0014	0.0014	0.12	ns
Trench	1	0.026	0.026	2.31	ns
Myco. x Trench	1	0.0003	0.0003	0.03	ns
Block	2	0.019	0.019	1.69	ns
Error	5	0.067	0.011		
Total	11	0.011			

Appendix II - 34 : Total treatment effect for final volume (log transformed values) of *Cedrela toona*.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.0245	0.0245	2.76	ns
Treatments	5	0.0268	0.0053	0.61	ns
Block	2	0.0811	0.0405	4.57	*
Error	9	0.0798	0.0089		
Total	17	0.2754			

Appendix II - 35 : Mulch and trench effects of *Toona ciliata* for final volume (log values) by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.002	0.002	0.43	ns
Mulch	1	0.178	0.017	3.33	ns
Trench	1	0.003	0.003	0.59	ns
Mulch x Trench	1	0.009	0.009	1.76	ns
Block	2	0.105	0.052	9.87	*
Error	5	0.026	0.005		
Total	11	0.211			

Appendix II - 36 : Mycorrhiza and trench effects of *Toona ciliata* for final volume (log values) by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1	0.021	0.021	1.26	ns
Myco.	1	0.006	0.006	0.41	ns
Trench	1	0.001	0.001	0.06	ns
Myco. x Trench	1	0.0009	0.0009	0.06	ns
Block	2	0.02	0.02	1.48	ns
Error	5	0.099	0.016		
Total	11	0.171			

Appendix II - 37 : Survival percentage (arc sine transformed values) of *Cedrela toona.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	5	210.26	42.05	0.88	ns
Block	2	24.72	12.36	0.26	ns
Error	10	476.14	47.61		
Total	17	711.13			

Appendix II - 38 : Total treatment effect for final height of *Swietenia macrophylla.*

Source of variation	df	ss	ms	F - value	Level of significance
Covariate-1 (initial height)	1	17.47	17.47	11.17	*
Covariate-2 (light level)	1	15.83	15.83	10.13	*
Treatments	4	78.85	19.71	12.61	**
Block	2	71.85	35.92	22.97	**
Error	6	9.38	1.56		
Total	14	268.75			

Appendix II - 39 : Mulch and trench effects of *Swietenia macrophylla* for final height by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate - 1	1	14.40	14.40	7.00	ns
Covariate - 2	1	13.82	13.82	6.72	ns
Mulch	1	56.95	56.95	27.68	**
Trench	1	7.28	7.28	3.58	ns
Mulch x Trench	1	5.57	5.57	2.71	ns
Block	2	53.9	26.9	13.1	*
Error	5	8.23	2.05		
Total	11	244.58*			

* sequential ss

Appendix II - 40 : Mycorrhiza and trench effects of *Swietenia macrophylla* for final height by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate - 1	1	15.03	15.03	12.0	*
Covariate - 2	1	12.86	12.86	10.3	*
Myco.	1	11.21	11.21	7.99	ns
Trench	1	12.07	12.07	7.93	ns
Myco. x Trench	1	0.548	0.548	0.44	ns
Block	2	54.14	27.07	21.7	**
Error	5	4.99	1.248		
Total	11	192.58*			

* sequential ss

Appendix II - 41 : Total treatment effect for final diameter of *Swietenia macrophylla.*

Source of variation	df	ss	ms	F - value	Level of significance
Covariate-1 (initial height)	1	0.0002	0.0002	0.05	ns
Covariate-2 (light level)	1	0.0011	0.0011	0.22	ns
Treatments	4	0.0115	0.0028	0.54	ns
Block	2	0.0290	0.0145	2.72	ns
Error	6	0.0319	0.0053		
Total	14	0.0933			

Appendix II - 42 : Mulch and trench effects of *Swietenia macrophylla* for final diameter by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate - 1	1	0.0026	0.0026	0.40	ns
Covariate - 2	1	0.0004	0.0004	0.06	ns
Mulch	1	0.0012	0.0012	0.19	ns
Trench	1	0.0087	0.0087	1.31	ns
Mulch x Trench	1	0.0004	0.0004	0.06	ns
Block	2	0.032	0.016	2.41	ns
Error	5	0.026	0.0067		
Total	11	0.0058*			

