THE VEGETATIVE PROPAGATION

&

EARLY DEVELOPMENT OF DIPTEROCARP CUTTINGS

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I confirm that this thesis is my own work and has not been submitted in any previous application for a degree. The results presented are from analyses that were carried out by myself unless otherwise acknowledged.

Glen Reynolds

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For my Nan and Des, who taught me how to grow plants, and my Mum

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ABSTRACT

Many of the lowland rainforests of SE Asia have been degraded by logging and shifting cultivation, are lacking in natural recruitment (particularly among the dipterocarps) and are in critical need of rehabilitation. Enrichment planting is an established method of rainforest rehabilitation but this depends upon a reliable supply of dipterocarp seedlings. However, due to their habit of mass flowering, the supply of dipterocarp seed, and hence planting material, is sporadic. It is therefore of critical importance that alternative methods for the large-scale production of dipterocarps are developed. Vegetative propagation by cuttings would in theory be ideal but few rehabilitation projects are propagating dipterocarps by this method. The reasons for this are two-fold: questions remain at the propagation phase (particularly the influence of light and applied hormones on rooting) and, more importantly, there is almost no evidence to indicate how dipterocarp cuttings develop after planting.

The role of light and plant growth regulators on rooting in cuttings of *Dryobalanops lanceolata*, *Parashorea malaanonan* and *Shorea leprosula* was investigated. The responses of these species to the level of irradiance were plastic and there were no effects on cutting survival, rooting percentage or root development. Previous research on the use of plant growth regulators to promote rooting in dipterocarp cuttings has been inconclusive. Several concentrations of indole-butyric acid (IBA) were applied to cuttings of the same species for various durations. High concentration IBA combined with long exposure duration treatments resulted in high cutting mortality. Application of IBA did not significantly improve either root initiation or subsequent development.

Cuttings showed higher mortality than seedlings up to 20 months after planting though, for both plant types, survival was similar to that reported in previous research on enrichment-planted and naturally-recruited dipterocarp seedlings. Relative growth rates were higher in cuttings than seedlings. Cuttings had a lower root:shoot ratio at planting, and lower above- and below-ground biomass, but after 20 months these values had converged towards those of seedlings. After eight years cuttings and seedlings of *D. lanceolata* had similar above- and below-ground biomass. Cuttings tended to have a higher root:shoot ratio but there were no differences in rooting depth or root distribution down the soil profile. Cuttings produced a 'pseudo-taproot' of similar form and extent to the taproot produced by seedlings.

In conclusion, the propagation of dipterocarps by cuttings could provide a viable alternative for the large-scale production of planting material. Cuttings showed similar development to seedlings after planting and it can be reported with some confidence that the root systems of dipterocarp cuttings would likely be capable of supporting the tree to maturity.

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ACRONYMS & ABREVIATIONS

FACE – Forests Absorbing Carbon dioxide Emissions (Foundation)

INFAPRO – Innoprise-FACE Foundation Rainforest Rehabilitation Project

INIKEA – Innoprise-IKEA Rainforest Rehabilitation Project

SEARRP – (The Royal Society) South East Asia Rainforest Research Programme

YSFMA – Yayasan Sabah Forest Management Area

DVFC – Danum Valley Field Centre

DVCA – Danum Valley Conservation Area

DL – *Dryobalanops lanceolata*

PM – *Parashorea malaanonan*

SL – *Shorea leprosula*

ha – Hectares

DBH – Diameter at Breast Height

GLM – Generalised Linear Model

LM – Linear Model

LME – Linear Mixed-Effects model

ANOVA – Analysis of Variance

ANODEV – Analysis of Deviance

LOWESS – Locally Weighted Regression

AIC – Akaike Information Criterion

ENSO – El Niño Southern Oscillation

rgr – Relative growth rate

IBA – Indole-Butyric Acid

NAA – Napthalene Acetic Acid

CHAPTER 1

1. INTRODUCTION

This research was based at the Danum Valley Field Centre and Innoprise-FACE Foundation Rainforest Rehabilitation Project in Sabah, Malaysia and was part of the Royal Society's South East Asia Rainforest Research Programme. The overall research objectives were to answer specific questions relating to the propagation of dipterocarps by cuttings and to compare the establishment and development of dipterocarp cuttings and seedlings planted as part of a large-scale rainforest rehabilitation project. This chapter sets the project in context by describing the:

i. Basic ecology and ecophysiology of the Dipterocarpaceae
ii. Importance, current status and threats to rainforests globally, with particular reference to SE Asia and Borneo
iii. Rehabilitation of degraded lowland dipterocarp forest by enrichment planting
iv. Role of vegetative propagation in supplying dipterocarp planting material
v. Project rationale
vi. Research aims and objectives

Figure 1.1: *The primary lowland rainforest of the Danum Valley Conservation Area, Sabah*

1.1 The family Dipterocarpaceae

The Dipterocarpaceae is a family of mostly evergreen trees found only in the tropics. The family is represented in South America (by two species in Guyana), equatorial Africa, the Indian sub-continent and China. However, by far the greatest diversity of dipterocarps is found in SE Asia, particularly the floristic region known as Malesia. Their range extends from Sumatra and Malaysia in the west (including all of Indonesia) to the Philippines in the north and east to Papua New Guinea. Very few dipterocarps are found east of the Wallace Line and only two species are shared between Borneo and Sulawesi. None occur as far east as the Bismark Archipeleago or as far south as Australia. The centre of diversity is the island of Borneo. (Symington *et al.*, 2004; Whitmore, 1984; Ashton, 1982, Maguire & Ashton, 1977).

Figure 1.2: *The distinctive buttresses of a mature dipterocarp*

Dipterocarps dominate the lowland forests of SE Asia and in the richest stands, which are found on Borneo, the family accounts for up to 10% (by abundance) of all tree species and over 80% of upper canopy trees (Whitmore, 1990). It is this stand

density combined with the pre-eminence of the dipterocarps in the international hardwood trade that make the lowland rainforests of SE Asia the most valuable timber forests in the tropics (FAO, 2001).

The larger dipterocarps can reach heights well in excess of 80 m and are often distinctively buttressed (Meijer & Wood, 1964; Figures 1.1, 1.2, 1.3). Distribution is generally limited to areas with annual rainfall greater than *c.* 1,000 mm and to elevations up to *c.* 1,000 m, although a handful of species persist to 1,500 m (Ashton, 1982). Recent research using radiocarbon dating techniques indicates that dipterocarps reach an age of at least 350 years (Robertson *et al.*, 2004). The SE Asian dipterocarps are monophyletic (Kajita *et al.*, 1998).

Figure 1.3: *Mature dipterocarps showing the characteristic form & great height of many members of the family. For scale note the person at the bottom of the frame (circled)*

One of the most striking and distinctive characteristics of the Malesian Dipterocarpaceae is their habit of synchronous or mass flowering followed by mast fruiting (Ashton *et al.*, 1988; Figures 1.4, 1.8). This occurs on a supra-annual cycle

and appears to be correlated with El Niño Southern Oscillation (ENSO) events. Although the precise flowering cue has yet to be conclusively established, low night temperatures associated with the onset of an ENSO event appears to be the most likely trigger (Ashton *et al.*, 1988; LaFrankie & Chan, 1991; Appanah, 1993).

Figure 1.4: *'Seed rain' during dipterocarp mast fruiting at Danum Valley, Sabah. Note the distinctive winged seed (Picture courtesy of Konstans Wells)*

The spatial extent of mass flowering is highly variable and can range from as limited an area as a single valley or series of hill-tops to general flowering covering almost the entire Malesian region (Wood, 1956; Appanah, 1993). The mass flowering of dipterocarps is perhaps the most spectacular event in tropical biology; at the peak of flowering each individual dipterocarp tree may present over a million heavily fragrant blossoms in a single night – multiplied over hundreds of thousands, even millions, of hectares of forest then this truly represents one of the world's great natural phenomena (Ashton *et al.*, 1988). Mass flowering occurs nowhere else in the tropics

and most likely evolved as a mechanism to satiate seed predators (Janzen, 1974; Ashton *et al.,* 1988; Sakai, 2002). It has also been suggested that synchronous flowering may have developed as a response to the more favourable light conditions for seedling establishment (resulting from increased mortality of canopy trees and general defoliation) which follow ENSO-related droughts (Williamson & Ickes, 2002).

The SE Asian dipterocarps are insect-pollinated, obligate out-crossers. Flowers are bisexual, generally small and star-shaped and are usually white or cream in colour. They have numerous perianths in which the sepals spiral, overlap and often elongate to form distinctive 'wings' as the seed matures (Figure 1.4). In spite of their often impressively winged fruit, dipterocarps disperse rather poorly by wind, which is seldom strong in the SE Asian tropics, and gyration alone is probably the main mechanism of dispersal (Ashton *et al.*, 1988). The role of secondary dispersal agents is almost certainly minor; rats, squirrels and other small mammals are known to scatter-hoard dipterocarp fruits, though probably not far from the parent tree (Curran *et al.*, 2000; Wells & Bagchi, 2005). Dipterocarp seeds are recalcitrant and germinate within days of release from the parent tree (Ashton, 1988; Curran *et al.*, 1999).

Following mast fruiting, dipterocarp seedlings quite literally carpet the forest and are highly adapted to survival in the dark, cool conditions on the forest floor (Ashton, 1988; Zipperlen & Press, 1996; Press *et al.*, 1996; Whitmore & Brown, 1996). They allocate considerable resources to defence against herbivory and are able to persist for long periods, often through inter-masting years, until gap formation occurs and light levels increase (Blundell & Peart, 2001; Kurokawa *et al.*, 2004). Following gap formation, dipterocarp seedlings are able to re-partition resources and adjust architecture, morphology, leaf structure and various ecophysiological attributes in order to capitalise on the sudden increase in light and, as a result, maximise growth (Whitmore & Brown, 1996; Zipperlen & Press, 1996; Barker *et al.*, 1997). These regenerative strategies are well understood by foresters and are the basis of the sylvicultural systems designed for the management of Malaysia's inland forests, most

particularly the Malayan Uniform System with its emphasis on enhancing the natural regenerative capacity of dipterocarp forest (Strugnell, 1947; Walton, 1948; Wyatt-Smith, 1963; Whitmore, 1984). These characteristics have major implications for the conservation of lowland dipterocarp forests and, perhaps more importantly, the rehabilitation of forests that have been degraded through logging (Wyatt-Smith, 1963; Appanah & Weinland, 1993; Appanah, 2001).

1.2 Tropical rainforests – importance, threats & current status

The crucial role of rainforests in ecosystem function, particularly in supporting biodiversity, is becoming increasingly evident. Despite covering only 10% of the total land area, the tropical rainforests act as the Earth's primary reservoir of terrestrial biodiversity and house approximately two-thirds of all known species (Pimm *et al.*, 2001). During recent years the ecological role of the rainforests, their value to human populations and the need for co-ordinated conservation and restoration programmes, has been recognised in major international agreements including the United Nations Framework on Climate Change, the Convention on Biological Diversity and the United Nations Forum on Forests. It has been estimated that the total economic value of ecosystem services provided by rainforests (climate regulation, erosion control, nutrient cycling, production of raw materials, tourism etc) exceeds US$3.8 trillion/year at mid-1990s prices (Constanza *et al.*, 1997, Pimm, 1997). However, and despite this clear ecological importance and economic value, anthropogenic impacts have resulted in large-scale rainforest clearance and degradation in all tropical regions – and at a seemingly ever increasing rate. The full effects of this are as yet unclear but to highlight just one of many possible consequences, recent studies have indicated that forest loss is likely to have a greater impact on global biodiversity than the combined effects of climate change, nitrogen deposition, biotic exchange and increasing atmospheric CO_2 concentration (Sala *et al.*, 2000).

In 1997 the humid tropical forests covered some 1,116 million ha, with the bulk accounted for by the Latin American rainforests (653 million ha). The SE Asian rainforests accounted for 270 million ha, with 193 million ha in equatorial Africa. From 1990 to 1997 the estimated area of rainforest cleared, across all tropical regions, was 4.9 (±1.3) million ha/year. This represented a deforestation rate of the order of 0.43%/year. Deforestation rates for Latin America and equatorial Africa were 0.33 and 0.36%/year respectively. In SE Asia, however, the rate was roughly double this at 0.71%/year, equating to the annual loss of 2 million ha of rainforest (Mayaux *et al.*, 2005). The rate of forest loss in SE Asia shows no signs of slowing. From 2000 to 2005 the annual loss of forest in SE Asia was 0.98% as compared to the global mean of 0.18%/year (FAO, 2005).

1.3 The SE Asian situation

Due largely to a unique and complex geological history, including the presence of numerous oceanic islands and a stable climate with abundant rainfall, the forests of the SE Asian region are extraordinarily species-rich and show a high degree of endemism (Sodhi *et al.*, 2004). Undoubtedly the rainforests of SE Asia are the most complex, species-rich terrestrial ecosystems which ever existed and, of the 25 global biodiversity 'hotspots', 4 overlap in the SE Asian tropics (Whitmore, 1984; Myers *et al.*, 2000). The evolution of the unique reproductive strategy of the dipterocarps also exerts a strong influence on the ecology and diversity of the SE Asian rainforests and has important implications for their recovery after disturbance (Whitmore, 1984; Ashton *et al.*, 1988; Appanah, 1999; Curran *et al.*, 1999; Curran *et al.*, 2004).

The main drivers of forest loss, degradation and fragmentation in SE Asia are conversion to plantation, selective logging and shifting cultivation. As recently as the early 1800s almost the entire region was under natural forest cover, with any clearance associated with population centres and small-scale subsistence agriculture. Larger-scale deforestation began only around 200 years ago as a result

of the increasing regional and global demand for rice (*Oryza sativa*), although from the early 1900s substantial areas of forest were cleared to make way for perennial export crops including rubber (*Hevea brasiliensis*), coconut (*Cocos nucifera*), cocoa (*Theobroma cacao*) and, more recently, oil palm (*Elaeis guineensis*) (Sodhi *et al.*, 2004). Until the 1950s the timber industry was relatively limited in extent and capacity. However, following widespread mechanisation after WWII, combined with a hugely increased demand for SE Asian timber, the rate of exploitation of the forests increased exponentially. Timbers from the SE Asian forests are particularly sought after in the international market; the dipterocarps, in particular, have uniformly excellent properties for construction and plywood production, and logs from the numerous species of dipterocarp can be grouped into just a handful of end-use classes allowing standardised processing and marketing (Whitmore, 1984; Whitmore, 1998). These properties, and the richness of dipterocarp stands, have given rise to the industrial-scale logging and timber processing operations which have dominated forestry in SE Asia for the past 50 years.

Today, at the beginning of the 21st century, the rainforests of SE Asia are in a generally dismal condition. The forests of north-east India have been extensively exploited for timber, degraded through shifting cultivation and cleared for large-scale agricultural plantations. Selective logging and clear felling have led to the loss of much of the lowland forests of Burma, Laos and Vietnam and the impact of shifting cultivation is also believed to be increasing in these countries, especially Burma. The Indonesian forests have been exceptionally hard-hit and show probably the highest recent deforestation rates of any tropical nation. On the island of Sumatra which, second to Borneo, once housed the greatest expanse of dipterocarp forest, the lowland rainforests have virtually disappeared under the pressure of logging and conversion to plantation. A similar situation is now developing in Kalimantan. The Philippines, which until the early 1980s probably exported more timber than any other single nation in the tropics, has been virtually denuded with the only significant areas

of forest remaining in the far north and on small islands in the Mindanao region (reviewed by Mayaux *et al.*, 2005; FAO, 2001; Sodhi *et al.*, 2004; Whitmore, 1984). Currently less than half of the original SE Asian forests remain and it has been estimated that by 2100 SE Asia will have lost 75% of its original forest cover (FAO, 2001; Sodhi *et al.*, 2004).

Figure 1.5: *Huge dipterocarp logs being trucked from the rainforests of eastern Sabah*

Although the number of species extinctions in SE Asia is not currently alarming, this situation is unlikely to remain (IUCN, 2003). Recent work based on the island of Singapore, which is the most deforested nation in SE Asia having lost 95% of its original forest cover in less than 200 years, indicates that future biodiversity losses in the wider region will be catastrophic. By extrapolating from the observed effects of deforestation on Singapore, and inferred extinction rates over the region, it has been estimated that up to 42% of species in SE Asia will be lost during the next century. Due to the high levels of endemism at least half of these losses would represent global extinctions (Brook *et al.*, 2003; Sodhi *et al.*, 2004).

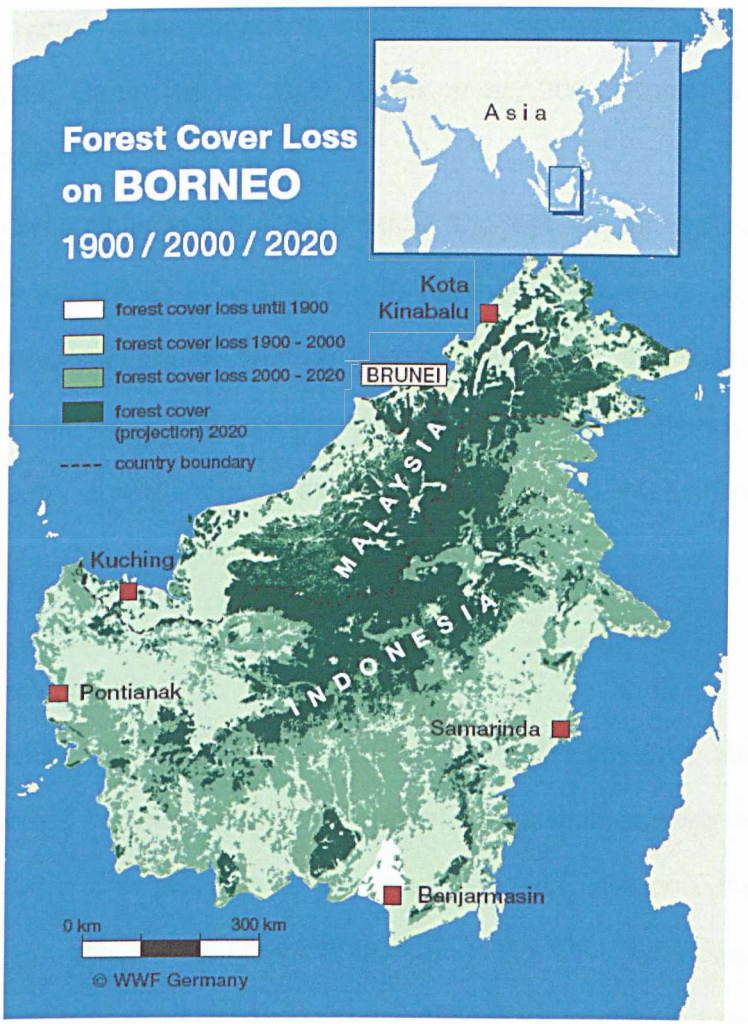
1.4 The rainforests of Borneo

Borneo is one of the world's largest islands with a total land area of *c.* 745,000 km^2 and is shared by 3 states: Indonesia, Malaysia and Brunei. The Indonesian part of Borneo, Kalimantan, is by far the largest and covers *c.* 540,000 km^2. The Malaysian states of Sabah (*c.* 74,000 km^2) and Sarawak (*c.* 125,000 km^2) occupy the north-east and northern parts of the island respectively with the tiny sultanate of Brunei (*c.* 6,000 km^2) lying between Sabah and Sarawak on the north-west coast. Borneo straddles the equator and, lying below the monsoon belt, has a relatively equitable climate (Walsh & Newbery, 1999). Until the mid-20th century the island was almost completely forest-covered including extensive lowland rainforests in Sabah, Sarawak and north-east and south-west Kalimantan. Upland, hill and sub-montane forests dominate in the mountainous spine running from central-west Kalimantan though to Mount Kinabalu in Sabah. Much of southern and western Kalimantan is covered by swamp forests (MacKinnon *et al.*, 1997).

The Dipterocarpaceae reach their zenith on Borneo, both in terms of diversity and stature. The family comprises 269 species of 13 genera (Symington *et al.*, 2004) and they dominate the upper canopy layer of the lowland and hill forests to a degree not seen elsewhere in SE Asia (Whitmore, 1998). The lowland forests of Borneo are the tallest found in the humid tropics with an upper canopy in the 60 - 70 m range and emergent trees reaching heights of over 80 m in ideal conditions (Meijer & Wood, 1964). It is this stand density, combined with the enormous size of the individual trees, which made the lowland dipterocarp forests of Borneo the most valuable timberlands in the tropics; from 1975 to 1995 the volume of timber exported solely from Borneo exceeded all timber exports from equatorial Africa and Latin America combined (FAO, 2001). During the 'timber boom' of the 1970s and 1980s, when most of the prime timber forests of Sabah and Sarawak were initially logged, harvesting volumes in excess of 120 m^3 ha were not uncommon, with over 160 m^3 ha felled in the richest stands (Putz *et al.*, 2001; Moura-Costa & Karolus, 1992). Even in the face

of a dwindling resource base and, as recently as 2004, Sabah alone produced 5.4 million m^3 of timber from its natural forests (Sabah Forest Department, 2005). However, almost all the accessible lowlands of Borneo have now been heavily logged, usually more than once, and timber production has long since shifted to the upland forests (Appanah, 2001). Protected areas have not escaped this general degradation and recent research has shown that Kalimantan's protected lowland forests declined by over 50% from 1985 to 2001, mainly as a result of illegal logging and shifting cultivation (Curran *et al.*, 2004). Projections for future forest conversion on Borneo are alarming and predict almost complete loss of the island's lowland forests by 2020 (Figure 1.6; Rautner *et al.*, 2005).

Figure 1.6: *Map showing forest cover and loss from 1900 to 2000 and projected to 2020 (courtesy of WWF-Germany)*



Perhaps more ominously, it appears that ENSO events, which in many respects are responsible for driving the ecology of the Bornean rainforests, are becoming increasingly frequent and severe. The most immediate and dramatic impact has been fire and during the ENSO-associated droughts of 1982-83 and 1997-98 well over 5 million ha^{-1} of forests on Borneo burned (Leighton & Wirawan, 1986; Sodhi *et al.*, 2004; Mayaux *et al.*, 2005). However, the more insidious and potentially serious long-term threat is to the regenerative system on which dipterocarp forests depend. Instead of acting as the 'engine' of dipterocarp regeneration, ENSO related droughts now appear to be disrupting the recruitment and survival of seedlings, even in large and well-buffered primary forest protected areas. It is possible, perhaps even likely, that mast fruiting is simply no longer functioning; dipterocarps in degraded forests may not be producing seed in sufficient quantity to satiate predators and, where seedlings do recruit, they appear to succumb quickly to the effects of drought (Whitmore, 1998; Curran *et al.*, 1999; Brook *et al.*, 2003; Kohler & Huth, 2004; Curran *et al.*, 2004).

If the factors contributing to forest degradation and loss are indeed interacting with increasingly severe ENSO events, to the detriment of dipterocarp recruitment, the implications are potentially disastrous. It could be argued that the rainforests of Borneo, at least in their current dipterocarp-dominated form, are already persisting as a 'living mortuary' and without some form of restorative intervention have little prospect of continuity beyond the current generation.

1.5 Forest rehabilitation

Forest rehabilitation can be defined as a treatment to "*re-establish the productivity and some, but not necessarily all, of the plant and animal species thought to be originally present at the site. For ecological or economic reasons, the new forest might also include species not originally present at the site. The protective function and many of the ecological services of the original forest may be re-established*"

(Lamb, 2001 cited in Evans & Turnbull, 2004). Restoration, by contrast, aims to return the forest to near original condition. Given the level of degradation of much of the remaining SE Asian forests, and the extreme difficulty, cost and time that would be required to re-establish systems even approaching the complexity and richness of a primary lowland rainforest, rehabilitation by enrichment planting – rather than full-scale restoration – is likely to be the favoured option in SE Asia (Evans & Turnbull, 2004). In Malaysia, had the Malayan Uniform System (Strugnell, 1947; Walton, 1948) been fully implemented, with its emphasis on protecting and tending natural regeneration, then today there would unlikely be any requirement for the rehabilitation of the countries' lowland forests. However, this system was never followed through a proper rotation anywhere in Malaysia. Moreover, and as a result of the extensive clearance and degradation of the lowland forests of Malaysia over the past 40 years, the Malayan Uniform System "*found itself without the forest for which it was principally designed*" (Appanah & Weinland, 1993). As Appanah and Weinland (1993) adroitly state: "*The 'cure' had been found but the 'patients' were gone*". The likely need for the rehabilitation of Malaysia's forests was identified as long ago as the 1960s when Wyatt-Smith (1963) published his standard work on the silviculture of Malaysia's inland forests in which he devotes an entire chapter to enrichment planting. However, it was many years before any large-scale enrichment planting programmes were instituted either in Malaysia or elsewhere in the tropics.

Over recent years there has been considerable interest in rainforest rehabilitation by enrichment planting with indigenous tree species in both the old world (e.g. Pinso & Moura Costa, 1993; Schulze *et al.*, 1994; Ådjers *et al.*, 1995; Korpelainen *et al.*, 1995; Ashton *et al.*, 2001) and new world tropics (e.g. Montagnini *et al.*, 1997; Ricker *et al.*, 1999; Peña-Claros *et al.*, 2002; Martínez-Garza & Howe, 2003; Griscom *et al.*, 2005). In the Malaysian and SE Asian context the rehabilitation of lowland forest essentially involves a combination of release cutting (usually in lightly disturbed areas) to reduce competition on naturally regenerating dipterocarp seedlings and

enrichment planting with dipterocarps and other canopy species, either in lines or patches, in more degraded areas where natural regeneration is lacking (Ådjers *et al.*, 1995; Moura-Costa *et al.*, 1996; Evans & Turnbull, 2004). In highly degraded areas (e.g. old skidding tracks or log landings), where no forest canopy remains and/or where the topsoil may be extremely compacted, it would probably be necessary to carry out soil ripping treatments and establish a cover of fast-growing indigenous pioneers, or even exotic species such as *Acacia mangium*, prior to underplanting with dipterocarps (Pinard *et al.*, 1992; Nussbaum *et al.*, 1995). However, due to the cost and time involved, this rarely occurs in practice and highly degraded areas are often abandoned to *Imperata* grassland (Figure 1.7).

Figure 1.7: *Degraded rainforest approximately 20 years after logging, showing distinctive pioneer-dominated canopy & large open area colonised by grass & other herbaceous species*

Two of SE Asia's largest rehabilitation projects, covering a combined total of almost 50,000 ha, are located in Sabah and are managed by Yayasan Sabah (the Innoprise-FACE (INFAPRO) and Innoprise-IKEA (INIKEA) rainforest rehabilitation projects). Given the scale of many rehabilitation programmes, the number of seedlings required

for enrichment planting can be very large. At present almost all planting material is derived from seed-based systems but this can present huge problems due to the highly erratic nature of dipterocarp reproduction, as earlier described, and hence the lack of seed availability during inter-masting years. This not only has implications for the production of sufficient quantities of seedlings but also the number of species available for replanting. Many rehabilitation programmes would ideally plant with a broadly similar complement of dipterocarp species to that which occurred naturally in a given area prior to logging. However, other than in years immediately following a mast fruiting, this is rarely possible and planting frequently relies on sporadic seed production among the limited number of dipterocarp species which flower in the intervening periods between mast events. For example, during the first few years of the INFAPRO project in Sabah, several thousand hectares of forest were enrichment planted using only a handful of dipterocarp species (mostly *Dryobalanops lanceolata* and *Shorea leprosula*) out of the possible 30 or more species abundant in the project area (Yap, 2005 *pers. comm.*). The long-term impacts of reducing dipterocarp diversity in enrichment-planted areas, particularly on ecosystem function and overall biodiversity, is far from clear and is the subject of ongoing research at Danum Valley (Sherer-Lorenzen *et al.*, 2005)

In order to provide large-scale enrichment planting programmes with a regular supply of dipterocarp planting material, over a wide species range, it is necessary to explore alternative, vegetative-based, production methods.

1.6 Vegetative propagation

Vegetative propagation, in its various forms, has been used by horticulturalists and foresters for thousands of years to propagate both crop and ornamental plants. Ancient Chinese literature indicates that *Cunninghamia lanceolata*, one of the most important timber species in China, has been propagated by cuttings for over 1,000 years (Ritchie, 1994, Minghe & Ritchie, 1999). In Japan vegetative propagation has

been used with the indigenous conifer *Cryptomeria japonica* for *c.* 500 years and, as long ago as the 1600s, Japanese horticulturalists had published detailed technical manuals describing propagation methods for this species (Ohba, 1993). In Europe, the Romans were propagating English elm (*Ulmus procera*) by cuttings (over 2,000 years ago) for the purposes of producing material for training grape vines (Gil *et al.*, 2004).

Vegetative propagation is most often used as a means of mass multiplication and is especially useful in cases where seed is either problematic to obtain, difficult to germinate or recalcitrant and impossible to store (Tompsett, 1987; Itoh *et al.*, 2002). Vegetative propagation also plays an important role in the production of clonal material from plants that have been genetically improved through breeding or selection programmes (Hartmann *et al.*, 2002; Evans & Turnbull, 2004). More recently various methods of vegetative propagation have been used in *ex-situ* conservation programmes to increase numbers in species that are critically endangered in their natural habitats. For example, vegetative propagation by stem cuttings has been successfully used to supplement a tiny population of the recently-discovered Wollemi pine (*Wollemia nobilis*) in south-eastern Australia (Pohio *et al.*, 2005).

There are many well established methods of vegetative propagation including grafting, budding, division, layering and root or stem cuttings. More recently, these have been supplemented by the laboratory-based micro-propagation techniques of somatic embryogenesis, synthetic seed, cell and tissue culture and micro cuttings (comprehensively reviewed in Hartmann *et al.*, 2002). These techniques have all found use in the humid tropics but by far the most important propagation method for the large-scale production of tropical timber and other forestry species is stem cuttings (Evans, 1999; Evans & Turnbull, 2004). Propagation by cuttings is well understood, is relatively easy and inexpensive to apply and, in respect to rainforest rehabilitation projects which often operate in remote locations and within limited

budgets, the great advantage of using cuttings is that sophisticated propagation facilities or a regular power supply are not prerequisites and several simple, low-tech propagation methods have been developed with these situations in mind. (e.g. Leakey & Longmann, 1988; Newton & Jones, 1993[a,b]; Kantarli, 1993[a,b]; Leakey & Newton, 1994; Pollisco, 1994[a,b]).

Although propagation by stem cuttings is an established technique, there are a number of difficulties which must be recognised and addressed if the system is to be implemented successfully, especially with regard to dipterocarp enrichment planting programmes:

1.6.1 *Stockplant management*

Cuttings of most tree species will only root successfully if taken from physiologically juvenile parent material. Cuttings taken from physiologically mature plants are rarely viable, at least not without the application of time consuming pre-treatments such as whole-plant etiolation, stem banding or girdling (e.g. Hare, 1977; Maynard & Basuk, 1985, 1987; Howard & Ridout, 1992; Hartmann *et al.*, 2002).

To provide a continuous supply of readily available cuttings it is necessary to maintain parent stockplants in a juvenile state and in a form from which cuttings can easily be taken. This is often achieved by managing stockplants in hard-pruned (coppiced) hedge-orchards (e.g. Howard *et al.*, 1985; Hartmann *et al.*, 2002). However, the cost of maintaining a hedge-orchard and the area of land it requires are often major disincentives to their establishment (Evans & Turnbull, 2004). Moreover, hedging techniques can only be applied effectively to species which have the ability to coppice. In dipterocarps, for example, not only is the capacity for basal regeneration limited, the few orthotropic shoots which arise from dipterocarps managed as hedge-orchards often have extremely long internodes and are wholly unsuitable as cutting material (*personal observation*).

An alternative to hedging for the management of stockplants, which has been used with species that coppice poorly (including the dipterocarps), involves bending the main branches and staking or tying them into position (Leakey, 1983; Moura-Costa, 1993, 1994; Smits, 1992; Smits *et al.,* 1994). This breaks apical dominance and gives rise to a flush of orthotropic shoots along the bent branch. However, it is a tedious and time consuming technique, difficult to apply on a large scale and, in the case of the dipterocarps (and as with dipterocarp hedge-orchards), the shoots which arise often have an architecture and internodal length which render them unsuitable as cutting material (*personal observation*).

Another factor which can seriously limit the productive capacity of stockplants is plagiotropy (Evans & Turnbull, 2004). In a number of tree species, including the dipterocarps (Moura-Costa 1993, *personal observation*) and several conifers such as *Podocarpus falcatus* (Negash, 2003) and *Pinus abies* (Dekker-Robertson & Kleinschmit, 1991) cuttings taken from plagiotropic shoots often continue to grow plagiotropically long after rooting. In some species (e.g. Pinus abies) serial propagation has been used to overcome plagiotropism (Dekker-Robertson & Kleinschmit, 1991) but this has never been attempted with the dipterocarps.

1.6.2 *Propagation environment*

The role of the propagation environment is to:

i) provide conditions of low evaporative demand which allow cuttings to survive the immediate post-severance 'shock'

ii) maintain physiological processes, including (potentially) photosynthesis, at levels necessary for root initiation and subsequent development (Hartmann *et al.*, 2002).

Although the optimal environmental conditions necessary for successful propagation are known for many commercially important species, for plants which are not usually

propagated by cuttings these have often not been established. This is the case for many dipterocarp species.

1.6.3 *Rooting*

Not all plants root easily from stem cuttings and a number of important tropical timber species including most of the dipterocarps, several eucalypts, *Acacia* and *Pinus* species, have been found shy to root (Appanah & Weinland, 1993; Hartmann *et al.*, 2002; Evans & Turnbull, 2004). There are a number of physical (e.g. wounding, stem blanching, girdling) and hormonal treatments which can be applied to cuttings to improve rooting, and some of these have been used successfully with tropical hardwoods (Hartmann *et al.*, 2002), but responses are often species-specific (sometimes even genotype specific) and treatment regimes have yet to be established for many species. Again, this is especially true of species which are normally propagated by seed rather than cuttings.

1.6.4 *Long-term growth*

For a propagation method to have general application, it must not have a detrimental effect on the growth characteristics of the resulting plant. However, for many species, especially in the humid tropics, the long-term effects of propagation by vegetative means are unknown and few studies have compared the development of cutting and seedling propagated plants. The relatively limited body of research which exists for timber plantation species (temperate or tropical) indicates that cutting and seedling root systems can show significant architectural and structural differences, particularly in terms of rooting depth, and that cuttings of some species can be more prone than seedlings to water stress, root competition, wind-throw and toppling (e.g. Sasse & Sands, 1996,1997; Mulatya *et al.*, 2002). Cuttings of some tree species (e.g. *Eucalyptus globulus*) have also been shown to have a lower root:shoot ratio than seedlings (Sasse & Sands, 1997). Reduced root:shoot ratios have been associated

by several authors with decreased stability of juvenile trees (Coutts, 1983; Nielsen, 1992; Evans & Turnbull, 2004). It is not known if or how the root systems of dipterocarp cuttings and seedlings differ.

1.7 Propagating dipterocarps by cuttings

Vegetative propagation by stem cuttings would potentially be an ideal method for the production of dipterocarp planting material (Smits, 1985, 1986; Appanah & Weinland, 1993; Aminah 1996, 1999; Dick & Aminah, 1994; Evans & Turnbull, 2004). It could, at least in theory, be implemented on a large scale and would allow production across a wide species range independent of major flowering events (Appanah & Cossalter, 1994). In view of the degradation of the dipterocarp forests in recent decades, vegetative propagation could also play an important role in the *ex-situ* conservation of particularly rare or threatened dipterocarp species.

The first attempts to propagate dipterocarps by stem cuttings were made by the Forest Department of Malaya at Kepong during the 1930s (at what is now the Forest Research Institute Malaysia - FRIM), and in Java, Indonesia during the 1950s (Malayan Forestry Department, 1937; Ardikiosoma & Noekamal, 1955). However, the main body of work in this field was conducted from the early 1980s to the mid 1990s, mostly in Malaysia, Indonesia and Thailand, and generally focused on cutting type and source, stock plant management, cutting treatment and the propagation environment (reviewed by Dick & Aminah, 1994). However, despite high expectations, success beyond the research nursery has been extremely limited (Appanah & Weinland, 1993; Mok, 1993; Appanah & Cossalter, 1994). In 1993 Dr. Appanah, then Head of the Natural Forests Division of FRIM, recorded the following opinion (Appanah & Weinland, 1993):

"*It seems like a good number of timber trees in Peninsular Malaysia can be vegetatively propagated in the laboratory, albeit with some difficulty. But mass propagation on an operational scale has yet to be tried out for any of these*

species.....In the 1950s vegetative propagation held no promise for raising plants of Malayan timber species. The situation is not any more promising today. For the near future, little possibility for vegetative propagation is seen on an operational scale for many of the important timber species in the region".

To date, few (if any) large-scale forest rehabilitation programmes in SE Asia have produced significant quantities of dipterocarp planting material by vegetative means (*Personal observation;* Appanah, 1999 *pers. comm.*). In Sabah, the INFAPRO and INIKEA projects are not currently producing dipterocarps by cuttings – both projects have, however, stated that they aim to develop vegetative propagation systems to supplement seedling supplies during periods of low seed availability.

1.8 Project rationale

There are a number of reasons for the apparent lack of interest and success in the large scale vegetative propagation of dipterocarps by cuttings; stockplants have been found difficult to manage and have limited capacity, dipterocarp cuttings appear to be relatively shy-to-root and nursery procedures have not been perfected across a wide species range. More importantly, there is a paucity of information on the post-planting performance of dipterocarp cuttings, particularly the development and characteristics of the root system. The relevant literature is reviewed and discussed in the experimental chapters (3, 4, 5 and 6) and in the General Discussion (Chapter 7).

1.9 Research aims & objectives

In order to address at least the most important of these issues, the project focused on three key areas:

i. Propagation phase – up to 8 weeks after the cutting is taken
ii. Establishment phase – up to 20 months after planting
iii. Post-establishment phase – up to 8 years after planting

The specific research questions were:

i. Does the light environment during propagation have any effect on cutting survival, rooting percentage or root development?

ii. Do exogenously applied hormones have any effect on cutting survival or rooting percentage?

iii. Could hormone treatments applied at the time of propagation have longer term effects on cuttings after planting?

iv. Are there differences between the survival, growth rate and development of dipterocarp cuttings and seedlings up to 20 months after planting?

v. Do dipterocarp cuttings and seedlings differ up to 8 years after planting? In particular, do dipterocarp cuttings develop a tap-root or other roots with a similar supportive function?

And as an aside:

i. Could overgrown nursery seedlings provide a viable source of cutting material?

The applied objectives of the research were to:

i. Improve propagation methods for dipterocarp cuttings

ii. Assess the longer-term growth and development of dipterocarp cuttings

iii. Establish whether cuttings could provide a viable alternative to seedlings as planting material for large-scale enrichment planting

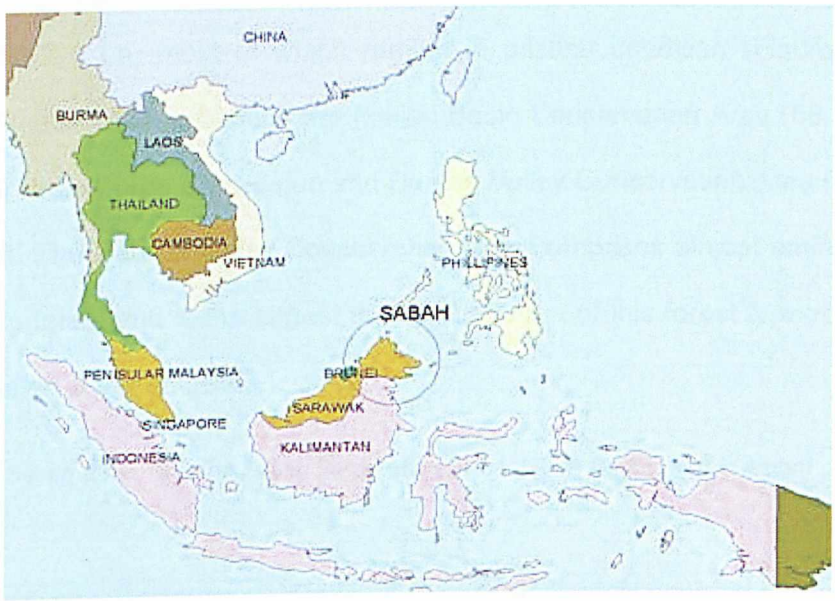
Figure 1.8: *Primary lowland rainforest at Danum Valley during a mast fruiting event*

CHAPTER 2

2. SITE DESCRIPTION & GENERAL METHODS

This project was based in the Malaysian state of Sabah, which occupies the northern portion of the island of Borneo (Figure 2.1). The study sites where located in a large forest concession managed by Yayasan Sabah.

Figure 2.1: *SE Asia – Sabah, part of the island of Borneo, is circled*



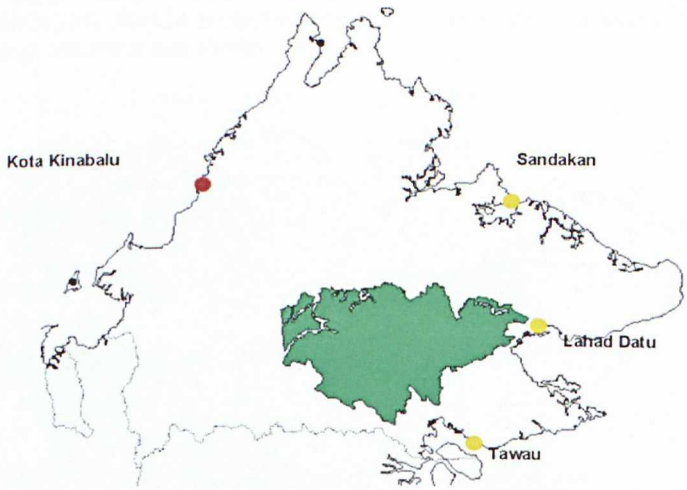
2.1 The Yayasan Sabah Forest Management Area

Yayasan Sabah ("The Sabah Foundation") was established in 1966 with the aim of improving the lives of Malaysians living in Sabah by the provision of welfare, medical and educational services. In order to provide a sustainable source of revenue to fund these activities Yayasan Sabah was granted management rights over a huge forest concession in south-eastern Sabah with a total area of over 1 million hectares (10,000 km^2). The concession is known as the Yayasan Sabah Forest Management Area (YSFMA) and is managed on behalf of Yayasan Sabah by its wholly-owned commercial subsidiary Innoprise Corporation (Figure 2.3). The YSFMA occupies

almost 14% of the entire land area of Sabah (Figure 2.2) and is one of the largest forest concessions in SE Asia (Marsh & Greer, 1992).

The commercially managed natural forests of the YSFMA, which have been selectively harvested from the early 1970s onwards, total approximately 750,000 ha. The concession includes approximately 60,000 ha of agricultural and exotic timber plantations with a further 80,000 ha earmarked for conversion to oil palm plantation before 2010 (Marsh & Greer, 1992; Pinso, *pers. com*). The YSFMA also includes a number of fully-protected conservation areas and virgin jungle reserves covering almost 150,000 ha, most of which remain in pristine condition (Figure 2.4). The largest of these protected areas are Maliau Basin Conservation Area (58,840 ha) on the western side of the concession and Danum Valley Conservation Area (43,800 ha) in the east. The Danum Valley Conservation Area comprises almost entirely lowland dipterocarp forest and is the largest undisturbed area of this forest type remaining in Sabah (Marsh & Greer, 1992).

Figure 2.2: *Sabah & the Yayasan Sabah Forest Management Area (highlighted in green)*

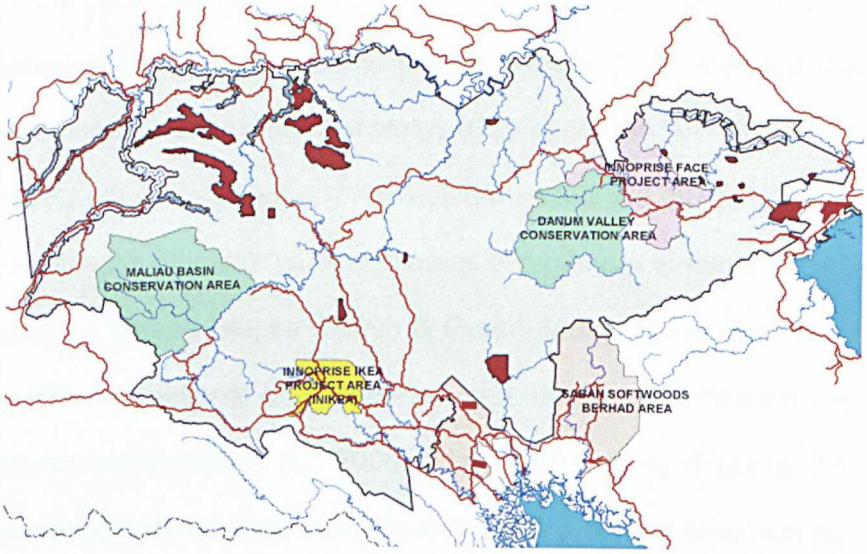


In 1985 Yayasan Sabah and a number of local and international partners including the Royal Society of London established the Danum Valley Field Centre (Figure 2.3). This is situated on the eastern border of the Conservation Area and acts as a base

for scientific research and environmental education (Marsh, 1995). Danum Valley is now among the best studied sites anywhere in the old-world tropics.

Figure 2.3: *The Danum Valley Field Centre, Sabah, Malaysia*

Figure 2.4: *The Yayasan Sabah Forest Management Area. The INFAPRO project (to the east of Danum Valley) shown in pink, INIKEA project in yellow, the Danum Valley & Maliau Basin Conservation Areas in green. Other protected areas shown in red*



Embedded within the YSFMA are two large-scale forest rehabilitation projects. In the south-west is the Innoprise-IKEA forest rehabilitation project (INIKEA), which is

financed by the furniture group IKEA, and covers an area of approximately 14,000 ha. The aim of INIKEA is to increase biodiversity in the heavily logged and fire-damaged forest of the project area (Sinun, 2005 *pers. comm.*). Lying on the eastern flank of the Danum Valley Conservation Area is the 30,000 ha Innoprise-FACE Foundation Rainforest Rehabilitation Project (INFAPRO), of which this research was part.

2.2 The Innoprise-FACE Foundation Rainforest Rehabilitation Project

INFAPRO was established in 1992 as a joint venture between Innoprise Corporation and FACE Foundation (Forests Absorbing CO_2 Emissions) of the Netherlands. The aim of INFAPRO is to promote the regeneration of 30,000 ha of highly degraded logged forest, largely by enrichment planting, and thereby to increase capacity for CO_2 sequestration (Pinso & Moura Costa, 1993). To date, over 10,000 ha of forest has been enrichment planted by the INFAPRO project (Yap, 2005 *pers. comm.*). The forest of the INFAPRO area, which is part of the Ulu Segama Forest Reserve (5° 0'N, 117° 30'E), is covered by dipterocarp forest (Newbery *et al.*, 1992). The complex geology of the area has resulted in the formation of a highly heterogeneous range of soils including acrisols, cambisols and luvisols (Wright, 1975; Marsh & Greer, 1992) with a concomitantly variable nutrient status (Goh *et al.*, 1993).

The INFAPRO area was selectively harvested from the mid 1970s to the early 1990s using a combination of tractor yarding in areas of moderate terrain and cable or 'high-lead' yarding on steeper slopes (Marsh & Greer, 1992). These harvesting methods resulted in different patterns of disturbance, and usually have differing requirements for subsequent rehabilitation (Li, 2006). High-lead yarding (Figures 2.5 and 2.6) involved winching logs up or down a slope towards a central collection point around the machine itself. Forest in the immediate vicinity of the machine set-up (which may total as much as 20 ha) was often completely degraded with further severe damage extending outwards along winching 'corridors' (Marsh & Greer, 1992).

Figure 2.5: *A high-lead yarding machine. When in use the telescopic winching tower is erected*

Figure 2.6: *A high-lead site approximately 20 years after logging. The area remains dominated by herbaceous species with only minimal regeneration among pioneer or canopy species. During logging the high-lead machine would have stood at the point at which the photograph was taken*

Tractor yarding resulted in a random mosaic of damage including highly degraded areas such as skid tracks (Figure 2.7) through lightly disturbed to completely untouched forest remnants. High-lead yarding was probably the more damaging technique in its impact on vegetation but generally caused less soil compaction, erosion and nutrient leaching than tractors (Marsh & Greer, 1992; Li, 2006).

Figure 2.7: *A skid track along which logs would have been dragged by a tractor*

In lightly to moderately disturbed areas, where dipterocarp seedlings either survived the logging or recruited subsequently, rehabilitation may simply involve cutting back the competing vegetation (release cutting) which would otherwise hamper the growth of regenerating seedlings. In more degraded areas, especially where high lead machines had been deployed, it is almost always necessary to enrichment plant.

Figure 2.8: *Dipterocarp seedlings at the INFAPRO nursery*

The INFAPRO project rehabilitates between 1,000 and 2,000 ha of forest annually and, depending on the level of enrichment planting, has an annual requirement of between 100,000 and 250,000 dipterocarp seedlings (Figure 2.8). At present, these are almost all propagated from seed (Moura-Costa *et al.*, 1996; Li, 2006).

2.3 The climate of Sabah

The temperature and relative humidity of south-eastern Sabah (based on the 20 year Danum Valley records) are typical of the equatorial rainforests with mean monthly temperatures ranging less than 2°C around the annual mean of 26.7°C. Temperatures in excess of 34°C are rare, occurring only during prolonged dry periods. The highest temperature recorded at Danum Valley was 36.3°C (during the 1997-98 ENSO event) and the lowest 19.2°C. Mean relative humidity at 14.00 hours averages 72% and at 08.00 hours 94%. Mean annual rainfall (1985-2000) is 2768mm; the lowest annual rainfall of 1918mm occurred in 1997, which was an ENSO year, and the highest, 3,501mm, in 2000. Mean monthly rainfall ranges from 155mm in April to 311mm in January and tends to be highest in the transition months following the equinoxes (May-June and October-November) and also during the northerly monsoon months of December-January. Rainfall is generally lowest during March and April, which are the most drought-prone months during ENSO events, also in August and September when the south-westerly monsoon is at its height. The climate of Danum Valley is aseasonal but subject, as in 1997-98, to occasional severe droughts and is intermediate between the less drought-prone north-western Borneo and the more drought-prone east coast (Walsh & Newbery, 1999).

2.4 Species selection

Three dipterocarp species were selected for this research: *Dryobalanops lanceolata, Parashorea malaanonan* and *Shorea leprosula*. They were selected on the basis of

their suitability for enrichment planting, relative abundance, wide distribution and high value as timber species. *D. lanceolata, P. malaanonan* and *S. leprosula* are particularly common in the lowland forests of south-eastern Sabah (Meijer & Wood, 1964).

2.4.1 *Dryobalanops lanceolata* Burck

Botanical references: Burck in Ann. Jard. Bot. Buitenz. 6.244 (1887), Wyatt-Smith in Malayan Forester 18:115 (1955). Vernacular name: Kapur paji.

D. lanceolata is endemic to Borneo where it is found in all parts of the island except the far south and is the commonest of the *Dryobalanops* species found in Sabah. Its preferred habitat is lowland forest up to an elevation of approx. 700 m. It often forms gregarious stands, especially on slopes, ridges and close to streams. *D. lanceolata* is one of the largest of all the dipterocarps, reaching heights of over 80 m in ideal conditions with a dbh of up to 2 m. The crown is dense with few, irregularly spaced branches. Buttresses are few and relatively small, rarely exceeding 1 metre in height. *D. lanceolata* is one of the most important commercial species in Sabah. Its timber is of medium weight, strong and durable and is used in construction, flooring and in the manufacture of plywood (Meijer & Wood, 1964; Symington *et al.*, 2004).

D. lanceolata is a highly desirable species for enrichment planting as it is relatively fast growing, able to withstand a wide range of environmental conditions from open areas (high light, low relative humidity often with severely compacted soil) to closed canopy forest (very low light) and shows high resistance to insect herbivory (Yap, *pers. com.*).

2.4.2 Parashorea malaanonan *(Blanco) Merr.*

Botanical references: Merrill in Spec. Blanco 271 (1918) et Enum. Philip. Fl. Pl. 3:100 (1923), van Slooten in Bull. Jard. Bot. Buitenz, Ser. Iii, 8:370 (1927), Symington in

Gardens Bull. 9:334 (1938), Brown, Forest Trees of Sarawak & Brunei, 128 (1955). Vernacular name: Urat mata daun licin.

P. malaanonan is common in northern Borneo, including north-east Kalimantan, and the Philippines. It is widely distributed across a range of forest types up to an elevation of over 1,200 m and sometimes occurs in gregarious stands. It is by far the most important commercial timber species in northern Borneo. *P. malaanonan* is a large tree reaching a height of up to 70 m with a dbh of up to 2 m. The crown is very large and conically shaped with regularly arranged branches. Buttresses are large – up to 5 metres in height. *P. malaanonan* timber has a wide variety of uses and due to its attractive, pale colour is one of the most important species for the production of plywood face veneers (Meijer & Wood, 1964; Symington *et al.*, 2004).

2.4.3 *Shorea leprosula* Miq.

Botanical references: Miquel in Fl. Ind. Suppl.: 487 (1860), Foxworthy, Dipterocarpaceae of the Malay Peninsula, Malayan Forest Records, No. 10:220 (1932), Symington, Foresters' Manual of Dipterocarps: 75 (1943), Van Slooten in Bull. Bot. Gard. Buitenz. III, 18:262 (1949). Vernacular name: Seraya tembaga.

S. leprosula is distributed throughout Thailand, Peninsular Malaysia, Sumatra and Borneo. It is a common species in Sabah in lowland forests up to an elevation of *c.* 500 m. On poorly drained soils it is often the most common of the red saraya group of dipterocarps. *S. leprosula* is a large tree reaching a height of up to 70 m and dbh of 1.5 m. The crown is broad, umbrella shaped and has a distinctive coppery shading when viewed from below. Buttresses are prominent but not large. *S. leprosula* timber is relatively light and is used for construction, furniture and is an important species for use in the production of plywood core veneers (Meijer & Wood, 1964; Symington *et al.*, 2004).

S. leprosula, like *D. lanceolata*, is a useful species for enrichment planting. It is fast growing and is particularly useful for planting open areas.

2.5 Methods for vegetative propagation

The following section describes the nursery facilities used for the research, cutting source and type, propagation media and containers. Propagation methods used were largely adapted from Hartmann and colleagues (2002) and Macdonald (1986).

2.5.1 Cutting source & type

All cuttings used during this research were taken from the orthotropic shoots of overgrown nursery seedlings. It was the intention to use cutting material derived from hedge orchard stock plants, however, this was impossible due to the limited number of cuttings which could be taken even from INFAPRO's extensive hedge orchards. This issue will be addressed in detail in the General Discussion (Chapter 7).

Prior to cutting removal, seedlings from which the cuttings were to be taken were kept under a double layer of 70% shade netting for a period of 2 months. Apical cuttings were removed using secateurs (Figure 2.9) making a sloping cut just below a node to give a shoot length of between 150 and 200 mm consisting of 3 to 5 nodes.

Figure 2.9: *Taking cuttings of Dryobalanops lanceolata from overgrown nursery seedlings (cuttings being taken by Adrian Karolus)*

In cuttings of *D. lanceolata* and *S. leprosula* lower leaves were removed, retaining the top-most 2 to 3 fully expanded leaves. In *P. malaanonan*, which has relatively large leaves, 1 to 2 fully expanded leaves were retained but, where necessary, leaves were trimmed by up to 50% to reduce the risk of excessive evapotranspiration (Figure 2.10). This is an established technique in propagation by stem cuttings (Hartmann *et al.*, 2002).

Figure 2.10: *Dryobalanops lanceolata cutting after rooting (scale is a 300 mm rule)*

2.5.2 Propagation media & containers

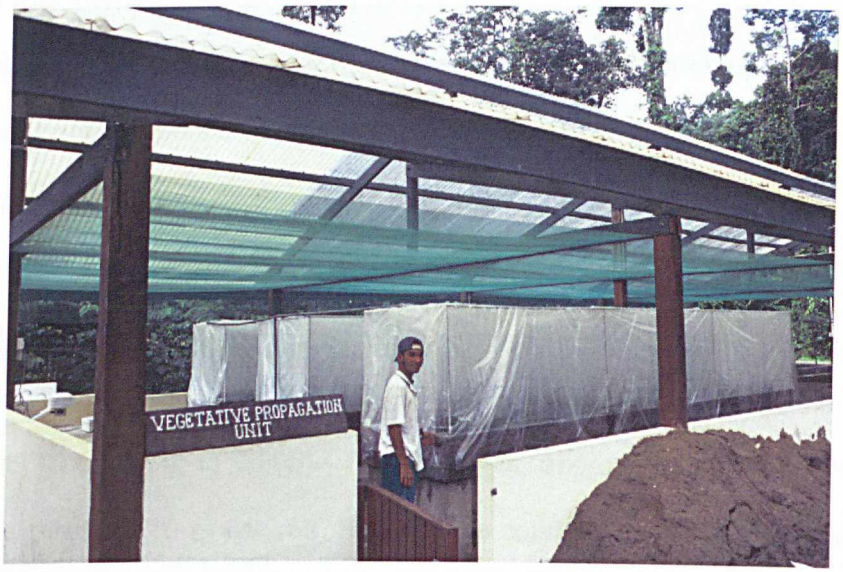
The propagation medium consisted of 40% composted sawdust (single source from a local sawmill), 40% river sand and 20% forest topsoil. Several m^3 of composted sawdust was purchased locally at the start of the project from a single batch. River sand and topsoil were collected within the vicinity of the INFAPRO nursery. The constituents were thoroughly mixed and steam-sterilised for 2 hours in order to eradicate soil-borne pests and pathogens. Cuttings were either struck directly into the

propagation beds, or into polythene bags measuring 50 mm x 200 mm (standard size bags for dipterocarp seedlings). Further details are given in the methods for each chapter.

2.5.3 Nursery facilities

Nursery facilities for this research were located at the INFAPRO headquarters (about 12 km by road from the Danum Valley Field Centre), in the Ulu Segama Forest Reserve. The nursery was built specifically for this project and consisted of 6 raised concrete beds under a corrugated clear plastic roof with a single layer of 30% shade netting (figure 2.11). Each bed was 1 m high and measured 5 m long by 1 m wide by 20 cm deep. The base of each bed was covered with a 5 cm layer of granite chips and drained via a number of large holes running into floor drains. The beds were covered with an aluminium frame to a height of approximately 1 m (from the bed surface) which in turn was covered with a layer of 100 micron polythene sheet and shade netting (figure 2.12). Prior to the insertion of each batch of cuttings the beds were drenched with a solution of the fungicide benomyl (ICI Benlate)[1].

Figure 2.11: *INFAPRO research nursery just after construction. Three of the six propagation beds shown covered with polythene sheeting*



[1] Note: Benomyl is banned for use in Europe and North America.

Irrigation was provided by a pumped, pressurised system consisting of two 1.5 hp electric centrifugal pumps operating in parallel. These supplied overhead spray nozzles suspended 50 cm above the propagation beds. The nozzles (RainBird Ltd, Australia) were of a micro-irrigation type generating a circular spray pattern of relatively large droplets.

Figure 2.12: *Cuttings of Dryobalanops lanceolata, Parashorea malaanonan & Shorea leprosula*

The system was controlled by an electrical two-stage timer. The first stage allowed setting of the interval between spray bursts and the second the spray. The typical setting used was 15 minutes between bursts with a spray duration of 30 seconds. The interval between bursts was reduced to 10 minutes or less during periods of high evaporative demand.

2.6 Field planting

Planting followed the standard INFAPRO system (Moura-Costa, 1993; Moura-Costa *et al.*, 1996; Yap, 1998; Li, 2006). Planting lines, approx. 2 m wide, were cleared through the forest at 10 m centres. Plants were carefully removed from their plastic containers and planted at 3 m centres, where possible (Figure 2.13). Every 3 to 4

months the planting lines were cleared and competing vegetation cut back. No fertilisers, insecticides or herbicides were used during the experimental period.

Figure 2.13: *Field planting of dipterocarp seedling (Shorea leprosula) in logged-over forest*

2.7 Plant measurements

Above ground measurements (*in-vivo*) were typically made of plant height (in mm to the nearest 5 mm), stem diameter at base (10 mm from soil surface, in mm to 2 decimal places), diameter at breast height (approximately 1,300 mm from soil surface, in mm to 2 decimal places) and leaf number (fully expanded leaves only). Below ground measurements (*in-vivo*) were restricted to rooting depth (maximum depth of soil exploited by the root system, in mm) and maximum root length (in mm). For destructive measurements, aerial parts of the plant were separated into stems and leaves. Root systems were separated into 3 diameter classes: < 2 mm, 2 to 5 mm and > 5 mm. Where necessary, root and stem sections were cut into manageable lengths prior to drying. Plant parts were oven dried at 65°C for 2 weeks. Dry weights were measured (in g) to 2 decimal places. Any variation from these methods will be noted in the chapter methods.

2.8 Overview of statistical analyses

All data were analysed and graphs generated using the GPL statistical package 'R' (The R Foundation for Statistical Computing version 2.0.1).

Data with normally distributed errors were analysed by the traditional methods of analysis of variance (where explanatory variables were categorical) and regression analysis (for continuous explanatory variables). When data included both categorical and continuous explanatory variables general linear model analyses were used (Crawley, 2002; Dalgaard, 2002; Maindonald & Braun, 2003; Crawley, 2005).

When diagnostic plots showed that distribution of residuals was not normal, or where variances were unequal, data were transformed until they met the assumptions of the analysis. The transformations used have been specified in the methods sections of the experimental chapters. For data with non-normally distributed errors that could not be transformed (i.e. for binary survival or rooting data, or proportional data) generalised linear models (GLMs) were used that replaced the normal distribution with another more appropriate distribution from the exponential family (i.e. Poisson or Binomial). Again, details are given in the methods for each experiment.

Some of the experimental designs used were of the split-plot type which had multiple error terms; one for each different plots and split-plots. At every level the signal associated with the treatment is compared to the residual differences between plots (or split-plots) at the level in question (after the treatment effect had been removed). Split-plot designs require the use of linear mixed or mixed-effects models which properly account for the fixed (i.e. treatment) and random (i.e. residual error term) effects. For split-plot designs with data which was not normally distributed (e.g. the survival and rooting analyses in Chapter 4 of this thesis) a generalised linear mixed-effects model (or GLMM) was used. In this type of analyses, deviance rather than sums of squares is applied. The deviance is divided by the degrees of freedom to give a mean deviance and these mean deviances are used to perform the

approximate F tests in an exactly analogous way to a standard ANOVA. (Pinhero & Bates, 2000; Crawley, 2002; Dalgaard, 2002; Maindonald & Braun, 2003; Hector, 2004; Crawley, 2005).

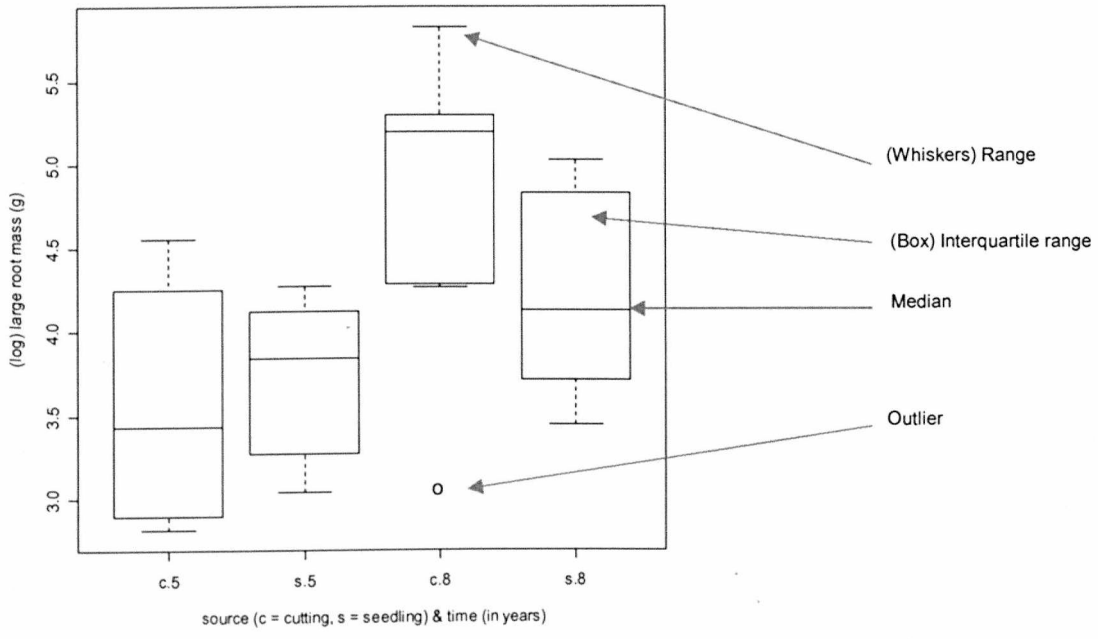
More modern approaches to hypothesis tests in GLMMs are in the process of being introduced (Hector, 2006 *pers. comm.)* but since this work is still in development the simple mean deviance approach is applied here.

Data are presented as ANOVA tables with output rounded to two significant figures. A full step-wise analysis for each experiment, with R coding, is included in Appendices 1, 2, 3 and 4.

2.8.4 *Graphs*

Box and whisker plots are the main graph type used to display data (Figure 2.14). These show the median (central horizontal line), interquartile range (box) and the data range (whiskers). Outliers are indicated by open circles (Maindonald & Braun, 2003).

Figure 2.14: *Example of the box & whisker plots used to display much of the data in this research*



CHAPTER 3

3. THE PROPAGATION PHASE: VARYING THE LEVEL OF IRRADIANCE

Experimental aims were to:

i. Establish if the light regime during propagation has any effect on survival and rooting percentage in cuttings of *D. lanceolata, P. malaanonan* and *S. leprosula*

ii. Establish if light has any effect on the extent of root and shoot formation or on root:shoot ratio

With the hypothesis that:

High irradiance during propagation is detrimental to cutting survival and root initiation, especially in shade-tolerant species, but that root and shoot development in cuttings that initiate roots is enhanced by increased irradiance.

3.1 Background & supporting literature

Initiation and development of adventitious roots is influenced by the interaction of various physiological and environmental factors. Successful rooting can be attributed to maintaining a propagation environment that enables cuttings to survive the immediate post-severance period and in which physiological processes are subsequently able to operate at optimal levels for root development (Blazich, 1888; Leakey *et al.*, 1994; Mesén *et al.*, 1997; Hartmann *et al.*, 2002; Lebude *et al.*, 2004). However, despite the importance and widespread use of cutting-based propagation systems, it remains uncertain if photosynthesis plays a significant role in root initiation or, perhaps more importantly at an applied level, the extent to which photosynthetic activity influences subsequent root growth and development (Mesén *et al.*, 1997; Mesén *et al.*, 2001; Bruce *et al.*, 2001; Hartmann *et al.*, 2002; Pohio *et al.*, 2005). Photosynthesis is almost certainly not an absolute prerequisite for root initiation; leafy cuttings have been shown to initiate roots in complete darkness

(Davis & Potter, 1981) and many temperate species are capable of rooting as leafless cuttings (Hartmann *et al.*, 2002). It has even been suggested that it is root production which influences photosynthesis in cuttings and not *vice versa* (Okoro & Grace, 1976). It can probably be concluded that while photosynthesis (and hence the level of irradiance during propagation) is probably not a crucial factor in root initiation, at least for most species, it is likely to play a much more important role in early root development. Several studies on both temperate and tropical species have indicated this to be the case – but results for tropical species in particular are somewhat inconsistent and there is almost no experimental evidence to indicate how light may affect the root development of dipterocarp cuttings.

Dipterocarp seedlings are adapted to a wide range of light environments from deep shade under a closed forest canopy to direct sunlight after gap formation (Ashton, 1988; Zipperlen & Press, 1996; Press *et al.*, 1996; Brown, 1996; Whitmore & Brown, 1996; Barker *et al.*, 1997) but it is unclear at what point on this continuum, if any, lies the optimal level of irradiance for root development in dipterocarp cuttings. Given this wide tolerance, and the relatively low light compensation and saturation points of seedlings of most dipterocarp species (Sasaki & Mory, 1981), it is possible that the responses of dipterocarp cuttings to differing light regimes are relatively plastic and that, providing irradiance is not so high or low as to cause damage, the precise level might have little or no effect on survival and/or root development. It is also possible that the responses of cuttings from different dipterocarp species might vary according to their basic ecology or habitat preference, i.e. light demanding species (such as *Shorea leprosula*) might show a different response to those which are more shade tolerant (e.g. *Dryobalanops lanceolata*). Previous work has attempted to assess rooting in dipterocarp cuttings in relation to species-level preferences in terms of elevation, slope, soil and coppicing ability (Itoh *et al.*, 2002) but shade tolerance has not been considered.

In the only published study to specifically investigate the influence of light on dipterocarp cuttings, rooting percentage in *Shorea leprosula* cuttings grown under intermediate irradiation (up to 360 micro mol m^{-2} s^{-1}) was significantly higher than in those grown under higher or lower light levels (of 658 and 98 micro mol m^{-2} s^{-1} respectively). There was, however, no effect of light on the number of roots formed per cutting (Aminah *et al.*, 1997). There has been no comparative research in refereed literature to determine optimal light levels across a range of species.

In more general work on dipterocarp cuttings, which did not specifically investigate the effects of light, it has been recommended that incident irradiation be reduced by levels of *c.* 50% (Aminah, 1991, 1995; Moura-Costa, 1993; Sakai *et al.*, 1994), to 70% (Kantarli, 1993[a,b]) and 90% (Momose, 1978). However, the reasons why these levels of shade were applied was not discussed, and no research has attempted to quantify (in terms of root length or root mass) the influence of different light regimes on the extent of root formation.

Experimental evidence for the effects of light during the propagation of other tropical broadleaves is relatively scant. In research on the African trees *Irvingia gabonensis* and *Triplochiton scleroxylon* rooting percentage was highest in cuttings with the largest leaf area (Shiembo *et al.*, 1996; Nketiah, 1998). Similarly, in the South American species *Inga feuillei,* cuttings in which several leaves were retained rooted successfully, while cuttings in which leaves had been removed failed completely to root (Brennan & Mudge 1998). Similar results were reported in the east African timber tree *Terminalia spinosa* where cuttings were shown to be actively photosynthesising during the propagation period and that the presence of leaves was essential for rooting (Newton *et al.*, 1992). However, in research which compared rooting in leafy and leafless cuttings of the Central American multi-purpose tree *Leucaena leucephala*, although cuttings with leaves rooted more successfully (71% of cuttings forming roots) leafless cuttings also rooted, albeit less successfully (39% rooting) (Dick *et al.*, 1999). In the Mexican timber species *Cordia alliodora* the highest

rooting percentage was in treatments that combined high irradiance with a moderate reduction in leaf area, suggesting that varying leaf area influenced rooting through balancing the processes of transpiration and photosynthesis (Mesén *et al.*, 1997).

These results are somewhat contrary to the earlier statement that photosynthesis does not play a significant part in root initiation; it appears that in a number of tropical species photosynthesis may indeed be important in the rooting process. However, this is difficult to establish conclusively since it is near-impossible to vary photosynthetic rate independent of the other factors, either environmental or physiological, which may influence rooting. Altering photosynthetic rate by varying irradiance or leaf area will affect other factors in the cutting such as vapour pressure deficit, temperature, auxin concentration and wounding responses (following leaf removal or trimming); all of which might play important roles in root initiation and/or development (Morison & Gifford, 1984; Davis 1988; Mesén *et al.*, 1997).

There is more evidence on the influence of irradiance during propagation for temperate species, although results are similarly inconsistent. In research on *Pinus sylvestris* there was no difference in rooting responses in cuttings grown under high (180 micro mol m^{-2} s^{-1}) or low (36 micro mol m^{-2} s^{-1}) light regimes either in rooting percentage or the number of roots formed in each cutting (Hansen *et al.*, 1978). In a similar experiment on aspen (*Populus tremula* x *tremuloides*), which is regarded as a shy-rooting species, rooting percentage was highest in cuttings grown under low-light (8 w m^2) compared to high-light (40 w m^2) treatments. In the easier-rooting willow (*Salix caprea* x *viminalis*) light level had no affect on rooting percentage (Eliasson & Brunes, 1980). Results showing the positive effects of a low irradiance regime (or, perhaps more likely, negative effects of high irradiance) were also found in cuttings of *Forsythia* and *Weigelia* spp. (Loach & Gay, 1979). In contrast, both Eliasson (1978) and Davis & Potter (1981), in work on *Pisum sativum*, found that rooting improved with increasing irradiance and suggested that the response was due to enhanced photosynthesis. In research on rooting in cuttings of a recently-discovered Australian

pine, *Wollemia nobilis*, it was found, in contrast to the results presented by Mesén and colleagues (1997) on *C. alliodora*, that although photochemical efficiency declined markedly during periods of environmental stress, particularly in the immediate post-severance period, this did not appear to inhibit subsequent root initiation or development. Shading treatments which alleviated photoinhibition did not increase rooting percentage and the authors concluded that cuttings of *W. nobilis* remained capable of rooting even after severe photoinhibition (Pohio *et al.*, 2005).

Notwithstanding the difficulties in isolating the possible light-effects from concomitant changes in other environmental and/or ecophysiological factors, it is important to establish if the responses of dipterocarp cuttings to differing light regimes under standard nursery conditions are, as would seem likely, relatively plastic and whether light could prove to be a major factor in root initiation or early development. A supplementary aim was to provide some indication if the rooting ability of dipterocarp cuttings may be related to the basic ecology of individual species, and hence if the propagation environment would require species or genera-specific modifications, i.e. would a shade tolerant species like *D. lanceolata* root better under low light conditions. Of greater importance was to establish if the light regime influenced the extent of root formation. Most of the studies cited have reported either the absence or presence of roots or simple count or categorical data on the number of roots formed per cutting. Despite the possible implications of early root development on cutting survival and growth after planting, and longer-term effects on stability and/or water and nutrient uptake, very few studies have attempted to quantify the extent of root development in dipterocarp cuttings. This represents a significant gap in current knowledge as it has been shown in species as diverse as *Hevea brasiliensis*, *Eucalyptus globulus*, *Melia volkensii* and *Pinus radiata* that root development during the propagation phase can have major implications for long-term growth of the adult plant (Tinley, 1963; Sasse & Sands, 1996, 1997; Mulatya *et al.*, 2002; Watson & Tombleson, 2002).

3.2 Materials & methods

The general nursery procedure used for raising the cuttings is described in the General Methods[1]. All cuttings were sourced from overgrown nursery seedlings and rooted in 50 x 200 mm potting bags. For a period of at least 2 months prior to the start of the experiment, all seedlings were kept under a standard irradiance of approx. 50% of incident.

The experiment was set up in a completely randomised block design. The 6 propagation beds (acting as blocks) were divided into 3 compartments with a light treatment randomly assigned to each, giving a total of 6 replicates per light treatment (Figure 3.1). Sixty six cuttings (22 of each species) were placed in each compartment, giving a total of 1,188 cuttings used in the experiment (22 cuttings x 3 species x 3 treatments x 6 replicates = 1,188).

Figure 3.1: *Experimental design & light treatment allocation (3 treatment levels – 90%, 75% & 60% light interception)*

The cuttings were randomised by species and arranged in the central portion of each compartment to avoid treatment 'overlap' at the compartment edge (Figure 3.2 – following page).

[1] *See Chapter 2 – page 46*

Figure 3.2: *Cuttings of D. lanceolata, P. malaanonan & S. leprosula under 75% shade (foreground) & 60% shade*

Shading for the houses was provided by polypropylene nursery shade netting (30% light interception) in single, double or triple layers. In combination with the nursery roofing and polythene sheeting covering the individual propagation beds, the total light interception for the treatments were *c.* 60% (high light), 75% (medium) and 90% (low light) respectively. Irrigation was provided by a semi-automated pump system as described in the General Methods.

Cutting survival was recorded on a weekly basis and any dead cuttings removed to reduce the risk of infection from fungal pathogens. After a period of 8 weeks the cuttings were removed from the containers and the presence or absence of roots recorded. The propagation medium was gently washed from the root system and the cuttings destructively harvested as described in the General Methods.

Binomial survival and rooting data were analysed using a Generalised Linear Model specifying binary logistic regression of proportions in the test. Data from the destructive harvest (root and shoot mass etc) were analysed using a Linear Mixed-Effects Model.[1]

[1] *For full details of the various analyses & additional ANOVA tables see Appendix 1 – page 182*

3.3 Results

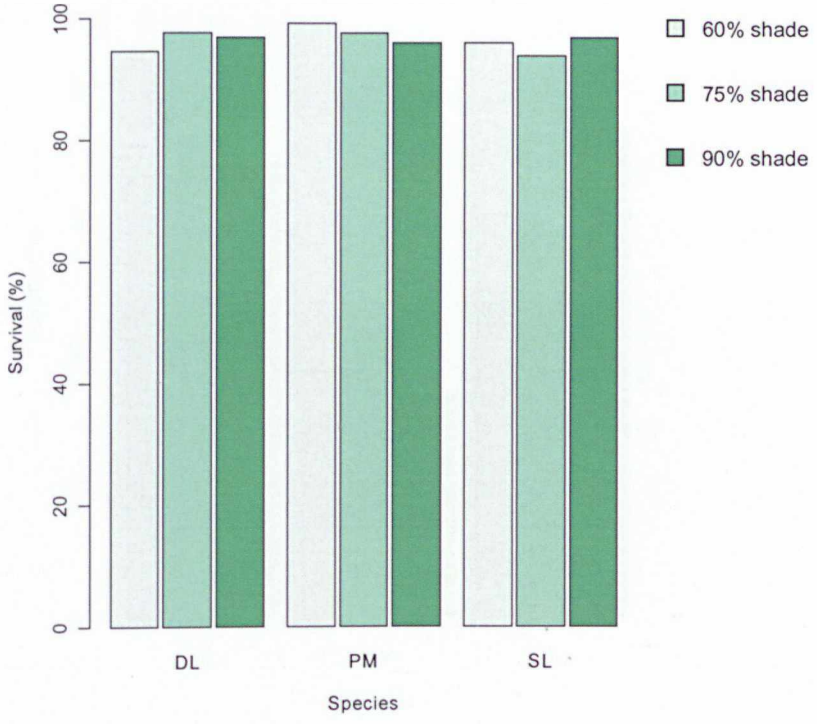
3.3.1 *Survival*

Survival did not vary significantly between treatments and there was no interaction between species and light level (Table 3.1, Figure 3.3). Survival was uniformly high (> 90%) in all species.

Table 3.1: *GLM analysis (using binary logistic regression on proportions) for the effect of light on survival in cuttings of D. lanceolata, P. malaanonan & S. leprosula after a period of 8 weeks*

Source	df	Dev.	Res.df	Res.Dev	p (>Chi)
null			53	61.2	
block	5	2.17	48	59.03	0.83
light	2	0.051	46	58.98	0.98
species	2	2.64	44	56.34	0.27
light:species	4	6.34	40	49	0.18

Figure 3.3: *Survival in cuttings of D. lanceolata, P. malaanonan & S. leprosula grown under 60, 75 and 90% shade after 8 weeks.*



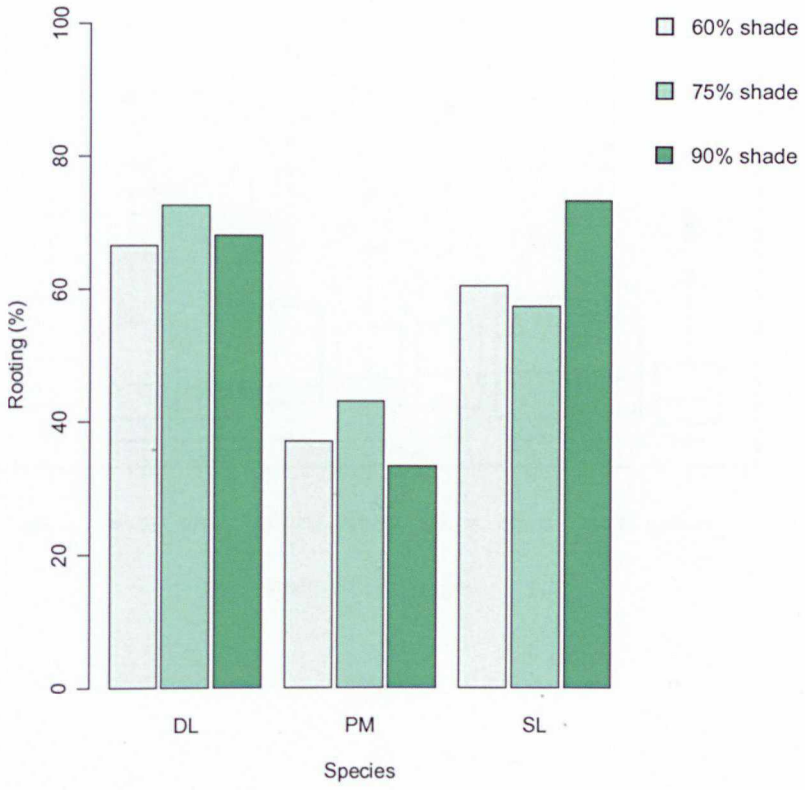
3.3.2 *Rooting percentage*

As with survival, there was no significant treatment effect on rooting percentage. There were significant species differences (Table 3.2). Mean rooting percentage in the 3 species was 69% in *D. lanceolata,* 38% in *P. malaanonan* and 64% in *S. leprosula* (Figure 3.4). There was a significant block effect – most likely as a result of the lower rooting percentage recorded for cuttings in block 4.

Table 3.2: *GLM analysis (using binary logistic regression on proportions) for the effect of light on rooting percentage in cuttings of D. lanceolata, P. malaanonan & S. leprosula after 8 weeks*

Source	df	Dev.	Res.df	Res.Dev	f	p (>f)
null			53	216.76		
block	5	32.078	48	184.69	3.34	0.013
light	2	1.21	46	183.47	0.32	0.73
species	2	93.88	44	89.59	24.49	<0.0001
light:species	4	11.437	40	78.157	1.49	0.22

Figure 3.4: *Rooting percentage (after 8 weeks) in cuttings of D. lanceolata, P. malaanonan & S. leprosula under 60, 75 & 90% shade*



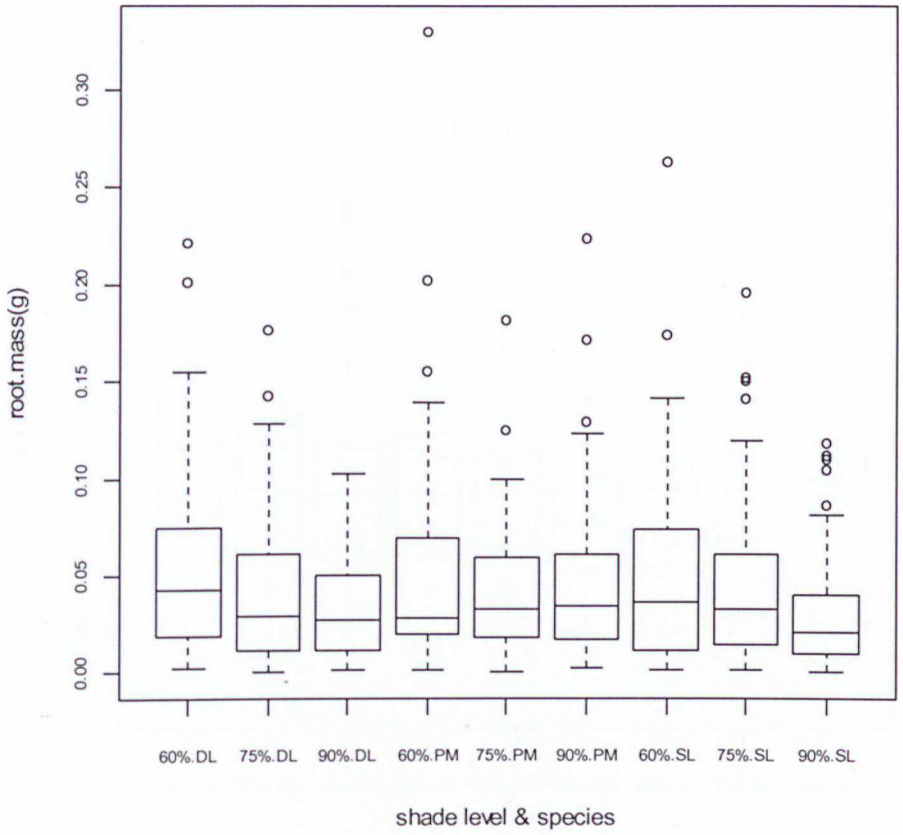
3.3.3 *Destructive measurements*

Of the cuttings that formed roots, there were no treatment or species effects on root mass (Table 3.3, Figure 3.5).

Table 3.3: *LME analysis for the effect of light on root mass in cuttings of D. lanceolata, P. malaanonan & S. leprosula after 8 weeks*

Source	df	den.df	F	p
(intercept)	1	492	2351.74	<0.0001
light	2	10	2.52	0.13
species	2	30	1.84	0.18
light:species	4	30	1.68	0.18

Figure 3.5: *Effect of light on root mass in cuttings of D. lanceolata (DL), P. malaanonan (PM) & S. leprosula (SL) after 8 weeks*

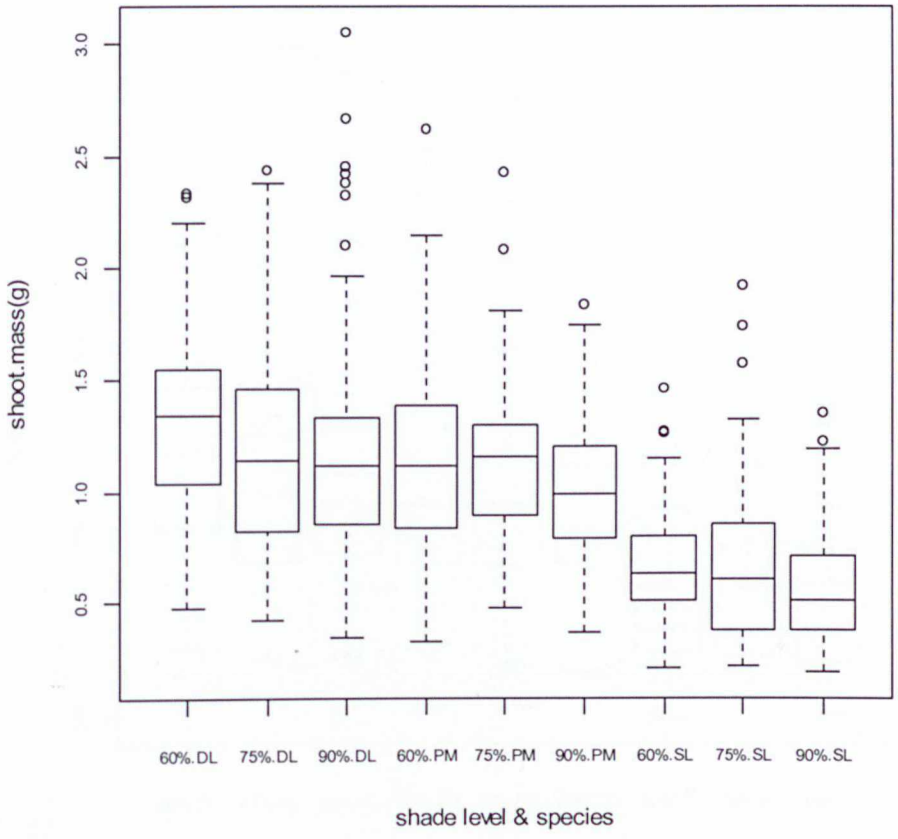


Shoot mass was significantly greater in cuttings grown under higher irradiance (Table 3.4, Figure 3.6). There were species differences with *S. leprosula* having a lowest shoot mass, though there was no light:species interaction.

Table 3.4: *LME analysis for the effect of light on shoot mass in cuttings of D. lanceolata, P. malaanonan & S. leprosula after 8 weeks*

Source	df	den.df	F	p
(intercept)	1	492	34.24	<0.0001
light	2	10	4.79	0.035
species	2	30	132.63	<0.0001
light:species	4	30	0.55	0.70

Figure 3.6: *Effect of light on shoot mass in cuttings of D. lanceolata, P. malaanonan & S. leprosula after 8 weeks*

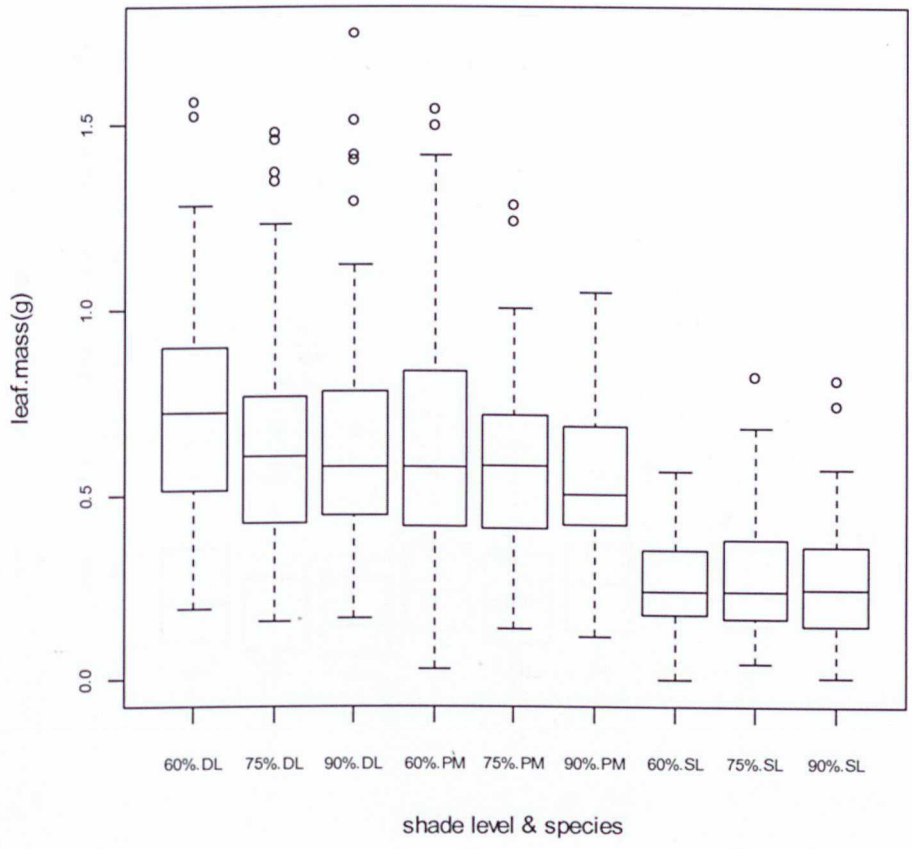


Leaf mass varied significantly between species, with *S. leprosula* having a significantly lower leaf mass than either *D. lanceolata* or *P. malanonaan*. There was no treatment effect or species:treatment interactions (Table 3.5, Figure 3.7).