* sequential ss

Appendix II - 43 : Mycorrhiza and trench effects of *Swietenia macrophylla* for final diameter by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate - 1	1	0.00007	0.00007	0.01	ns
Covariate - 2	1	0.0023	0.0023	0.35	ns
Myco.	1	0.0009	0.0009	0.14	ns
Trench	1	0.0077	0.0077	1.13	ns
Myco. x Trench	1	0.00007	0.00007	0.01	ns
Block	2	0.0215	0.0107	1.58	ns
Error	5	0.0272	0.0068		
Total	11	0.0726*			

* sequential ss

Appendix II - 44 : Total treatment effect for final volume (log transformed values) of *Swietenia macrophylla.*

Source of variation	df	ss	ms	F - value	Level of significance
Covariate-1 (initial height)	1	0.0030	0.0030	0.28	ns
Covariate-2 (light level)	1	0.0003	0.0003	0.03	ns
Treatments	4	0.0261	0.0065	0.59	ns
Block	2	0.1000	0.0500	4.55	ns
Error	7	0.0659	0.0110		
Total	14	0.2233			

Appendix II - 45 : Mulch and trench effects of *Swietenia macrophylla* for final volume (log values) by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate - 1	1	0.0057	0.0057	0.64	ns
Covariate - 2	1	0.0004	0.0004	0.05	ns
Mulch	1	0.0080	0.0087	0.87	ns
Trench	1	0.017	0.017	1.94	ns
Mulch x Trench	1	0.007	0.007	0.83	ns
Block	2	0.118	0.059	6.55	ns
Error	5	0.036	0.009		
Total	11	0.219*			

* sequential ss

Appendix II - 46 : Mycorrhiza and trench effects of *Swietenia macrophylla* for final volume (log values) by factorial analysis.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate - 1	1	0.006	0.006	0.52	ns
Covariate - 2	1	0.00004	0.00004	0.00	ns
Myco.	1	0.0039	0.0039	0.33	ns
Trench	1	0.015	0.015	1.27	ns
Myco. x Trench	1	0.057	0.057	0.48	ns
Block	2	0.116	0.058	4.9	ns
Error	5	0.047	0.118		
Total	11	0.216*			

* sequential ss

APPENDIX III

ANOVA TABLES FOR RESULTS IN CHAPTER 5

(only those with statistically significant results are presented except for breakdown analysis with interactions)

Appendix III - 1 : Mulch effect for total dry weight of *Alstonia macrophylla.*

Source of variation	Degrees of freedom (df)	Sum of squares (ss)	Mean squares (ms)	F - value	Level of significance
Treatments	1	225502	225502	9.95	**
Block	2	119775	59888	2.64	ns
Error	8	181309	22664		
Total	11	526586			

Symbols : ns = not significant at p=0.05
* = significant at p=0.05
** = significant at p=0.01
*** = significant at p=0.001

Appendix III - 2 : Mulch and trench effects for total dry weight of *Alstonia macrophylla.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	225502	225502	8.04	*
Trench	1	990	990	0.04	ns
Mulch x Trench	1	12097	12097	0.43	ns
Block	2	119775	59888	2.14	ns
Error	6	168222	28037		
Total	11	526586			

Appendix III - 3 : Mycorrhiza and trench effects for total dry weight of *Alstonia macrophylla.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	690	690	0.01	ns
Trench	1	23852	23852	0.30	ns
Myco. x Trench	1	87552	87552	1.12	ns
Block	2	119813	59906	0.77	ns
Error	6	469672	78279		
Total	11	701579			

Appendix III - 4 : Mulch effect for RGR of *Alstonia macrophylla.*

Source of variation	df	ss	ms	F - value	Level of significance
Mulch	1	0.0001687	0.0001687	10.98	**
Block	2	0.0000151	0.0000075	0.49	ns
Error	8	0.0001230	0.0000153		
Total	11	0.0003069			

Appendix III - 5 : Mulch and trench effects for RGR of *Alstonia macrophylla.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	0.00016	0.00016	9.36	*
Trench	1	0.00000075	0.00000075	0.04	ns
Mulch x Trench	1	0.000014	0.000014	0.78	ns
Block	2	0.000015	0.0000075	0.42	ns
Error	6	0.00010	0.000018		
Total	11	0.00030			

Appendix III - 6 : Mycorrhiza and trench effects for RGR of *Alstonia macrophylla.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	0.000008	0.000008	0.12	ns
Trench	1	0.000016	0.000016	0.24	ns
Myco. x Trench	1	0.000075	0.000075	1.12	ns
Block	2	0.0000045	0.0000022	0.03	ns
Error	6	0.000402	0.000067		
Total	11	0.00050			