Table 3.5: *LME analysis for the effect of light on leaf mass in cuttings of D. lanceolata, P. malaanonan & S. leprosula after 8 weeks*

Source	df	den.df	F	p
(intercept)	1	492	489.48	<0.0001
light	2	10	1.036	0.39
species	2	30	110.86	<0.0001
light:species	4	30	1.57	0.21

Figure 3.7: *Effect of light on leaf mass in cuttings of D. lanceolata, P. malaanonan & S. leprosula after 8 weeks*

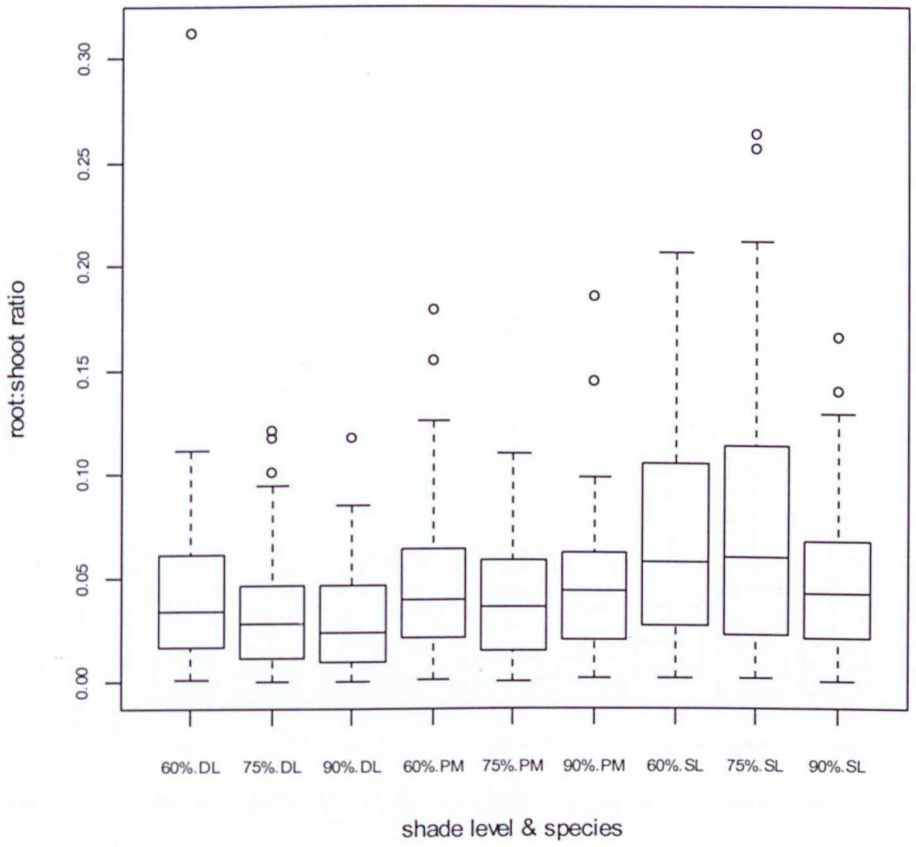


There were no effects of light on root:shoot ratio. There were species differences, with *S. leprosula* having the highest root:shoot ratio, but the light:species interaction was not significant (Table 3.6, Figure 3.8).

Table 3.6: *LME analysis for the effect of light on root:shoot ratio in cuttings of D. lanceolata, P. malaanonan & S. leprosula after 8 weeks*

Source	df	den.df	F	p
(intercept)	1	492	1466.086	<0.0001
light	2	10	1.086	0.37
species	2	30	17.52	<0.0001
light:species	4	30	1.43	0.25

Figure 3.8: *Effect of light on root:shoot ratio in cuttings of D. lanceolata, P. malaanonan & S.leprosula after 8 weeks*

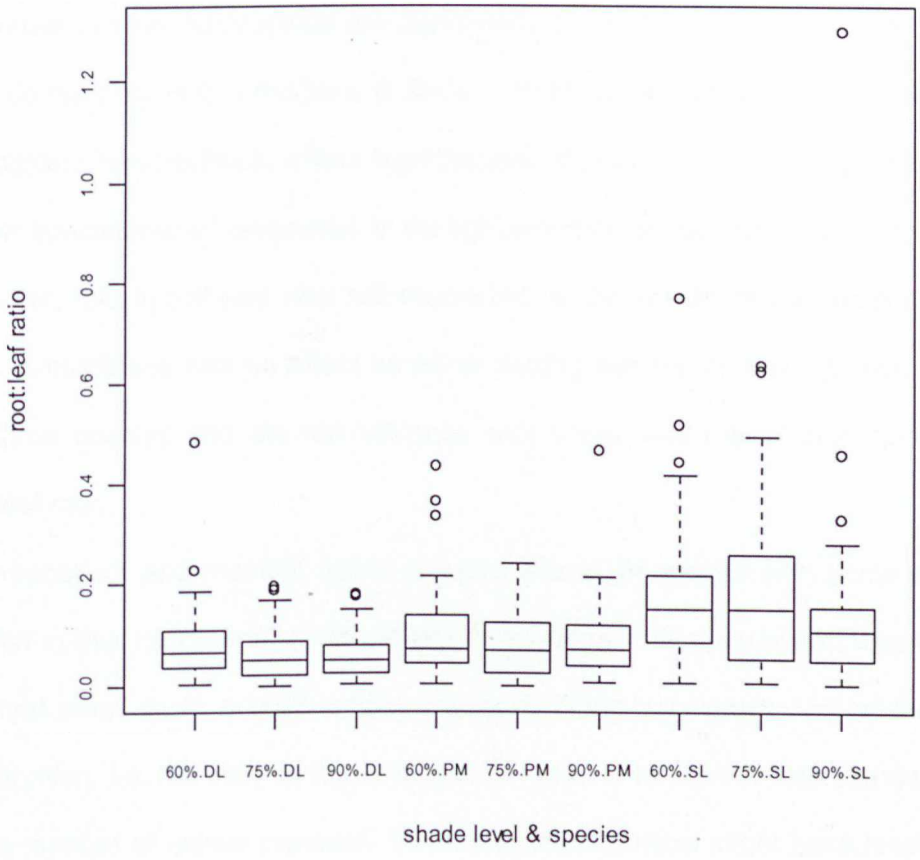


As with root:shoot ratio, there was a significant species effect on root:leaf ratio with *S. leprosula* showing a higher ratio than the other species. Light effects were not significant at $p<0.05$, but there was marginal significance at $p<0.1$. There were no treatment:species interactions (Table 3.7, Figure 3.9).

Table 3.7: *LME analysis for the effect of light on root:leaf ratio in cuttings of D. lanceolata, P. malaanonan & S. leprosula after 8 weeks*

Source	df	den.df	F	p
(intercept)	1	492	1285	<0.0001
light	2	10	3.71	0.062
species	2	30	37.94	<0.0001
light:species	4	30	1.059	0.39

Figure 3.9: *Effect of light on root:leaf ratio in cuttings of D. lanceolata, P. malaanonan & S. leprosula after 8 weeks*



3.4 Discussion

Evidence from a range of tropical and temperate tree species indicates that the precise nature of the propagation environment, in terms of light and other factors, can critically influence adventitious root formation in cuttings (Hartmann *et al.*, 2002). Indeed, cuttings of some particularly sensitive species will only form roots if environmental variables are maintained within tight limits (e.g. Eliason & Brunes, 1980; Newton *et al.*, 1992; Brennan & Mudge, 1998; Dick *et al.*, 1999). Conversely, cuttings of other species show considerable tolerance to variance in the propagation environment (e.g. Hansen *et al.*, 1978) and, in some cases, are able to root successfully even after periods of severe photoinhibition (Pohio *et al.*, 2005).

Naturally recruited dipterocarp seedlings show considerable plasticity in their response to environmental variables, particularly light (e.g. Ashton, 1988; Barker *et al.*, 1997), though there is a considerable degree of species-specificity in their precise responses; some dipterocarps are particularly shade tolerant while others are more light demanding (e.g. Whitmore & Brown, 1996; Brown *et al.*, 1999). Given these ecological characteristics, it was hypothesised that dipterocarp cuttings would show similar species-based responses to the light environment during propagation.

However, this hypothesis was not supported by the results of the experiment. The level of irradiance had no effect on either cutting survival or root initiation in any of the three species and did not influence root mass, leaf mass, root:shoot ratio or root:leaf ratio.

The root:shoot and root:leaf ratios reported should be treated with some degree of caution in that root formation in cuttings is an entirely *de novo* event, whereas stem and leaf mass is, to a large extent, *de facto,* being very much 'set' at the time of propagation, i.e. the stem of the cutting is trimmed to a more-or-less standard length and a number of leaves removed. While root development might have responded to the treatment regime during propagation (8 weeks in this experiment), this may not have been the case with shoots unless either new leaves were produced or existing

leaves senesced. However, assessment of root:shoot and root:leaf ratios did allow for the extent of root formation to be assessed while controlling for shoot and leaf mass (and hence likely photosynthetic potential).

Survival was uniformly high across both treatment and species, indicating that environmental conditions during propagation were maintained within acceptable limits in the immediate post-severance period. Rooting percentage in cuttings of *D. lanceolata, P. malaanonan* and *S. leprosula* were similar to those reported in previous research (e.g. Srivastrava & Manggil, 1981; Muckadell & Malim, 1983; Appanah & Weinland, 1993; Dick & Aminah, 1994; Smits, 1992; Smits *et al.*, 1994; Moura-Costa & Lundoh, 1994; Moura-Costa *et al.*, 1996).

These results, and those from previous research, suggest that light in the range 10-50% of incident provides a suitable environment for cutting survival and supports the physiological processes necessary for subsequent root initiation and development. As cuttings were assessed after a relatively short period (8 weeks), had there been a treatment effect then this would likely have been obvious at this early stage. It can therefore be reported with some confidence that the precise level of irradiance has little or no influence on survival or root development in dipterocarp cuttings.

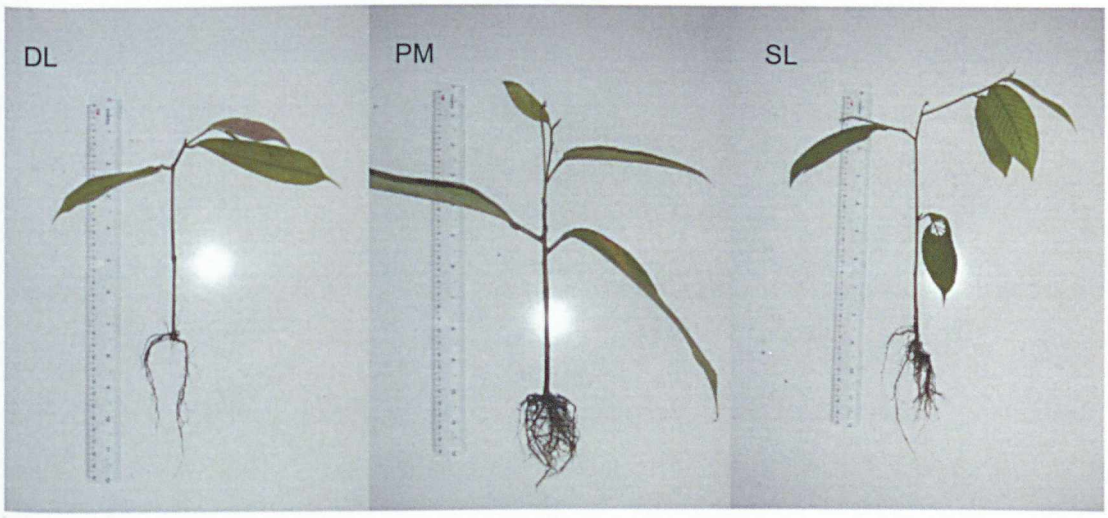
There were no significant light:species interactions in any of the measured parameters. This again suggests that responses of dipterocarp cuttings showed considerably plasticity and that, for example, even a light-demanding species such as *S. leprosula* (Symington *et al.*, 2004) was able to successfully initiate and develop roots under conditions of low irradiance. Equally, cuttings of the more shade-tolerant *D. lanceolata* (Meijer & Wood, 1964) grown under the high light treatment showed similar rooting success and development to those grown in lower light. The rooting response of *S. leprosula* cuttings in this experiment was quite different to the results reported by Aminah and colleagues (1997) who found that *S. leprosula* cuttings were relatively sensitive to the light environment during propagation and rooted most

successfully under intermediate irradiation. Rooting was negatively impacted in both higher and lower light treatments (Aminah *et al.*, 1997).

Block effects were significant on rooting percentage. Although the reasons for this are not immediately apparent, it is possible that environmental variation between blocks was responsible. The research nursery and individual propagation beds were both shaded, which prevented direct sunlight striking the propagation beds during the main part of the day. However, due to the orientation of the nursery and gaps in surrounding vegetation, the 60% shade treatment in Block 4 (Figure 3.1) was struck by direct sunshine in the latter part of the afternoon. This may have resulted in much higher temperatures, lower relative humidity and greater evaporative demand and negatively impacted rooting percentage in this part of the propagation bed.

Visually, the root systems developed by *D. lanceolata*, *P. malaanonan* and *S. leprosula* cuttings during the experimental period appeared to be relatively extensive, well-formed and strongly geotropic (Figure 3.10). Although morphology at this stage is difficult to assess quantitatively, there was nothing obvious in the development of the root systems in these species which would raise concerns in the longer term. Post-planting development in the root systems of cutting-propagated dipterocarps will be considered in Chapters 5 and 6.

Figure 3.10: *Example of D. lanceolata (DL), P. malaanonan (PM) & S. leprosula (SL) cuttings rooted as part of the light experiment (scale is a 300 mm rule)*



It is highly likely that the level of irradiance would have strongly influenced the temperature and relative humidity of the propagation environment. Given the lack of response of the cuttings to light, it is therefore reasonable to assume that dipterocarp cuttings show considerable tolerance to variation in these factors. This assumption is borne out by previous research which has utilised a range of different light regimes during propagation from 50% shade (e.g. Moura-Costa, 1993) to 90% shade (e.g. Momose, 1978) and varying in sophistication from polythene bags shaded by palm fronds (Pollisco, 1993[a]; Kantarli, 1993[b]) to computer controlled hydroponic systems (Smits *et al.*, 1994; reviewed by Dick & Aminah, 1994). The use of sophisticated facilities is clearly not a pre-requisite to the successful propagation of dipterocarp cuttings. Their apparent tolerance to variation in the propagation environment may be particularly important for forest rehabilitation projects that are not able to invest in expensive nursery facilities or do not have access to reliable electrical or water supplies.

CHAPTER 4

4. THE PROPAGATION PHASE: USE OF PLANT GROWTH REGULATORS

Experimental aims were to:

i. Establish if varying the concentration of IBA solution, and the duration of exposure to these solutions, had any effect on survival and root initiation in cuttings of *D. lanceolata, P. malaanonan* and *S. leprosula*

ii. Establish if the various IBA treatments had any effect on root and shoot development

With the hypothesis that:

Root initiation and development in cuttings of *D. lanceolata, P. malaanonan* and *S. leprosula* is improved when cuttings are treated with increasing exposure to IBA solutions of increasing strength[1].

4.1 Background & supporting literature

The critical role of auxins in root initiation was established as long ago as the 1930s and over the past seventy years numerous studies have confirmed that auxins, either endogenous or applied, are essential for the formation of adventitious roots in cuttings (Thimann & Koepfli, 1935; reviewed in: Davis, 1988; Davis & Haissig, 1994; Hartmann *et al.*, 2002). Indole-3-acetic acid (IAA), an endogenous auxin, has been shown to have a strong stimulatory effect on adventitious rooting and, in its synthetic form, IAA was the first plant growth regulator applied to cuttings to improve rooting performance (Hartmann *et al.*, 2002). In the mid-1930s it was also shown that the synthetic auxins indole-butyric acid (IBA) and naphthalene-acetic acid (NAA) were more effective than IAA in stimulating adventitious rooting and IBA and NAA remain the most commonly used applied auxins in vegetative propagation by stem cuttings

[1] *In the range 0 – 3,000 ppm IBA concentration, 1 second to 120 hours exposure duration*

(Hartmann *et al.*, 2002). IBA is widely accepted as being the most effective general use auxin; it has been shown to promote rooting in a great many species, has low phytotoxicity over a broad concentration range and, with refrigeration and protection from light, can be stored for long periods (Macdonald, 1986; Hartmann *et al.*, 2002). Although there are exceptions, it is almost always the case that if a cutting does not respond to IBA then other auxins will not compensate. However, the benefits of applied plant growth regulators are not universal and, especially in difficult-to-root species, factors other than auxin supply may actually determine root initiation and development (Hartmann *et al.*, 2002).

The concentration of auxin applied to cuttings is usually in the range of between 500 and 1,250 ppm for softwood cuttings of herbaceous plants and 1,000 to 3,000 ppm for semi-hardwood cuttings of shrub and tree species (the dipterocarp cuttings taken as part of this project were all semi-hardwood) although concentrations of up to 5,000 ppm have been used with some semi-hardwood cuttings and to 10,000 ppm with dormant, hardwood cuttings of some temperate species (Macdonald, 1986; Hartmann *et al.*, 2002).

As responses to applied auxins are often species-specific there have been numerous studies to determine treatment regimes, particularly for the more important crop and ornamental plants. This work has been comprehensively reviewed in a number of standard texts on vegetative propagation and adventitious root formation (e.g. Macdonald, 1986; Davies *et al.*, 1988; Davies *et al.*, 1994; Hartmann *et al.*, 2002). This review, therefore, will largely be restricted to research on tropical species and that relating specifically to dipterocarps.

Experimental evidence for the action of auxins on dipterocarp cuttings is inconclusive and often contradictory with both negative and positive effects reported (reviewed by Dick & Aminah, 1994). In one of the few recent studies, Brodie (2003) tested a number of IBA concentrations on rooting in *Dryobalanops oblongifolia* and *Shorea splendida* stem cuttings but found no significant treatment affect. Moura-Costa &

Lundoh (1994), in the only published study to compare the action of different auxin types on dipterocarp cuttings, investigated the effects of IBA, NAA and 2-4 D at three concentrations (200, 800 and 3,000 ppm) on rooting in *Dryobalanops lanceolata*. They reported that all three auxins had a negative impact on rooting, with NAA (at all concentrations) having the most suppressing effect. Untreated cuttings showed the highest rooting percentage.

In earlier work by Hallé and Kamil (1981) on the dipterocarp *Vatica pauciflora*, in which a range of IBA concentrations were tested, cuttings treated with a solution of 2,000 ppm showed the highest rooting percentage. Rooting percentage was lower in cuttings treated with either higher or lower concentrations of IBA, although their work was somewhat confounded by minimal replication and the absence of a control. Conversely, in cuttings of *Shorea macrophylla*, it was found that IBA applied at concentrations of 1,200, 3,600 and 10,800 ppm had a negative impact on rooting percentage as compared to a pure water control. However, among those cuttings that did form roots, treatment with IBA promoted a significant increase in the number of roots formed (Lo, 1985). Similarly, in experiments on *Shorea bracteolata, S. leprosula, Anisoptera scaphula* and *Dipterocarpus charteceus,* Srivastava & Manngil (1981) found that IBA did not improve rooting percentage in any of the concentrations tested (100, 500, 1,000 and 2,000 ppm) but that IBA promoted what the authors described as 'heavier' rooting in *S. bracteolata* at 500 ppm and in *A. scaphula* and *S. leprosula* at 2,000 ppm – though no data were presented to quantify the extent of the apparent increased root development.

These results were further supported in a later study on *Shorea leprosula* cuttings (Aminah *et al.*, 1994). IBA significantly increased rooting percentage up to a concentration of 2,000 ppm, although at higher concentrations rooting was negatively affected. However, and in common with Srivastava & Manngil (1981) and Lo (1985), all of the IBA concentrations enhanced root development in terms of the number of roots formed.

One of the few published studies to demonstrate a clear relationship between the application of IBA and root *initiation* (as opposed to root *development*) in dipterocarp cuttings was carried out by Pollisco (1994[b]) in the Philippines on two *Shorea* species. Although responses to IBA varied between species the study suggested that applied IBA was critically important for root initiation as untreated cuttings failed completely to root. In *S. contorta* the precise concentration of IBA appeared to be significant (only cuttings treated with 2,000 ppm IBA produced roots), whereas rooting percentage in *S. guiso* was similar at each of the IBA concentrations used.

Research on other tropical tree species has also shown that auxins, generally, have little effect on root initiation but that root development, either in terms of rate or extent, can be enhanced. In cuttings of the West African tree *Irvingia gabonensis,* IBA application had no effect on either rooting percentage or the number of roots formed per cutting, although it did significantly improve the speed of root development (Shiembo *et al.*, 2002). In leafy softwood cuttings of the South American tree *Inga feullei* IBA did not improve rooting percentage but did increase the number of roots formed per cutting (Brennan & Mudge, 1998). Similarly, IBA had no effect on root initiation in cuttings of the African timber species *Milicia excelsa* but did increase the number of roots per cutting. Somewhat surprisingly, given that IBA is not regarded as being phytotoxic, its application to *M. excelsa* was strongly correlated with cutting mortality. The authors attributed this to increased leaf abscission in the treated cuttings (Ofori *et al.*, 1996).

Cuttings of some species have shown a particularly strong response to auxin application. In teak (*Tectona grandis*) cuttings, IBA was found to improve rooting percentage, mean number of roots per cutting and root length, number of shoots, leaves and overall shoot length (Husen & Pal, 2003). A similar suite of positive effects were also reported following IBA application to cuttings of African mahogany (*Khaja ivorensis*) (Tchoundjeu & Leakey, 1996), to the North American *Robinia*

pseudoacacia and *Grewia optiva* (Swamy *et al.*, 2002) and Australasian *Eucalyptus globulus* and *E. saligna* (Fogaça & Fett-Neto, 2005).

Methods for applying IBA and other auxins to stem cuttings are well-established. Powder preparations, where IBA is carried in a talc-based medium, are commonly used and easily applied on a small scale, but ensuring uniformity of application is problematic and this method is seldom used on large nurseries. In commercial horticulture and forestry, liquid 'quick-dip' IBA solutions are very widely used and have generally been found more effective in promoting rooting than talc-based formulae (Chong *et al.*, 1992; Hartmann *et al.*, 2002). Complete immersion of cuttings in dilute IBA solutions, or spraying cutting stems and foliage prior to insertion, have been used with some species, though not widely (Hartmann *et al.*, 2002).

The technique of soaking the cutting base in a dilute auxin solution prior to striking has somewhat fallen from favour in recent years and is now hardly used in commercial horticulture (Hartmann *et al.*, 2002). Although the effectiveness of this technique is often variable (Loach, 1985), and setting-up treatments is relatively time consuming, it has been shown to promote rooting in a number of difficult-to-root tree and shrub species (Macdonald, 1986).

4.2 Materials & methods

The general procedure used for raising the cuttings is described in the General Methods[1]. All cuttings were sourced from overgrown nursery seedlings and rooted directly into the nursery beds.

A stock solution of 10,000 ppm IBA was prepared by dissolving 10 g of technical grade IBA in 20 ml of 95% ethanol and then topped-up to 1,000 ml using distilled water. Solutions of 100, 300, 1,000 and 3,000 ppm IBA were then prepared by decanting the appropriate amount of stock solution (10, 30, 100 and 300 ml respectively) and, again, topping-up to 1,000 ml using de-ionised water.

Each of these solutions, and a de-ionised water control, were decanted into separate opaque plastic tanks and colour coded using a drop of vegetable-based food colouring. The solutions were aerated using an aquarium pump and bubble de-fractionator. Cuttings of each species were randomly assigned to each treatment and placed in solutions for durations of 1 second, 1 hour, 12 hours, 48 hours and 120 hours. The total number of treatments was therefore 25 (4 IBA concentrations + control x 5 exposure durations).

Three nursery beds were prepared (acting as blocks) and each block was divided into 3 main species plots. As the cuttings were placed in close proximity within the beds it was necessary to separate the species to avoid the much larger-leaved *P. malaanonan* shading-out, in particular, the smaller-leaved *S. leprosula*. The main species plots were divided into 25 subplots and each of the 25 treatments were randomly assigned to each subplot. Eight cuttings were placed in each subplot. The total number of cuttings used in this experiment was 1,800 (8 cuttings x 3 species x 25 treatments x 3 replicates (blocks) = 1,800 cuttings). The experimental design is shown in Figure 4.1.

[1] *See Chapter 2 – page 46*

Figure 4.1: *Experimental design/treatment allocation (sub-plot number shown in green, treatment code (1-25) shown in blue)*

BLOCK 3

Plot 7 *Shorea leprosula*										Plot 8 *Dryobalanops lanceolata*										Plot 9 *Parashorea malaanonan*									
155	18	160	19	165	16	170	13	175	2	180	9	185	11	190	20	195	19	200	7	205	25	210	24	215	9	220	2	225	3
154	22	159	3	164	14	169	6	174	21	179	8	184	25	189	18	194	2	199	15	204	19	209	13	214	16	219	1	224	12
153	15	158	20	163	23	168	10	173	12	178	12	183	17	188	3	193	16	198	21	203	23	208	4	213	20	218	6	223	22
152	8	157	7	162	4	167	25	172	11	177	24	182	6	187	10	192	5	197	4	202	8	207	5	212	18	217	10	222	21
151	24	156	5	161	9	166	17	171	1	176	13	181	22	186	14	191	1	196	23	201	11	206	7	211	15	216	17	221	14

BLOCK 2

Plot 4 *Shorea leprosula*										Plot 5 *Parashorea malaanonan*										Plot 6 *Dryobalanops lanceolata*									
80	20	85	1	90	24	95	2	100	11	105	10	110	8	115	16	120	12	125	5	130	5	135	17	140	19	145	18	150	12
79	7	84	6	89	12	94	22	99	8	104	3	109	25	114	23	119	19	124	21	129	13	134	9	139	23	144	11	149	16
78	21	83	13	88	25	93	16	98	3	103	13	108	17	113	20	118	22	123	2	128	24	133	8	138	1	143	14	148	20
77	14	82	19	87	17	92	10	97	9	102	6	107	24	112	14	117	15	122	4	127	6	132	10	137	25	142	22	147	21
76	5	81	4	86	18	91	23	96	15	101	7	106	18	111	1	116	11	121	9	126	4	131	3	136	2	141	7	146	15

BLOCK 1

Plot 1 *Dryobalanops lanceolata*										Plot 2 *Parashorea malaanonan*										Plot 3 *Shorea leprosula*									
5	2	10	1	15	20	20	17	25	13	30	8	35	3	40	2	45	13	50	5	55	19	60	8	65	3	70	14	75	4
4	11	9	15	14	12	19	8	24	21	29	4	34	21	39	17	44	19	49	1	54	16	59	22	64	20	69	10	74	12
3	25	8	4	13	10	18	3	23	6	28	6	33	25	38	11	43	24	48	15	53	17	58	23	63	21	68	9	73	11
2	9	7	24	12	16	17	7	22	14	27	18	32	9	37	23	42	22	47	16	52	13	57	1	62	15	67	18	72	7
1	5	6	19	11	23	16	22	21	18	26	12	31	7	36	14	41	20	46	10	51	25	56	24	61	6	66	2	71	5

Sub-plot number in green

Treatment code in blue (concentration x exposure - 5 x 5 = 25 treatments)

Cutting survival was monitored on a weekly basis, with dead cuttings recorded and removed from the propagation beds (to avoid pathogen infection of healthy cuttings). After 8 weeks all surviving cuttings were lifted and the presence or absence of roots recorded.

A subset of rooted cuttings from each of the surviving treatments was randomly selected and harvested destructively as described in the General Methods. Due to limited replicates[1] treatments were grouped as indicated in Figure 4.2.

Figure 4.2: *Treatment groupings for destructive harvest*

	0 ppm IBA	*100 ppm IBA*	*300 ppm IBA*	*1,000 ppm IBA*	*3,000 ppm IBA*
1 sec	1	2	3	4	5
1 hour	6	7	8	9	10
12 hours	11	12	13	14	15
48 hours	16	17	18	19	20
120 hours	21	22	23	24	25

Group 1	24 cuttings
Group 2	48 cuttings
Group 3	46 cuttings

Binomial survival and rooting data were analysed using a Generalised Linear Model (binary logistic regression with split-plot ANODEV). Data from the destructive harvest were analysed using a Linear Model[2]. Most results were plotted using box-and-whisker plots (Maindonald & Braun, 2003). Lattice scatter plots were used for the survival and rooting percentage analyses with LOWESS curves fitted (Maindonald & Braun, 2003; Cleveland, 1981).

[1] *Most of the rooted cuttings were required for the field planting experiment. See Chapter 5 – page 92*
[2] *For full details of the various analyses see Appendix 2 – page 189*

4.3 Results

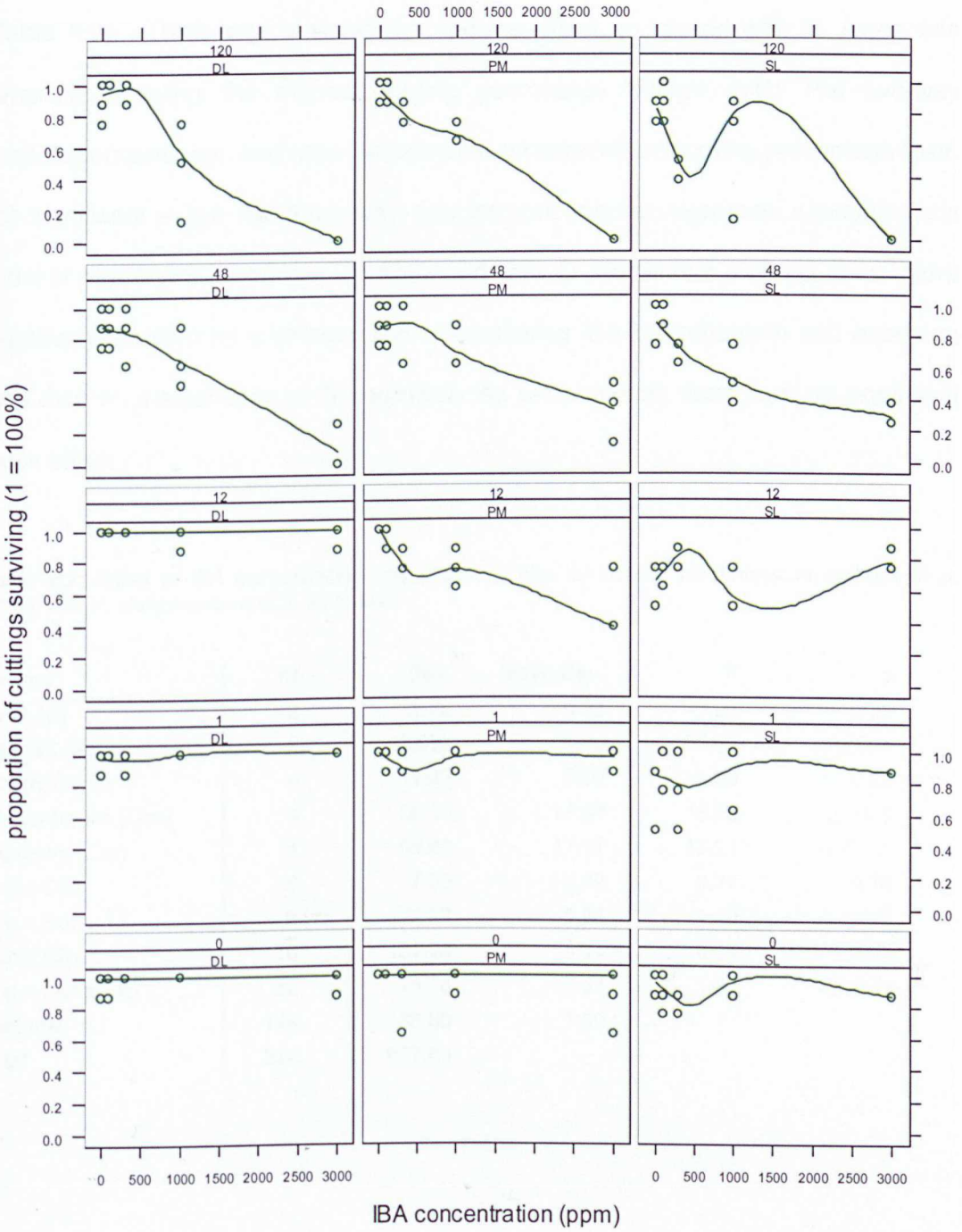
4.3.1 *Survival*

Survival was significantly different between the three species with *D. lanceolata* showing the highest survival rates and *S. leprosula* the lowest (Table 4.1). There were significant concentration and exposure effects on survival with, generally, survival decreasing with increasing IBA concentration and exposure time (Figure 4.3). The two-way species:concentration and species:exposure interactions were highly significant, as was the three-way species:concentration:exposure interaction with *P. malaanonan* and *S. leprosula* cuttings showing the more strongly negative response to increasing IBA concentration and exposure time, both independently and in combination. The highest IBA concentration (3,000 ppm), combined with the longest exposure (120 hours), resulted in 100% mortality in all species. No block effects were noted.

Table 4.1: *GLM analysis on the effect of IBA concentration and exposure time on survival in cuttings of D. lanceolata, P. malaanonan and S. leprosula. Significant values (p<0.05) shown in red*

Source	df	Dev.	Mean Dev.	F	p
Block (B)	2	0.65	0.33	1.031	0.44
Species (Spp)	2	29.67	14.84	46.38	0.0017
Plot (B x Spp)	4	1.29	0.32	0.29	0.88
Concentration (Con)	4	186.83	46.71	43.25	<0.0001
Exposure (Exp)	4	167.5	41.88	38.78	<0.0001
Spp x Con	8	24.17	3.02	2.80	<0.0001
Spp x Exp	8	37.62	4.7	4.35	<0.0001
Con x Exp	16	167.73	10.48	9.70	<0.0001
Spp x Con x Exp	32	42.52	1.33	1.23	<0.0001
Residual	144	155.9	1.08		
Total	224	813.88			

Figure 4.3: *Effect of IBA concentration and exposure time on survival in cuttings of D. lanceolata, P. malaanonan and S. leprosula (concentration plotted again exposure time and species). LOWESS curve fitted*



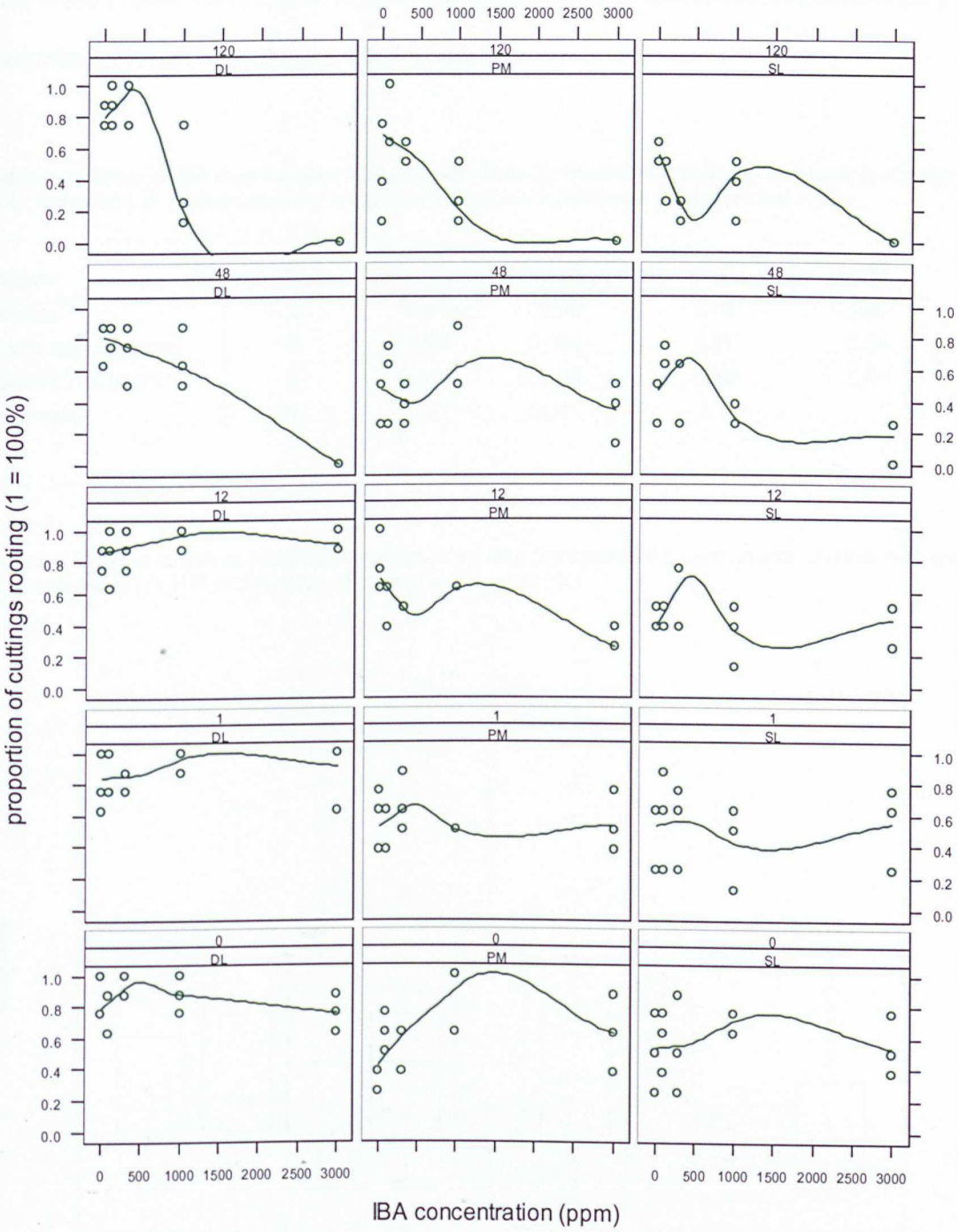
4.3.2 *Rooting percentage*

Both concentration and exposure had a significant effect on rooting percentage which, generally, decreased with increasing IBA concentration and exposure time (Table 4.2). There was a significant species effect on rooting with *D. lanceolata* generally showing the highest rooting percentage (Figure 4.4). The two-way species:concentration and species:exposure interactions on rooting percentage were not significant – but the three-way species:concentration:exposure interaction did show a significant response. It appeared that *D. lanceolata* cuttings were more negatively affected by a combination of increasing IBA concentration and exposure time than *P. malaanonan* or *S. leprosula.* As with survival, there was no significant block effect.

Table 4.2: *Effect of IBA concentration and exposure time on rooting percentage in cuttings of D. lanceolata, P. malaanonan and S. leprosula*

Source	df	Dev.	Mean Dev.	F	p
Block (B)	2	1.26	0.63	1.26	0.38
Species (Spp)	2	133.82	66.91	133.82	<0.0001
Plot (B x Spp)	4	1.99	0.50	0.39	0.82
Concentration (Con)	4	68.05	17.01	13.09	<0.0001
Exposure (Exp)	4	68.68	17.17	13.21	<0.0001
Spp x Con	8	7.33	0.92	0.71	0.78
Spp x Exp	8	12.33	1.54	1.19	0.78
Con x Exp	16	131.78	8.24	6.34	0.31
Spp x Con x Exp	32	75.76	2.37	1.82	<0.0001
Residual	144	186.60	1.30		
Total	224	687.60			

Figure 4.4: *Effect of IBA concentration and exposure time on rooting percentage in cuttings of D. lanceolata, P. malaanonan and S. leprosula (concentration plotted against exposure time and species). LOWESS curve fitted.*



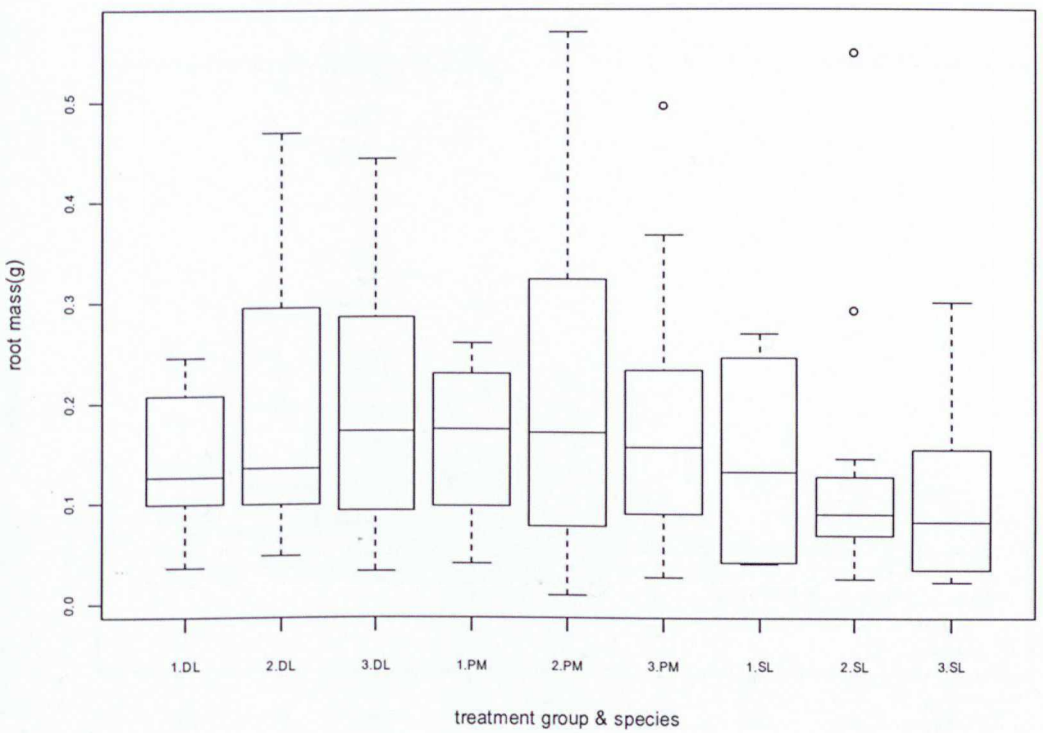
4.3.3 *Destructive measurements*

There were no treatment effects of either IBA concentration or exposure duration on root mass (Table 4.3 & Figure 4.5). There appeared to be some species difference in root mass, though only at the $p < 0.1$ level.

Table 4.3: *Effect of IBA concentration and exposure time (by treatment group) on root mass in cuttings of D. lanceolata, P. malaanonan and S. leprosula. Marginal significance (p<0.1) shown in blue*

Source	df	Sum sq	Mean sq	F	p (>F)
Species	2	0.079	0.040	2.74	0.069
Treatment (*by group*)	2	0.028	0.014	0.97	0.38
Species:Treatment	6	0.019	0.0048	0.33	0.86
Residuals	106	1.57	0.014		

Figure 4.5: *Effect of IBA concentration and exposure time (by treatment group) on root mass in cuttings of D. lanceolata (DL), P. malaanonan (PM) and S. leprosula (SL)*

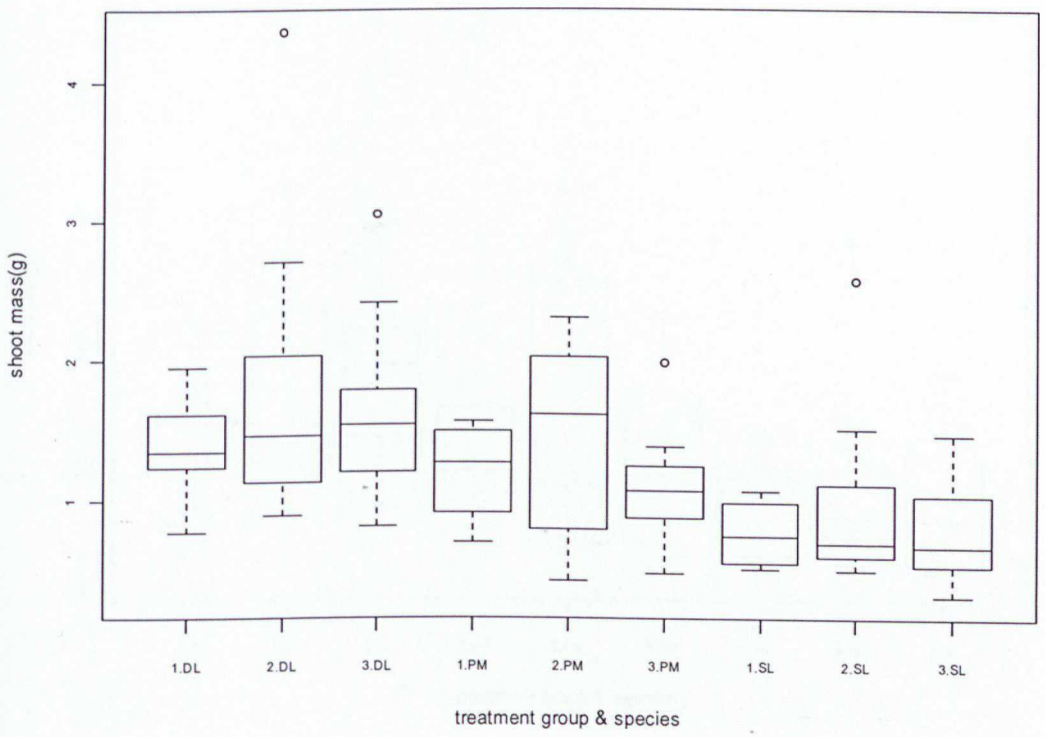


There were highly significant species differences in shoot mass, though no interaction with treatment (Table 4.4 and Figure 4.6). Leaf mass in *S. leprosula* was lower than in either *D. lanceolata* and *P. malaanonan*. The treatment effect showed only marginal significance, the direction of which was not obvious.

Table 4.4: *Effect of IBA concentration and exposure time (by treatment group) on shoot mass in cuttings of D. lanceolata, P. malaanonan and S. leprosula*

Source	df	Sum sq	Mean sq	F	p (>F)
Species	2	10.58	5.29	17.93	<0.0001
Treatment	2	1.52	0.76	2.58	0.080
Species:Treatment	4	0.44	0.011	0.37	0.83
Residuals	109	32.16	0.30		

Figure 4.6: *Effect of IBA concentration and exposure time (by treatment group) on shoot mass in cuttings of D. lanceolata, P. malaanonan and S. leprosula*

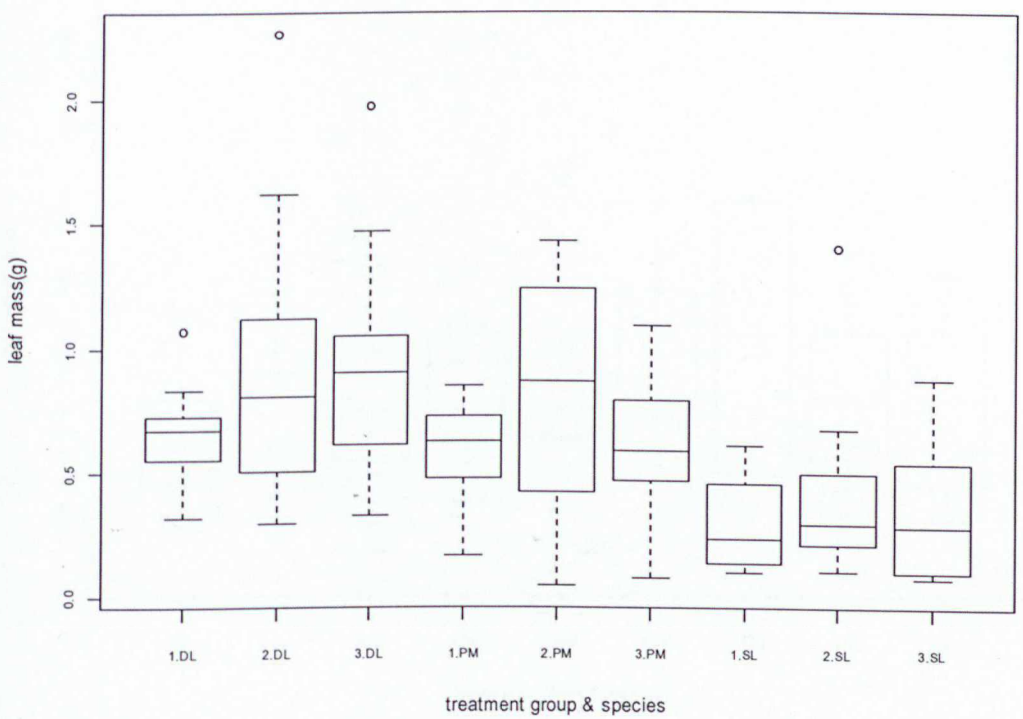


There were significant species differences in leaf mass though, as with the analysis of shoot mass, no interaction with treatment (Table 4.5 and Figure 4.7). *S. leprosula* had a lower leaf mass than either *D. lanceolata* or *P. malaanonan*. There were no treatment effects.

Table 4.5: *Effect of IBA concentration and exposure time (by treatment group) on leaf mass in cuttings of D. lanceolata, P. malaanonan and S. leprosula*

Source	df	Sum sq	Mean sq	F	p (>F)
Species	2	4.32	2.16	16.50	<0.0001
Treatment	2	0.71	0.35	2.70	0.79
Species:Treatment	4	0.34	0.085	0.65	0.63
Residuals	109	14.27	0.13		

Figure 4.7*: Effect of IBA concentration and exposure time (by treatment group) on leaf mass in cuttings of D. lanceolata, P. malaanonan and S. leprosula*

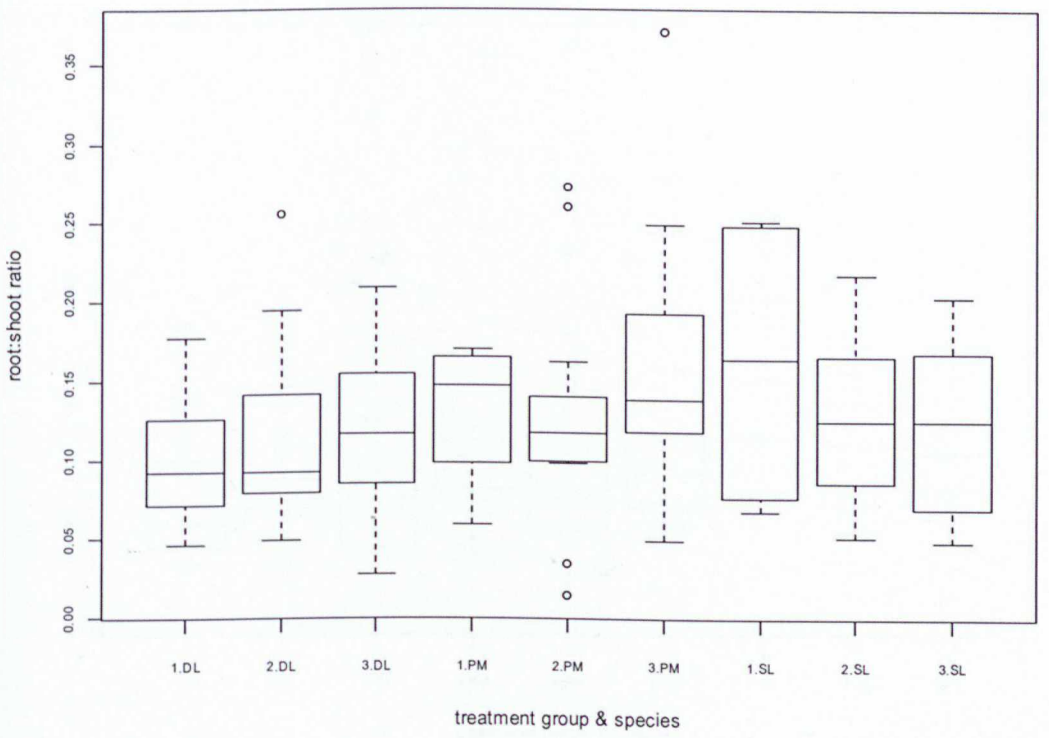


There were marginal species differences in root:shoot ratio with *D. lanceolata* having a slightly lower root:shoot ratio that *P. malaanonan* and *S. leprosula* (Table 4.6 and Figure 4.8). However, there were no significant treatment effects on root:shoot ratio.

Table 4.6: *Effect of IBA concentration and exposure time (by treatment group) on root:shoot ratio in cuttings of D. lanceolata, P. malaanonan and S. leprosula*

Source	df	Sum sq	Mean sq	F	p (>F)
Species	2	0.018	0.0088	2.48	0.089
Treatment	2	0.002	0.001	0.28	0.76
Species:Treatment	4	0.012	0.0031	0.87	0.48
Residuals	109	0.39	0.0036		

Figure 4.8: *Effect of IBA concentration and exposure time (by treatment group) on root:shoot ratio in cuttings of D. lanceolata, P. malaanonan and S. leprosula*

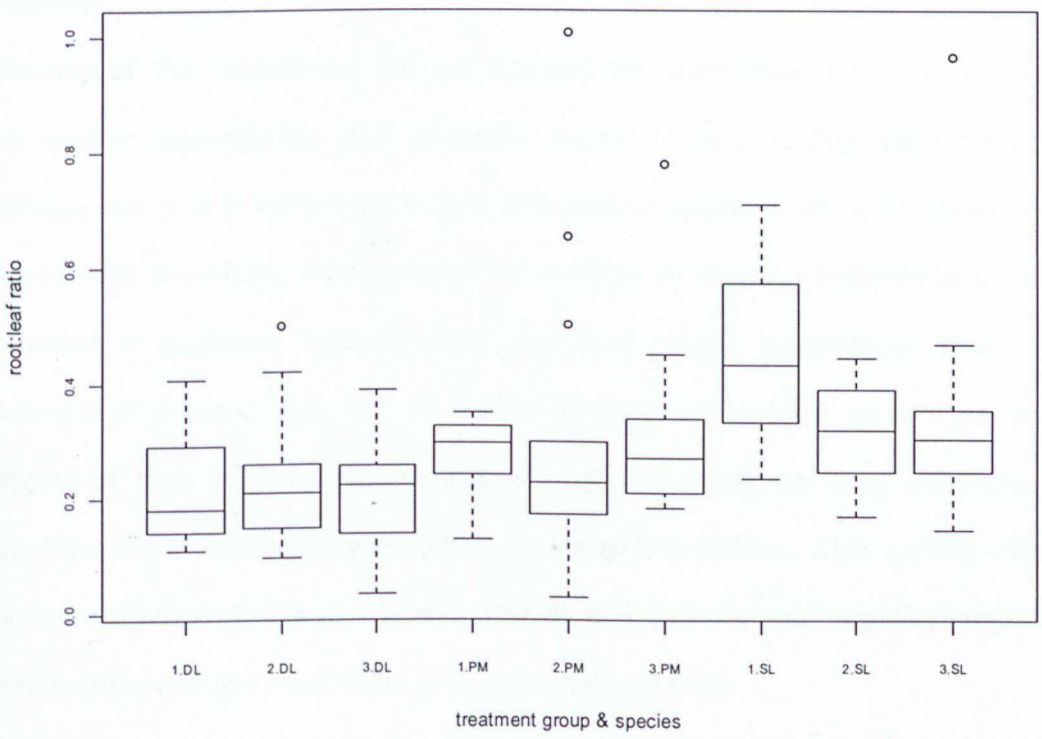


There were species differences in root:leaf ratio with, again, *D. lanceolata* having a lower ratio than either *P. malaanonan* and *S. leprosula* (Table 4.7 and Figure 4.9). As with root:shoot ratio, there were no treatment effects on root:leaf ratio – and no interaction with species.

Table 4.7: *Effect of IBA concentration and exposure time (by treatment group) on root:leaf ratio in cuttings of D. lanceolata, P. malaanonan and S. leprosula*

Source	df	Sum sq	Mean sq	F	p (>F)
Species	2	0.34	0.17	7.90	0.00063
Treatment	2	0.0021	0.0011	0.05	0.95
Species:Treatment	4	0.062	0.016	0.73	0.58
Residuals	109	2.33	0.021		

Figure 4.9: *Effect of IBA concentration and exposure time (by treatment group) on root:leaf ratio in cuttings of D. lanceolata, P. malaanonan and S. leprosula*



4.4 Discussion

Previous research indicated that the application of IBA to dipterocarp cuttings did not, generally, have a strong stimulatory affect on root initiation but that greater root development may have been promoted in several species, especially when applied at a concentration of approximately 2,000 ppm. However, results were inconclusive and well designed and replicated studies in this field are rare, with most using only relatively simplistic measures (root count) to assess root development. No published studies have attempted to assess the extent of root formation using destructive measurements or on resource partitioning between roots and shoots.

In all of the cited literature relating to dipterocarps, plant growth regulators were applied as quick-dip liquid solutions. No published literature has reported the use of alternative application methods, including soaking the cutting base in dilute IBA solutions prior to insertion. Given the somewhat inconclusive results from previous research, the use of alternative methods of IBA application certainly merited attention.

Results of this experiment did not support the hypothesis that IBA applied in increasing concentration and exposure would improve rooting percentage and subsequent root development. In fact, the reverse appeared to be the case. It was found that increasing the exposure of cuttings to higher concentrations of IBA resulted in increased mortality and decreased rooting percentage. There were species differences in terms of cutting survival and rooting percentage and it appeared that the negative impacts of high concentration, long exposure IBA treatments were particularly severe in *D. lanceolata* cuttings. This agreed with the findings of Moura-Costa and Lundoh (1994) who also reported negative impacts on rooting following IBA application to *D. lanceolata* cuttings.

Moreover, and in contrast to a number of the studies cited, there were no obvious ancillary benefits in terms of root development as none of the treatments affected root mass. Although there were clear species differences in a number of the

parameters measured as part of the destructive harvest, none of the treatment:species interactions were significant indicating that dipterocarp cuttings, in terms of both root and shoot development, showed no discernible response to IBA.

As with the previous experiment[1], results based on shoot and leaf measurements must be treated with some caution as these parameters are to some extent set at the time of cutting removal from the parent plant. However, the analysis of root:shoot and root:leaf ratios did allow for the extent of root formation to be assessed while controlling for the overall size of the cutting.

Increased cutting mortality in the higher concentration/long exposure treatments was unexpected, especially given the reported low phytotoxicity of IBA (e.g. Hartmann *et al.*, 2002). Cuttings in these more extreme treatments, particularly those in the 3,000 ppm concentration IBA/120 hour exposure treatment, showed severe stem scorching and almost complete defoliation (Figures 4.10 and 4.11).

Figure 4.10: *Severe damage in D. lanceolata cuttings treated with 3,000 ppm IBA for 120 hours*

Given that de-ionised water was used as the primary solute for the IBA preparations, it is probable that IBA itself was the causal agent for this damage; cuttings exposed for long durations in the control and low IBA concentration treatments showed no obvious signs of physical damage or physiological stress.

[1] *Chapter 3 – page 53*

Figure 4.11: *Severe damage in S. leprosula cuttings treated with 3,000 ppm IBA for 120 hours*

Although IBA soaking treatments were clearly unsuccessful in promoting increased root initiation or development, the technique yielded the potentially important finding that dipterocarps showed some degree of phytoxicity to applied IBA. Negative impacts of IBA on cutting survival, although rarely reported, are not unknown; Ofori and colleagues (1996) showed increased mortality of cuttings of *Milicia excelsa* following the application of IBA.

In retrospect, and in order to have determined if IBA application had influenced, even if only subtly, the rate of root emergence, there may have been some merit in making sequential rooting assessments. However, given that there were no differences in root development by the time of the destructive harvest after 8 weeks, it is unlikely that the rate of root formation was affected in any significant way.

There were drawbacks with the experimental procedures and subsequent analysis used during this experiment. Certainly a more complete destructive harvest would have been desirable. This was, unfortunately, impossible as several hundred of the cuttings rooted during this experiment were required for field planting[1].

[1] *See Chapter 5 – page 92*

A number of treatments, especially those which resulted in higher levels of cutting mortality, were relatively under-represented in the grouped-treatments which formed the basis of the destructive analysis. However, given the lack of significance, especially in the key parameter of root mass, results can be reported with some confidence. Obviously there was some degree of subjectivity in deciding which treatment should be placed in each of the 3 treatment groups. However, several combinations of treatment groupings were analysed, all of which showed a very similar result and significance levels.

These results were, in essence, similar to those of Brodie (2003) and Moura-Costa & Lundoh (1994) but in contradiction to the majority of studies cited in which the benefits of IBA application, in dipterocarps and other tropical tree species, have been widely reported. On the basis of this research there is no evidence to support the use of IBA in the rooting of dipterocarp cuttings, at least in the species tested. There may be some merit in establishing trials to assess the possible benefits of plant growth regulator application to a wider range of species – especially those dipterocarps which have been found particularly slow or difficult to root. However, given the possible phytotoxic response of *D. lanceolata*, *P. malaanonan* and *S. leprosula* to IBA, it would seem unlikely that any significant benefit would accrue from its application with a broader species range. There may also be some merit in investigating the use of alternative auxin sources, possibly NAA. However, numerous studies have shown IBA to be the most effective auxin source for most species, and that if IBA does not promote improved rooting performance then other plant growth regulators are unlikely to be any more effective (Hartmann *et al*, 2002). The use of alternative hormones would, therefore, probably not yield any significant gains in rooting performance. It is possible that factors other than auxin supply, either physical or physiological, are inhibiting rooting performance in dipterocarp cuttings and further research in this area should be considered.

CHAPTER 5

5. THE ESTABLISHMENT PHASE: SURVIVAL & GROWTH AFTER PLANTING

Experimental aims were to:

i. Establish if the propagation method of dipterocarp planting material (cuttings or seedlings) affected survival rates up to 20 months after planting

ii. Establish if the growth rates of cuttings were similar to those of seedlings

iii. Determine the responses of cuttings and seedlings to differences in canopy openness

iv. Compare root and shoot development in cuttings and seedlings up to 20 months after planting

v. Establish if the IBA treatments applied during the previous experiment (Chapter 4) have any affect on post-planting survival and development

With the hypothesis that:

Cuttings and seedlings of *D. lanceolata, P. malaanonan* and *S. leprosula* show similar survival and growth rates up to 20 months after planting, but that cuttings have a significantly lower root mass and root:shoot ratio.

5.1 Background & supporting literature

It is crucial to the success of any planting programme that survival and growth rates of planted seedlings (or cuttings) are within acceptable limits. High early mortality and abnormally slow growth are two of the main causes for the failure of plantations in the tropics and these are often associated with the 'quality' of planting material, particularly the root system (Evans & Turnbull, 2004). Vegetative propagation by stem cuttings can provide a viable method for the production of dipterocarp planting material only if cuttings show similar survival and growth rates to seedlings.

The ecophysiology of dipterocarp seedlings and their recruitment, survival and early growth are influenced by a series of environmental and physiological interactions and these have been the subject of much research (reviewed in the following section). There is also a considerable body of applied research on forest rehabilitation by enrichment planting including methods for maximising the survival and growth rates of planted dipterocarp seedlings (e.g. Moura-Costa *et al.*, 1996; Schulze *et al.*, 1994; Ådjers *et al.*, 1995; Nussbaum *et al.*, 1995; Montagnini *et al.*, 1997; Yap, 1998; Li, 2006). However, there are no published data to indicate how dipterocarp cuttings perform after planting or how their development compares to that of seedlings; evidence from other tree species, either tropical or temperate, is relatively scant.

Naturally recruited dipterocarp seedlings tend to show relatively high mortality in the first year after germination, regularly in excess of 30% (Turner, 1990; Itoh, 1995). However, following periods of low rainfall, such as during an ENSO event, attrition rates may be considerably higher (Walsh & Newbery, 1999; Bebber *et al.*, 2004). After this initial die-off, mortality rates generally stabilise and the surviving seedlings may persist for several years, possibly even decades (Whitmore, 1984; Ashton, 1988; Brown *et al.*, 1999; Delissio *et al.*, 2002).

Light is probably the main environmental factor determining the survival of dipterocarp seedlings. As long ago as the 1930s Foxworthy (1932) noted that "*in certain very dark places, where the canopy cover is very dense, little or no regeneration survives. In other places seedlings of many species may persist for a number of years in a state of arrested development*". Although light is clearly very important, the survivorship of dipterocarp seedlings is governed by the interaction of a number of variables including canopy openness associated with gap formation, seedling size when the gap forms, drought, herbivory (including root herbivory), nutrient availability, mycorrhizal development, root competition and physical damage (caused by tree and branch falls). Rather oddly, there is little evidence from the literature that fungal pathogens have any impact on the survival of dipterocarp

seedlings. These factors have been the subject of a large body of research and some debate (reviewed by Brown *et al.*, 1999; also: Hubbell & Foster, 1986; Ashton, 1988; Turner *et al.*, 1993; Burslem *et al.*, 1995, 1996; Itoh *et al.*, 1995; Grubb, 1996; Press *et al.*, 1996; Becker *et al.*, 1998; Turner, 2001; Bebber *et al.*, 2004; Tanner *et al.*, 2005). In general though, and as originally proposed by Brown and Whitmore (1992), it is probably true to say that species surviving in a seedling bank will simply be those that are able to persist for longest in the understory (i.e. the most shade tolerant species). However, in circumstances where gap formation occurs soon after the germination, the faster-growing, more light-demanding dipterocarps which would be unlikely to survive long under a closed canopy, would probably win through (Brown and Whitmore, 1992; Brown, 1996; Brown *et al.*, 1999).

Results from a number of both operational projects and academic studies indicate that mortality rates for enrichment planted dipterocarps in well-tended plantations largely mirror those reported for populations of naturally-recruited seedlings. Based on surveys of several thousand hectares of enrichment planted forest in the Malaysian states of Perak and Selangor, Appanah and Weinland (1993) recommended basing planning decisions on mean annual mortality of 10% for the first three years after planting and 5% annually thereafter (Appanah & Weinland, 1993). The authors also noted the considerable between-species variability in survival with rates (after approximately 15 years) ranging from less than 30% in *Shorea curtisii* to almost 80% in *Parashorea stellata* (Appanah & Weinland, 1993).

In work on a forest rehabilitation project in South Kalimantan, Ådjers and colleagues (1995) tested the effects of planting line width, line direction and maintenance regime on survival and growth rates in three *Shorea species* (*S. johorensis, S. leprosula and S. parvifolia*) enrichment planted in logged forest. They monitored growth and survival up to 2 years after planting and reported that line width, line direction and maintenance method had no effect on survival with mean values (across treatments)

of 50% for *S. johorensis*, 64% for *S. leprosula* and 55% for *S. parvifolia* (Ådjers *et al.*, 1995).

In research based on the INFAPRO project in Sabah, focussing on 5 dipterocarp species (*Hopea nervosa*, *H. sangal*, *Shorea ovalis*, *S. beccariana* and *Parashorea tomentella*), Li (2006) demonstrated that survival 3 months after planting was strongly influenced by slope, elevation, logging method (tractor *versus* high-lead yarding) and canopy openness. It appeared that survival of planted seedlings was highest on slopes of 15 – 30° and in areas logged by high-lead machines rather than tractor. These correlations are somewhat difficult to interpret into causal relationships in that the steeper slopes of the INFAPRO area were often logged by high-lead machines (Marsh & Greer, 1992; Li, 2006) and that, generally, greater volumes of timber were removed from the low-lying compartments of moderate terrain (Moura-Costa & Karolus, 1992). The remnant forest in these areas was also left in a considerably more degraded condition than the steeper slopes, with a greater density of skid-tracks, log-landings and open grassland (Marsh & Greer, 1992; Nussbaum *et al.*, 1995; Pinard *et al.*, 1996; Pinard *et al.*, 2000; *personal observation*). At 3 years after planting, survival appeared most strongly influenced by logging method with, as with the 3 month data, higher survival in areas logged using high-lead machines. Timber extraction volume (higher survival associated with lower extraction volumes) and forest type (higher survival associated with less disturbed forest with greater stocking volumes) also had significant effects on the survival of planted dipterocarp seedlings (Li, 2006). Overall survival rates on the INFAPRO project are considerably higher than those stated for other rehabilitation projects, either in SE Asia or tropical South America. The possible reasons for this are discussed in section 5.5. Survival rates for other dipterocarp enrichment planting programmes in Sabah and Kalimantan have been reported by Ådjers and colleagues (1995), Liew and Wong (1973), Chai (1974) and Garcia (1995, *pers. comm.)*, with rates in the 40 to 70% range at 2 to 3 years after planting.

Due to the somewhat unusual reproductive strategy and ecophysiology of the dipterocarps, drawing inferences from enrichment planting programmes elsewhere in the tropics is perhaps not terribly instructive. However, similar levels of survival have been reported for enrichment planting programmes in Argentina (Montagnini *et al.*, 1997), Brazil (d'Oliveira, 2000) and central Panama (Griscom *et al.*, 2005).

Despite the relatively large body of work which exists on the vegetative propagation of dipterocarps (reviewed by Dick & Aminah, 1994), there are no published data to indicate the survivorship of dipterocarp cuttings after planting. There is a paucity of information on the post-planting survival of cuttings from other tropical species; the only examples of research in this area are from the temperate literature, and these are relatively few. In research on *Picea abies*, which compared the field performance of cuttings and seedlings up to 14 years after planting, there was no difference in survival between the two plant types. Cuttings and seedlings showed survival of 80 and 78% respectively, with most mortality occurring in the first 4 years after planting (Hannerz & Wilhelmsson, 1998). In comparative research on *Eucalyptus globulus* cuttings and seedlings, higher mortality was noted in cuttings when plants were subjected to water stress treatments. The authors attributed this greater susceptibility to water stress to the lower root:shoot ratio of cuttings (Sasse & Sands, 1996). A high root:shoot ratio is regarded as being an important indicator of the quality of planting material and in their standard work on plantation forestry in the tropics, Evans and Turnbull (2004) highlight the importance of the root system, particularly a high root:shoot ratio, in maintaining survival rates in the immediate post-planting period (Evans & Turnbull, 2004).

The growth of dipterocarps has been studied by foresters and silviculturalists for over 70 years (e.g. Foxworthy, 1927; 1932; Strugnell, 1947; Walton, 1948; Wyatt-Smith, 1963; reviewed by Whitmore, 1984, 1990; Richards, 1996). Given the dominance of the dipterocarps in SE Asia, their ecosystem importance, unusual reproductive strategies and ecophysiological traits, the growth of dipterocarp seedlings has also

been the subject of numerous academic studies, both pure and applied. Many of these have investigated the apparent trade-off between growth, shade-tolerance and responses to gap formation, timber density of the particular species, insect herbivory, nutrient availability, drought and the affects of neighbourhood composition (e.g. Burslem *et al.*, 1996; Press *et al.*, 1996; Newbery *et al.*, 1999; Brown *et al.*, 1999; Walsh & Newbery, 1999; Blundell & Peart, 2001; Bungard *et al.*, 2002; Leakey *et al.*, 2003; Kurokawa *et al.*, 2004; King *et al.*, 2005; Stoll & Newbery 2005; Massey *et al.*, 2006). A detailed review of this literature is beyond the scope of this thesis, but the following provides a summary of the factors that influence dipterocarp growth rates:

Growth rates are strongly correlated with the size of gap in which seedlings are growing with, unsurprisingly, higher growth in larger gaps (Brown *et al.*, 1999), although the spatial and temporal pattern of the available light, especially sunfleck activity, has also been shown to be an important growth determinant (Leakey *et al.*, 2004). In the case of enrichment planting programmes, the width of the planting line or size of the planting gap are important in supporting growth rates (Ådjers *et al.*, 1995, Bebber *et al.*, 2002). King and colleagues (King *et al.*, 2005) suggested that much of both the within and between species variability in dipterocarp growth rates could be accounted for by the mechanistic assumption that, within a given size class, growth was proportional to light interception and the wood density of the species.

Nutrients may be more important in supporting higher growth rates in light-demanding species such as *Shorea leprosula* rather than in more shade-tolerant species (e.g. *Dryobalanops lanceolata*), though where light is not limiting growth is unlikely to be affected by low nutrient availability (Bungard *et al.*, 2002). However, for seedlings growing in the deep shade of the understory prior to gap formation, nutrients may, in addition to light, become limiting (Burslem *et al.*, 1996). In enrichment planting programmes, such as those carried out by INFAPRO, it has been shown that nutrients do not limit the growth of planted dipterocarp seedlings across a range of both light-demanding and shade tolerant species (Yap, 1999).

Dipterocarps invest considerable resources to defence against herbivory (Kurokawa *et al.*, 2004) and it appears that the growth or survival of dipterocarps is hardly impacted by the action of insect herbivores (Blundell & Peart, 2001). There is no reason to assume that herbivory would have a greater impact in enrichment planted rather than naturally recruited seedlings, although macro herbivores (e.g. deer, pigs, elephants) may have a greater influence given that they appear to preferentially browse along planting lines (*personal observation*; Yap, 2005 *pers. comm.*).

Recent work based at Danum Valley has indicated that growth rates of dipterocarp seedlings may be influenced by neighbourhood composition with seedlings growing at a faster rate in conspecific rather than heterospecific stands (Stoll & Newbery, 2005; Massey *et al.*, 2006). There is, at present, no evidence to indicate if the species composition of seedlings planted as part of enrichment planting programmes influences growth rate (or survival). This is the subject of ongoing research at Danum Valley and elsewhere (Sherer-Lorenzen *et al.*, 2005).

Given the range of environmental factors that may affect the growth of dipterocarp seedlings, predicting growth rates for individual dipterocarp species in an enrichment planting situation is problematic. However, Appanah and Weinland (1993) suggest that growth rates in properly maintained plantations would be in the order of 1.2 – 1.8 m $year^{-1}$ height and 1.3 – 1.5 cm $year^{-1}$ diameter. Many of the seedlings planted at the start of the INFAPRO project are now, some 10 - 12 years after planting, well over 15 metres in height (personal observation).

As with survival, there is almost no evidence from the literature, relating to either tropical or temperate tree species, to indicate how growth rates between cuttings and seedlings may vary; the little work that has been done in this area has focused on coniferous plantation species. In a study based in New Zealand that compared growth in cuttings and seedlings of *Pinus radiata*, Watson & Tombleson (2002) found no difference in total root mass or root:shoot ratio between the two plant types, although there were morphological differences in root depth and the extent of lateral

root development. In particular, cuttings showed greater biomass allocation in roots immediately adjoining the main stem. The authors suggested that the apparent bulk of the root/stem interface may improve eventual resistance to wind-throw (Watson & Tombleson, 2002). Gemmel and colleagues (1991) reported that height growth in 8 year old cuttings of *Picea abies* was 15% greater than in seedlings of the same genetic origin (Gemmel *et al.*, 1991). Similarly, and also in research comparing cutting and seedling growth in *P. abies*, Roulund and colleagues (1985) reported that although cuttings were 9% shorter at planting than seedlings, after 13 years growth cuttings were 18% taller (Roulund *et al.*, 1985). Rouland and Bergstedt (1982) reported similar findings from comparative work on *Picea sitchensis* cuttings and seedlings in which cuttings were 25% taller than seedlings 10 years after planting (Rouland & Bergstedt, 1982 cited in Hannerz & Wilhelmsson, 1998). In research comparing growth in cuttings and seedlings of *P. abies* over a 14 year period, Hannerz and Wilhelmsson (1998) reported that height growth in cuttings was uniformly greater than in seedlings, though the increase did not prove statistically significant at the $p < 0.05$ level. The authors suggested that the possible increased growth of cuttings was not due to genotypic effects (cuttings were taken from seedlings rather than clonal hedge-orchards) but rather a physiological gain – although they did not specify what this might be (Hannerz & Wilhelmsson, 1998). This or other work does not indicate why, if genetic effects are not responsible, cuttings should exhibit faster initial growth than seedlings.

In probably the only published research on the post-planting growth of dipterocarp cuttings, Aminah (1999) reported that cuttings of *Shorea leprosula* had annual height and diameter growth rates of 1.1 m and 1.3 cm respectively up to 5 years after planting. Cuttings of *Hopea odorata*, up to 6 years after planting, showed height and diameter growth rates of 1.7 m and 1.7 cm respectively. However, there was no assessment of survival or root growth and development.

5.2 Materials & methods

Cuttings and seedlings were planted into forest within the INFAPRO project area, Ulu Segama Forest Reserve. The planting area was logged in 1978, using tractor yarding methods, and originally enrichment planted during 1993 as described in Chapter 2.

Three x 1 hectare plots were established, each measuring 100m by 100m. The 3 plots were located within the same *c.* 50 ha logging compartment (coupe 78c) and spaced at approx. 200m from plot edge to plot edge. Existing planting lines (at 10m centres) were re-opened to a width of 2m and the cuttings and seedlings inter-planted with existing trees according to a completely randomised design. Immediately prior to planting the canopy cover at each planting point was estimated using a spherical densiometer (Model A, Forest Densiometers, Arlington, Virginia, USA)[1] consisting of a convex mirror divided into a cross-shaped grid of 24 squares. The densiometer was held at waist height (at approximately arm's length from the body). The observer counted in how many of four points, equally spaced within each grid square, open sky was visible and then summed these quantities. Measurements were taken at four cardinal directions at each planting point and divided by 96 to obtain a measurement of canopy cover (Lemmon, 1956).

Prior to planting, cuttings and seedlings were conditioned by placing them under similar nursery conditions (under 70% shade cloth with an identical irrigation regime) for a period of 1 month. Each plot was planted with 125 cuttings and 125 seedlings comprising 120 *D. lanceolata* (60 cuttings, 60 seedlings), 80 *P. malaanonan* (40 cuttings, 40 seedlings), and 50 *S. leprosula* (25 cuttings, 25 seedlings). Cuttings were derived from the experiments carried out as part of Chapter 4, which investigated the effects of hormone application. Seedlings were selected from the general INFAPRO nursery stock. Planting was carried-out at 3 metre centres along each line with each cutting/seedling randomly allocated to each planting point.

[1] Spherical densiometers have been shown to provide a quick and accurate method of assessing the openness of forest canopies (Englund *et al.*, 2005).

Immediately prior to planting 164 cuttings and seedlings were destructively harvested as described in the general methods[1]. The height, stem diameter and leaf number of all planted cuttings and seedlings were measured.

At intervals of 4 months the cuttings and seedlings were surveyed, recording survival, height, diameter (at base) and leaf number. Canopy openness at each planting point was estimated using a spherical densiometer, using the method as previously described. A total of 5 surveys were conducted up to 20 months after planting.

Twenty months after planting 16 cuttings and seedlings of each species were selected at random and harvested destructively as described in General Methods.

Survival data were analysed using a Generalised Linear Model (binary logistic regression). After analysing a full (saturated) model, non-significant interactions were removed through stepwise backwards deletion and new models tested against the saturated model using Akaike Information Criterion (Dalgaard, 2002; Maindonald & Braun, 2003; Hector, 2004)[2].

In order to establish if the hormone treatments from the previous experiment[3] had any longer term effects on cutting survival, a separate analysis was carried out on cuttings only with the treatment groups from the previous experiment carried forward and included in the analyses as a covariate. The basis of these groupings is shown in Figure 5.1.

Figure 5.1: *Treatment groupings from previous experiment*

	0 ppm IBA	*100 ppm IBA*	*300 ppm IBA*	*1,000 ppm IBA*	*3,000 ppm IBA*
1 sec	1	2	3	4	5
1 hour	6	7	8	9	10
12 hours	11	12	13	14	15
48 hours	16	17	18	19	20
120 hours	21	22	23	24	25

Treatment group 1	87 cuttings
Treatment group 2	139 cuttings
Treatment group 3	149 cuttings

[1] *See Chapter 2, Section 2.7 – page 50*
[2] *For further details of the analyses used see Appendix 3 – page 192*
[3] *For further details see Chapter 4, Section 4.2 – page 76*

Relative growth rates are presented as mm growth in diameter or height/month (all data log transformed). These were calculated by subtracting the initial measurements of diameter and height from the final measurements (at 20 months after planting) and dividing by the length of monitoring period (20 months). Data from the destructive harvests were analysed using a Linear Model.

5.3 Results

5.3.1 *Survival*

There was no significant difference in survival between cuttings (in any of the species) at 4 months after planting (Table 5.1). The survival percentage for each species (cuttings and seedlings) are shown in Table 5.3. The interaction between species, initial height and canopy opening had a significant effect on survival; it appeared that *D. lanceolata* that were taller at planting survived less well under open canopy, with the reverse being the case in *S. leprosula* (Figure 5.7).

Table 5.1: *GLM analysis for survival in cuttings and seedlings of D. lanceolata, P. malaanonan & S. leprosula 4 months after planting*

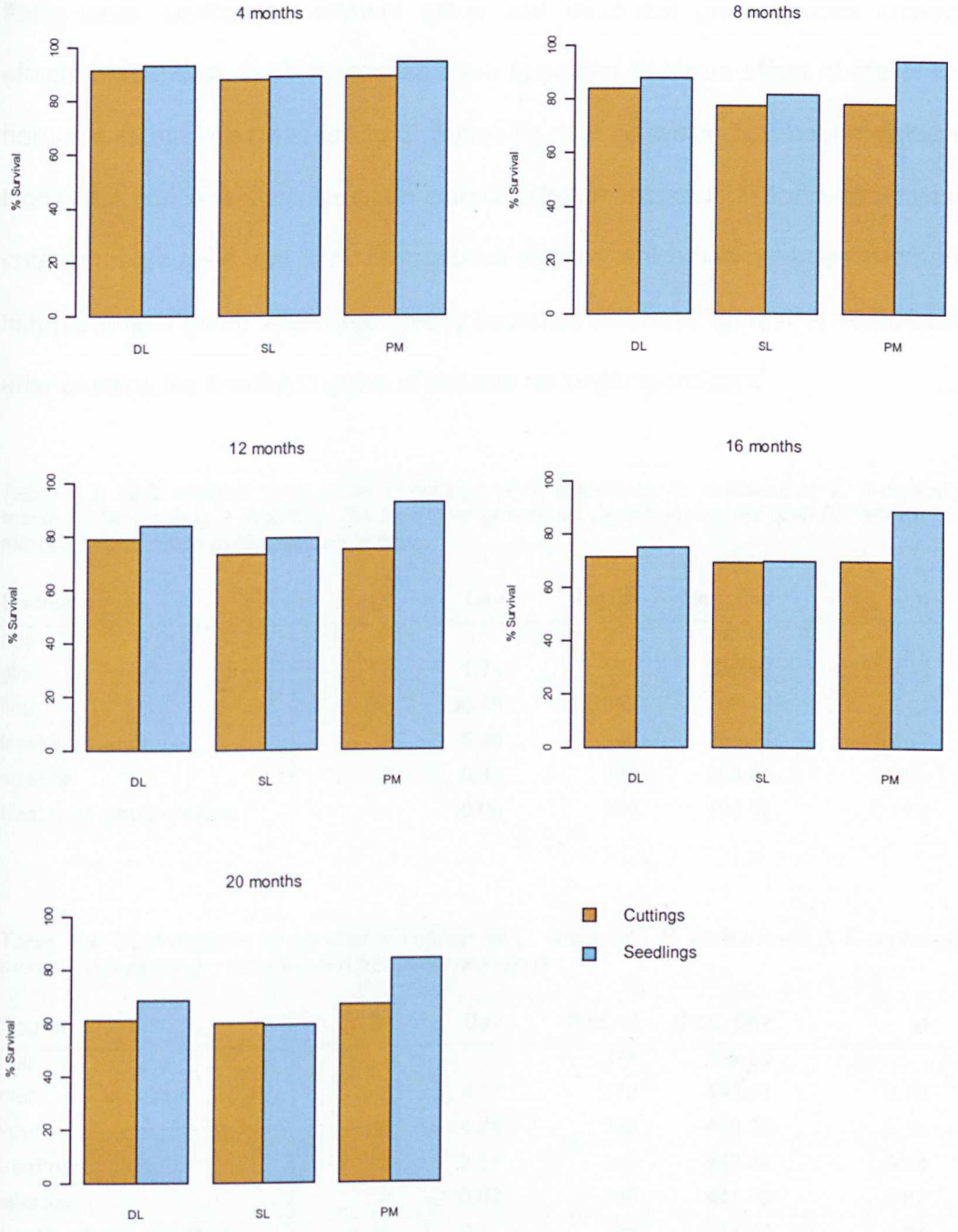
Source	Df	Dev	Res. df	Res. Dev	p
null			749	437.41	
plot	2	1.71	747	435.70	0.43
treatment *(cutting/seedling)*	1	1.72	746	433.98	0.19
species	2	1.62	744	432.36	0.44
initial height	1	1.62	743	430.74	0.20
canopy (*openness*)	1	2.08	742	428.65	0.15
treatment:species	2	1.06	740	427.59	0.59
treatment:initial height	1	0.01	739	427.58	0.92
species:initial height	2	1.62	737	425.96	0.44
treatment:canopy	1	1.33	736	424.63	0.25
species:canopy	2	1.55	734	423.08	0.46
initial height:canopy	1	3.07	733	420.01	0.08
treatment:species:initial height	2	0.18	731	419.83	0.92
treatment:species:canopy	2	2.18	729	417.65	0.34
treatment:initial height:canopy	1	2.60	728	415.05	0.11
species:initial height:canopy	2	9.98	726	405.07	0.01

At 20 months after planting there was a significant treatment effect on survival with seedlings surviving better than cuttings (Table 5.2, Figures 5.2, 5.4, 5.5). *P. malaanonan* showed higher survival than either *D. lanceolata* or *S. leprosula* (Figures 5.2, 5.4, 5.6). The interaction between species and canopy openness had a significant effect on survival (Figure 5.8). *S. leprosula* showed the greatest improvement in survival as canopy openness increased, with a similar response in *P. malaanonan*. The survival response of *D. lanceolata* to more open canopy was relatively flat.

Table 5.2: *GLM analysis for survival in cuttings and seedlings of D. lanceolata, P. malaanonan & S. leprosula 20 months after planting*

Source	Df	Dev	Res. df	Res. Dev	p
null			749	954.77	
plot	2	5.45	747	949.32	0.07
treatment *(cutting/seedling)*	1	6.20	746	943.12	0.01
species	2	11.35	744	931.77	0.0034
initial height	1	0.02	743	931.75	0.88
canopy (*openness*)	1	0.13	742	931.62	0.72
treatment:species	2	4.67	740	926.95	0.10
treatment:initial height	1	2.30	739	924.65	0.13
species:initial height	2	1.75	737	922.91	0.42
treatment:canopy	1	0.02	736	922.89	0.89
species:canopy	2	7.26	734	915.63	0.03
initial height:canopy	1	1.40	733	914.23	0.24
treatment:species:initial height	2	4.98	731	909.25	0.08

Figure 5.2: *Survival in cuttings and seedlings of D. lanceolata (DL), S. leprosula (SL) & P. malaanonan (PM) at 4, 8, 12, 16 & 20 months after planting*



Tables 5.3 and 5.4 show analyses for survival in cuttings at 4 and 20 months after planting with hormone treatment groupings included[1]. At 4 months after planting there were significant treatment group and treatment group:species interaction effects on survival. In *D. lanceolata* there appeared to be no effect of the previous hormone treatments whereas in *S. leprosula* cuttings which had been treated with higher IBA concentrations/exposure duration (treatment group 3) survived better than cuttings in groups 1 and 2. *P. malaanonan* cuttings which had not been treated with IBA (treatment group 1) showed greatly improved survival (Figure 5.3). At 20 months after planting the treatment group effect was no longer significant[2].

Table 5.3: *GLM analysis for survival in cuttings of D. lanceolata, P. malaanonan & S. leprosula 4 months after planting – including IBA treatment groupings. Significant values (p<0.05) shown in red, marginal significance (p<0.1) shown in blue.*

Source	Df	Dev	Res. df	Res. Dev	p
null			374	241.61	
plot	2	1.74	372	239.87	0.42
line	30	30.45	342	209.42	0.44
treatment group	2	5.96	340	203.47	0.051
species	2	0.42	338	203.05	0.81
treatment group:species	4	10.08	334	192.97	0.039

Table 5.4: *GLM analysis for survival in cuttings of D. lanceolata, P. malaanonan & S. leprosula 20 months after planting – including IBA treatment groupings*

Source	Df	Dev	Res. df	Res. Dev	p
null			374	496.55	
plot	2	4.12	372	492.43	0.13
line	30	44.24	342	448.20	0.05
treatments group	2	2.85	340	445.34	0.24
species	2	0.82	338	444.53	0.67
treatment group:species	4	3.11	334	441.42	0.54

[1] *See Figure 5.1, page 101*
[2] *For further details of the analyses used see Appendix 3 – page 192*

Figure 5.3: *Survival in cuttings of D. lanceolata (DL), S. leprosula (SL) & P. malaanonan (PM) including IBA treatment groupings (for details see figure 5.1, page 101)*

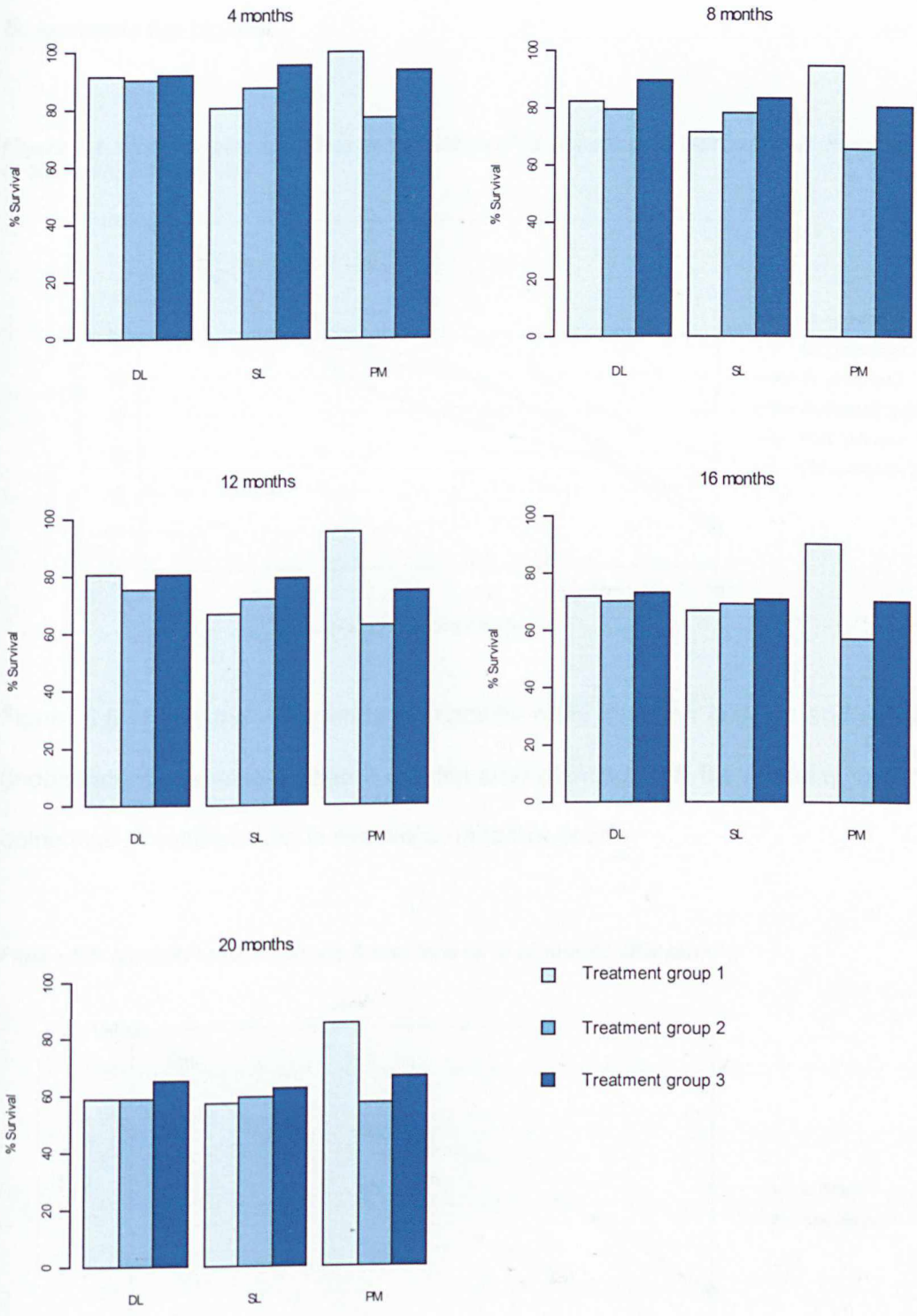


Figure 5.4 indicates the differences in mortality rates between cuttings and seedlings of each species, with *P. malaanonan* seedlings showing the lowest mortality rate and *S. leprosula* the highest.