Appendix III - 7 : Mulch effect for NAR of *Alstonia macrophylla.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	4.687	4.6687	6.97	*
Block	2	8.748	4.374	6.51	*
Error	8	5.379	0.672		
Total	11	18.816			

Appendix III - 8 : Mulch and trench effects for NAR of *Alstonia macrophylla.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	4.68	4.68	5.97	*
Trench	1	0.60	0.60	0.77	ns
Mulch x Trench	1	0.059	0.059	0.07	ns
Block	2	8.74	4.37	5.57	*
Error	6	4.71	0.78		
Total	11	18.8			

Appendix III - 9 : Mycorrhiza and trench effects for NAR of *Alstonia macrophylla.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	1.16	1.16	0.69	ns
Trench	1	2.07	2.07	1.24	ns
Myco. x Trench	1	0.816	0.816	0.49	ns
Block	2	7.2	3.6	2.14	ns
Error	6	10.1	1.7		
Total	11	21.3			

Appendix III - 10 : Total treatment effect for total dry weight of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	5	3886.2	777.2	5.19	**
Block	2	863.8	431.9	2.9	ns
Error	10	1498.5	149.9		
Total	17	6248.5			

Appendix III - 11 : Mulch treatment effect for total dry weight of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	3221.0	3221.0	18.2	**
Block	2	633.9	317.0	1.79	ns
Error	8	1415.9	177.0		
Total	11	5270.8			

Appendix III - 12 : Mycorrhiza treatment effect for total dry weight of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	446.52	446.52	6.23	*
Block	2	509.12	254.56	3.55	ns
Error	8	573.20	71.65		
Total	11	1528.84			

Appendix III - 13 : Mulch and trench effects for total dry weight of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	3221	3221	23.5	**
Trench	1	387.6	387.6	2.83	ns
Mulch x Trench	1	206.7	206.7	1.51	ns
Block	2	633.9	317.0	2.31	ns
Error	6	821.7	136.9		
Total	11	5270.8			

Appendix III - 14 : Mycorrhiza and trench effects for total dry weight of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	446.5	446.5	4.8	ns
Trench	1	3.85	3.85	0.04	ns
Myco. x Trench	1	11.2	11.2	0.12	ns
Block	2	509.1	254.5	2.74	ns
Error	6	558.1	93.0		
Total	11	1528.8			

Appendix III - 15 : Total treatment effect for stem dry weight of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	5	692.65	138.53	6.12	**
Block	2	157.00	78.50	3.47	ns
Error	10	226.43	22.64		
Total	17	1076.08			

Appendix III - 16 : Mulch treatment effect for stem dry weight of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	578.24	578.24	20.25	***
Block	2	113.37	56.69	1.99	ns
Error	8	228.46	28.56		
Total	11	920.07			

Appendix III - 17 : Mulch and trench effects for stem dry weight of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	578.3	578.3	24.6	**
Trench	1	44.5	44.5	1.89	ns
Mulch x Trench	1	42.9	42.9	1.83	ns
Block	2	113.4	56.7	2.41	ns
Error	6	141.0	23.5		
Total	11	920.0			

Appendix III - 18 : Mycorrhiza and trench effects for stem dry weight of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	92.9	92.9	6.8	ns
Trench	1	10.1	10.1	0.73	ns
Myco. x Trench	1	9.36	9.36	0.68	ns
Block	2	74.8	37.41	2.73	ns
Error	6	82.34	13.7		
Total	11	269.6			

Appendix III - 19 : Total treatment effect for leaf dry weight of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	5	823.73	164.75	4.13	*
Block	2	228.76	114.38	2.87	ns
Error	10	398.63	39.86		
Total	17	1451.12			

Appendix III - 20 : Mulch treatment effect for leaf dry weight of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	588.0	588.0	13.81	**
Block	2	172.53	86.30	2.03	ns
Error	8	340.54	42.57		
Total	11	1101.07			

Appendix III - 21 : Mulch and trench effects for leaf dry weight of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	588.0	588.0	21.5	**
Trench	1	105.6	105.6	3.87	ns
Mulch x Trench	1	71.0	71.0	2.6	ns
Block	2	172.5	86.3	3.2	ns
Error	6	163.9	27.3		
Total	11	1101.0			