Figure 5.4: *Mortality rates in cuttings and seedlings of D. lanceolata, S. leprosula & P. malaanonan up to 20 months after planting*

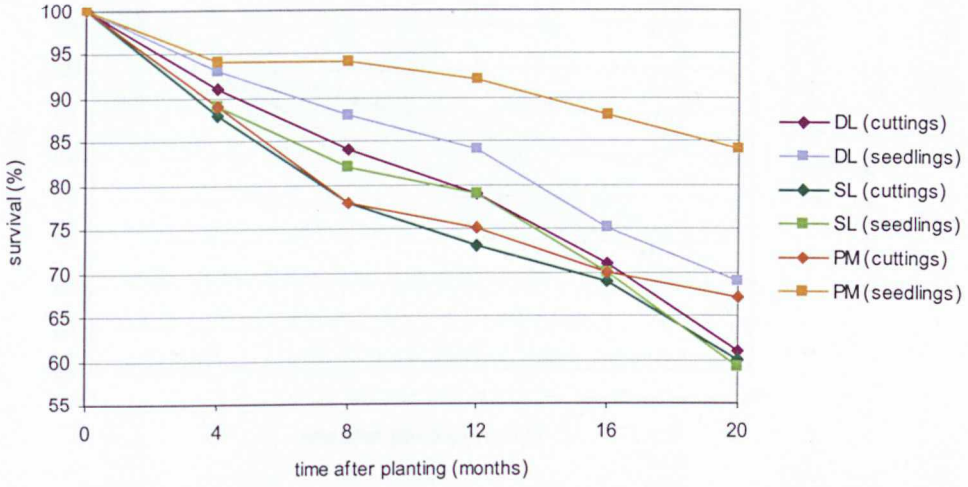


Figure 5.5 shows the divergence of mortality rates between cuttings and seedlings (independent of species) up to 8 months after planting, with the mortality in cuttings being high in cuttings than in seedlings up to this point.

Figure 5.5: *Mortality rates in cuttings & seedlings up to 20 months after planting*

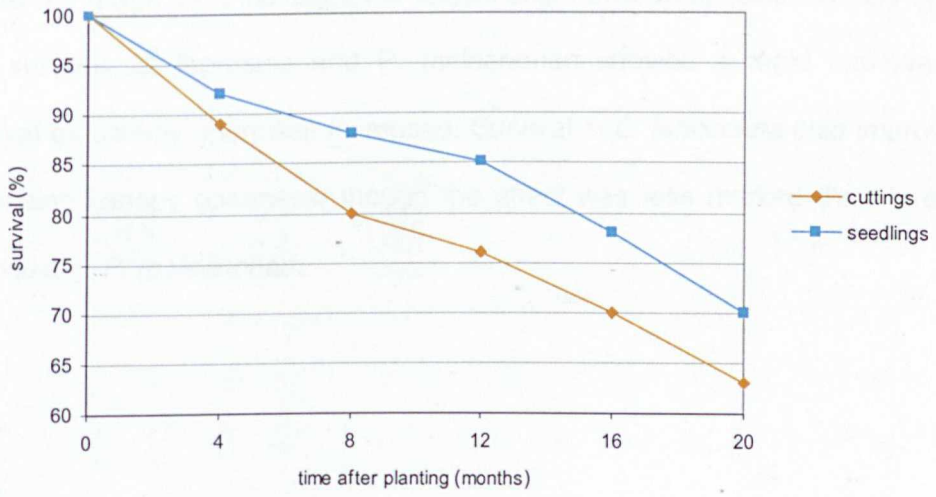


Figure 5.6 shows the difference mortality rates between species (independent of source i.e. cuttings/seedlings). Mortality was highest in *S. leprosula* and lowest in *P. malaanonan.*

Figure 5.6: *Mortality rates in D. lanceolata, S. leprosula & P. malaanonan up to 20 months after planting*

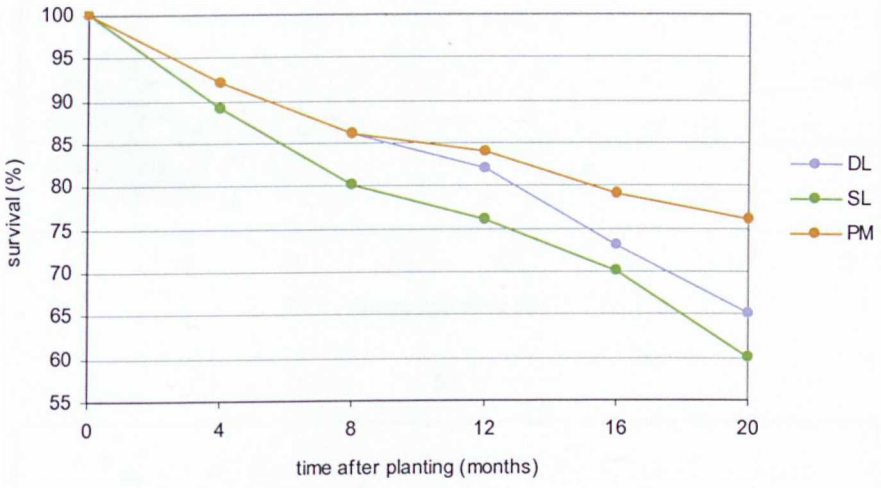


Figure 5.7 (following page) shows the relationship between species, planting height and canopy openness on survival. *S. leprosula* which were taller at planting survived better under more open canopy than shorted plants. In *D. lanceolata*, there was greater mortality in shorter plants planted in open canopy. Responses in *P. malaanonan* were relatively flat.

Figure 5.8 (page 111) indicates the relationship between species, canopy openness and survival. S. leprosula and P. malaanonan showed a rapid improvement in survival as canopy openness increased. Survival in *D. lanceolata* also improved with increasing canopy openness, though the effect was less marked than in either *S. leprosula* or *P. malaanonan*.

Figure 5.7: *Survival in D. lanceolata (DL), S. leprosula (SL) & P. malaanonan (PM) cuttings & seedlings plotted against initial height & canopy openness at 4 months after planting. Open black points indicate surviving plants, open orange points indicate dead plants*

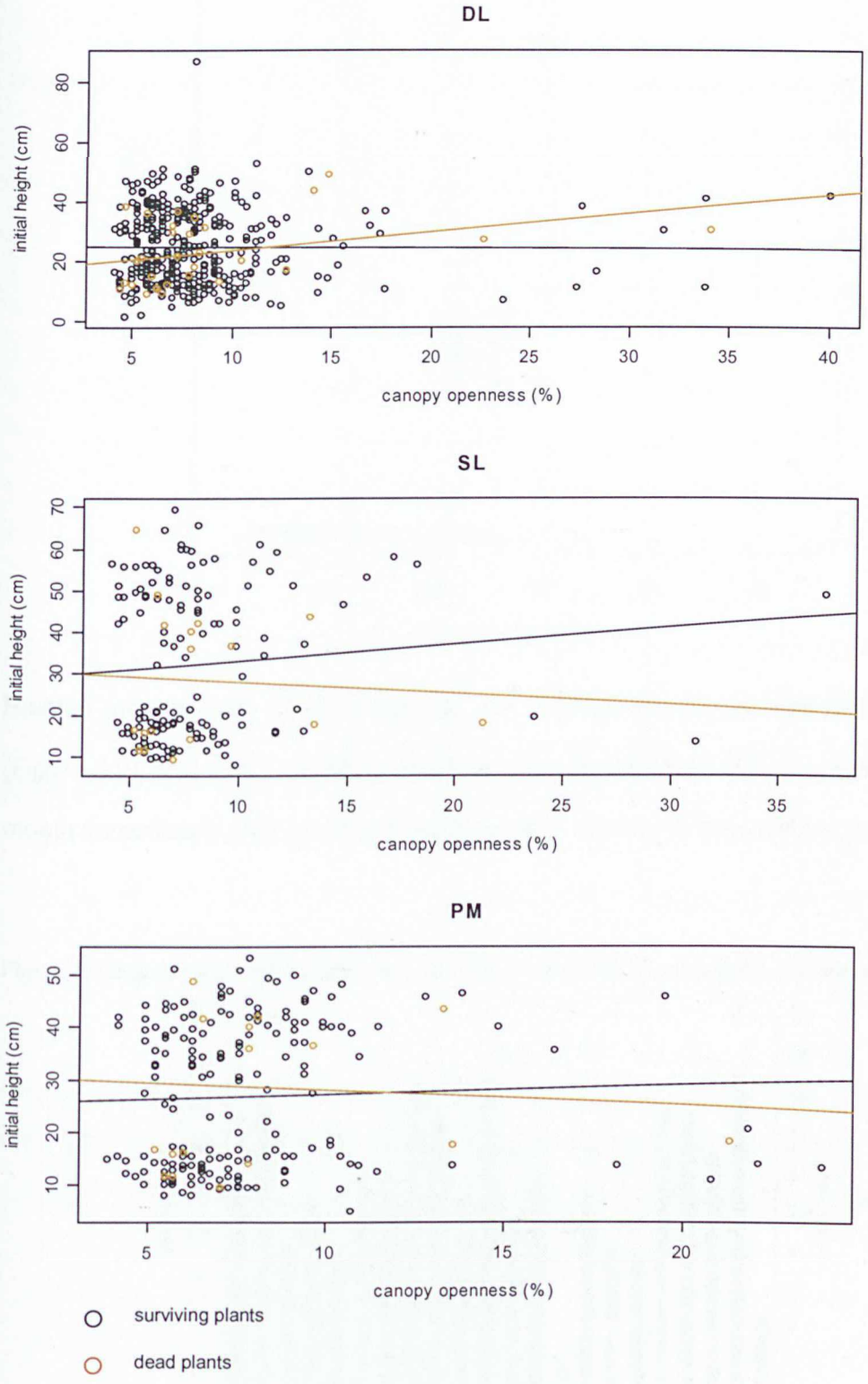
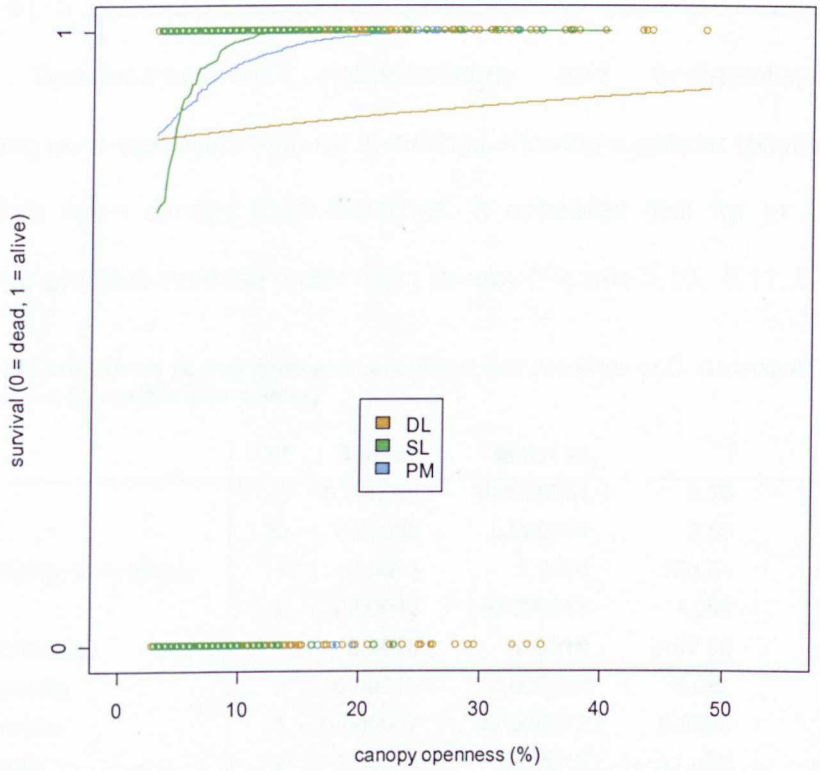
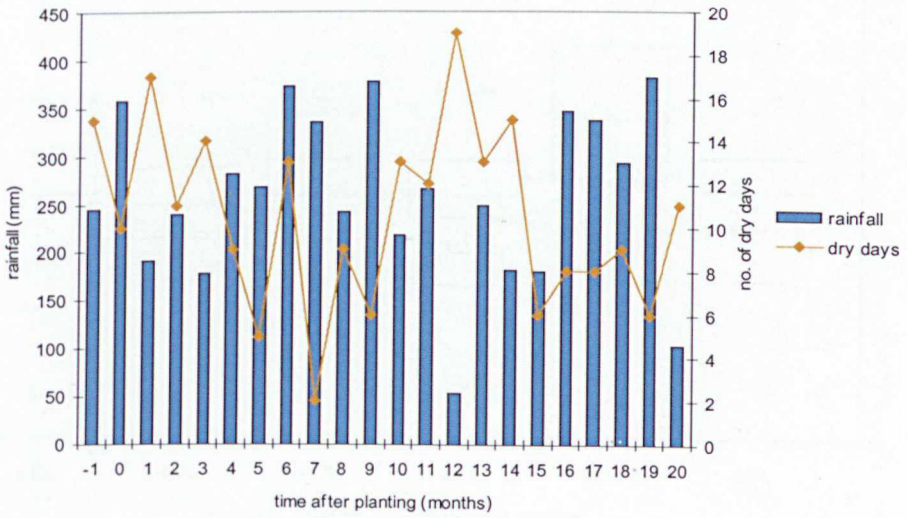


Figure 5.8: *Survival in D. lanceolata (DL), P. malaanonan (PM) & S. leprosula (SL) (cuttings & seedlings) plotted against canopy openness at 20 months after planting*



Rainfall records from DVFC show that the assessment period was generally wet (Figure 5.9), with only 1 month in which rainfall was less than 100 mm. However, the month immediately after planting (month 1) had a total of 18 days without rain.

Figure 5.9: *Rainfall & dry days during the period one month before planting to the end of the experiment*



5.3.2 *Relative growth rate*

Relative growth rate (rgr) diameter was significantly higher in cuttings than seedlings (Table 5.5). *S. leprosula* showed the highest rgr. Rgr was higher under more open canopy. Species:treatment, species:canopy and treatment:species:canopy interactions were significant with rgr in cuttings showing a greater (positive) response under more open canopy than seedlings. It appeared that rgr in *D. lanceolata* showed the greatest increase under open canopy (Figures 5.10, 5.11, 5.14).

Table 5.5: *LM analysis on (log)rgr (diameter) in cuttings and seedlings of D. lanceolata, P. malaanonan & S. leprosula at 20 months after planting*

Source	df	Sum sq	Mean sq	f	p
plot	2	0.000016	0.0000081	0.75	0.48
line	30	0.00083	0.000028	2.55	<0.0001
treatment *(cuttings/seedlings)*	1	0.0014	0.0014	126.61	<0.0001
species	2	0.00015	0.000077	7.099	0.00092
canopy (openness)	1	0.0018	0.0018	167.89	<0.0001
treatment:species	2	0.00013	0.000066	6.082	0.0025
treatment:canopy	1	0.000007	0.0000072	0.6606	0.42
species:canopy	2	0.00024	0.00012	11.069	<0.0001
treatment:species:canopy	2	0.00011	0.000057	5.26	0.0055
residuals	456	0.0049	0.000011		

Figure 5.10: *Rgr diameter (mm/month) at 20 months after planting in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula*

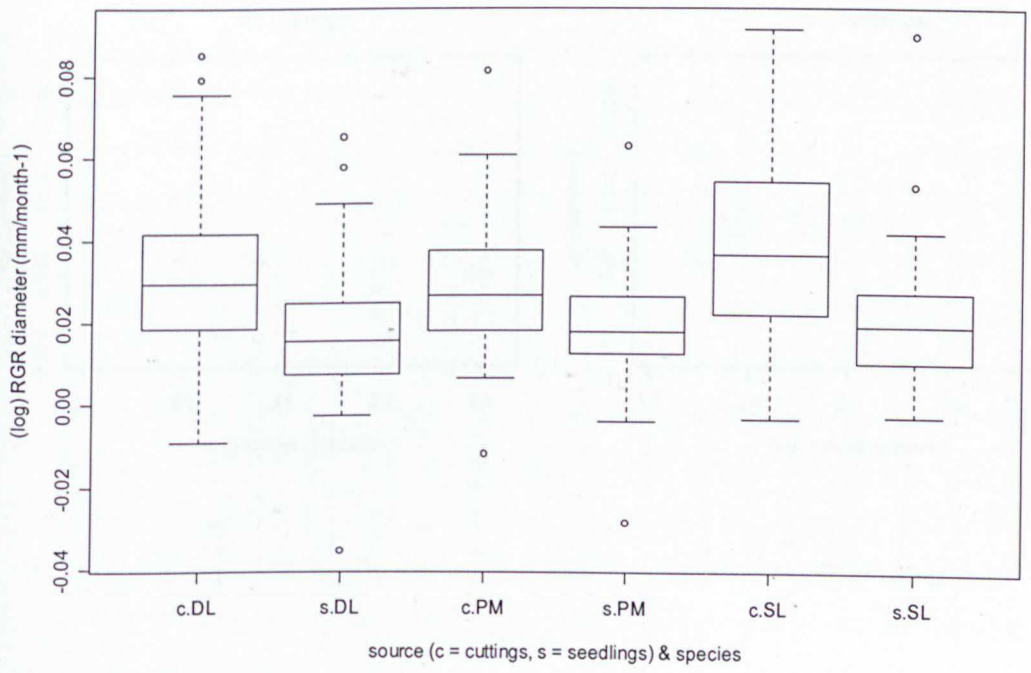
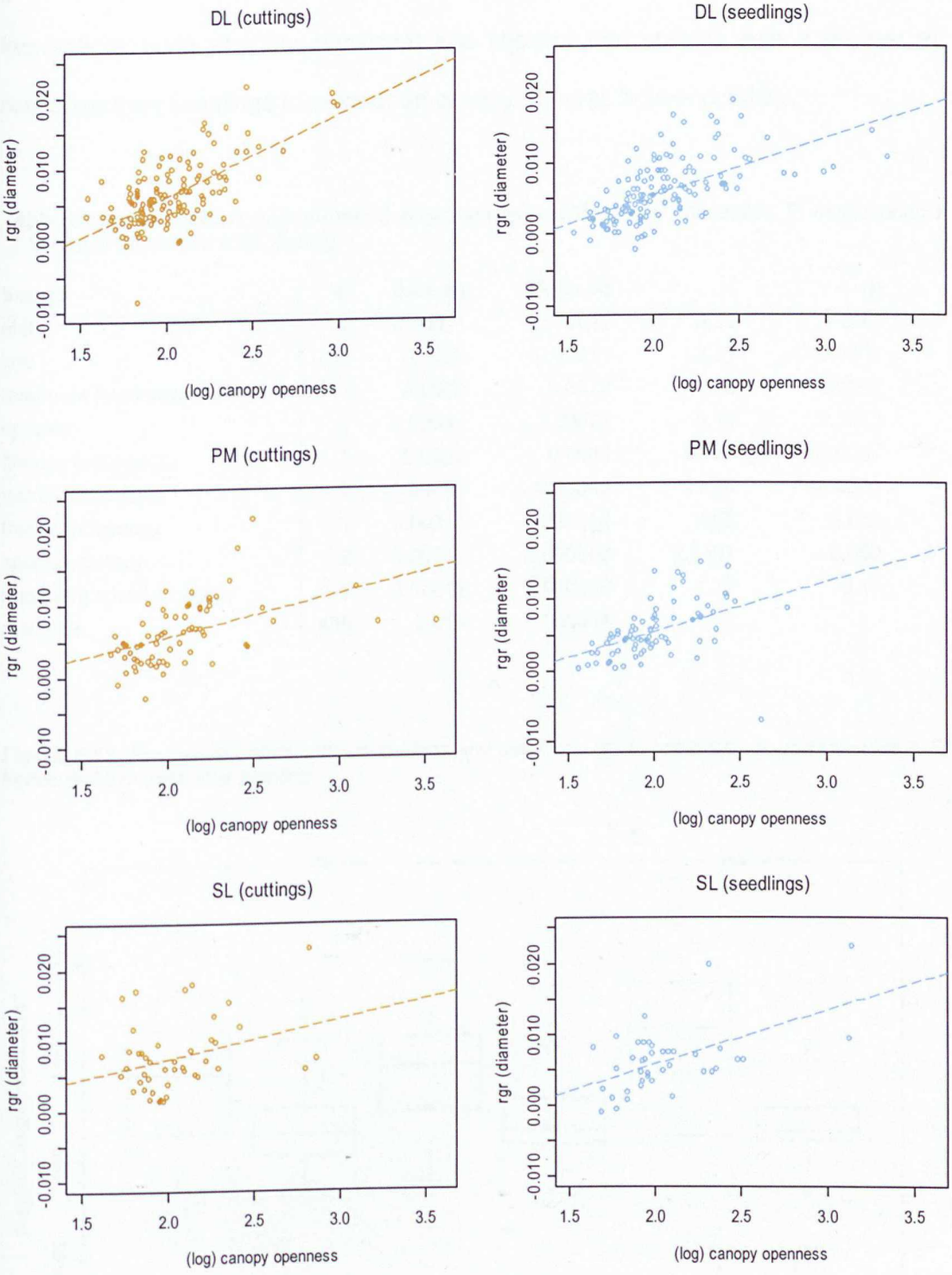


Figure 5.11: *Rgr (diameter) at 20 months after planting in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula. Cuttings (left-hand panels) shown in orange, seedlings (right-hand panels) shown in blue*



Rgr in height rgr was significantly higher in cuttings (Table 5.6 and Figure 5.12). There were strong species and canopy effects with *D. lanceolata* showing the greatest rgr response to more open canopy (Figure 5.13). The treatment:canopy interactions were strongly significant and showed that cuttings had a greater rgr response than seedlings to more open canopy (Figures 5.14 and 5.15).

Table 5.6: *LM analysis on (log)rgr (height) in cuttings and seedlings of D. lanceolata, P. malaanonan & S. leprosula 20 months after planting*

Source	df	Sum sq	Mean sq	f	p
plot	2	0.000021	0.000011	0.32	0.73
line	30	0.0033	0.00011	3.31	<0.0001
treatment (cuttings/seedlings)	1	0.0072	0.0072	212.76	<0.0001
species	2	0.00041	0.00021	6.15	0.0023
canopy (openness)	1	0.0032	0.0032	94.27	<0.0001
treatment:species	2	0.00090	0.00045	13.36	<0.0001
treatment:canopy	1	0.00014	0.00014	4.05	0.045
species:canopy	2	0.00019	0.000096	2.8491	0.060
treatment:species:canopy	2	0.00012	0.000059	1.77	0.17
residuals	456	0.015	0.000034		

Figure 5.12: *Rgr height (mm/month) in cuttings and seedlings of D. lanceolata, P. malaanonan & S. leprosula 20 months after planting*

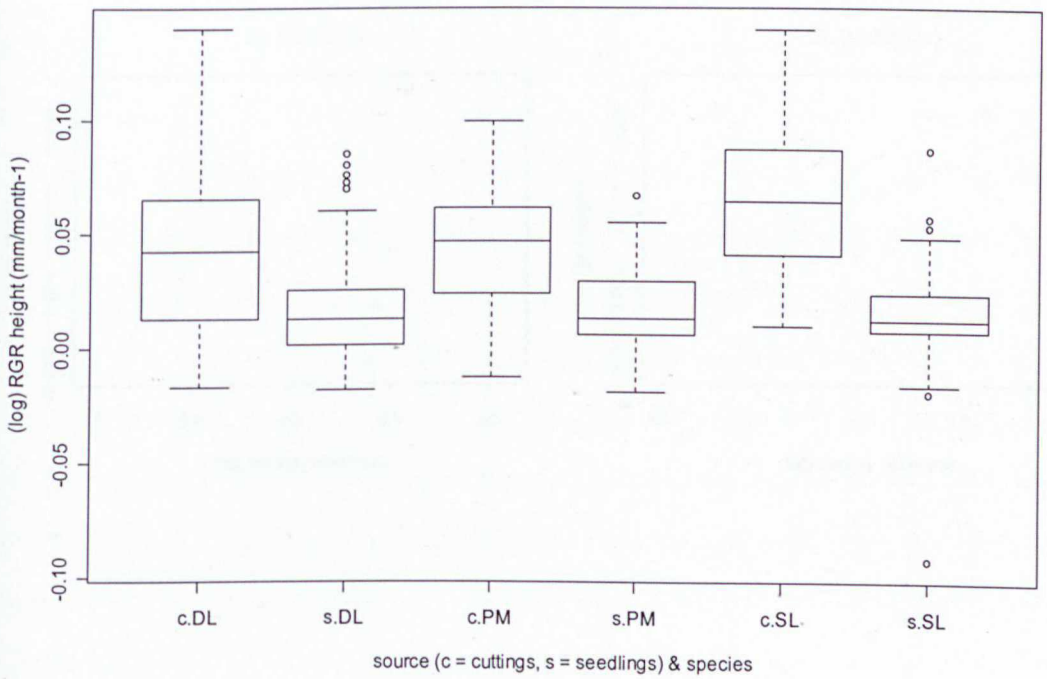


Figure 5.13: *Rgr (height) at 20 months after planting in cuttings and seedlings of D. lanceolata, P. malaanonan & S. leprosula. Cuttings (left-hand panels) shown in orange, seedlings (right-hand panels) shown in blue*

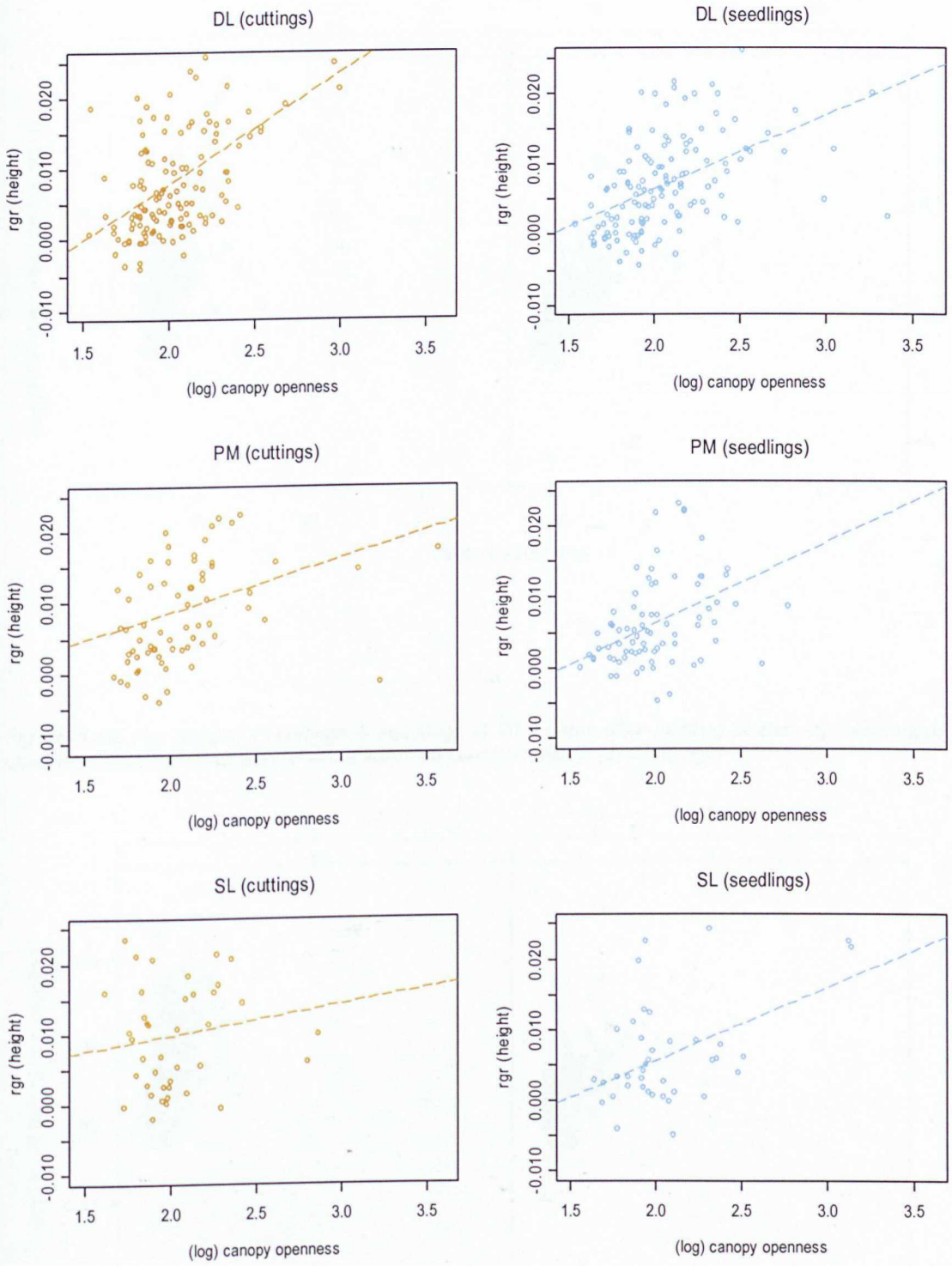


Figure 5.14: *Rgr (diameter) in cuttings & seedlings at 20 months after planting plotted against canopy openness. Cuttings (c) displayed in the left-hand panel, seedlings (s) in the right*

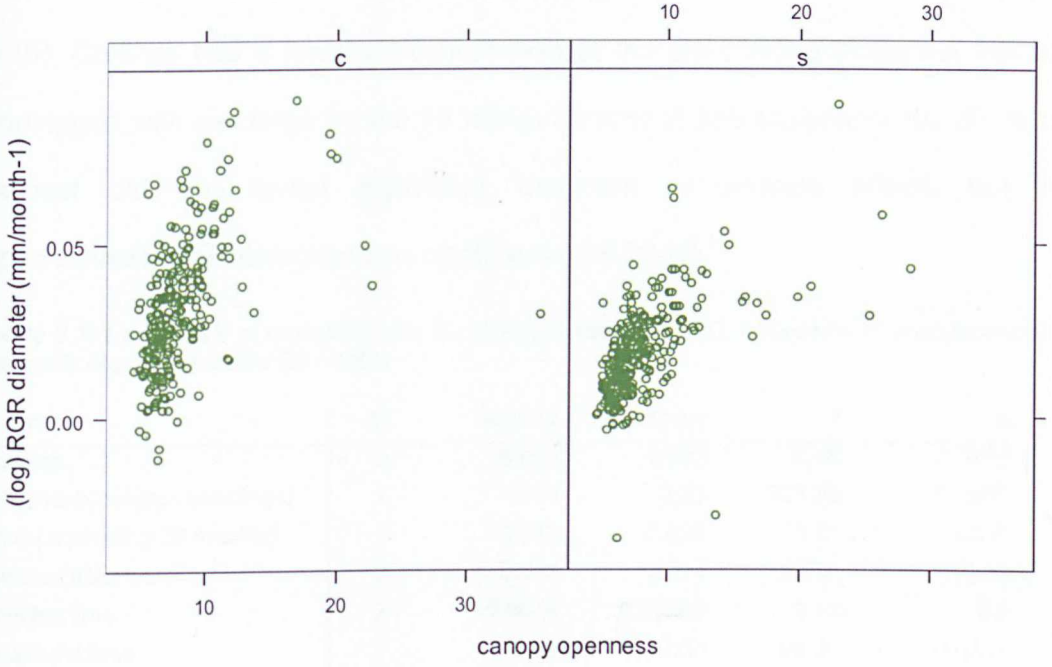
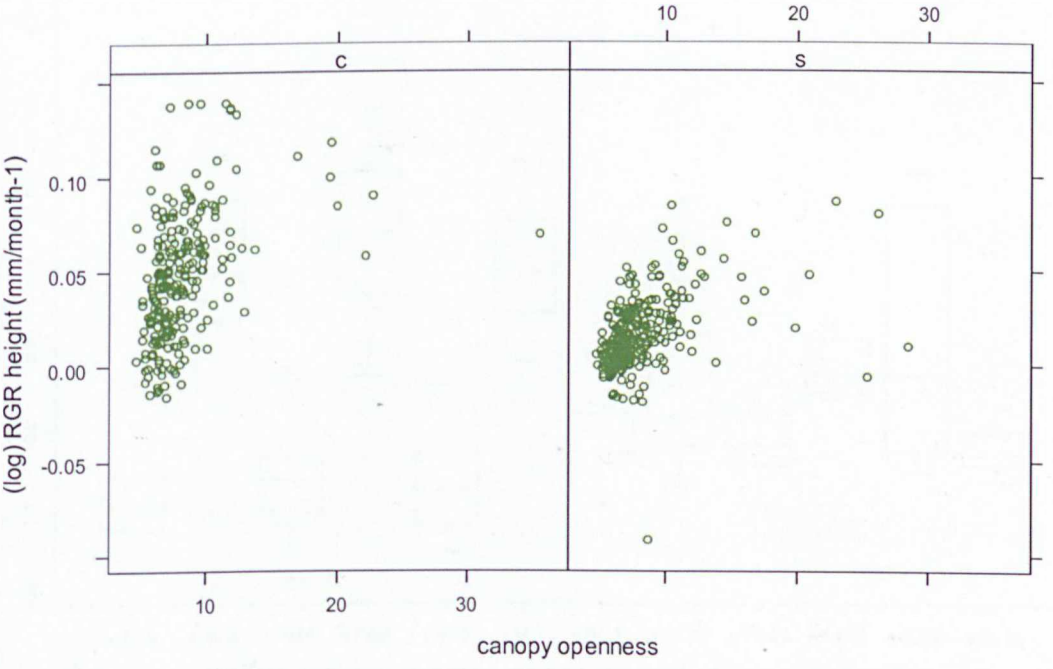


Figure 5.15: *Rgr (height) in cuttings & seedlings at 20 months after planting plotted against canopy openness. Cuttings (c) displayed in the left-hand panel, seedlings (s) in the right*



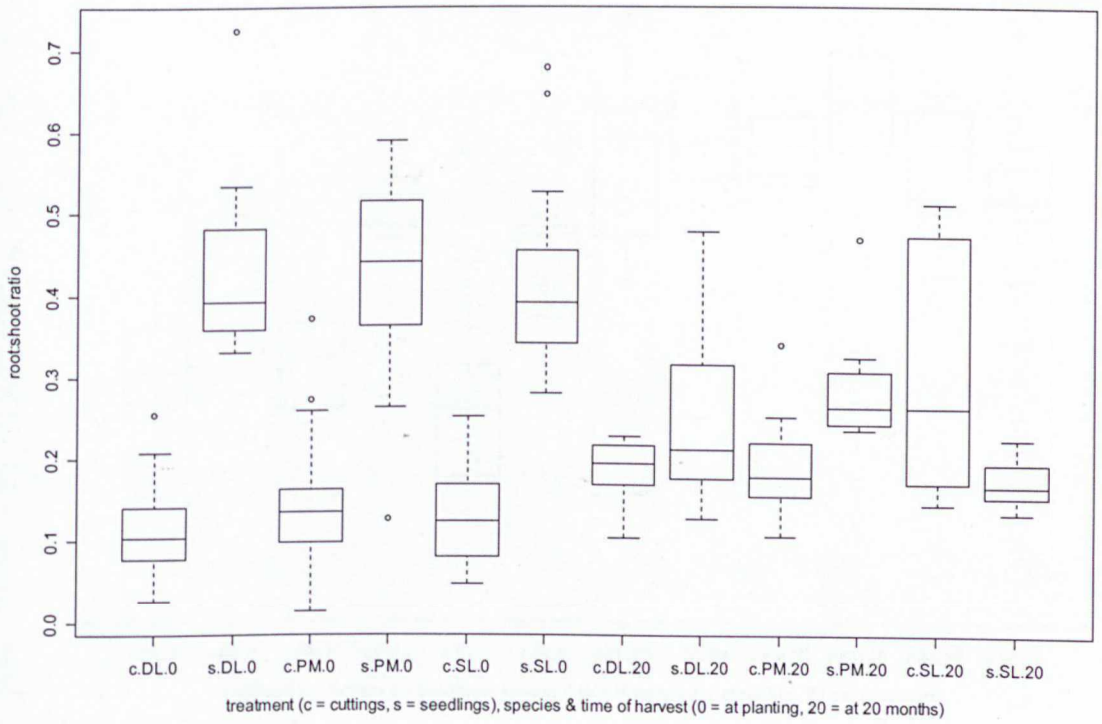
5.3.3 *Destructive measurements*

Root shoot ratio (Table 5.7) was significantly different between species and treatments and varied between the pre-planting and 20 month sub-samples (figure 5.16). Cuttings had a lower root:shoot ratio at the pre-planting stage but this had converged with seedlings by the 20 month harvest. A sub-analysis of the 20 month harvest did not reveal significant treatment or species effects but the species:treatment interaction was significant (p=0.0044).[1]

Table 5.7: *LM analysis of root:shoot ratio in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting & after 20 months*

Source	df	Sum sq	Mean sq	f	p
species	2	0.086	0.043	6.48	0.0019
treatment *(cuttings/seedlings)*	1	2.23	2.23	338.36	<0.0001
time *(at planting/20 months)*	1	0.038	0.038	5.71	0.018
species:treatment	2	0.027	0.014	2.046	0.13
species:time	2	0.0014	0.00069	0.11	0.9
treatment:time	1	0.63	0.63	95.26	<0.0001
species:treatment:time	2	0.079	0.04	6.018	0.0029
residuals	195	1.29	0.0066		

Figure 5.16: *Root:shoot ratio in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting and after 20 months*



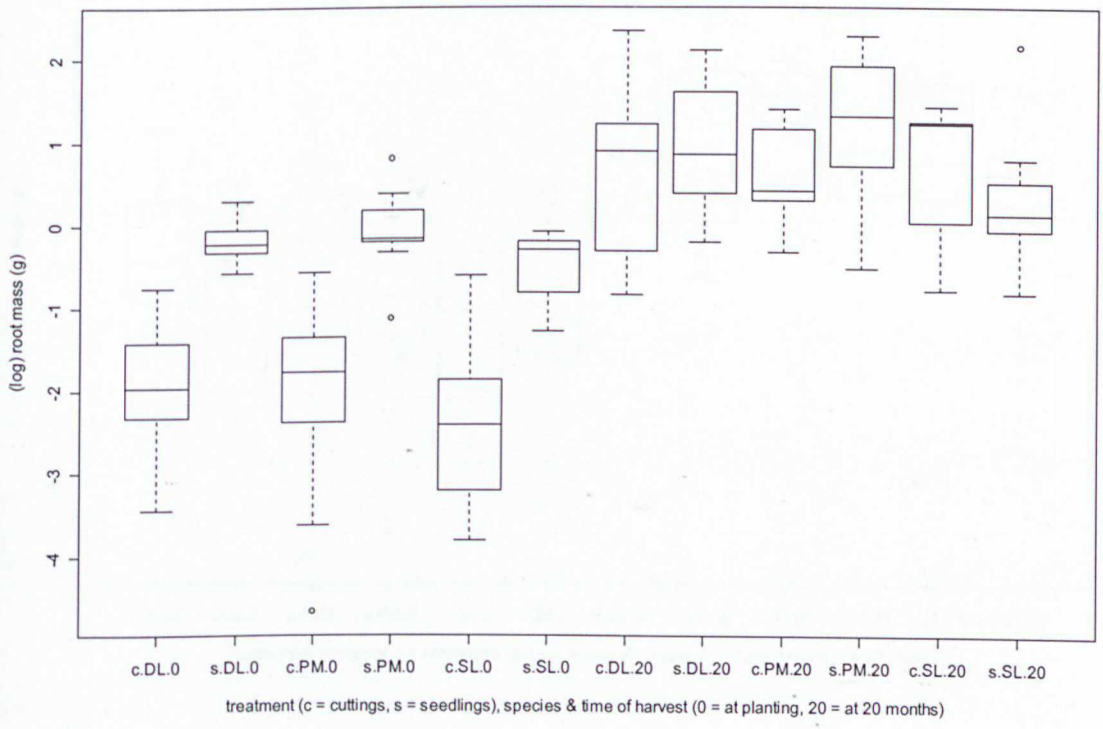
[1] *For sub-analysis of the 20 month harvest see Appendix 3, Section 3.4 – page 201*

Total root mass (Table 5.8, Figure 5.17) was significantly higher in seedlings than in cuttings at the time of planting. There were species differences (with *P. malaanonan* having the greatest root mass) although no interaction with treatment. At 20 months after planting root mass in seedlings and cuttings had converged – a sub-analysis of the 20 month harvest confirmed that there were no treatment or species differences.

Table 5.8: *LM analysis of total root mass in cutting & seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting & after 20 months*

Source	df	Sum sq	Mean sq	f	p
species	2	6.42	3.21	5.95	0.0031
treatment *(cuttings/seedlings)*	1	145.099	145.099	268.89	<0.0001
time *(at planting/20 months)*	1	123.73	123.73	229.29	<0.0001
species:treatment	2	0.45	0.22	0.41	0.66
species:time	2	0.046	0.023	0.043	0.96
treatment:time	1	20.47	20.47	37.94	<0.0001
species:treatment:time	2	1.25	0.62	1.15	0.32
residuals	195	105.27	0.54		

Figure 5.17: *Total root mass in cuttings and seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting & after 20 months*

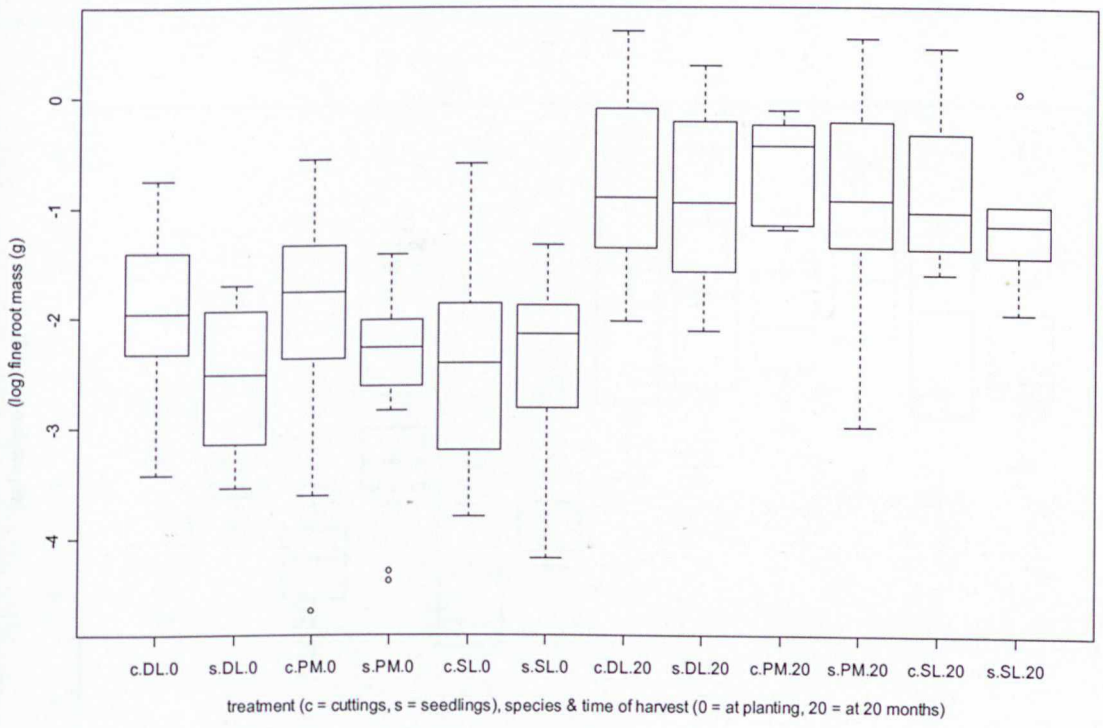


Analysis of fine root mass (Table 5.9) indicated that there may have been differences between species, but that significance was only marginal (p = 0.053). Fine root mass increased over time (Figure 5.18), but none of the interactions were significant.

Table 5.9: *LM analysis of fine root mass in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting & after 20 months*

Source	df	Sum sq	Mean sq	f	p
species	2	3.66	1.83	2.99	0.053
treatment *(cuttings/seedlings)*	1	0.40	0.40	0.65	0.42
time *(at planting/20 months)*	1	62.87	62.87	102.62	<0.0001
species:treatment	2	2.47	1.23	2.012	0.14
species:time	2	0.067	0.033	0.054	0.95
treatment:time	1	0.15	0.15	0.24	0.62
species:treatment:time	2	1.25	0.62	1.017	0.36
residuals	195	119.47	0.61		

Figure 5.18: *Fine root mass in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting and after 20 months*

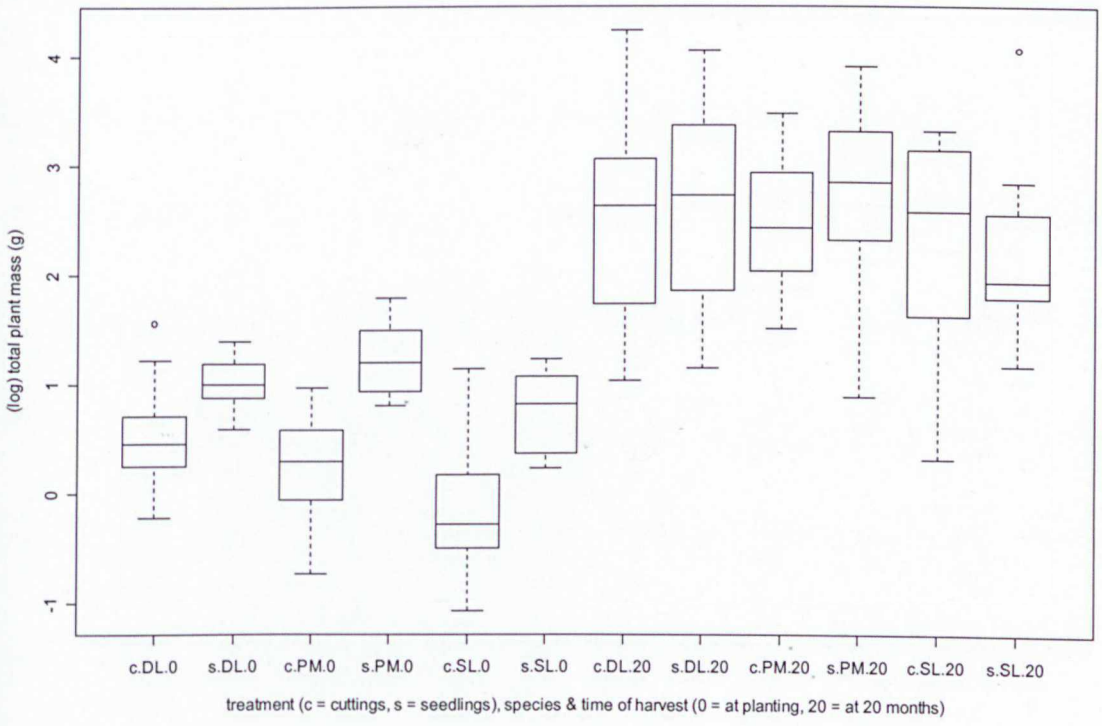


Total plant mass (Table 5.10, Figure 5.19) was varied between species, treatment and time. *S. leprosula* appeared to have a lower mass than the other species. Overall, seedlings had a significantly higher mass at planting than cuttings. The treatment:time interaction was significant suggesting a convergence in mass between cuttings and seedlings by 20 months after planting. There was no difference between cuttings and seedlings (or species) at the 20 month harvest.

Table 5.10: *LM analysis of total plant mass in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting & after 20 months*

Source	df	Sum sq	Mean sq	f	p
species	2	7.300	3.650	12.2359	<0.0001
treatment *(cuttings/seedlings)*	1	41.379	41.379	138.7242	<0.0001
time *(at planting/20 months)*	1	114.696	114.696	384.5186	<0.0001
species:treatment	2	1.120	0.560	1.8778	0.16
species:time	2	0.034	0.017	0.0563	0.95
treatment:time	1	3.125	3.125	10.4757	0.0014
species:treatment:time	2	0.244	0.122	0.4084	0.67
residuals	195	58.166	0.298		

Figure 5.19: *Total plant mass in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting & after 20 months*

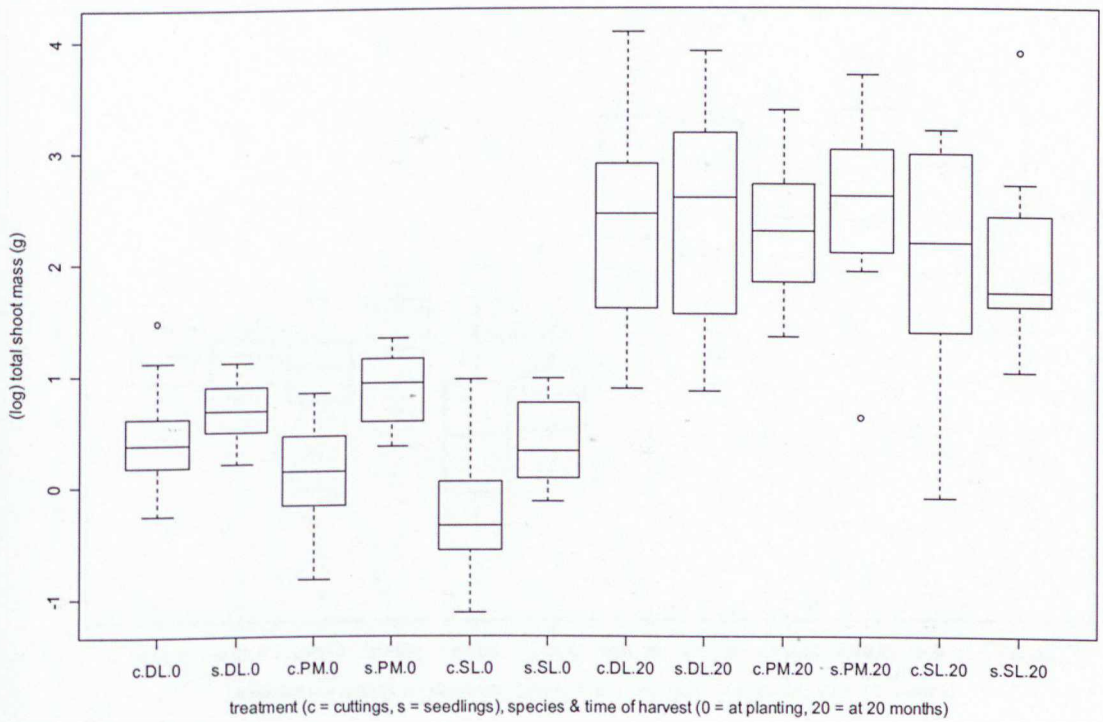


Analysis of shoot mass (comprising leaves and stems) indicates a similar pattern to the analysis of total plant mass (Table 5.11, Figure 5.20). Seedlings had a higher shoot mass at the time of planting, with convergence by the 20 month harvest. There were species differences – *S. leprosula* had lower shoot mass (in both cuttings and seedlings) than *D. lanceolata* or *P. malaanonan*. A sub-analysis of the 20 month dataset did not reveal any treatment or species effects.

Table 5.11: *LM analysis of total shoot mass in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting & after 20 months*

Source	df	Sum sq	Mean sq	f	p
species	2	7.84	3.92	13.089	<0.0001
treatment *(cuttings/seedlings)*	1	27.61	27.61	92.15	<0.0001
time *(at planting/20 months)*	1	117.29	117.29	391.44	<0.0001
species:treatment	2	1.33	0.67	2.22	0.11
species:time	2	0.041	0.020	0.068	0.93
treatment:time	1	1.33	1.33	4.43	0.037
species:treatment:time	2	0.21	0.10	0.34	0.71
residuals	195	58.43	0.30		

Figure 5.20: *Total shoot mass in cuttings & seedlings of D. lanceolata, P. malaanonan and S. leprosula at planting & after 20 months*

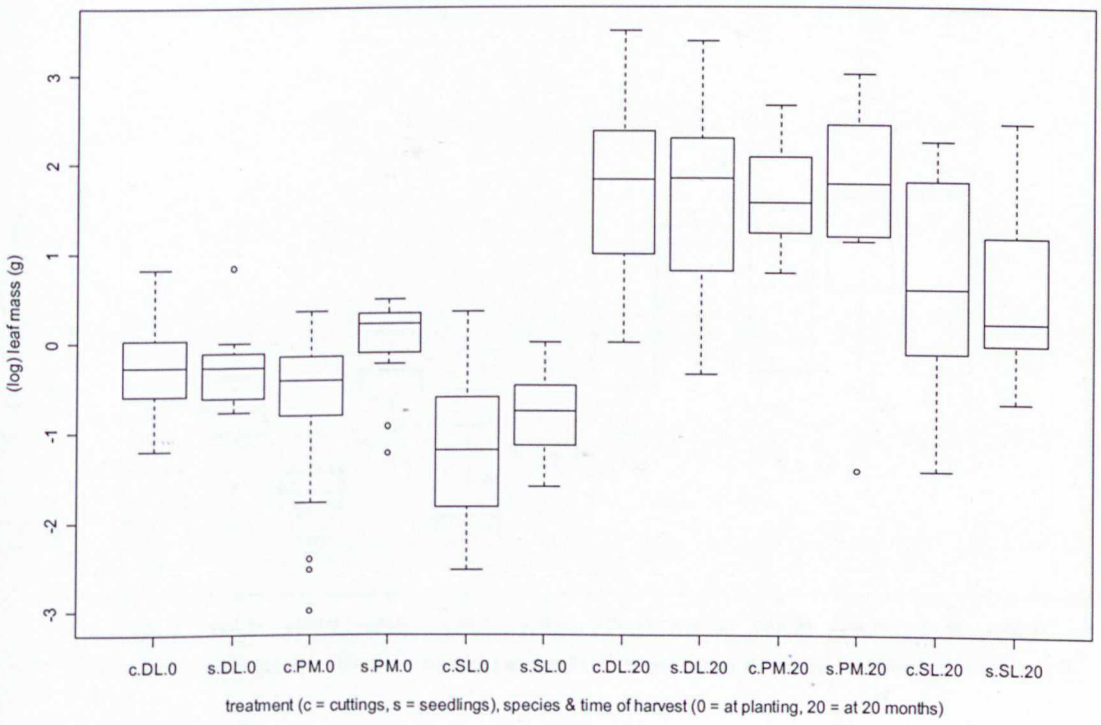


Analysis of leaf mass, as with shoot and total plant mass, showed significant differences between species and treatment, and varied over time (Tables 5.12, Figure 5.21). However, the treatment:time interaction showed only marginal significance (p = 0.098). The general trend shown in previous analyses, i.e. seedlings having a higher mass at planting with convergence after 20 months, was maintained.

Table 5.12: *LM analysis of leaf mass in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting & after 20 months*

Source	df	Sum sq	Mean sq	f	p
species	2	27.97	13.99	25.28	<0.0001
treatment *(cuttings/seedlings)*	1	15.36	15.36	27.76	<0.0001
time *(at planting/20 months)*	1	113.063	113.063	204.33	<0.0001
species:treatment	2	2.13	1.066	1.93	0.15
species:time	2	0.58	0.29	0.52	0.59
treatment:time	1	1.53	1.53	2.76	0.098
species:treatment:time	2	0.67	0.34	0.61	0.55
residuals	195	107.90	0.55		

Figure 5.21: *Leaf mass in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting & after 20 months*



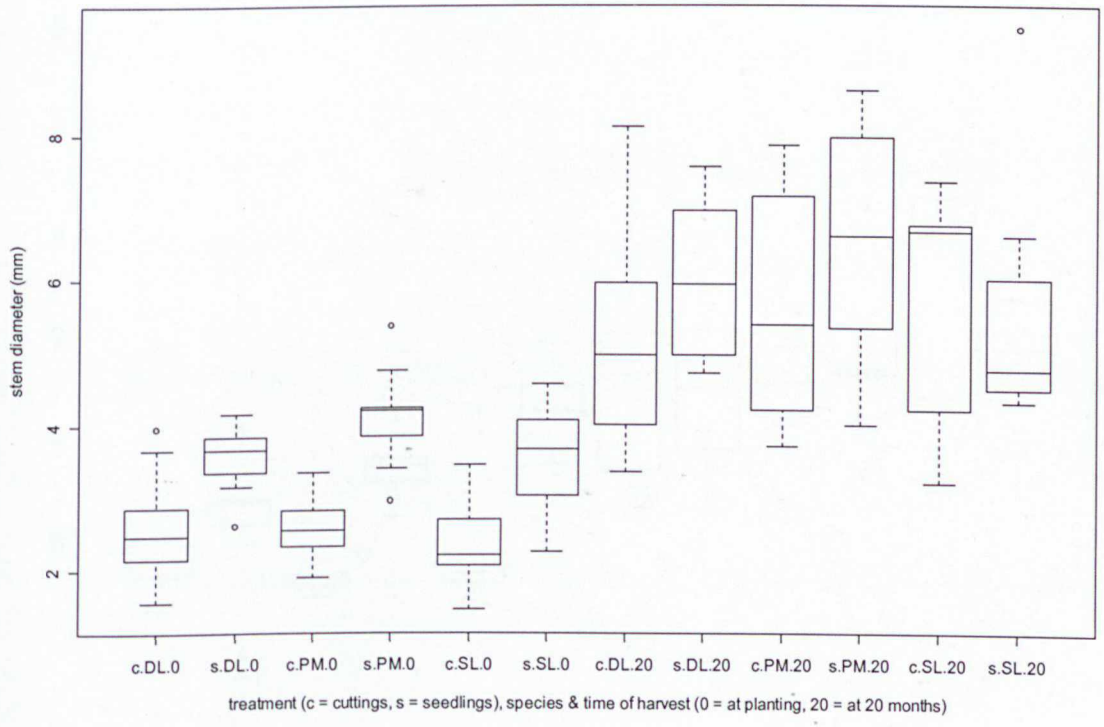
5.3.4 *Diameter & height*

Analysis of stem diameter showed significant differences between species, treatment and time (Table 5.13, Figure 5.22). Seedlings had greater diameter at the time of planting, but had converged by the 20 month harvest. There were species differences with *P. malaanonan* having a higher diameter at planting and after 20 months. In a sub-analysis at 20 months none of the variables were significant.

Table 5.13: *LM analysis of stem diameter in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting & after 20 months*

Source	df	Sum sq	Mean sq	f	p
species	2	9.44	4.72	6.81	0.0014
treatment *(cuttings/seedlings)*	1	110.74	110.74	159.71	<0.0001
time *(at planting/20 months)*	1	233.11	233.11	336.19	<0.0001
species:treatment	2	1.91	0.95	1.37	0.26
species:time	2	0.39	0.20	0.28	0.75
treatment:time	1	2.93	2.93	4.23	0.041
species:treatment:time	2	1.21	0.61	0.87	0.42
residuals	195	135.21	0.69		

Figure 5.22: *Stem diameter in cuttings & seedlings of D. lanceolata, P. malaanonan and S. leprosula at planting & after 20 months*

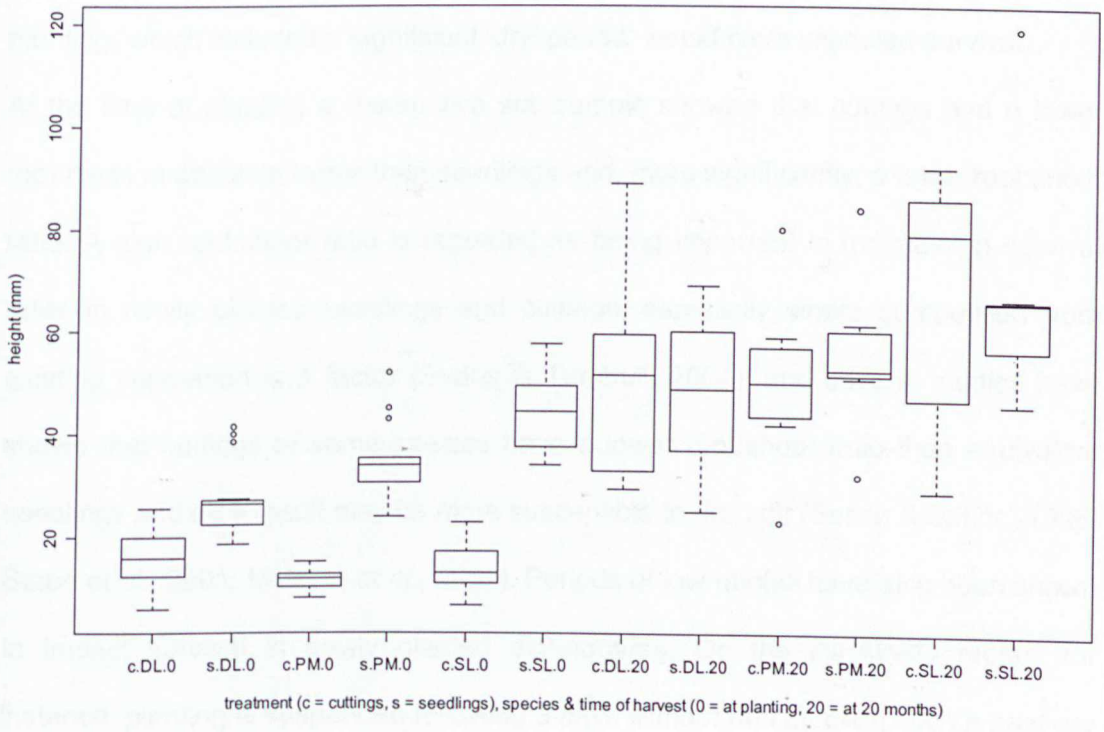


Analysis of plant height (Table 5.14, Figure 5.23) indicated similar results to that for stem diameter. There were significant differences in height between species, between cuttings and seedlings and over time. Seedlings were taller than cuttings at the time of planting with, again, convergence by the 20 month measurement. A sub-analysis of the 20 month harvest indicated that there may have been species differences with *S. leprosula* (cuttings and seedlings) apparently taller at this stage, though significance was marginal (p=0.052).[1]

Table 5.14: *LM analysis of height in cuttings & seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting & after 20 months*

Source	df	Sum sq	Mean sq	f	p
species	2	2964	1482	15.79	<0.0001
treatment *(cuttings/seedlings)*	1	21331	21331	227.27	<0.0001
time *(at planting/20 months)*	1	32897	32897	350.49	<0.0001
species:treatment	2	2413	1207	12.85	<0.0001
species:time	2	394	197	2.10	0.13
treatment:time	1	3066	3066	32.67	<0.0001
species:treatment:time	2	302	151	1.61	0.20
residuals	195	18303	94		

Figure 5.23: *Height in cuttings and seedlings of D. lanceolata, P. malaanonan & S. leprosula at planting & after 20 months*



[1] *See Appendix 3, Section 3.4 – page 201*

5.4 Discussion

A number of studies have shown that rainfall patterns, particularly ENSO events, play a critical role in driving the dynamics of the SE Asian rainforests and the survival of dipterocarp seedlings (e.g. Curran *et al.*, 1999; Walsh & Newbery, 1999; Brook *et al.*, 2003; Kohler & Huth, 2004; Curran *et al.*, 2004). Rainfall during this experiment was generally high, with only 1 of the 20 months having less than 100 mm of rain. This level of rainfall, 100 mm or less in a 1 month period, has been identified by Walsh and Newbery (1999) as a 'dry month' which they suggest may impact tree survival in the SE Asian humid tropics. The year in which the experiment was established was the wettest on record at Danum Valley with over 3,500 mm of rain. In the month preceding planting there was 244 mm of rain (a moderate level), with 358 mm (high rainfall) in the month during which the plots were actually planted. In the month immediately after planting, although rainfall was not especially low in overall terms (191.2 mm), there was a total of 17 days with no rain including a 7 day period with only 0.4 mm rainfall. Approximately 80% of the rain which fell in the month did so in just 4 storm events. It is possible that such a sporadic rainfall pattern so soon after planting, which included a significant 'dry' period, would have impacted survival.

At the time of planting a destructive sub-sample showed that cuttings had a lower root mass in absolute terms than seedlings and, more significantly, a lower root:shoot ratio. A high root:shoot ratio is regarded as being important in maintaining survival rates in newly planted seedlings and cuttings, especially where competition from existing vegetation is a factor (Evans & Turnbull, 2004), and several studies have shown that cuttings of some species have a lower root:shoot ratio than equivalent seedlings and as a result may be more susceptible to drought (Sasse & Sands, 1996; Stape *et al.*, 2001; Mulatya *et al.*, 2002). Periods of low rainfall have also been shown to impact survival in newly planted dipterocarps. On the INFAPRO project for instance, planting is suspended following 3 days without rain as even such a brief dry period has been found to increase mortality in planted seedlings (Li, 2006). Given the

relatively low root:shoot ratio of cuttings at the start of the experiment, the impact of the dry period immediately after planting, albeit relatively brief, could have been more severe on cuttings and resulted in the divergence of mortality rates in the first 8 months after planting.

Plotting survival independent of species showed quite clearly that cutting and seedling mortality rates began to converge after 8 months. It is possible that by this stage, 8 – 12 months after planting, root development and root:shoot ratio in cuttings and seedlings were broadly similar and hence that their responses to the various environmental factors that govern mortality would also have been similar. Data from the destructive harvest confirmed that root:shoot ratio and total root mass in cuttings had surpassed that in seedlings after 20 months, again suggesting convergence mid-way through the experiment.

There was a clear difference in survival between species with *P. malaanonan* showing significantly higher survival than either *D. lanceolata* or *S. leprosula* (Figure 5.2). This is a somewhat surprising result given that on the INFAPRO project *D. lanceolata* is regarded as having generally low mortality over a range of environmental conditions from open areas, with often highly compacted soil, to deep shade in the less-disturbed forest understory (Yap, *pers. comm.*; *personal observation*) and is highly resistant to insect herbivory (Bebber *et al.*, 2002). *S. leprosula*, as a light demanding species, has been found particularly useful for planting open, highly degraded areas (Yap, *pers. com.*) but would be expected to show higher mortality under closed canopies. By contrast, mortality rates reported for *P. malaanonan* are generally higher than for other light-demanding species (Bebber *et al.*, 2002; Yap, *pers. comm.*) and are often subject to both root and foliar herbivory (Bebber *et al.*, 2002).

The 3-way interaction between species, initial height and canopy openness had a significant effect on survival, though by 20 months the significance of the interaction had disappeared. Although the effect is difficult to interpret, it appears that taller

cuttings and seedlings of *D. lanceolata* survived less well under more open canopy than shorter plants, with the reverse being true in *S. leprosula*. The survival response of *P. malaanonan* to the initial height:canopy openness interaction was relatively flat. It is possible that the apparently temporal nature of the interaction was as a result of the several large tree falls which occurred in the plots during the experimental period. These created large canopy openings and patchy mortality patterns; this could explain the ephemeral nature of the effect which dropped in and out of significance between the survey dates.

There was no evidence that canopy openness had a greater impact on cutting rather than seedling survival. *S. leprosula* and *P. malaanonan* showed sharply improved survival as canopy openness increased. As both these species are regarded as being light-demanding this was to be expected (Brown *et al.*, 1999, Symington *et al.*, 2004). *D. lanceolata*, as a more shade-tolerant species, showed less marked survival gains under a more open canopy.

The IBA treatments applied to cuttings during propagation appeared to have had some residual affect on survival although, again, results were difficult to interpret. There was little or no effect on *D. lanceolata* cuttings whereas in *P. malaanonan* there was a strongly negative effect on survival following treatment with IBA (even at only moderate concentration and exposure duration). In *S. leprosula*, the reverse was the case with the lowest survival in untreated cuttings. No evidence was found in published literature to indicate why treatment with root-promoting hormones would have had either a detrimental or positive affect on the survival of cuttings after planting and it is possible that these effects were purely stochastic. By 20 months after planting the effects of IBA application were no longer significant but survival did differ between planting lines. This was almost certainly due to large tree falls as in a number of cases these were oriented along planting lines resulting in an atypical mortality pattern.

Overall mortality rates for cuttings and seedlings planted as part of this research were broadly in line with those reported for populations of naturally recruited seedlings (Turner, 1990; Itoh, 1995). In comparison with other enrichment planting programmes in SE Asia, survival after 20 months was at the upper end of the range reported by Appanah and Weinland (1993), Ådjers and colleagues (1995), Garcia (2005 *pers. comm.*) and Chai (1974) but lower than reported by Li (2006) for the INFAPRO project. Interpretation of the INFAPRO dataset is complicated by the method used to account for seedling mortality as this combines counts for planted and naturally regenerating seedlings. It is therefore difficult to track the fate of individual seedlings, either planted or naturally occurring, and hence to determine actual as opposed to derived survival rates. In a recently established enrichment planting experiment in Sabah ("The Sabah Biodiversity Experiment", Sherer-Lorenzen *et al.*, 2005) survival rates for *Dryobalanops lanceolata*, *Shorea leprosula* and *Parashorea malaanonan* were 31%, 36% and 44% respectively approximately 2 years after planting (Philipson 2006, *pers. comm.*.). These rates are lower than those reported in this research. There was, however, a mild ENSO event soon after the experiment was established which may have had impacted survival.

Cuttings showed a higher growth rate than seedlings in all 3 species. Similar results have been reported in a number of conifer species, though there is no obvious explanation as to why this may have been the case (e.g. Rouland & Bergstedt, 1982; Roulund *et al.*, 1985; Gemmel *et al.*, 1991; Hannerz & Wilhelmsson, 1998). In the analysis of rgr for diameter, *S. leprosula* cuttings showed increased growth under a more open canopy in comparison to seedlings. Given the basic ecology of *S. leprosula*, which is regarded as a fast-growing, light-demanding species (Appanah & Weinland, 1993; Symington *et al.*, 2004) it is not surprising that this species shows a greater response to increased light, though it is not at all clear why rgr was higher in cuttings than seedlings.

In the rgr analysis on height the position was somewhat more straightforward. Cuttings, irrespective of species, showed significantly higher growth rates under more open canopy in comparison to seedlings – as with diameter, *S. leprosula* cuttings showed the greatest increase in height. It is most unlikely that genotypic differences were responsible for higher growth rate in cuttings. The cuttings were taken from seedlings that formed the same population that provided the seedling planting material. Perhaps the most likely explanation is that the cuttings, having only recently been propagated, were simply in a more active growth phase than seedlings, which were at least 18 months old at the start of the experiment. It is also possible that the increased root:shoot ratio of cuttings, which likely surpassed that of seedlings mid-way through the experiment, may have supported increased above ground growth towards the end of the monitoring period.

The pre- and post-planting destructive sub samples indicated that cuttings had a lower biomass at the start of the experiment in all measured parameters with the exception of fine (< 2 mm diameter) root mass. This was in part due to the different structure of the cutting and seedling root systems at this early stage. In cuttings, all roots at the first harvest fell into the fine (< 2 mm) diameter class, whereas in seedlings the bulk of the root system was accounted for by a relatively well-defined tap root that fell into the 2 – 5 mm diameter class.

As already discussed, root:shoot ratio at planting was considerably lower in cuttings than seedlings. Although this may have been in part due to developmental or morphological differences between cuttings and seedlings, it must be remembered that to a greater extent the shoot mass of a cutting is heavily manipulated after removal from the parent plant, i.e. the stem is cut to a more-or-less standard length and the leaf number reduced. By the end of the experiment however, and in line with the greater rgr measurements, all of these measures (total root mass, total plant mass, total shoot mass and leaf mass) had converged with seedlings.

In summary, the original hypothesis that cuttings and seedlings would show similar survival and growth rates was not supported. Cuttings showed higher overall mortality than seedlings, though the difference was relatively minimal, at least in *D. lanceolata* and *S. leprosula*. Cutting and seedling development did show differences, though in a rather unexpected direction with higher growth rate in the cuttings of all 3 species. Cuttings had a uniformly lower above and below ground biomass than seedlings at the start of the experiment, but after 20 months these measurements had converged. Perhaps most importantly, root:shoot ratio, which was initially very much lower in cuttings, was similar to the seedlings' root:shoot ratio by the end of the experiment.

The aim of this experiment were to establish if there was any indications in the early growth and development of dipterocarp cuttings which could have raised concerns in their use as an alternative to seedlings in the production of planting material. It can be reported with some confidence that, in the species used, and although there were differences in survival, there was nothing to indicate that cuttings showed any major deleterious traits up to 20 months after planting. It is, however, important to determine how dipterocarp cuttings develop in the longer term and this will be addressed in the following chapter.

CHAPTER 6

6. THE POST ESTABLISHMENT PHASE: DEVELOPMENT AFTER 8 YEARS

Experimental aims were to:

i. Compare root and shoot development in *D. lanceolata* cuttings and seedlings at 5 and 8 years after planting

ii. Compare root distribution in *D. lanceolata* cuttings and seedlings 8 years after planting

With the hypothesis that:

Root architecture and development in cutting and seed-propagated *D. lanceolata* trees is significantly different; cuttings are shallower rooting than seedlings and do not develop a taproot.

6.1 Background & supporting literature

Evidence from this project[1] indicates that survival in dipterocarp cuttings in the immediate post-planting period is within acceptable limits and broadly comparable to both naturally recruited and enrichment planted seedlings. Growth and development in cuttings and seedlings was essentially similar and, perhaps more importantly, cuttings showed no obviously deleterious developmental traits up to 20 months after planting. However, if vegetative propagation is to provide a viable alternative for the production of dipterocarp planting material it is important to establish how cutting and seedling development compares in the longer term – and particularly if the root systems of cutting-propagated dipterocarps have the characteristics to support the tree to maturity.

The architecture of root systems plays a major role in both a tree's mechanical stability and its ability to acquire water and nutrients (e.g. Coutts, 1983; Fitter, 1991;

[1] *See Chapter 5 – page 92*

Cao & Ohkubo, 1998; Crook & Ennos, 1998; Danjon *et al.*, 2005). However, despite this clear importance the nature of the root systems of the majority of tropical trees remain almost entirely unknown (Richards, 1996). This is especially true of the dipterocarps and there is no published data whatsoever to indicate how the root systems of dipterocarp cuttings develop after planting.

A number of studies have shown that root systems in some tree species propagated by stem cuttings show significant morphological and structural differences to the roots of seed-derived trees, and that these differences can be detrimental (e.g. Tinley, 1963; Sasse & Sands, 1997; Stape *et al.*, 2001). For example, from the early 1900s until the mid 20th century attempts were made to propagate selected genotypes of rubber (*Hevea brasiliensis*) by stem cuttings. However, these have now been largely abandoned (Carron *et al.*, 2000). Cuttings did not produce a taproot or other support roots and the resulting trees were more susceptible to wind-throw than trees grown from seed. Cutting-propagated *H. brasiliensis* were also shallower rooted and consequently less resistant to drought than seedlings (Rubber Research Institute Malaysia, 1966; Tinley, 1963). Similarly, cutting-propagated *Eucalyptus globulus* have been shown to have shallower root systems and were significantly more prone to water stress than seedlings (Sasse & Sands, 1996). Moreover, and as with *H. brasiliensis*, *E. globulus* cuttings failed to produce taproots or roots with a similar supportive function up to 1 year after propagation and had a lower root:shoot ratio than seedlings raising concerns for the long-term stability of the adult tree (Sasse & Sands, 1997).

In Brazil, where over 3.5 million hectares of *Eucalyptus* plantations have been established (Stape *et al.*, 2001), vegetative propagation by conventional stem cuttings was until recently the most common method for the production of planting material (due mainly to the requirement to establish clonal plantations). However, cuttings were found to be more susceptible to water stress than seedlings in the immediate post-planting period. The authors attributed this to shallower root

morphology and in recent years propagation by conventional stem cuttings has been superseded by the use of micro-cuttings (Stape *et al.*, 2001). These apparently have a superior root system to conventional cuttings and show greater drought tolerance (Reis *et al.*, 1988; Yang *et al.*, 1995).

The African tree *Melia volkensii* is commonly used in arid agro-forestry systems and is often inter-planted with annual crop plants. As the supply of seed from *M. volkensii* can be unreliable there is considerable interest in propagation by cuttings (Mulatya *et al.*, 2002). In a comparative study on the post-planting performance of *M. volkensii* cuttings and seedlings it was found that cuttings had, as with *Eucalyptus* and *Hevea*, a significantly shallower root system. This caused instability in the adult tree and, due to greater root competition in upper soil layers, reduced yields among inter-planted crops (Stewart & Blomley, 1994; Mulatya *et al.*, 2002). The cuttings of several temperate broadleaves, including English oak (*Quercus robur*) and *Populus sp.*, have also been reported as having shallower root systems than seedlings (Riedacker & Belgrand, 1983; Khurana *et al.*, 1997).

It is, however, not always the case that differences between cutting and seedling root systems are deleterious. In comparative research on Douglas-fir (*Pseudotsuga menziesii*), cuttings were found to have a greater root mass, root:shoot ratio and were deeper rooting than seedlings (Ritchie *et al.*, 1992). Cuttings developed what the authors described as a 'coarser' root system which they suggested might help to improve stability in the mature tree (Ritchie *et al.*, 1992). In a detailed study on three-year old seedlings and cuttings of *Pinus radiata* in New Zealand, Watson and Tombleson (2002) reported that differences between cuttings and seedlings in total below-ground biomass, taproot and sinker root biomass were not significant. Mean root length was significantly greater in seedlings than cuttings but there was no difference in root:shoot ratio. The authors suggested that the most important factor determining stability was resource allocation to lateral roots proximal to the main stem and that as cutting propagated *P. radiata* showed increased biomass

accumulation in this zone, cuttings would potentially show greater resistance to wind-throw than seedlings (Watson & Tombleson, 2002).

In perhaps the only published study to date on the development of dipterocarp cuttings after planting, Aminah (1999) monitored growth in *Shorea leprosula* and *Hopea odorata* cuttings over a period of 6 years. The author concluded, on the basis of above-ground development in these species, that vegetative propagation could provide an alternative for the production of dipterocarp planting material (Aminah, 1999). However, given that no assessment was made of root development and that cuttings were not considered in comparison with seedlings, this assertion is not supported by the evidence and significant questions remain as to the long-term development of dipterocarp cuttings, especially the root system.

6.2 Materials & methods

The study site was part of the 1983 logging coupe within the Ulu Segama Forest Reserve approximately 10 km to the south east of the Danum Valley Field Centre. The area was selectively logged by tractor in 1983 and enrichment-planted in 1993 as part of the INFAPRO project using cuttings and seedlings of *D. lanceolata*. Soils in the area are of the Bang association and consist of orthic acrisols. Topography of the area is gently sloping. The remnant forest cover in both the seedling and cutting blocks consisted of *Macaranga* and other pioneer species. Cuttings and seedlings were planted in adjacent trial blocks of approximately 200 plants each. The planting system followed standard INFAPRO practise with 2 m wide planting lines cleared at 10 m centres with planting at 3 m centres along the lines.

At 5 years after planting, 16 *D. lanceolata* (8 cuttings, 8 seedlings) were selected at random from the cutting and seedling blocks. Trees less than 1.2 m in height were rejected on the basis that they might have been heavily or repeatedly browsed or subject to some other physical damage of the leader shoot that could have resulted in atypical root architecture or development. Aerial parts of the plant were measured in the field. The plants were then lifted, excavating the soil from the immediate root zone by hand, ensuring that the entire root system (including fine roots <2 mm diameter) remained intact. A destructive harvest was carried out as described in the General Methods. At 8 years after planting a further 12 individuals (6 cuttings, 6 seedlings) were randomly selected from the same population. Aerial parts of the plant were measured and the trees lifted as described above with the exception that roots were harvested by depth, dividing the system into 3 zones: 0 - 30 cm, 30 – 60 cm and > 60 cm from the soil surface. Data were analysed using a Linear Model and displayed as ANOVA tables with output rounded to 2 significant figures.[1]

[1] *For full details of the various analyses & additional ANOVA tables see Appendix 4 – page 204*

6.3 Results

Analyses were carried out for root:shoot ratio, total plant mass, root mass (by diameter class), shoot mass, leaf mass, root depth, plant height and root depth:plant height ratio. ANOVA tables for each analysis can be found in Appendix 4, page 204. Significant results have been summarised in Tables 6.1 and 6.2.

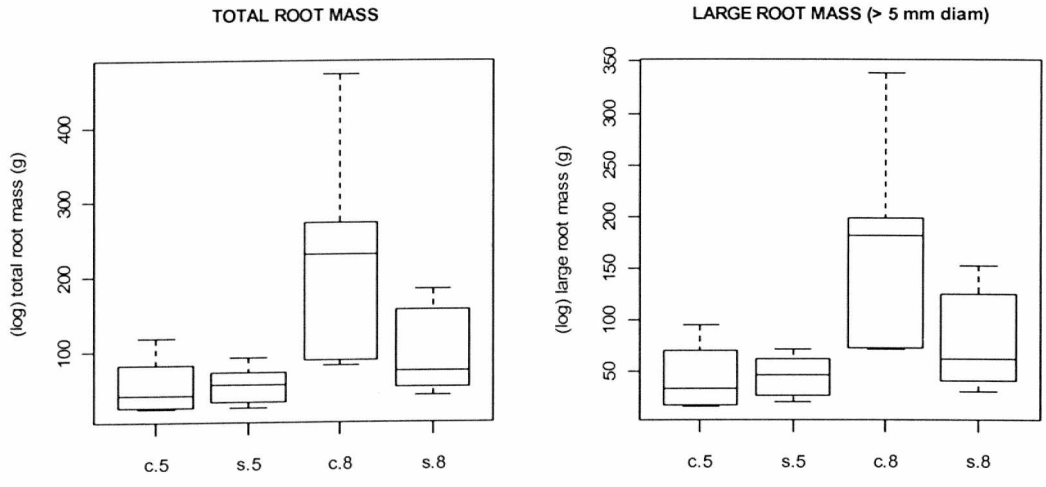
Table 6.1: *Summary of significant results from analyses of cuttings & seedlings at 5 & 8 years after planting (p < 0.05 shown in red, p < 0.1 shown in blue)*

Parameter measured	Significant source/interaction	p value
root:shoot ratio	treatment (cuttings/seedlings):time after planting	0.0026
root depth:plant height	time after planting	0.027
root depth	time after planting	0.024
total root mass	time after planting	0.00028
total root mass	treatment (cuttings/seedlings):time after planting	0.058
large root mass (>5mm diam)	time after planting	0.00042
large root mass (>5mm diam)	treatment (cuttings/seedlings):time after planting	0.055
med. root mass (2-5mm diam)	treatment (cuttings/seedlings)	0.036
med. root mass (2-5mm diam)	time after planting	0.018
fine root mass (>2mm diam)	time after planting	<0.0001
total plant mass	time after planting	<0.0001
total shoot mass	time after planting	<0.0001
plant height	time after planting	<0.0001

6.3.1 *Root mass*

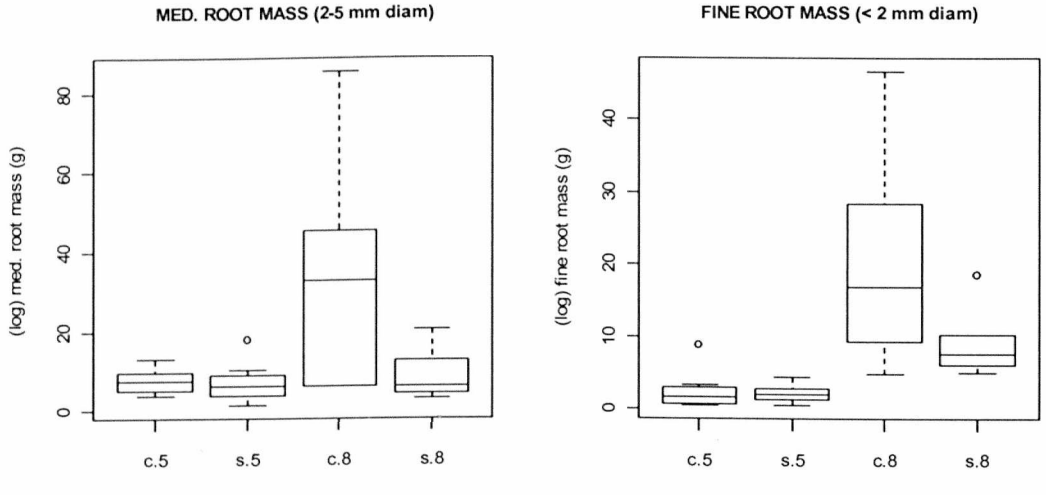
Total root mass varied significantly between 5 and 8 years after planting. At the 8 year harvest cuttings had a higher root mass than seedlings though significance was just outside the 95% confidence level at p = 0.058 (Table 6.1 and Figure 6.1). Large root mass (roots > 5 mm diameter) appeared to be higher in cuttings after 8 years (Table 6.1 and Figure 6.2 – following page) though significance was just outside the 95% confidence level (p = 0.055).

Figures 6.1 & 6.2: *Total root mass & large root mass plotted against source (c = cuttings, s = seedlings) & time after planting (in years)*



Medium root mass (2 – 5 mm diameter) varied significantly between cuttings and seedlings at both 5 and 8 years after planting with cuttings having a greater mass in this size class (Figure 6.3). Difference in fine root mass (< 2 mm diameter) between cuttings and seedlings was not significant at either harvest (Figure 6.4).

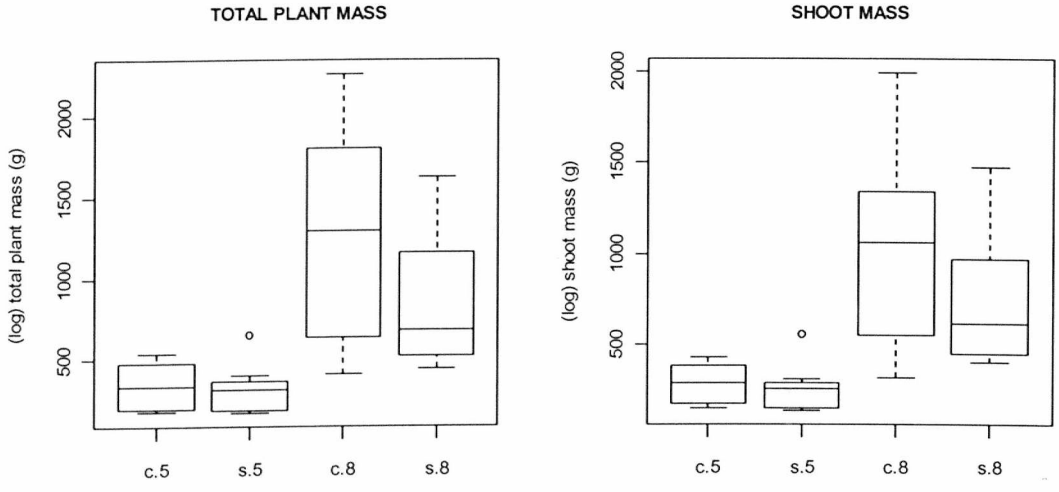
Figure 6.3 & 6.4: *Medium root mass & fine root mass plotted against source (c = cuttings, s = seedlings) & time after planting (in years)*



6.3.2 *Total plant mass & shoot mass*

Total shoot mass and total plant mass were higher 8 years after planting but did not vary between cuttings and seedlings at either 5 or 8 years (Figures 6.5 and 6.6).

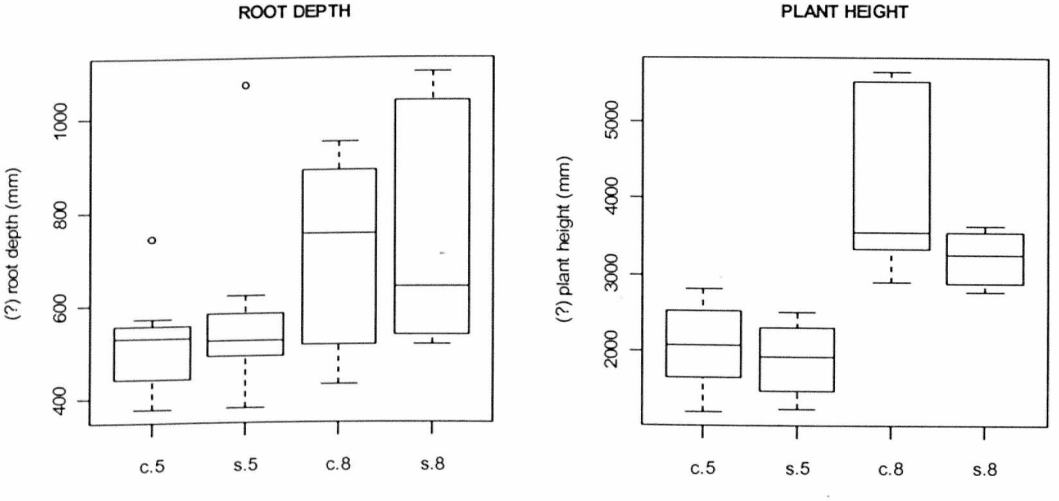
Figures 6.5 & 6.6: *Total plant mass & shoot mass plotted against source (c = cuttings, s = seedlings) & time after planting (in years)*



6.3.3 *Root depth & plant height*

Root depth and plant height did not vary between cuttings and seedlings at either harvesting date (Table 6.1 and Figures 6.7 and 6.8). There was no difference in root depth:plant height ratio between cuttings and seedlings, though there was a significant reduction in the root depth:plant height ratio (in both cuttings and seedlings) between 5 and 8 years after planting.