Appendix III - 22 : Mycorrhiza and trench effects for leaf dry weight of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	30.7	30.7	1.8	ns
Trench	1	0.01	0.01	0.00	ns
Myco. x Trench	1	3.0	3.0	0.2	ns
Block	2	227.7	113.8	6.66	*
Error	6	102.5	17.1		
Total	11	364.0			

Appendix III - 23 : Mulch treatment effect for root dry weight of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	72.03	72.03	9.6	**
Block	2	13.16	6.58	0.88	ns
Error	8	60.04	7.50		
Total	11	145.27			

Appendix III - 24 : Mulch and trench effects for root dry weight of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	72.03	72.03	8.27	*
Trench	1	7.36	7.36	0.85	ns
Mulch x Trench	1	0.4	0.4	0.05	ns
Block	2	13.2	6.58	0.76	ns
Error	6	52.27	8.72		
Total	11	145.23			

Appendix III - 25 : Mycorrhiza and trench effects for root dry weight of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	0.05	0.05	0.00	ns
Trench	1	19.25	19.25	1.27	ns
Myco. x Trench	1	1.08	1.08	0.07	ns
Block	2	47.33	23.7	1.55	ns
Error	6	91.31	15.22		
Total	11	159.0			

Appendix III - 26 : Mulch treatment effect for leaf area of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	788481	788481	5.26	*
Block	2	232913	116456	0.78	ns
Error	8	1198332	149791		
Total	11	2219726			

Appendix III - 27 : Mulch and trench effects for leaf area of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	788481	788481	5.24	ns
Trench	1	190008	190008	1.26	ns
Mulch x Trench	1	105281	105281	0.7	ns
Block	2	232913	116456	0.77	ns
Error	6	903042	150507		
Total	11	2219726			

Appendix III - 28 : Mycorrhiza and trench effects for leaf area of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	48896	48896	0.39	ns
Trench	1	242536	242536	1.92	ns
Myco. x Trench	1	71765	71765	0.57	ns
Block	2	173501	86750	0.69	ns
Error	6	759406	126568		
Total	11	1296105			

Appendix III - 29 : Mulch treatment effect for root:shoot ratio of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	0.020833	0.020833	12.85	**
Block	2	0.000800	0.000400	0.25	ns
Error	8	0.012967	0.001621		
Total	11	0.034600			

Appendix III - 30 : Mulch and trench effects for root:shoot ratio of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	0.0208	0.0208	12.5	**
Trench	1	0.0021	0.0021	1.28	ns
Mulch x Trench	1	0.0008	0.0008	0.50	ns
Block	2	0.0008	0.0004	0.24	ns
Error	6	0.01	0.001		
Total	11	0.034			

Appendix III - 31 : Mycorrhiza and trench effects for root:shoot of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	0.016	0.016	3.85	ns
Trench	1	0.001	0.001	0.29	ns
Myco. x Trench	1	0.003	0.003	0.64	ns
Block	2	0.003	0.0015	0.38	ns
Error	6	0.025	0.004		
Total	11	0.048			

Appendix III - 32 : Total treatment effect for RGR of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	5	0.00028	0.000056	3.82	*
Block	2	0.00015	0.000075	5.08	*
Error	10	0.00014	0.000015		
Total	17	0.00058			

Appendix III - 33 : Mulch treatment effect for RGR of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	0.00026	0.00026	23.71	***
Block	2	0.00004	0.00002	1.96	ns
Error	8	0.00008	0.00001		
Total	11	0.00039			

Appendix III - 34 : Mycorrhiza treatment effect for RGR of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	0.00006	0.00006	5.09	*
Block	2	0.00018	0.00009	7.79	*
Error	8	0.00009	0.00001		
Total	11	0.00034			

Appendix III - 35 : Mulch and trench effects for RGR of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	0.00026	0.00026	22.8	**
Trench	1	0.000003	0.000003	0.26	ns
Mulch x Trench	1	0.000016	0.000016	1.42	ns
Block	2	0.000043	0.000021	1.88	ns
Error	6	0.000068	0.000011		
Total	11	0.00039			

Appendix III - 36 : Mycorrhiza and trench effects for RGR of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	0.000060	0.000060	3.99	ns
Trench	1	0.0000040	0.0000040	0.27	ns
Myco. x Trench	1	0.00000008	0.00000008	0.01	ns
Block	2	0.00018	0.000093	6.11	*
Error	6	0.000091	0.000015		
Total	11	0.00034			

Appendix III - 37 : Mulch treatment effect for NAR of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	76.30	76.30	12.71	**
Block	2	10.68	5.34	0.89	ns
Error	8	48.02	6.003		
Total	11	135.01			

Appendix III - 38 : Mycorrhiza treatment effect for NAR of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	38.52	38.52	13.43	**
Block	2	19.92	9.96	3.47	ns
Error	8	22.94	2.86		
Total	11	81.38			

Appendix III - 39 : Mulch and trench effects for NAR of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	76.30	76.30	12.8	**
Trench	1	1.841	1.841	0.31	ns
Mulch x Trench	1	10.3	10.3	1.72	ns
Block	2	10.7	5.34	0.89	ns
Error	6	35.91	5.98		
Total	11	135.0			

Appendix III - 40 : Mycorrhiza and trench effects for NAR of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	38.52	38.52	11.8	**
Trench	1	3.27	3.27	1.0	ns
Myco. x Trench	1	0.002	0.002	0.00	ns
Block	2	19.9	9.96	3.04	ns
Error	6	19.67	3.3		
Total	11	81.4			

Appendix III - 41 : Mycorrhiza treatment effect for LAR of *Khaya senegalensis.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	168.75	168.75	8.43	*
Block	2	29.49	14.74	0.74	ns
Error	8	160.23	20.03		
Total	11	358.5			

Appendix III - 42 : Mulch and trench effects for LAR of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	120.3	120.3	3.00	ns
Trench	1	0.03	0.03	0.00	ns
Mulch x Trench	1	69.1	69.1	1.72	ns
Block	2	129.5	64.7	1.61	ns
Error	6	241.1	40.1		
Total	11	560.1			

Appendix III - 43 : Mycorrhiza and trench effects for LAR of *Khaya senegalensis.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	168.8	168.8	8.9	*
Trench	1	38.16	38.16	1.96	ns
Myco. x Trench	1	5.33	5.33	0.27	ns
Block	2	29.5	14.7	0.8	ns
Error	6	116.7	19.5		
Total	11	358.5			

Appendix III - 44 : Mulch treatment effect for leaf number of *Toona ciliata.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	23.24	23.24	27.81	**
Block	2	5.32	2.66	3.18	ns
Error	8	6.68	0.83		
Total	11	35.24			

Appendix III - 45 : Mulch and trench effects for leaf number *Toona ciliata.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	23.2	23.2	21.4	**
Trench	1	0.19	0.19	0.17	ns
Mulch x Trench	1	0.001	0.001	0.00	ns
Block	2	5.33	2.67	2.46	ns
Error	6	6.5	1.08		
Total	11	35.25			

Appendix III - 46 : Mycorrhiza and trench effects for leaf number of *Toona ciliata.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	12.0	12.0	2.58	ns
Trench	1	2.61	2.61	0.56	ns
Myco. x Trench	1	4.32	4.32	0.93	ns
Block	2	19.3	9.62	2.07	ns
Error	6	27.9	4.65		
Total	11	66.1			

Appendix III - 47 : Mulch treatment effect for leaf area of *Toona ciliata.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	78894	78894	14.14	**
Block	2	150538	75269	13.49	**
Error	8	44635	5579		
Total	11	274066			

Appendix III - 48 : Mulch and trench effects for leaf area of *Toona ciliata.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	78894	78894	10.7	*
Trench	1	234	234	0.03	ns
Mulch x Trench	1	19	19	0.00	ns
Block	2	150538	75269	10.2	*
Error	6	44382			
Total	11	274066			

Appendix III - 49 : Mycorrhiza and trench effects for leaf area of *Toona ciliata.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	22881	22881	1.22	ns
Trench	1	14008	14008	0.75	ns
Myco. x Trench	1	11532	11532	0.61	ns
Block	2	194941	97470	5.2	ns
Error	6	112815	18803		
Total	11	356178			

Appendix III - 50 : Mulch treatment effect for LWR of *Toona ciliata.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	0.044	0.044	6.30	*
Block	2	0.002	0.001	0.15	ns
Error	8	0.056	0.007		
Total	11	0.102			

Appendix III - 51 : Mulch and trench effects for LWR of *Toona ciliata.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	0.044	0.044	5.68	*
Trench	1	0.009	0.009	1.16	ns
Mulch x Trench	1	0.0004	0.0004	0.05	ns
Block	2	0.0021	0.0010	0.14	ns
Error	6	0.0468	0.007		
Total	11	0.102			