Figures 6.7 & 6.8: *Root depth & plant height plotted against source (c = cuttings, s = seedlings) & time after planting (in years)*



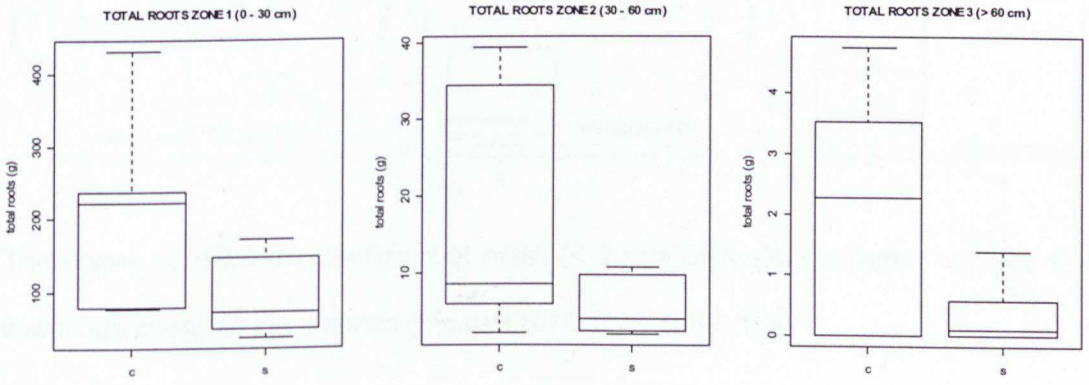
6.3.4 *Root distribution (8 year harvest)*

Table 6.2: *Summary of significant results (marginal significance – p < 0.1 level) from analyses of root distribution in cuttings & seedlings of at 8 years after planting*

Parameter measured	Source/interaction	p value
total root mass in zone 1 (0-30 cm below ground)	treatment (cuttings/seedlings)	0.057
total root mass in zone 3 (>60 cm below ground)	treatment (cuttings/seedlings)	0.052
large root mass in zone 1 (0-30 cm below ground)	treatment (cuttings/seedlings)	0.056
med. root mass in zone 1 (0-30 cm below ground)	treatment (cuttings/seedlings)	0.092
med. root mass in zone 3 (>60 cm below ground)	treatment (cuttings/seedlings)	0.06

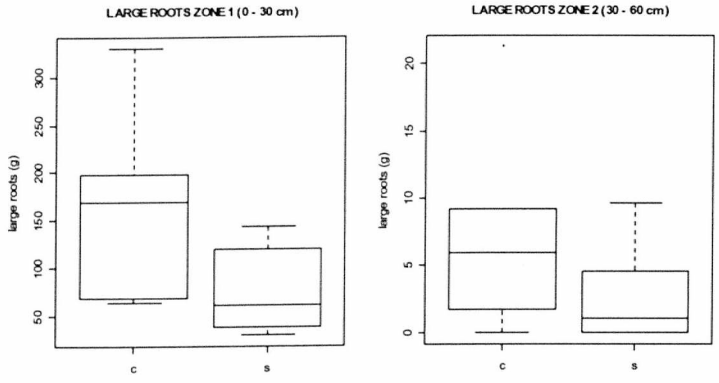
Total cutting root mass in zones 1 (0 – 30 cm from the soil surface) and 3 (> 60 cm from the soil surface) was higher than in seedlings though significance was just marginal at p = 0.057 and p = 0.052 respectively. There was no difference in cutting and seedling root mass in zone 2 (30 – 60 cm) (Table 6.2 and Figures 6.9, 6.10 and 6.11).

Figures 6.9, 6.10 & 6.11: *Root (total mass) distribution plotted against source (c = cuttings, s = seedlings) in zone 1 (0-30 cm), zone 2 (30-60 cm) & zone 3 (> 60 cm)*



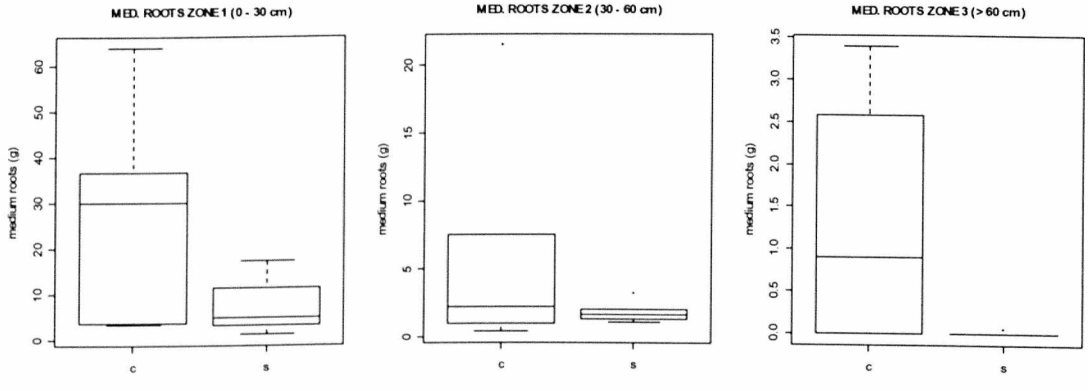
Large root mass (> 5 mm diameter) was higher in cuttings in zone 1 – though significance was marginal (p = 0.056). There was no significant difference in large root mass between cuttings and seedlings in zone 2, and no large roots were found in zone 3 in either cuttings or seedlings (Table 6.2 and Figure 6.12 and 6.13 – following page).

Figures 6.12 & 6.13: *Large root mass (> 5 mm diameter) distribution plotted against source (c = cuttings, s = seedlings). Note – there were no large roots in Zone 3 (> 90 cm depth)*



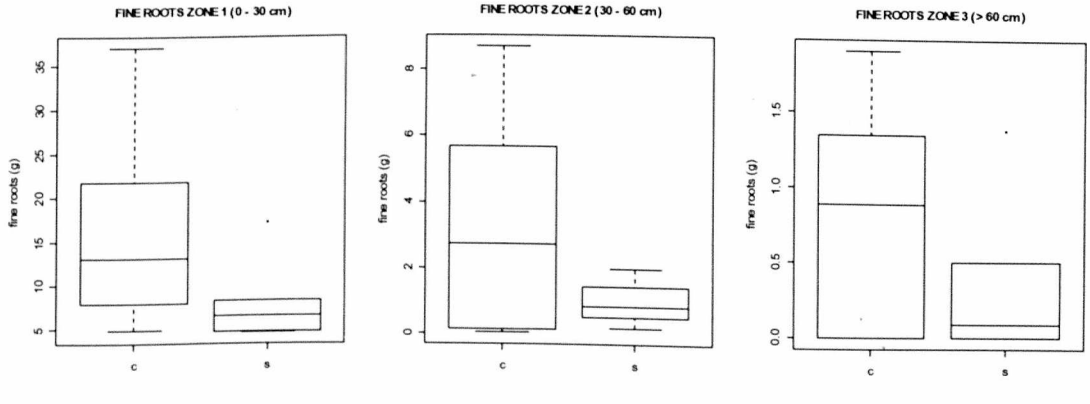
Medium root mass (2 – 5 mm diameter) was higher in cuttings than seedlings in zones 1 and 3, though only at the $p < 0.1$ level (Figures 6.14, 6.15 and 6.16).

Figure 6.14, 6.15 & 6.16: *Medium root mass (2-5 mm diameter) distribution plotted against source (c = cuttings, s = seedlings)*



There was no difference in fine root mass (< 2 mm diameter) between cuttings and seedlings in any of the 3 zones (Figures 6.17, 6.18 and 6.19).

Figure 6.17, 6.18 & 6.19: *Fine root mass (< 2 mm diameter) distribution plotted against source (c = cuttings, s = seedlings)*



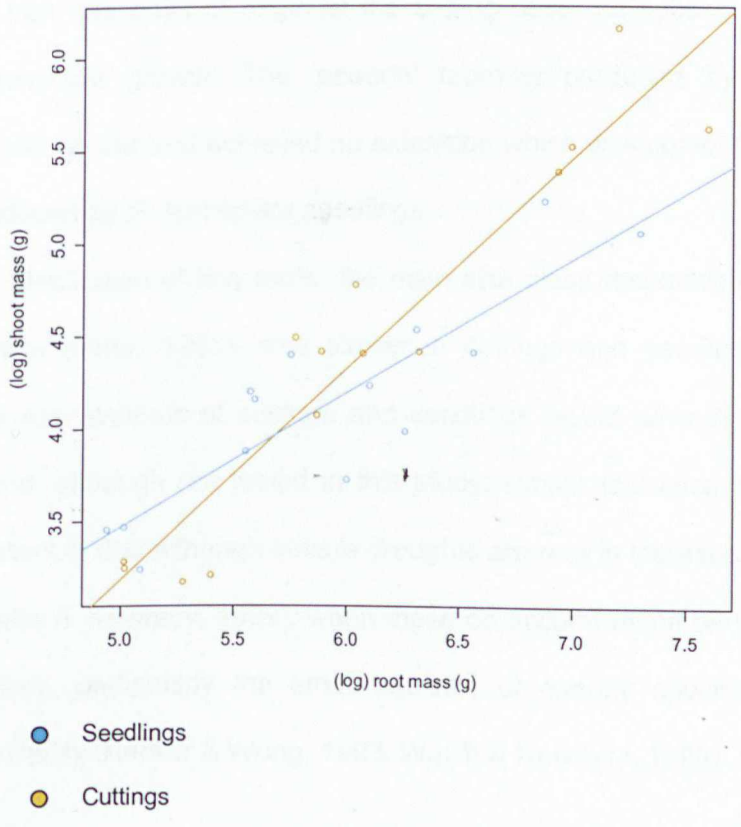
6.3.5 *Root:shoot relationship*

Root mass was positively correlated with shoot mass in both cuttings and seedlings (Table 6.3 and Figure 6.20) at 5 and 8 years after planting. There were significant interactions between root mass, shoot mass and source (i.e. cuttings/seedlings) with cuttings having a higher root mass relative to shoot mass than seedlings.

Table 6.3: *LM analysis describing the relationship between root mass (response variable) & shoot mass & time after planting in D. lanceolata cuttings & seedlings. Significant values (p < 0.05) shown in red. Marginal significance (p < 0.1) shown in blue. Output rounded to 2 significant figures. Root & shoot mass data log transformed*

Source	df	Sum sq	Mean sq	f	p
shoot mass	1	14.43	14.43	176.45	<0.0001
source *(cuttings/seedlings)*	1	0.12	0.12	1.46	0.24
time *(after planting)*	1	0.19	0.19	2.33	0.14
shoot mass:source	1	0.58	0.58	7.14	0.015
shoot mass:time	1	0.069	0.069	0.85	0.37
source:time	1	0.3	0.3	3.64	0.071
shoot mass:source:time	1	0.13	0.13	1.59	0.22
residuals	20	1.64	0.082		

Figure 6.20: *Root mass plotted against shoot mass in D. lanceolata cuttings & seedlings*



6.4 Discussion

Saplings of tropical canopy tree species are generally regarded as being deep rooted with a taproot-based structure (Becker & Castillo, 1990; Becker *et al.*, 1998) and this has been confirmed for a number of dipterocarp species, including *D. lanceolata* (Yamada *et al.*, 2005). It has been suggested that deep rooted saplings are more drought resistant than shallower rooted shrubs and understory trees, and show greater stability on often fragile tropical soils (Becker & Castillo, 1990; Condit *et al.*, 1995, Yamada *et al.*, 2005). As discussed in section 6.1, cuttings of some species have been shown to have shallower root systems and were more susceptible to water stress than equivalent seedlings (e.g. Tinley, 1963; Sasse & Sands, 1997; Stape *et al.*, 2001). Evidence from this study indicates that cuttings of *D. lanceolata* are as deep rooted as seedlings. Although difficult to assess quantitatively, it was clear that *D. lanceolata* cuttings had a structurally very similar root system to seedlings; visually, the deep roots produced by cuttings were comparable in all respects to the taproots of seedlings. Initially these roots grew more-or-less horizontally from the point of origin at the cutting base but subsequently assumed positively geotropic growth. The 'pseudo' taproots produced by cuttings were morphologically similar and achieved an extension which was comparable to the true taproots produced by *D. lanceolata* seedlings.

The vertical distribution of fine roots, the main size class responsible for water and nutrient uptake (Fitter, 1991), was similar in cuttings and seedlings. This would suggest that root systems of cuttings and seedlings would have similar absorptive properties and, although not tested in this study, similar tolerance to water stress. This is important in that although severe droughts are rare in the aseasonal tropics of SE Asia (Walsh & Newbery, 1999), when these do occur it might be the smaller size classes of tree, particularly the small saplings of canopy species, which show increased mortality (Becker & Wong, 1993; Walsh & Newbery, 1999).

The root:shoot ratio of *D. lanceolata* seedlings declined markedly between the 5 and 8 year harvests. This is consistent with a number of studies which have shown that root:shoot ratio decreases with increasing tree size (e.g. Shukla & Ramakrishnan, 1984; Walters & Reich, 1996; Cao & Ohkubo, 1998), although higher cutting root:shoot ratios in cuttings have been reported for the conifer *Pseudotsuga menziesii* (Ritchie *et al.*, 1992). It has been suggested that the greater resources allocated to the root system in the early growth stages is beneficial for both tree establishment and survival in shade (Cannell & Dewar, 1994; Kitajima, 1994; Cao & Ohkubo, 1998). However, in *D. lanceolata* cuttings, the root:shoot ratio remained relatively constant between the 5 and 8 year harvests. It is not clear what the long-term implications for *D. lanceolata* cuttings might be if a high root:shoot ratio were to be maintained to maturity and further harvests would be necessary to determine if *D. lanceolata* cutting and seedling root:shoot ratios converge over time. It is possible that there would be a trade-off in resource allocation and that below ground development in cuttings could be at the expense of above ground biomass accumulation. However, based on the finding from this study, it can be stated with some confidence that the root systems of *D. lanceloata* cuttings, up to 8 years after planting, show no obviously deleterious traits and are, in essence, morphologically and structurally comparable to the root system produced by *D. lanceolata* seedlings. As an aside, and although not quantified as part of this study, the presence of ecto-myccorhiza was noted in both cutting and seedling root systems at similar levels.

In terms of mechanical support, dipterocarps often have large and distinctive root buttresses (e.g. Meijer & Wood, 1964; Richards, 1996; Symington *et al.*, 2004) and it is likely that these are the primary means of anchorage in the mature tree (Richards, 1996; Crook *et al.*, 1997). However, given that buttresses do not develop for many years, it is the mechanical strength of the root system which is key to stability in the early growth stages with the taproot providing the main element of support (Crook *et al.*, 1997). As already discussed, rooting depth in *D. lanceolata* cuttings was similar

to that of seedlings and the pseudo-taproot produced by cuttings appeared to be comparable in all respects to the taproot of seedling *D. lanceolata*. Although not specifically tested, the similarity of the cutting pseudo-taproot and the seedling taproot would suggest that, functionally, they would have comparable performance in supporting the tree.

The relationship between plant height and root depth was similar in cuttings and seedlings. The root depth:plant height ratio did, however, decline from the 5th to the 8th year harvest, possibly reflecting a re-partitioning of resources to favour above ground rather than below ground growth.

Cuttings had a greater mass of large roots in the upper soil profile (0 – 30 cm from the soil surface) than seedlings. This probably reflects the secondary thickening which occurs at the union between the adventitious roots formed at the cutting base. Furthermore, in seedlings a single taproot is produced that is fully contiguous with the stem and it is from this structure that the rest of the root system is generated. In cuttings it is often the case that several large roots emerge from the cutting base and that, in the immediate vicinity of the stem base, the root system has a more 'branching' structure than in seedlings.

There is no evidence to suggest that the differences in distribution of roots in the large and medium size classes would render cuttings any less stable than cuttings – in fact, and as suggested for cutting-propagated *Pseudotsuga menziesii* (Ritchie *et al.*, 1992), it is possible that *D. lanceolata* cuttings may show greater stability than seedlings prior to buttress formation.

Results from this study suggest that cuttings of *D. lanceolata* produce a root system of broadly similar structure and morphology to *D. lanceolata* seedlings both in terms of the roots responsible for support and anchorage, water and nutrient uptake. However, these findings must be treated with some caution in that the study was based on relatively few replicates. This was unavoidable given available time and resources; to lift each tree with the root system intact required 8-12 man days. The

datasets showed considerable variability, particularly in the fine and medium root size classes. This variability is to some extent inherent in the assessment of root systems; up to 30-fold differences have been reported in fine root length between within species samples (Cao & Ohkubo, 1998). Further assessments of root structure as the trees reach maturity could yield valuable information on the long-term development of the cutting root system. The three-dimensional digitising techniques developed for analysing the extensive root systems of mature *Pinus pinaster* (Danjon *et al.*, 2005) would seem to be ideal for use with dipterocarps. This would require the use of a mechanical back-hoe to excavate the tree but, as these machines are widely used for road and bridge building as part of logging operations in SE Asia, this would be an option.

It would have been instructive to have tested the functionality of cutting root systems in comparison to seedlings, both in terms of mechanical strength and water and nutrient uptake, and this should form the basis of further studies. Following the methods of Crook and colleagues (Crook *et al.*, 1997), it would be useful to test the strength of the pseudo-taproots produced by *D. lanceolata* cuttings and it should also be a priority to monitor the development of buttress roots in cuttings and seedlings over the longer term. There is no evidence in the published literature to suggest if the cuttings of rainforest trees are able to produce buttresses and no dipterocarp cuttings have been monitored over a sufficiently long period to confirm buttress formation.

These findings are based on only one dipterocarp species. Although there is no reason to assume that cuttings of other dipterocarp species would show developmental differences to *D. lanceolata* (especially given the results presented in Chapter 5 of this thesis which investigated cuttings of *Shorea* and *Parashorea* species) this assumption should certainly be tested.

Notwithstanding these experimental shortcomings, it can be concluded that the root systems of *D. lanceolata* cuttings were essentially similar to those of seedlings and the original hypothesis of this experiment can be rejected.

CHAPTER 7

7. GENERAL DISCUSSION

The main themes of this research were, i) addressing specific questions relating to the propagation of dipterocarp cuttings, ii) comparing the immediate post-planting survival and development of cuttings and seedlings and, iii) comparing their longer-term development. Before drawing together these themes and the specific findings of this research, it is important to take a step back and briefly discuss some of the issues surrounding the management of dipterocarp stockplants and hence the availability of cutting material.

7.1 Stockplant management & the supply of dipterocarp cuttings

It had been intended to use the INFAPRO and Danum Valley hedge orchards as the main source of cutting material for this research. However, following an assessment some 18 months prior to the start of the project, it was clear that too few cuttings were available from these hedge orchards to supply experimental requirements.

There are three main reasons for the lack of capacity in traditionally-managed dipterocarp hedge orchards. Firstly, dipterocarps do not generally coppice well. There are exceptions, some of the *Hopea* species for example (Kantarli, 1993[b]; Aminah, 1996), but of the major dipterocarp genera used on enrichment planting programmes in SE Asia (*Shorea*, *Parashorea*, *Dryobalanops* and *Dipterocarpus* species) none appear to produce a profusion of orthotropic shoots after hard pruning. Secondly, the few orthotropic shoots that are produced after coppicing, because of very long internodes, make unsuitable cutting material and, thirdly, the received wisdom is that cuttings taken from plagiotropic shoots (which do develop relatively well after coppicing) do not re-assume orthotropic growth. There is little or no evidence from the literature to support any of these assertions, but to set up

experiments to properly test questions related to stockplant management would have been beyond the scope and time-scale of this research.

Recognising that this project would have been impossible without a reliable supply of cutting material, approximately 1 year before the start of the first experiment small-scale trials were instituted to establish if plagiotropic stockplant shoots might in fact be capable of providing suitable cutting material. Cuttings were taken from plagiotropic shoots of *Dryobalanops lanceolata* and several *Hopea*, *Shorea* and *Parashorea* species. Although the amount of cutting material produced was plentiful, and the resulting cuttings generally rooted well, all the cuttings were still growing plagiotropically almost 2 years later. These results were further confirmed after assessing a batch of cuttings of *D. lanceolata*, also taken from plagiotropic shoots, which had been field-planted at the start of the INFAPRO project in 1992. These cuttings were still growing plagiotropically more than 10 years later with no sign of any resumption of orthotropic growth. Given the problems of plagiotropy, and the general lack of capacity, it was clear that hedge orchards could not provide either a suitable or reliable source of cuttings. This presented potentially serious difficulties for this project and, more importantly, for the supply of cuttings for planting material should seedlings be in short supply.

The only alternative source of cuttings available were the existing seedlings growing at the INFAPRO nursery. Under normal circumstances using seedlings as stockplants would make no sense; taking a dipterocarp cutting from a seedling gives a multiplication factor of only 1:1 or at best 1:2. In most cases, only one cutting can be taken from each seedling as it is only the apical, leafy, semi-hardwood zone of the seedling which can provide a viable cutting. In older seedlings the lower portion of the stem is usually heavily lignified and has few or no leaves. These parts of the stem would almost certainly not provide cutting material as leafless, hardwood cuttings of tropical evergreens are usually not able to form roots (Hartmann *et al.*, 2002).

Due to the mast fruiting habit of dipterocarps the most pressing issue in providing planting material to a large-scale forest rehabilitation programme is not so much one of supply but rather scheduling nursery production, which is almost impossible using a seed-based propagation system. Immediately following a fruiting event seed is readily available across a broad range of species and, notwithstanding the logistical difficulties of collecting, processing and sowing these seeds, it is a relatively trivial matter to grow a huge number of seedlings. On the INFAPRO project, for example, nursery stocks after fruiting can total well over one million seedlings from 30 or more species. However, although dipterocarp seedlings can survive for relatively long periods in dense shade (Blundell & Peart, 2001; Kurokawa *et al.*, 2004), they can only be 'held' at a plantable size for perhaps three or at most four years before they become either too large or too pot-bound to plant (*personal observation*). The current practice is to cull these overgrown seedlings and this can leave enrichment planting projects critically short of planting material from around the fourth year after a major mast fruiting event – given that these events can be anything up to 10 years apart (Ashton *et al.*, 1988, Appanah, 1993).

Although overgrown or pot-bound seedlings may no longer be suitable for planting, they can provide an almost ideal source of stem cuttings. Seedlings remain physiologically juvenile with a strongly orthotropic main shoot, are often available in very large numbers across a broad species range and, as they would otherwise be destroyed, the fact that only one cutting may be taken from each seedling is largely irrelevant. Under these circumstances vegetative propagation can be regarded as a means of 'rejuvenating' otherwise unusable nursery stock rather than as a method of mass multiplication. An important additional benefit of taking cuttings from seedlings, rather than from a limited number of hedge orchard stockplants, is that the genetic diversity of planting material is maintained.

In conclusion, the main purpose of propagating dipterocarps by cuttings in the context of forest rehabilitation would be to provide an alternative method for the

production of planting material once seed-propagated plants become unplantable. Taking cuttings from overgrown seedlings would allow the 'rejuvenation' of nursery stock at precisely the time when the supply of seedlings of a plantable size begins to dwindle. The expense and time involved in establishing extensive hedge orchards, which have very limited capacity, and that would, in any case, only be called into production infrequently, is almost certainly not worthwhile. There is a strong argument that enrichment planting programmes should grow as many seedlings as possible during a mast fruiting event, not only to provide planting material for the immediate 3 to 4 year period, but also as stockplants from which cuttings can be taken as the seedlings themselves become unplantable.

7.2 Propagating dipterocarps by cuttings

The great majority of lowland dipterocarp forests in SE Asia are in a highly degraded condition (e.g. Mayaux *et al.*, 2005) and often show a serious lack of natural recruitment (e.g. Curran *et al.*, 1999). Large tracts of the region's lowland forests are therefore in considerable need of restorative intervention, with enrichment planting likely to be the key element of any rehabilitation effort (e.g. Wyatt-Smitt, 1963; Appanah & Weinland, 1993). Enrichment planting programmes frequently operate over extensive areas, tens of thousands of hectares in some cases, and hence the requirement for planting material can be enormous. However, due to the irregularity of dipterocarp fruiting (e.g. Ashton *et al.*, 1988), a seed-based propagation system cannot be relied upon as the sole production method. It is of critical importance that alternative methods are in place for the large-scale propagation of dipterocarps.

Given the financial and logistic constraints under which many enrichment planting programmes operate, vegetative propagation by stem cuttings, as a well-established and simple method, could in theory provide a viable alternative to seed-based production systems. However, despite a considerable body of research and some success in developing cutting-based propagation methods that could be scaled to

meet the demands of a large-scale planting operation (reviewed by Dick & Aminah, 1994), few rehabilitation projects are producing significant quantities of dipterocarps by cuttings (Appanah & Weinland, 1993; Appanah, *pers. com.*). This lack of interest is probably due in large part to concerns relating to the longer-term development of dipterocarp cuttings after planting; addressing this issue was the main aim of this project and will be discussed in the following section. However, significant gaps in knowledge remain at the propagation stage. In particular, the influence of light on rooting in dipterocarp cuttings has never been studied, while the efficacy of applied hormones to promote rooting has not been conclusively established.

Despite the importance and widespread use of vegetative propagation in commercial horticulture and forestry, it remains unclear for many species if photosynthesis plays any part in the root initiation process in leafy stem cuttings (e.g. Mesén *et al.*, 1997; Mesén *et al.*, 2001; Bruce *et al.*, 2001; Hartmann *et al.*, 2002). If a generalisation is possible, photosynthesis (and hence the level of irradiance) is probably more important after root initiation, at which stage it may influence the rate of root emergence and the extent of root development (Hartmann *et al.*, 2002).

There have been numerous studies on the responses of naturally recruited dipterocarps to light, many of which have focused on its role in determining the survival and growth of seedlings and in structuring dipterocarp populations (reviewed by: Brown *et al.*, 1999, also Ashton, 1988; Press *et al.*, 1996; Barker *et al.*, 1997). In view of its central role in dipterocarp ecology, in particular the rapid growth of dipterocarp seedlings in response to gap size (e.g. Brown & Whitmore, 1996), it was hypothesised that the level of irradiance might play an equally important role in the rooting and other growth responses of dipterocarp cuttings, particularly root development. However, results from this research indicated that survival, root initiation and root development in cuttings of *D. lanceolata*, *P. malaanonan* and *S. leprosula* were unaffected by varying the level of irradiance (within the range investigated), suggesting that these species have considerable plasticity in their

response to light. Although no previous studies have focussed specifically on the effects of light on root initiation in dipterocarp cuttings or how it may influence subsequent root development, recommendations for shading dipterocarp cuttings have ranged from <50% (e.g. Sakai *et al.*, 1994) to >90% (e.g. Momose, 1978). By implication this would support the proposition that the precise level of irradiance is largely irrelevant to rooting in dipterocarp cuttings. Moreover, given that light levels would influence other variables including temperature, relative humidity and vapour pressure deficit within the propagation environment, this also implies that dipterocarp cuttings show considerable tolerance to variation in these factors.

Aside from the physical propagation environment, adventitious root formation in cuttings is strongly influenced by the action of either endogenous or applied plant hormones (reviewed in: Davis, 1988; Haissig & Davis, 1994; Hartmann *et al.*, 2002). Numerous studies over a wide range of herbaceous and woody plant species have shown that hormones of the auxin group can significantly improve root initiation and development in cuttings. Of the range of natural and synthetic auxins used in vegetative propagation, IBA has proved to be the most effective for the majority of species (reviewed in: Macdonald, 1986; Hartmann *et al.*, 2002).

With rare exception, the cuttings of most dipterocarp species have been found relatively slow and difficult to root and a number of studies have investigated the use of IBA and other auxin-group hormones with a view to improving rooting performance (reviewed by Dick & Aminah, 1994). However, results have been inconclusive with both negative and positive effects having been reported. The use of IBA was re-visited in this project on cuttings of *D. lanceolata*, *P. malaanonan* and *S. leprosula* with the now seldom used horticultural technique of soaking cuttings in dilute auxin solutions (Hartmann *et al.*, 2002). This method had been found effective in promoting rooting in several difficult-to-root tree species (Macdonald, 1986) but has never been used with dipterocarp cuttings.

Results were relatively clear cut. Long exposure of cuttings to high concentrations of IBA resulted in increased cutting mortality. The treatment which combined the long exposure time tested (120 hours) with the highest concentration of IBA (3,000 ppm) caused 100% mortality in all species. This strongly suggested a phytotoxic response to IBA; a surprising result given that IBA is regarded has having extremely low phytotoxicity over a wide concentration (and species) range (Hartmann *et al.*, 2002). Phytotoxic responses to IBA, although rare, are not entirely unknown and have been reported in cuttings of the African tree *Milicia excelsa* (Ofori *et al.*, 1996).

IBA had a generally negative impact on rooting percentage, with the most pronounced affect on *D. lanceolata* cuttings. There was no evidence that IBA application improved root development. These results were in agreement with previous studies (on *D. lanceolata*) which have shown that IBA auxin-group hormones did not improve either root initiation or development (Moura-Costa & Lundoh, 1994; Brodie, 2003).

Given the possible phytotoxic response of *D. lanceolata*, *P. malaanonan* and *S. leprosula* to IBA, these results provide no basis to recommend its use with dipterocarp cuttings. In the absence of evidence from a wider range of species, the use of IBA with dipterocarp cuttings should for the time being be discouraged.

Further research in this area could include the use of other plant growth regulators, perhaps NAA or the more recently developed Phenyl indole-thiolobutyrate (P-ITB), which has been found effective in promoting rooting in a number of woody species (Dirr, 1990, 1994). However, it seems unlikely that the use of these substances would yield significant gains; if IBA had indeed induced a phytotoxic response, it is likely that other synthetic auxins would be similarly toxic to dipterocarp cuttings, and, in most cases, if a cutting shows no response to IBA the use of other root promoting substances would unlikely compensate (Hartmann *et al.*, 2002).

Survival and rooting percentages for cuttings grown as part of this project, in both the light and hormone experiments, were equivalent to or higher than those reported in

previous studies. However, in comparison with other plantation and horticultural tree species regularly propagated by stem cuttings, rooting success in *D. lanceolata*, *P. malaanonan* and *S. leprosula* is low (Appanah & Weinland, 1993). The reasons why rooting in dipterocarp cuttings is comparatively poor have not been conclusively established but results from this and previous studies do not suggest that the propagation environment (light level, misting regime, propagation media etc.) or applied hormones are significant as dipterocarp cuttings appear relatively plastic in their responses to variation in these factors.

A wide array of propagation facilities have been used for raising dipterocarp cuttings ranging from clear plastic bags filled with coir and shaded with palm fronds (Pollisco, 1994[a,b]) to highly sophisticated, computer-controlled, fully-automated hydroponic systems (Smits *et al.*, 1994). For individual enrichment planting projects the choice of propagation facility would largely depend on the availability of supporting staff, funding and infrastructure – in particular a reliable water and electrical supply. This project utilised relatively sophisticated semi-automated mist facilities and was supported by a highly-skilled staff, good infrastructure and a substantial budget. However, given the apparently wide tolerance of dipterocarp cuttings to the propagation environment, this level of sophistication may not be a pre-requisite to success and on a less well staffed, funded or more remotely located project, much simpler facilities could just as well be used.

7.3 Survival & development of dipterocarp cuttings after planting

There is no evidence to indicate how dipterocarp cuttings perform after planting or how their growth and development compares to that of seedlings. This is a serious gap in knowledge and it is unlikely that any major enrichment planting project would risk implementing a cutting-based propagation system without some degree of confidence that dipterocarp cuttings would show similar long-term survival, growth and developmental characteristics to seedlings.

In this project, mortality in cuttings was higher than in seedlings, particularly during the first 8 months after planting. However, it was notable that overall survival in both cuttings and seedlings was broadly comparable to survival data reported by enrichment projects and for naturally recruited dipterocarp seedlings (e.g. Moura Costa *et al.*, 1996; Schulze *et al.*, 1994; Ådjers *et al.*, 1995; Turner, 1990; Itoh, 1995). It is not clear what factors, environmental or physiological, were responsible for the difference in survival between cuttings and seedlings. It appears most likely that the explanation is related to the lower root:shoot ratio in cuttings at the time of planting, coinciding with a brief dry period immediately after planting. Several studies have shown that in some tree species cuttings have a lower root:shoot ratio than seedlings and are more susceptible to water stress (Sasse & Sands, 1996; Stape *et al.*, 2001; Mulatya *et al.*, 2002).

Relative growth rate in cuttings (after 20 months growth) was significantly higher than in seedlings, independent of species. As a result, and although cuttings had a lower biomass (above and below ground), height and diameter than seedlings at the time of planting, by the end of the experiment these measurements had largely converged. There was no obvious explanation for this other than that cuttings, which had only recently been propagated, may simply have been in a more active growth phase at the start of the experiment. The seedlings, by contrast, were approximately 2 years old when planted and had been held under heavy nursery shade during this period. Root malformation is known to occur in plants that have been grown for too long in small containers (Zwolonski & Bayley, 2001; Evans & Turnball, 2004) and this may have been the case with the dipterocarp seedlings used in this research. It was possible, although certainly not obvious either at planting or the 20 month harvest, that the seedling root system had started to 'spiral' and that this may have impacted growth rate. As a general principle, and although there would be a cost implication, consideration should be given to using root trainer containers for raising both dipterocarp seedlings and cuttings. Such containers are now widely used in the

plantation industry and have been shown to improve root morphology and inhibit spiralling (Adjers & Strivastava, 1993 cited in Evans & Turnbull, 2004).

Canopy openness, and interactions between canopy openness, species and initial planting height, affected survival and growth rates in cuttings and seedlings – albeit temporarily. These interactions are extremely difficult to interpret, not least as the effects dropped in and out of significance during the experimental period. It is quite possible that canopy-related effects were artefacts caused by the several major tree falls which occurred within the plots during the experiment. Purely by chance, a number of the largest of the tree falls were oriented almost directly along the planting lines and this could explain the atypical, highly patchy mortality and/or growth patterns of the planted cuttings and seedlings.

Evidence from this research suggests that cutting growth in the immediate post-planting period is perfectly acceptable and broadly comparable to that of seedlings. Although there were differences in survival and growth between cuttings and seedlings during this period, it appears highly likely that these were driven by temporary factors, most particularly pre-planting differences in root:shoot ratio. It is also possible that the 'vigour' of cuttings and seedlings at the time of planting may have impacted comparative growth rates.

Based on the assessment of *D. lanceolata* cuttings and seedlings after 5 and 8 years, the differences between cuttings and seedlings did indeed appear to be temporal. A detailed comparative analysis, including measures of root mass and root distribution down the soil profile, indicated that development in cuttings and seedlings of *D. lanceolata* was essentially similar. There were no differences in the key parameters of root depth, total root mass, fine root mass or fine and large root mass distribution at either the 5 or 8 year harvests and above ground growth was similar in both cuttings and seedlings. Cuttings had a higher root:shoot ratio than seedlings at 8 years after planting, though the data showed considerable variability. Although difficult to assess quantitatively, perhaps the most significant finding of this part of the

project was that cuttings produced a 'pseudo' taproot of very similar form and extent to the taproot produced by the seed-derived trees.

In summary, up to 8 years after planting, by which stage some of the trees were well over 5 metres tall, the root systems of *D. lanceolata* cuttings and seedlings were essentially similar. Cuttings had a well-structured root system comprising both absorptive and support roots of similar extent, form and distribution to seedlings.

7.4 Conclusions

In the event of a shortage of seedlings, a large-scale enrichment planting project could reasonably be advised to initiate the propagation of dipterocarps by stem cuttings, most likely sourced from overgrown nursery seedlings. Such a project could also be advised, with some confidence, that the root system of cutting-propagated dipterocarps, being similar to that of seed-propagated trees in almost all respects, would be capable of supporting the planted trees to maturity.

7.5 Research limitations

In retrospect, the choice of study species would ideally have reflected a broader range of the ecological traits found among dipterocarps. It would probably have been sensible to have dropped one of the light demanding, fast growing species (either *P. malaanonan* or *S. leprosula* – both of which occupy a similar ecological niche) in favour of a more shade tolerant, slow growing, heavy-hardwood such as a *Hopea* or *Vatica* species. Unfortunately, neither these or similar species were available in sufficient quantity at the INFAPRO nursery to supply a properly replicated experiment.

Similarly, in the light experiment, a greater range of light treatments particularly in the higher range, could have been beneficial. Imposing higher light treatments would, however, have been difficult as the ambient shade level at the research nursery was already in the order of 50%. Characterising the environment within each of the light

treatments, especially in terms of temperature and relative humidity, would have been instructive and it was intended to take these measurements. Unfortunately, the data logging equipment provided by INFAPRO to measure these parameters malfunctioned at the start of the experiment and could not be repaired in time to be deployed.

At the propagation phase, it was a considerable oversight not to have made an assessment of cutting mass by destructive sub-sample at the time of removal from the stockplant. An analysis of above-ground biomass gains both during and after propagation was therefore impossible.

A sophisticated root-scanning system (Delta-T Devices RootScan) was purchased to make detailed assessments of root length of cuttings both immediately following rooting and for the analysis of the root system of field planted cuttings and seedlings. The RootScan system is based on a modified high-definition scanner, includes advanced software to assess root length, allows cuttings to be scanned *in-vivo* and subsequently planted; root development of an individual cutting or seedling could therefore have been measured immediately after propagation and re-measured at the end of the experiment, rather than relying on destructive pre- and post-planting sub-samples. Despite numerous attempts, the system could not be made to work with anything but the finest of roots (considerably less than 2 mm diameter). Roots in larger size classes caused 'shadowing' in the scanned image and this introduced unacceptable errors into the analyses. Moreover, even in the relatively fine root systems of newly propagated cuttings, the scanning resolution had to be altered for each root scan in order to account for differences in diameter class distribution. The alteration of scanning resolution between scans resulted in orders-of-magnitude differences in root length assessments between apparently similarly-sized root systems. Given these difficulties, root length data from these scans has not been presented.

Perhaps the most serious limitation of this research was in the assessment of cuttings and seedlings of *D. lanceolata* at 5 and 8 years after planting. Firstly, the cuttings and seedlings were planted as part of a forestry trial rather than as a properly designed field experiment. Cuttings were planted in one distinct 'block' with seedlings planted in a separate, albeit adjacent, block. The cutting and seedling blocks were located within the same logging compartment and there were no obvious difference in topography, soil type, forest type or canopy cover. However, because of this less than ideal arrangement, the findings from these analyses must be treated with a degree of caution. Despite these drawbacks, it was considered that the potential value of assessing dipterocarp cuttings at this stage of development far outweighed the limitations resulting from the experimental design, or rather the lack thereof (no randomized blocks, for example). Secondly, although the cuttings and seedlings were planted as part of a forestry trial, it appears that they had not been measured either before or after planting and no background survival or growth data were available up to the point of the 5 or 8 years assessments. The third major limitation was the minimal number of trees assessed at each of the harvests. This level of replication was due to the time involved in lifting the trees – especially during the 8 year harvest when some saplings were well over 5 metres in height. Each tree took 2 to 3 people up to 5 days to lift and was often interrupted by rain; the fine roots, in particular, could only be removed effectively without breakage from relatively dry, friable soil.

7.6 Possible directions & priorities for future research

Significant questions remain with regard to the vegetative propagation of dipterocarps by cuttings, both at the propagation stage and in the longer-term development of cuttings after planting. Based on the findings (and limitations) of this project, there are a number of areas which should be developed in any future research.

At the propagation stage research on a wider range of species to establish their suitability for propagation by cuttings would be useful. For example, several dipterocarps, including *Dipterocarpus* and some *Shorea* species, have a high resin content and it is possible that propagating such resinous species by conventional stem cuttings may prove difficult or even impossible (Hartmann *et al.*, 2002). However, these species-specific traits have yet to be established as most research in this area has focussed on a relatively few, high-value timber species. Information on the propagation of a wider range of dipterocarps would be extremely important in more conservation-focussed rehabilitation or restoration projects where planting with a wider range of species would be a priority.

There have been only very few studies on the use of micropropagation and other *in vitro* techniques with the dipterocarps, and the research that has been done has concentrated on an extremely limited range of species (Scott & Loh, 1995; Linington, 1991). Although it is often the case that if cuttings are difficult to root using conventional techniques then micropropagation also proves problematic, further work in this area may be merited, especially for dipterocarp species with particularly high conservation value – though given the cost and technical requirements of *in vitro* propagation it seems unlikely that the technique would find use with all but the best-funded rainforest rehabilitation projects.

Results from this research suggested that dipterocarp cuttings may be more susceptible to water stress than seedlings. It would, however, be useful to investigate this in a more controlled way, for example following the methods of Sasse and Sands (1997) who conducted pot trials to establish responses to water stress in cuttings and seedlings of *Eucalyptus* species. It would be useful to establish if dipterocarp cuttings have similar nutrient uptake levels to seedlings and, also in relation to nutrient uptake, the extent to which cutting and seedling root systems are colonised by mycorrhiza. Observational evidence from this research indicated that cutting root

systems were mycorrhizal but this should be established conclusively given the possible growth implications, especially on nutrient-poor soils.

Assessment of root architecture in dipterocarp cuttings and seedlings using the three-dimensional digitising techniques developed by Danjon and colleagues (1999, 2005) would be an obvious area of future research. Use of this technique, which essentially involves manually 'mapping' the root system and then analysing its structure using specially developed AMAPmod software (Danjon *et al.*, 1999, 2005), could shed new light on the development processes of dipterocarp cutting root systems and give a useful insight into the characteristics of the root systems of mature dipterocarps which have never been studied.

Although this research has suggested that the root systems of dipterocarp cuttings and seedlings are essentially similar, it is important to quantify the support function of cutting root systems. Methods have been developed for testing the mechanical strength of root systems (Crook *et al.*, 1997) and these could be employed in comparative research on dipterocarp cuttings and seedlings. It is also critical to establish if dipterocarp cuttings are capable of producing buttress roots; the 8 year-old *D. lanceolata* assessed as part of this experiment had not started to form buttresses, though in many species this does not appear to occur until the tree reaches 10 or more metres in height (Appanah & Weinland, 1993).

There is a pressing need for these issues to be addressed if the potential of vegetative propagation of dipterocarps is to be fully realised. The SE Asia rainforests face increasing threats from degradation through logging, shifting cultivation and clearance for agriculture; the propagation of dipterocarps by cuttings could play an important role in both forest rehabilitation and, potentially, the *ex-situ* conservation of individual dipterocarp species.

CHAPTER 8

8. KEY RECOMMENDATIONS

The overriding objective of this research was to provide information that would be of practical use to projects involved in the rehabilitation of lowland dipterocarp forests by enrichment planting. Based on the findings of this and related studies the following recommendations can be made:

8.1 Stockplant type & management

- Under most circumstances establishing hedge orchards to supply cutting material is not recommended. The exception would be for the conservation of rare or endangered dipterocarp species where seed may be difficult to obtain
- Overgrown nursery seedlings make excellent stockplants
- Plagiotropic stockplant shoots, either from hedge orchards or overgrown seedlings, cannot be used as sources of cutting material
- Following mast fruiting it would be advisable to collect sufficient seed to supply the planting operation for 3 to 4 years, plus a broadly equivalent quantity to provide enough cutting material to supply the planting operation until the next major fruiting event
- Seedling stockplants may be grown under the same conditions as the seedlings intended for planting

8.2 Propagation by cuttings

- The choice of propagation facilities depends on the availability of funds, trained staff, electrical and water supplies. Perfectly acceptable results can be obtained from low-tech facilities, though a more controllable propagation environment with automatic or semi-automatic irrigation may be easier to manage
- The propagation environment should be shaded at a level between 60 and 90%

- Standard semi-hardwood apical cuttings of about 150 to 200 mm length with 1 to 3 fully expanded leaves retained (trimmed if necessary to reduce leaf area) should be taken from the orthotropic shoots of seedling stockplants using a sloping cut just beneath a node
- The use of rooting hormones, IBA or similar, is not recommended
- It is perfectly possible to strike cuttings in the same bags (50 x 200 mm) as those used to raise seedlings. Once rooted cuttings may remain in these bags until planting
- In order to encourage mycorrhizal activity, the media used for propagation should ideally include a forest soil component. The media used in this research, which consisted of 40% composted sawdust, 40% river sand and 20% forest soil, supported good root development during propagation and by the 20 month harvest in the field planting experiment the cuttings had developed mycorrhizal associations. The choice of organic component would depend on locally available materials; coir, composted oil palm waste or composted rice husks would all, potentially, be suitable (following sterilization)

8.3 Enrichment planting with cuttings

- Cuttings can provide a viable alternative to seedlings to supply planting material and can be planted with some confidence that they will show similar survival, growth rates and long-term development to seedlings
- Cuttings should be 'weaned' from the propagation environment and acclimated under standard nursery conditions for at least one month prior to planting
- If cuttings are planted, a long-term measurement programme should be instituted to monitor their growth and development. Of particular importance would be to monitor experimentally cutting susceptibility to drought, wind-throw and, in the longer-term, the extent and nature of buttress formation

REFERENCES

Ådjers, G., Hadengganan, S., Kuusipalo, J., Nuryanto, K., Vesa, L. 1995. Enrichment planting of dipterocarps in logged-over secondary forests: effect of width, direction and maintenance method of planting on selected *Shorea* species. *Forest Ecology and Management,* ***73****, 259-270.*

Ådjers, G., Srivastava, P.B.L. 1993. Nursery practices. In: *Awang, K., Taylor, D. Acacia mangium: growing and utilization. Winrock International and the Food and Agriculture Organisation of the United Nations, Bangkok.*

Alexander, I., Ahmad, N., Lee, S.S. 1992. The role of mycorrhizas in the regeneration of some Malaysian forest trees. *Philosophical Transactions of the Royal Society of London (Series B),* ***335****, 379-388.*

Aminah, H. 1991. A note on the rooting of *Shorea bracteolata* stem cuttings. *Journal of Tropical Forest Science,* ***3****, 187-188.*

Aminah, H. 1995. Vegetative propagation of *Shorea leprosula* by stem cuttings. *Ph.D. Thesis, University of Edinburgh.*

Aminah, H. 1996. Vegetative propagation by stem cuttings as a potential method for production of clonal planting stock for indigenous forest tree species in Malaysia. In: *Dieters, M.J., Matheson, A.C., Nikles, D.G., Harwood, C.E., Walker, S.M. (Eds.) Tree Improvements for Sustainable Tropical Forestry. Proceedings of the QFRI-IUFRO Conference, Caloundra, Queensland, Australia. 27th October-1st November 1996.*

Aminah H. 1996. Rooting of *Hopea odorata* cuttings taken from coppice shoots and the growth performance of rooted cuttings at nursery stage. *Journal of Tropical Forest Science,* ***8****, 273-279.*

Aminah, H., Dick, J. McP., Leakey, R.R.B., Grace, J., Smith, R.I. 1995. Effect of indole butyric acid (IBA) on stem cuttings of *Shorea leprosula*. *Forest Ecology and Management,* ***72****, 199-206.*

Aminah, H., Dick, J.M., Grace, J. 1997. Influence of irradiance on water relations and carbon flux during rooting of *Shorea leprosula* leafy stem cuttings. *Tree Physiology,* ***17****, 445-452.*

Aminah, H. 1999. Propagation by stem cuttings is an alternative method of producing planting stocks of dipterocarps. In: *Marzalina, M., Khoo, K.C., Jayanthi, N., Tsan, F.Y., Krishnapilly, B. (Eds.) Recalcitrant Seeds: IUFRO Seed Symposium 1998 Proceedings. Forest Research Institute Malaysia.*

Appanah, S. 1993. Mass flowering of dipterocarp forests in the aseasonal tropics. *Journal of Bioscience,* ***18****, 457-474*

Appanah, S., Cossalter. C., 1994. Dipterocarps: State of knowledge and priorities and needs for future research. *5th Roundtable Conference on Dipterocarps, Chiangmi, Thailand. 7th - 10th November 1994.*

Appanah, S., Weinland, G. 1993. Planting Quality Timber Trees in Peninsular Malaysia - a Review. *Malayan Forestry Records No.38. Forest Research Institute Malaysia.*

Appanah, S. 2001. Sustainable management of Malaysian rainforests. In: *Evans, J. (Ed.). The Forests Handbook, Volume 2., 341-356.*

Ardikiosoma, R.I., Noekamal, M.T. 1955. Pertjobaan tanaman *Shorea leprosula* di Djawa. *Pengumuman Balai Penjelidikan Kehutanan No. 48.*

Ashton, P.S. 1982. Dipterocarpaceae. *Flora Malesiana Series 1*, ***9***.