Appendix III - 52 : Mycorrhiza and trench effects for LWR of *Toona ciliata.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	0.020	0.020	3.84	ns
Trench	1	0.0002	0.0002	0.04	ns
Myco. x Trench	1	0.0080	0.0080	1.54	ns
Block	2	0.0010	0.0005	0.10	ns
Error	6	0.0312	0.0052		
Total	11	0.0604			

Appendix III - 53 : Mycorrhiza treatment effect for root:shoot ratio of *Toona ciliata.*

Source of variation	df	ss	ms	F - value	Level of significance
Treatments	1	0.011	0.011	4.9	*
Block	2	0.012	0.0064	2.76	ns
Error	8	0.018	0.0023		
Total	11	0.043			

Appendix III - 54 : Mulch and trench effects for root:shoot ratio of *Toona ciliata.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Mulch	1	0.002	0.002	0.46	ns
Trench	1	0.0003	0.0001	0.03	ns
Mulch x Trench	1	0.0000	0.0000	0.00	ns
Block	2	0.025	0.012	2.71	ns
Error	6	0.279	0.004		
Total	11	0.055			

Appendix III - 55 : Mycorrhiza and trench effects for root:shoot ratio of *Toona ciliata.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F - value	Level of significance
Myco.	1	0.011	0.011	5.46	ns
Trench	1	0.004	0.004	1.76	ns
Myco. x Trench	1	0.002	0.002	1.15	ns
Block	2	0.012	0.006	3.10	ns
Error	6	0.012	0.002		
Total	11	0.042			

APPENDIX IV

ANCOVA TABLES FOR RESULTS IN CHAPTER 6

Appendix IV - 1 : Factorial analysis of final height of thinning trial at Kinigama.

Source of variation	Degrees of freedom (df)	Sum of squares (ss)	Mean squares (ms)	F - value	Level of significance
Covariate	1 (1)≠	493.87 (526.0)	493.87 (526.0)	25.86 (34.38)	*** (***)
Thinning	3 (3)	704.01 (704.7)	234.67 (234.9)	12.29 (15.35)	*** (***)
Species	3 (3)	221.48 (206.5)	73.83 (68.8)	3.87 (4.5)	* (**)
Thinning*Species	9	110.69	12.3	0.64	ns
Block	2 (2)	160.25 (129.5)	80.13 (64.7)	4.20 (4.23)	* (*)
Error	29 (38)	553.76 (581.5)	19.10 (15.3)		
Total	47 (47)	13524.37 (13353.7)			

Covariate = initial value of the trees at the start of the experiment

≠ = values within the paranthesis are from analysis without interaction term when it is non-significant.

Symbols : ns = not significant at p=0.05
* = significant at p=0.05
** = significant at p=0.01
*** = significant at p=0.001

Appendix IV - 2 : Factorial analysis of final diameter of thinning trial at Kinigama.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1 (1)	0.014 (0.022)	0.014 (0.022)	1.57 (3.08)	ns (ns)
Thinning	3 (3)	0.509	0.169	18.97	***
Species	3 (3)	0.062	0.020	2.31	ns
Thinning*Species	9	0.030	0.003	0.37	0.939
Block	2 (2)	0.185	0.092	10.36	***
Error	29 (38)	0.259	0.008		
Total	47 (47)	1.350			

Appendix IV - 3 : Factorial analysis of final volume (log transformed values) of thinning trial at Kinigama.

Source of variation	df	ss	ms	F - value	Level of significance
Covariate	1 (1)	0.187 (0.200)	0.187 (0.200)	13.2 (14.46)	*** (***)
Thinning	3 (3)	1.097 (1.114)	0.365 (0.371)	25.81 (26.82)	*** (***)
Species	3 (3)	0.040 (0.037)	0.013 (0.037)	0.96 (0.90)	ns
Thinning*Species	9	0.115	0.012	0.90	ns
Block	2 (2)	0.459 (0.446)	0.229 (0.223)	16.23 (16.84)	*** (***)
Error	29 (38)	0.411 (0.526)	0.014 (0.013)	0.90 (0.90)	
Total	47 (47)	3.186 (3.186)			

APPENDIX V

SOIL PROFILE DESCRIPTION

Location : Watawala
Slope : about 20%
Landscape position : Mid slope
Vegetation : Pine with some scattered perennial shrubs and grasses

Character	A layer (10-42 cm)	B1 layer (42-75 cm)	B2 Layer (75-92 cm)	B3 layer (92-148 cm)	B4 layer (148 + cm)
Colour (wet) (Munsell)	2.5Y 3/2 (brownish black)	7.5 YR 5/8 (bright brown)	Many stones and decomposing rock fragments	10YR 4/6 (brown)	10YR 5/8 (yellowish brown)
Texture	sandy clay loam	gravely clay loam		sandy loam	sandy loam
Structure*	weak, medium, s.a.b.	moderate, medium, s.a.b		moderate, fine, s.a.b.	moderate, fine, s.a.b.
Consistency	slightly sticky and plastic	sticky and plastic		non-sticky and non-plastic	slightly sticky and non-plastic
Pore Distribution	few, fine and many medium pores	many fine and few medium pores		average fine pores	few fine pores
Root Distribution	many fine and few medium roots	few fine and few medium roots		few fine roots	very few fine roots
Rock fragments	few, decomposing	few decomposing		nil	decomposing
Horizon boundary	wavy abrupt	wavy abrupt		wavy abrupt	wavy abrupt
Other characteristics	clay cutons around gravel particles	higher clay cutons than A layer, few Fe stones		no clay cutons, fine Mn stains and concretions, some Fe stones	few clay cutons, many quarts particles, fine Mn concretions

* structure includes stability, size and type of aggregrates
s.a.b. = sub angular blocky

SOIL PROFILE DESCRIPTION

Location : Deltota
Slope : about 10%
Landscape position : Mid slope
Vegetation : Pine with some scattered perennial shrubs and grasses

Character	A layer (0-6 cm)	B1 layer (6-48 cm)	B2 Layer (48-86 cm)	B3 layer (86-109 cm)	B4 layer (109 + cm)
Colour (wet) (Munsell)	10YR 4/6 (brown)	10YR 5/8 (yellowish brown)	7.5YR 5/8 (bright brown)	2.5YR 4/8 (reddish brown)	2.5YR 4/8 (reddish brown)
Texture	sandy clay loam	sandy loam	sandy loam	gravely loam	gravely clay loam
Structure*	moderate, fine s.a.b.	moderate, medium, s.a.b	strong, medium and s.a.b.	Gravel layer	moderate, fine, s.a.b.
Consistency	sticky and plastic	slightly sticky and plastic	slightly sticky and slightly plastic		slightly sticky and non-plastic
Pore Distribution	few, fine pores	medium, many fine pores	medium pores common		few fine pores
Root Distribution	many fine and medium roots	many medium and fine roots	few medium, fine roots		no roots
Rock fragments	nil	few decomposing	few quartz particles		sand and gravel particles
Horizon boundary	clear smooth	diffused smooth	clear and wavy		wavy abrupt
Other characteristics	nil	clay cutons present. silt deposited from A layer	Mn concretions present, reduced soil due to saturation		Many Mn concretions

* structure includes stability, size and type of aggregrates
s.a.b. = sub angular blocky

APPENDIX VI

Spore density and percentage of live spores observed in various experimental sites in pine plantations and mature tree blocks outside the experimental areas (Data based on 5-6 soil samples collected from topsoil in an area of 0.5 ha in each case)

Site and species	Number of spores per 50 g of soil	percentage of live spores
Experimental sites		
1. Panwila (*A. macrophylla*)	497	5.2
2. Deltota (*K. senegalensis*)	238	19.5
3. Watawala (*T. ciliata*)	660	3.3
4. Galaha (*S. macrophylla*)	176	0.5
Mature tree sites		
1. *A. macrophylla*	602	2.9
2. *K. senegalensis*	200	8.5
3. *S. macrophylla*	80	0.4
Trap cultures in pots (Soils of above experimental plots planted with millet and cowpea grown for about 6-7 months)	about 10,000	about 95.0

Endomycorrhizal types of which spores were observed in above samples.

1) *Glomus occultum* (Walker)
2) *Acaulospora morrowae* (Spain and Schenck)
3) *Acaulospora mellea* (Spain and Schenck)
4) *Acaulospora foveata* (Trappe and Janos)
5) *Gigaspora* species
6) *Scutellospora pellucida* (Nicolson and Schenck)

Some mycorrhizal fungal species observed in pine roots in experimental areas.

Ectomycorrhiza 1) *Suillus* species
2) *Thelephora* species
3) *Inocybe* species

Ectendomycorrhiza: 1) E strain