Ashton, P.S. 1988. Dipterocarp biology as a window to the understanding of tropical forest structure. *Annual Review of Ecological Systematics, **19**, 347-370.*

Ashton, P.S., Givinish, T.J., Appanah, S. 1988. Staggered flowering in the Dipterocarpaceae: New insights into floral induction and the evolution of mass flowering in the seasonal tropics. *The American Naturalist, **132,** 44-60.*

Ashton, M.S., Gunatilleke, C.V.S., Singhakumara, B.M.P., Gunatilleke, I.A.U.N. 2001. Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. *Forest Ecology and Management, **154**, 409-430.*

Barker, M.G., Press, M.C., Brown, N.D. 1997. Photosynthetic characteristics of dipterocarp seedlings in three tropical rain forest light environments: a basis for niche partitioning? *Oecologia, **112**, 453-463.*

Bebber, D., Brown, N., Speight, M. 2002. Drought and root herbivory in understory *Parashorea* Kurz (Dipterocarpaceae) seedlings in Borneo. *Journal of Tropical Ecology, **18**, 795-804.*

Bebber, D., Brown, N., Speight, M., Moura-Costa, P., Yap, S.W. 2002. Spatial structure of light and dipterocarp seedling growth in a tropical secondary forest. *Forest Ecology and Management, **157**, 65-75.*

Bebber, D.P., Brown, N.D., Speight, M.R. 2004. Dipterocarp seedling population dynamics in Bornean primary lowland forest during the 1997-8 El Niño-Southern Oscillation. *Journal of Tropical Ecology, **20**, 11-19.*

Becker, P., Castillo, A. 1990. Root architecture of shrubs and saplings in the understory of a tropical moist forest in lowland Panama. *Biotropica, **22**, 242-249.*

Becker, P., Ong, C.L., Goh, F. 1998. Selective drought mortality of Dipterocarp trees: no correlation with timber group distributions in Borneo. *Biotropica, **30**, 666-671.*

Becker, P., Sharbani, N., Yahya, R. 1998. Root architecture and root:shoot allocation of shrubs and saplings in two lowland tropical forests: implications for life-form composition. *Biotropica, **31**, 93-101.*

Blazich, F.A. 1988. Mineral nutrition and adventitious rooting. In: *Haissig, B.E., Davis, T.D. Adventitious Root Formation in Cuttings. Dioscorides Press, Oregon.*

Blundell, A.G., Peart, D.R. 2001. Growth strategies of a shade-tolerant tropical tree: the interactive effects of canopy gaps and simulated herbivory. *Journal of Ecology, **89**, 608-615.*

Brennan, E.B., Mudge, K.W. 1998. Vegetative propagation of *Inga feuillei* from shoot cuttings and air layering. *New Forests, **15**, 37-51.*

Brodie, J.F. 2003. The factors affecting the rooting ability of *Dryobalanops oblongifolia* and *Shorea splendida* (Dipterocarpaceae) stem cuttings. *Journal of Tropical Forest Science, **15**, 109-116.*

Brook, B.W., Sodhi., N.S., Ng, P.K.L. 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature, **424**, 420-423.*

Brown, N.D., Whitmore, T.C. 1992. Do dipterocarp seedlings really partition tropical rain forest gaps? *Philosophical Transactions of the Royal Society of London (Series B), **335**, 369-378.*

Brown. N. 1996. A gradient of seedling growth from the centre of a tropical rain forest canopy gap. *Forest Ecology and Management, **82**, 239-244.*

Brown, N., Press, M., Bebber, D. 1999. Growth and survivorship of dipterocarp seedlings: differences in shade persistence create a special case of dispersal limitation. *Philosophical Transaction of the Royal Society of London Series B, **354**, 1847-1855.*

Bruce, S.E., Rowe, D.B., Flore, J.A. 2001. Chlorophyll fluorescence and vegetative propagation of Taxus. *Hortscience, **36**, 971-975.*

Bungard, R.A., Zipperlen, S.A., Press, M.C., Scholes, J.D. 2002. The influence of nutrients on growth and photosynthesis of seedlings of two rainforest dipterocarp species. *Functional Plant Biology, **29**, 505-515.*

Burslem, D.F.R.P., Grubb, P.J., Turner, I.M. 1995. Responses of nutrient addition among shade-tolerant tree seedlings of lowland tropical rain forest in Singapore. *Journal of Ecology, **83**, 113-122.*

Burslem, D.F.R.P., Grubb, P.J., Turner, I.M. 1996. Responses to stimulated drought and elevated nutrient supply among shade-tolerant tree seedlings of lowland tropical forest in Singapore. *Biotropica, **28**, 636-648.*

Cameron, R.J., Thomson, G.V. 1969. The vegetative propagation of *Pinus radiata*: Root initiation in cuttings. *Botanical Gazette, **130**, 242-251.*

Cannell, M.G.R., Dewar, R.C. 1994. Carbon allocation in trees: a review of concepts modelling. *Advances in Ecological Research,* ***25****, 59-104.*

Cao, K.F., Ohkubo, T. 1998. Allometry, root/shoot ratio and root architecture in understory saplings of deciduous dicotyledonous trees in central Japan. *Ecological Research,* ***13****, 217-227.*

Carron, M.P., Le Roux, Y., Tison, J., Dea, B.G., Caussanel, V., Clair, J., Keli, J. 2000. Compared root system architectures in seedlings and *in vitro* plantlets of *Hevea brasiliensis*, in the initial years of growth in the field. *Plant and Soil,* ***223****, 73-85.*

Chai, D. 1975. Enrichment planting in Sabah. *The Malaysian Forester,* ***38****, 271-279.*

Chong, C., Allen, O.B., Barnes, H.W. 1992. Comparative rooting of stem cuttings of selected woody landscape shrub and tree taxa to varying concentrations of IBA in talc, ethanol and glycol carriers. *Journal of Environmental Horticulture,* ***10****, 245-250.*

Cleveland, S.W. 1981. LOWESS: a program for smoothing scatterplots by robust locally weighted regression. *The American Statistician,* ***35****, 54.*

Condit, R.S., Hubbell, S.P., Foster, R.B. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a sever drought. *Ecological Monographs,* ***65****, 419-439.*

Constanza, R., d'Arge, R., Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M. 1997. The value of the world's ecosystem services and natural capital. *Nature,* ***387****, 253-260.*

Coutts, M.P. 1983. Root architecture and tree stability. *Plant and Soil,* ***71****, 171-188.*

Crawley, M.J. 2002. Statistical Computing: An Introduction to Data Analysis Using S-Plus. *John Wiley, New York.*

Crawley, M.J. 2005. Statistics: An Introduction Using R. *John Wiley, New York.*

Crook, M.J., Ennos, A.R. 1998. The increase in anchorage with tree size of the tropical tap rooted tree *Mallotus wrayi*, King (Euphorbiaceae). *Annuls of Botany,* ***82****, 291-296.*

Crook, M.J., Ennos, A.R., Banks, J.R. 1997. The function of buttress roots: a comparative study of the anchorage systems of buttressed (*Aglaia* and *Nephelium ramboutan* species) and non-buttressed (*Mallotus wrayi*) tropical trees. *Journal of Experimental Botany,* ***48****, 1703-1716.*

Curran, L.M., Caniago, I., Paoli, G.D., Astianti, D., Kusneti, M., Leighton, M., Nirarita, C.E., Haeruman, H. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science,* ***286****, 2184-2188.*

Curran, L.M., Webb, C.O. 2000. Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecological Monographs,* ***70****, 129-148.*

Curran, L.M., Trigg, S.N., McDonald, A.K., Astiani, D., Hardiono, Y.M., Siregar, P., Caniago, I., Kasischke, E. 2004. Lowland forest loss in protected areas of Indonesian Borneo. *Science,* ***303****, 1000-1003.*

d'Oliveira, M.V.N. 2000. Artificial regeneration in gaps and skidding trails after mechanised forest exploitation in Acre, Brazil. *Forest Ecology and Management,* ***127****, 67-76.*

Dalgaard, P. 2002. Introductory Statistics with R. *Springer, New York.*

Danjon, F., Sinoquet, H., Godin, C., Colin, F., Drexhage, M. 1999. Characterisation of structural tree root architecture using 3-D digitising and AMAPmod software. *Plant and Soil,* ***211****, 241-258.*

Danjon, F., Fourcaud, T., Bert, D. 2005. Root architecture and wind-firmness of mature *Pinus pinaster. New Phytologist,* ***168****, 387-400.*

Davies, F.T., Davis, T.D., Kester, D.E. 1994. Commercial importance of adventitious rooting to horticulture. In: *Davis, T.D., Haissig, B, E. (Eds.). Biology of Adventitious Root Formation. Plenum Press, New York.*

Davies, F.T., Lazarte, J.E., Joiner, J.N. 1982. Initiation and development of roots in juvenile and mature leaf bud cuttings of *Ficus pumila. American Journal of Botany,* ***69****, 804-811.*

Davis, T.D. 1988. Photosynthesis during adventitious rooting. *Davis, T.D., Haissig, B.E., Sankhla, N. (Eds.) Adventitious Root Formation in Cuttings. Dioscorides Press, Oregon.*

Davis, T.D., Haissig, B.E (Eds.). 1994. Biology of Adventitious Root Formation. *Plenum Press, New York.*

Davis, T.D., Potter, J.R. 1981. Current photosynthesis as a limiting factor in adventitious root formation on leafy pea cuttings. *Journal of the American Society for Horticultural Science,* ***106****, 278-282.*

Dekker-Robertson, D.L., Kleinschmit, J. 1991. Serial propagation of Norway spruce (Picea abies (L) Karst) – results from later propagation cycles. *Silvae Genetica,* ***40****, 202-214.*

Delissio, L.J., Primack, R.B., Hall, P., Lee, H.S. 2002. A decade of canopy-tree seedling survival and growth in two Bornean rain forests: persistence and recovery from suppression. *Journal of Tropical Ecology,* ***18****, 645-658.*

Dick, J.McP., Aminah, H. 1994. Vegetative propagation of tree species indigenous to Malaysia, *Commonwealth Forestry Review,* ***73****, 164-171.*

Dick, J., Magingo, F., Smith, R.I., McBeath, C. 1999. Rooting ability of *Leucaena leucocephala* stem cuttings. *Agroforestry Systems, **42**, 149-157.*

Dirr, M.A. 1990. Effects of P-ITB and IBA on the rooting response of 19 landscape taxa. *Journal of Environmental Horticulture, **8**, 83-85.*

Dirr, M.A. 1994. The latest status of IBA and other root promoting chemicals. *Nursery Management, **10**, 24-25.*

Elliasson, L. 1978. Effects of nutrients and light on growth and root formation in *Pisum sativum* cuttings. *Physiologia Plantarum, **43**, 13-18.*

Eliasson, L., Brunes, L. 1980. Light effects on root formation in aspen willow cuttings. *Physiologia Plantarum, **48**, 261-265.*

Englund, S.R., O'Brien, J.J., Clark, D.B. 2000. Evaluation of digital and film hemispherical photography and spherical densiometer for measuring forest light environments. *Canadian Journal of Forest Research, **30**, 1999-2005.*

Evans, J. 1999. Planted forests of the wet and dry tropics: their variety, nature, and significance. *New Forests, **17**, 25-36.*

Evans, J., Turnbull, J. 2004. Plantation Forestry in the Tropics (3rd Edition). *Oxford University Press, Oxford.*

FAO, 2001. Global Forest Resources Assessment 2000. *Main Report, FAO Forestry Paper No. 140, Food and Agriculture Organisation of the United Nations.*

FAO, 2005. Global Forest Resources Assessment 2005. *Main Report, FAO Forestry Paper No. 147, Food and Agriculture Organisation of the United Nations.*

Fitter, A.H. 1991. The ecological significance of root system architecture: an economic approach. In: *Atkinson, D. (Ed.) Plant Root Growth: An Ecological Perspective. Blackwell Scientific Publications, Oxford.*

Fogaça, C.M., Fett-Neto, A.G. 2005. Role of auxin and its modulators in the adventitious rooting of *Eucalyptus* species differing in recalcitrance. *Plant Growth Regulation, **45**, 1-10.*

Foxworthy, F.W. 1927. Commercial timber trees of the Malay Peninsular. *Malayan Forest Records No. 3, Federated Malay States, Kuala Lumpur.*

Foxworthy, F.W. 1932. Dipterocarpaceae of the Malay Peninsula. *Malayan Forest Record No. 10, Forest Research Institute, Kepong, Malaya.*

Gemmel, P., Örlander, G., Högberg, K.A. 1991. Norway spruce cuttings perform better than seedlings of the same genetic origin. *Silvae Genetica, **40**, 198-202.*

Gil, L., Fuentes-Utrilla, P., Soto, A., Cervera, T., Collada, C. 2004. Phylogeography: English elm is a 2000-year-old Roman clone. *Nature, **431**, 1053.*

Goh, K.J., Kee, K.K., Chew, P.S. 1993. Soil fertility of some common soils in Sabah, Malaysia. *Applied Agricultural Research Sdn. Bhd. (Unpublished tech. report).*

Griscom, P.H., Ashton, P.M.S., Berlyn, G.P. 2005. Seedling survival and growth of native tree species in pastures: implication for dry tropical forest rehabilitation in central Panama. *Forest Ecology and Management, **218**, 306-318.*

Grubb, P.J. 1996. Rainforest dynamics: the need for new paradigms. In: *Edwards, D.S., Booth, W.E., Choy, S.C. (Eds.) Tropical Rainforest Research. Kluwer, The Netherlands.*

Haissig, B.E., Reimenschnieder, D.E. 1988. Genetic effects on adventitious rooting. In: *Davis, T.D., Haissig, B.E., Sankhla, N. (Eds.) Adventitious Root Formation in Cuttings. Dioscorides Press, Oregon.*

Hallé, F., Kamil, H. 1981. Vegetative propagation of Dipterocarps by stem cutting and air-layering. *The Malaysian Forester, **44**, 314-318.*

Hannerz, M., Wilhelmsson, L. 1998. Field performance during 14 years' growth of *Picea abies* cuttings and seedlings propagated in containers of varying size. *Forestry, **71**, 373-380.*

Hansen, J., Strömquist, L., Ericsson, A. 1978. Influence of the irradiance of carbohydrate content and rooting of cuttings of pine seedlings (*Pinus sylvestris* L.). *Plant Physiology, **61**, 975-979.*

Hare, R.C. 1977. Rooting of cuttings from mature water oak (*Quercus nigra*). *Southern Journal of Applied Forestry, **1**, 24-25.*

Hector, A. 2004. Statistics for Free I: Linear Models in R. *Institute of Environmental Science, University of Zurich.*

Hartmann, H.T., Kester, D.E., Davies, F.T., Geneve, R.L. 2002. Plant Propagation: Principles and Practices. *Prentice-Hall, New Jersey.*

Howard, B.H., Harrison-Murray, R.S., Arjyal, S.B. 1985. Responses of apple summer cuttings to severity of stockplant pruning and to stem blanching. *Journal of Horticultural Science, **60**, 145-152.*

Howard, B.H., Ridout, M.S. 1992. A mechanism to explain increased rooting in leafy cuttings of *Syringa vulgaris* 'Madame Lemoine' following dark treatment of the stockplant. *Journal of Horticultural Science, **67**, 103-114.*

Hubbell, S.*P., Foster*, R.B. 1986. Canopy gaps and dynamics of a neotropical forest. In: *Crawley, M.J. (Ed.) Plant Ecology. Blackwell Scientific Publications, Oxford.*

Huth, A., Ditzer, T. 2001. Long-term impacts of logging in a tropical rain forest – a simulation study. *Forest Ecology and Management*, ***142***, 33-51.

Husen, A., Pal, M. 2003. Clonal propagation of teak (*Tectona grandis* Linn. f.): effect of IBA application and adventitious root regeneration on vertically split cuttings. *Silvae Genetica, **52**, 173-176.*

Itoh, A., 1995. Effects of forest floor environment on germination and seedling establishment of two Bornean rainforest emergent species. *Journal of Tropical Ecology, **11**, 517-524.*

Itoh, A., Yamakura, T., Ogino, K., Lee, H.S. 1995. Survivorship and growth of seedlings of 4 dipterocarp species in a tropical rain-forest of Sarawak, East Malaysia. *Ecological Research, **10**, 327-338.*

Itoh, A., Yamakura, T., Kanzani, M., Ohkubo, T., Palmiotto, P.A., LaFrankie, J.V., Kendawang, J.J., Lee, H.S. 2002. Rooting ability of cuttings relates to phylogeny, habitat preference and growth characteristics of tropical rainforest trees. *Forest Ecology and Management, **168**, 275-287.*

IUCN. 2003. IUCN Red List of Threatened Species. *(http://www.redlist.org).*

Janzen, D.H. 1974. Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. *Biotropica, **6**, 69-103.*

Kajita, T., Kamiya, K., Nakamura, K., Tachida, H., Wickneswari, R., Tsumura, Y., Yoshimara, H., Yamazaki, T. 1998. Molecular phylogeny of Dipterocarpaceae in Southeast Asia based nucleotide sequences of matK, trnL intron, and trnL-trnF intergenic spacer region in chloroplast DNA. *Molecular Phylogenetics and Evolution, **10**, 202-209.*

Kantarli, M. 1993[a]. Vegetative Propagation of Dipterocarps by Cuttings in the ASEAN Region. *ASEAN-Canada Forest Tree Seed Centre Project. Review Paper No.1.*

Kantarli, M. 1993[b]. Vegetative propagation of *Hopea odorata* by cuttings: a low-cost technology. *ASEAN-Canada Forest Tree Seed Centre Project. Technical Publication 16.*

Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns in correlates of seedling shade tolerance of 13 tropical trees. *Oecologia, **98**, 419-428.*

Kennedy, D.N., Swaine, M.D. 1992. Germination and growth of colonizing species in artificial gaps of different sizes in dipterocarp rain forest. *Philosophical Transactions of the Royal Society of London (Series B), **335**, 357-366.*

Khurana, D.K., Narkhede, S., Parkash, N. 1997. Rooting behaviour and growth performance of new poplar clones under agroforestry. In: *International Workshop on Agroforestry for Sustainable Land-use. Institute National de la Recherche Agronomique, Montpelier, France, 311-314.*

King, D.A., Davies, S.J., Nur Supardi, M.N., Tan, S. 2005. Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Functional Ecology, **19**, 445-453.*

King, D.A., Davies, S.J., Tan, S., Nur Supardi, M.N. 2006. The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology, **94**, 670-680.*

Köhler, P., Huth, A. 2004. Simulating growth dynamics in a South-East Asian rainforest threatened by recruitment shortage and tree harvesting. *Climatic Change, **67**, 95-117.*

Korpelainen, H., Ådjers, G., Kuusipalo, J., Nuryanto, K., Otsamo, A. 1995. Profitability of rehabilitation of overlogged dipterocarp forest: a case study from South Kalimantan, Indonesia. *Forest Ecology and Management, **79**, 207-215.*

Kurokawa, H., Kitahashi, Y., Koike, T., Lai, J., Nakashizuka, T. 2004. Allocation to defense or growth in dipterocarp forest seedlings in Borneo. *Oecologia, **140**, 261-270.*

Kuusipalo, J., Hadengganan, S., Ådjers, G., Sagala, A.P.S. 1997. Effect of gap liberation on the performance and growth of dipterocarp trees in a logged-over rainforest. *Forest Ecology and Management, **92**, 209-219.*

Lamb, D. 2001. Reforestation. In: *Levin, S.A. (Ed.) Encyclopedia of Biodiversity, Academic Press, San Diego.*

Leakey, R.R.B. 1983. Stockplant factors affecting root initiation in cuttings of *Triplochiton scleroxylon*, an indigenous hardwood of West Africa. *Journal of Horticultural Science, **58**, 277-290.*

Leakey, R.R.B., Newton, A.C. (Eds.) 1994. Tropical Trees: the Potential for Domestication and the Rebuilding of Forest Resources. *HMSO Books for the Institute of Terrestrial Ecology.*

Leakey, R.R.B., Longman, K.A. 1988. Low-tech cloning of tropical trees. *Appropriate Technology, **15**, 6.*

Leakey, A.D.B., Press, M.C., Scholes, J.D. 2003. Patterns of dynamic irradiance affect the photosynthetic capacity and growth of dipterocarp tree seedling. *Oecologia, **135**, 184-193.*

Leakey, A.D.B., Scholes, J.D., Press, M.C. 2004. Physiological and ecological significance of sunflecks for dipterocarp seedlings. *Journal of Experimental Botany, **56**, 411, 469-482.*

Lebude, A.V., Goldfarb, B., Blazich, F.A., Wise, F.C., Frampton, J. 2004. Mist, substrate water potential anc cutting water potential influence rooting of stem cuttings of loblolly pine. *Tree Physiology, **24**, 823-831.*

LeFrankie, J.V., Chan, H.T. 1991. Confirmation of sequential flowering in *Shorea* (Dipterocarpaceae). *Biotropica, **23**, 200-2003.*

Lemmon, P.E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science, **2**, 314-320.*

Leighton, M., Wirawan, N. 1986. Catastrophic drought and fire in Borneo tropical rainforest associated with the 1982-83 El Niño Southern Oscillation event. In: *Prance, G.T. (Ed.), Tropical rain forests and the World Atmosphere. AAAS Symposium 10, Boulder, Colorado, 75-102.*

Leppe, D., Smits, W.T.M. 1988. Methoda pembuatan dan pemeliharaan Kebun Pangkas *Dipterocarpaceae. Forest Research Institute Samarinda. Special Edition No. 4.*

Li, F.Y. 2006. Factors affecting tree seedling establishment following rehabilitation management in logged-over tropical rain forest in Sabah, Malaysia. *PhD Thesis, Imperial College, University of London.*

Liew, T.C., Wong, F.O. 1973. Density, recruitment, mortality and growth of dipterocarp seedlings in virgin and logged-over forests in Sabah. *Malay Forester, **36**, 3-15.*

Linington, I.M. 1991. In vitro propagation of *Dipterocarpus alatus* and *Dipterocarpus intricatus. Plant Cell, Tissue and Organ Culture, **27**, 81-88.*

Lo, Y.N. 1985. Root initiation of *Shorea macrophylla* cuttings: effects of node position, growth regulators and misting regime. *Forest Ecology and Management, **12**, 43-52.*

Loach, K. 1985. Rooting of cuttings in relation to the propagation medium. *Combined Proceedings of the International Plant Propagators Society, **35**, 472-485.*

Macdonald, B. 1986. Practical woody plant propagation for nursery growers. *Timber Press, Oregon.*

MacKinnon, K., Hatta, G., Halim, H., Mangalik, A. 1997. The Ecology of Kalimantan. *Oxford University Press, Oxford.*

Maguire, B., Ashton, P.S. 1977. Pakaraimoideae, Dipterocarpaceae of the western hemisphere. II. Systematic, geographic and phyletic considerations. *Taxonomy, **26**, 342-368.*

Maindonald, J.H., Braun, J. 2003. Data Analysis and Graphics Using R: An Example-Based Approach. *Cambridge University Press, Cambridge.*

Malayan Forest Department. 1937. Headquarters Bulletin. *Forest Department, Federated Malay States, Kuala Lumpur.*

Marsh, C., Greer, A.G. 1992. Forest land-use in Sabah, Malaysia: An introduction to the Danum Valley. *Philosophical Transactions of the Royal Society of London (Series B), **335**, 331-340.*

Marsh, C. 1995. Danum Valley Conservation Area Management Plan. *The Danum Valley Management Committee/Yayasan Sabah.*

Martínez-Garza, C., Howe, H.F. 2003. Restoring tropical diversity: bearing the time tax on species loss. *Journal of Applied Ecology,* ***40****, 423-429.*

Massey, F.P., Massey, K., Press, M.C., Hartley, S.E. 2006. Neighbourhood composition determines growth, architecture and herbivory in tropical rain forest tree seedlings. *Journal of Ecology,* ***94****, 646-655.*

Mayaux, P., Holmgren, P., Archard, F., Eva, H., Stibig, H.J., Branthomme, A. 2005. Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical Transactions of the Royal Society of London (Series B),* ***360****, 373-384.*

Maynard, B.K., Bassuk, N.L. 1985. Etiolation as a tool for rooting cuttings of difficult to root woody plants. *Proceedings of the International Plant Propagators Society,* ***35****, 488-495.*

Maynard, B.K., Bassuk, N.L. 1987. Stock plant etiolation and blanching of woody plants prior to cutting propagation. *Journal of the American Society of Horticultural Science,* ***112****, 273-276.*

Meijer, W., Wood, G.H.S. 1964. Dipterocarps of Sabah (North Borneo). *Sabah Forest Record No.5. Forest Department, Sandakan.*

Mesén, F., Newton, A.C., Leakey, R.R.B. 1997. The effects of propagation environment and folia area on the rooting physiology of *Cordia alliodora* (Ruiz & Pavon) Ozken cuttings. *Trees,* ***11****, 404-411.*

Mesén, F., Newton, A.C., Leakey, R.R.B. 2001. The influence of stockplant environment on morphology, physiology and rooting of leafy stem cuttings of Albizia guachapele. *New Forests,* ***22****, 213-227.*

Minghe, L., Ritchie, G. 1999. Eight hundred years of clonal forestry in China: mass production of rooted cuttings of Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.). *New Forests,* ***18****, 143-159.*

Mok, S.T. 1993. Current research on artificial regeneration of dipterocarps. *Forestry Research Program for Asia & the Pacific (FORSPA). FORSPA Publication 8.*

Momose, Y. 1978. Vegetative propagation of Malaysian trees. *The Malaysian Forester,* ***41****, 219-223.*

Montagnini, F., Eibl, B., Grance, L., Maiocco, D., Nozzi, D. 1997. Enrichment planting in overexploited subtropical forest of the Paranaense region of Misiones, *Argentina. Forest Ecology and Management,* ***99****, 237-246.*

Morison, J.I.L., Gifford, R.M. 1984. Plant growth and water use with limited water supply in high CO_2 concentrations. I. Leaf area, water use and transpiration. *Australian Journal of Plant Physiology,* ***11****, 361-374.*

Moura-Costa, P.H., Karolus, A. 1992. Summary of felling data for the Ulu Segama region. *Innoprise Corporation Sdn. Bhd. (Unpublished data – internal report).*

Moura-Costa, P.H. 1993. Large scale enrichment planting with dipterocarps, methods and preliminary results. *Paper Presented to the BIO-REFOR Workshop, Yogyakarta, September 1993.*

Moura-Costa, P.H., Lundoh, L. 1994. The effects of auxins (IBA, NAA and 2,4-D) on rooting of *Dryobalanops lanceolata* (Kapur - Dipterocarpaceae) cuttings. *Journal of Tropical Forest Science,* ***7****, 338-340.*

Moura-Costa, P., Yap, S.W., Ong, C.L., Ganing, A., Nussbaum, R., Mojuin, T. 1996. Large-scale enrichment planting with dipterocarps as an alternative for carbon offset – methods and preliminary results. In: *Appanah, S., Khoo, K.C. (Eds.) Proceedings of the 5th Round Table Conference on Dipterocarps, Forest Research Institute Malaysia, Kuala Lumpur, 386-396.*

Muckadell, J.S., Malim, P. 1983. Preliminary results from rooting juvenile cuttings of some dipterocarp species. *Forest Research Centre Sepilok, Sabah, Malaysia. Working Paper 29.*

Mulatya, J.M., Wilson, J., Ong, C.K., Deans, J.D., Sprent, J.I. 2002. Root architecture of provenances, seedlings and cuttingsof *Melia volkensii*: implications for crop yield in dryland agroforestry. *Agroforestry Systems,* ***56****, 65-72.*

Munang, D.M., (Ed.). 1989. Forestry in Sabah. *Sabah Forestry Department.*

Myers, N., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature,* ***403****, 853-858.*

Negash, L. 2003. Vegetative propagation of the threatened East African yellow wood (*Podocarpus falcatus*). *South African Journal of Botany,* ***69****, 170-175.*

Newbery, D.M., Kennedy, D.N., Petol, G.H., Madani, L., Ridsdale, C.E. 1999. Primary forest dynamics in lowland dipterocarp forest at Danum Valley, Sabah, Malaysia, and the role of the understory. *Philosophical Transactions of the Royal Society of London (Series B),* ***354****, 1763-1782.*

Newton, A.C., Muthoka, P.N., Dick, J.McP. 1992. The influence of leaf area on the rooting physiology of leafy stem cuttings of *Terminalia spinosa*. *Trees,* ***6****, 210-215.*

Newton, A.C., Jones, A.C. 1993[a]. Characterisation of microclimate in mist and non-mist propagation systems. *Journal of Horticultural Science,* ***68****, 421-430.*

Newton, A.C., Jones, A.C. 1993[b]. The water status of four tropical tree species in mist and non-mist propagation systems. *Journal of Horticultural Science,* ***68****, 653-663.*

Nielson, C.C.N. 1992. Will traditional conifer tree breeding for enhanced stem production reduce wind stability: genetic variation is allocation of biomass to root classes and stem. *Silvae Genetica,* ***41****, 307-319.*

Nketiah, T., Newton, A.C., Leakey, R.R.B. 1998. Vegetative propagation of *Triplochiton scleroxylon* K. Schum in Ghana. *Forest Ecology and Management,* ***105****, 99-105.*

Nussbaum, R., Anderson, J., Spencer, T. 1995. Factors limiting the growth of indigenous tree seedlings planted on degraded rainforest soils in Sabah, Malaysia. *Forest Ecology and Management,* ***74****, 149-159.*

Ofori, D.A., Newton, A.C., Leakey, R.R.B., Grace, J. 1996. Vegetative propagation of Milicia excelsa by leafy stem cuttings: effects of auxin concentration, leaf area and rooting medium. *Forest Ecology and Management,* ***84****, 39-48.*

Ohba, K. 1993. Clonal forestry with sugi (*Cryptomeria japonica*). In: *Ahuja, M.R., Libby, W.J. (Eds.) Clonal Forestry: Genetics, Biotechnology and Application, Springer-Verlag, New York.*

Okoro, O.O., Grace, J. 1976. The physiology of rooting *Populus* cuttings. I. Carbohydrates and photosynthesis. *Physiol. Plant.,* ***36****, 133-138.*

Omom, M.R., Smits, W.T.M. 1989. Pengaruh IBA terhadap pertambuhan stek batang *Shorea lamellata. Buletin Penelitan Kehutanan,* ***5****, 103-112.*

Otsamo, R. 2000. Early development of three planed indigenous tree species and natural understory vegetation in artificial gaps in an *Acacia mangium* stand on an *Imperata cylindrica* grassland site in South Kalimantan, Indonesia. *New Forests,* ***19****, 51-68.*

Paz, H. 2003. Root/shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats and ecological groups. *Biotropica,* ***35****, 318-332.*

Peña-Claros, M., Boot, R.G.A., Dorado-Lora, J., Zonta, A. 2002. Enrichment planting of *Bertholletia excelsa* in secondary forest in the Bolivian Amazon: effect of cutting line width on survival, growth and crown traits. *Forest Ecology and Management,* ***161****, 159-168.*

Pimm, S.L. 1997. The value of everything. *Nature,* ***387****, 231-232.0*

Pimm, S.L., *et al.* (32 co-authors). 2001. Can we defy nature's end? *Science,* ***293****, 2207-2209.*

Pinard, M., Barker, M.G., Tay, J. 2000. Soil disturbance and post-logging recovery on bulldozer paths in Sabah, Malaysia. *Forest Ecology and Management, **130**, 213-225.*

Pinard, M., Ganing, A., Nussbaum, R. 1992. Disturbance and recovery in a tropical rain forest: a case study of the Ulu Segama Forest Reserve, Sabah, Malaysia. *MAB Regional Workshop on Rehabilitation of Degraded Secondary Forests. Kuala Lumpur, 17-20th February 1992.*

Pinard, M., Howlett, B., Davidson, D. 1996. Site conditions limit pioneer tree recruitment after logging dipterocarp forests in Sabah, Malaysia. *Biotropica, **28**, 2-12.*

Pinard, M.A., Putz, F.E. 1996. Retaining forest biomass by reducing logging damage. *Biotropica, **28**, 278-295.*

Pinhero, J.C., Bates, D.M. 2000. Mixed effects models in S and S-Plus. *Springer-Verlag, Berlin.*

Pinso, C., Moura-Costa, P. 1993. Greenhouse gas offset funding for enrichment planting: a case study from Sabah, Malaysia. *Commonwealth Forestry Review, **72**, 343.*

Pohio, K.E., Wallace, H.M., Peters, R.F., Smith, T.E., Trueman, S.J. 2005. Cuttings of Wollemi pine tolerate moderate photoinhibition and remain highly capable of root formation. *Trees, **19**, 587-595.*

Pollisco, M.T. 1994[a]. Propagating Philippine dipterocarps with non-mist system. *Canopy International, **20**, 4-7.*

Pollisco, M.T. 1994[b]. Two alternative asexual propagation techniques for some dipterocarp species. *Proceedings International Workshop BIO-REFOR, Kanger, Malaysia. 111-116.*

Press, M.C., Brown, N.D., Barker, M.G., Zipperlin, S.W. 1996. Photosynthetic responses to light in tropical rain forest tree seedlings. In: *Swaine, M.D. (Ed.) The Ecology of Tropical Forest Tree Seedlings, Paris, France: UNESCO.*

Putz, F.E., Blate, G.M., Redford, K.H., Fimbel, R., Robinson, J. 2001. Tropical forest management and conservation of biodiversity: an overview. *Conservation Biology, **15**, 7-20.*

Ramos, J., del Amo, S. 1991. Enrichment planting in a tropical secondary forest in Veracruz, Mexico. *Forest Ecology and Management, 54, 289-304.*

Rautner, M., Hardiono, M., Alfred, R.J. 2005. Borneo: treasure island at risk. *WWF Germany, Frankfurt am Main.*

Reis, G.G., Reis, M.G.F., Maestri, M. 1988. Growth and water relations of *Eucalyptus grandis* and *E. camaldulensis* seedlings in plastic tubes under three irrigation regimes. *Arvore, **12**, 183-195.*

Riedacker, A., Belgrand, M. 1983. Morphogenesis of root systems of seedlings and cuttings of *Quercus robus* L. *Plant and Soil, **71**, 131-146.*

Richards, P.W. 1996. The Tropical Rainforests (2nd Edition). *Cambridge University Press, Cambridge.*

Ricker, M., Medelsohn, R.O., Daly, D.C., Ángeles, G. 1999. Enriching the rainforests with native fruit trees: an ecological and economic analysis in Los Tuxtlas (Veracruz, Mexico). *Ecological Economics, **31**, 439-448.*

Ritchie, G.A., Tanaka, Y., Duke, S.D. 1992. Physiology and morphology of Douglas-fir rooted cuttings compared to seedlings and transplants. *Tree Physiology, **10**, 179-194.*

Rithcie, G.A. 1994. Commercial application of adventitious rooting to forestry. In: *Biology of Adventitious Root Formation (Eds. Davis, T.D., Haissig, B.E.). Plenum Press, New York.*

Robertson, I., Froyd, C.A., Walsh, R.P.D., Newbery, D.M., Woodborne, S., Ong, R.C. 2004. The dating of dipterocarp tree rings: establishing a record of carbon cycling and climatic change in the tropics. *Journal of Quaternary Science, **19**, 657-664.*

Roulund, H., Bergstedt, A. 1982. Sammenligning mellem frøplanter og stiklingsformerede kloner af sitkagran (Picea sitchensis (Bong.) Carr.). 10 års resultater. *Dan Skovforen. Tidskr, **67**, 218-235.*

Roulund, H., Wellendorf, H., Werner, M. 1985. A clonal experiment in Norway spruce (Picea abies (L.) Karst). 15 years results. *Forest Tree Improvement No. 17, Arboretet Hørsholm, Akaddemisk Forlag, København.*

Rubber Research Institute of Malaysia. 1966. Rooted cuttings. *Annual Report, 27.*

Sabah Forest Department. 2005. Annual Report 2004. *Sabah Forest Department, Malaysia.*

Sakai, C., Yamamoto, Y., Subiakto, A., Hendromono., Prameswari, D. 1994. Vegetative propagation of Dipterocarpaceae. *Proceedings International Workshop BIO-REFOR, Kangar, Malaysia.*

Sakai, S. 2002. General flowering in lowland mixed dipterocarp forests of SE Asia. *Biological Journal of the Linnean Society, **75**, 233-247.*

Sala, O.E., *et al.* 2000. Global biodiversity scenarios for the year 2100. *Science, **287**, 1770-1774.*

Sasaki, S., Mory, T. 1981. Growth responses of dipterocarp seedlings to light. *Malayan Forestry Records, **44**, 319-345.*

Sasse, J., Sands, R. 1996. Comparative responses of cuttings and seedlings of *Eucalyptus globulus* to water stress. *Tree Physiology, **16**, 287-294.*

Sasse, J., Sands, R. 1997. Configuration and development of root systems of cuttings and seedlings of *Eucolyptus globulus. New Forests, **14**, 85-105.*

Scott, E.S., Rao, A.N., Loh, C.S. 1988. Production of plantlets of *Shorea roxburghii* from embryogenic axes cultured *in vitro. Annuls of Botany, **61**, 233-236.*

Scott, E.S., Rao, A.N., Loh, C.S. 1995. Preliminary studies of micropropagation of Hopea oderata, a dipterocarp tree. *Plant Cell, Tissue and Organ Culture, **41**, 193-196.*

Shiembo, P.N., Newton, A.C., Leakey, R.R.B. 1996. Vegetative propagation of *Irvingia gabonensis*, a West African fruit tree. *Forest Ecology and Management, **87**, 185-192.*

Shukla, R.P., Ramakrishnan, P.S. 1984. Biomass allocation strategies and productivity of tropical trees related to successional status. *Forest Ecology and Management, **9**, 315-324.*

Shukor, N, A., Ling, T.T. 1994. A note on the rooting of *Shorea acuminata* and *Shorea parvifolia* leafy stem cuttings. *Journal of Tropical Forest Science, **6**, 206-208.*

Schulze, P.C., Leighton, M., Peart, D.R. 1994. Enrichment planting in selectively logged rain forest: a combined ecological and economic analysis. *Ecological Applications, **4**, 581-592.*

Smits, W.T.M. 1985. Production of Dipterocarp planting stock in nurseries. *Proceedings of the Third Round Table Conference on Dipterocarps, Mulawarman University, East Kalimantan, Indonesia.*

Smits, W.T.M. 1986. Vegetative propagation and possibilities for its use with dipterocarps. *Diskusi Terbatas Beberapa Aspek Pembangunan Hutan, Jakarta.*

Smits, W.T.M. 1992. Mass propagation of dipterocarps by vegetative propagation in Indonesia. In: *Regional Symposium on Mass Clonal Multiplication of Forestry Trees for Plantation Programmes. Cisarua, Bogor, Indonesia. 1st-9th Dec 1992.*

Smits, W.T.M., de Fraiture, A.C., Yasman, I. 1994. Production of dipterocarp planting stock by cuttings in Indonesia. In: *Leakey R.R.B., Newton, A.C. (Eds.) Tropical Trees: the potential for domestication and the rebuilding of forest resources. HMSO Books for the Institute of Terrestrial Ecology.*

Scherer-Lorenzen, M., Potvin, C., Koricheva, J., Bornik, Z., Hector, A., Reynolds, G., & Schmid, B. 2005. The design of experimental tree plantations for functional biodiversity research. In: *Scherer-Lorenzen, M., Körner, C., Schulze, E.D. (Eds) The functional significance of forest diversity. Springer, Berlin.*

Sodhi, N.S., Koh, L.P., Brook, B.W., Ng, P.K.L. 2004. Southeast Asian biodiversity: an impending disaster. *TRENDS in Ecology and Evolution, **19**, 654-660.*

Srivastrava, P.B.L., Manggil, P. 1981. Vegetative propagation of some Dipterocarps by cuttings. *The Malaysian Forester, **44**, 301-313.*

Stape, J.L., Gonçalves, J.L.M., Gonçalves, A.N. 2001. Relationships between nursery practices and field performance for *Eucalyptus* plantations in Brazil. *New Forests, **22**, 19-41.*

Stewart, M., Blomley, T. 1994. Use of *Melia volkensii* in a semi-arid agroforestry system in Kenya. *Commonwealth Forestry Review, **73**, 128-131.*

Stoll, P., Newbery, D.M. 2005. Evidence of species-specific neighbourhood effects in the Dipterocarpaceae of a Bornean rain forest. *Ecology, **86**, 3048-3062.*

Strugnell, E.J. 1947. Development in silvicultural practice in Malayan evergreen forests. *Malayan Forester, **11**, 37-41.*

Swamy, S.L., Puri, S., Singh, A.K. 2002. Effects of auxins (IBA and NAA) and season on rooting of juvenile and mature hardwood cuttings of *Robinia pseudoacacia* and *Grewia optiva*. *New Forests, **23**, 143-157.*

Symington, C.F. (revised by Ashton, P., Appanah, S.) 2004. Forester's Manual of Dipterocarps. *Malayan Forestry Record No.16.*

Tanner, E.V.J., Teo, V.K., Coomes, D.A., Midgley, J.J. 2005. Pair-wise competition-trials amongst seedlings of ten dipterocarp species; the role of initial height, growth rate and leaf attributes. *Journal of Tropical Ecology, **21**, 317-328.*

Tchoundjeu, Z., Leakey, R.R.B. 1996. Vegetative propagation of African mahogany: effects of auxin, node position, leaf area and cutting length. *New Forests, **11**, 125-136.*

Thimann, K.V., Koepfli, J.B. 1935. Identity of the growth-promoting and root-forming substances of plants. *Nature, **135**, 101-102.*

Thomas, I.K. 1987. Research on the rooting of juvenile cuttings of fast-growing hardwood exotics: Progress over the period from October 1984 to February 1987. *FRC Publication No. 33. Forest Research Centre, Sabah, Malaysia.*

Tinley, G.H. 1963. Recent developments in propagating and planting rubber. *World Crops, **9**, 307-311.*

Tompsett, P.B. 1987. Desiccation and storage studies on dipterocarp seeds. *Annuls of Applied Biology, **110**, 371-379.*

Tuomela, K., Kuusipalo, J., Vesa, L., Nuryanto, K., Sagala, A.P.S., Ådjers, G. 1996. Growth of dipterocarp seedlings in artifical gaps: an experiment in a logged-over rainforest in South Kalimantan, Indonesia. *Forest Ecology and Management, **81**, 95-100.*

Turner, I.M., Newton, A.C. 1990. Initial responses of some tropical rain forest tree seedlings to a large gap environment. *Journal of Applied Ecology, **27**, 605-608.*

Turner, I.M., Brown, N.D., Newton, A.C. 1993. The effect of fertilizer application on dipterocarp seedling growth and mycorrhizal infection. *Forest Ecology and Management, **57**, 329-337.*

Turner, I.M. 2001. The Ecology of Trees in the Tropical Rain Forest. *Cambridge University Press, Cambridge.*

Walsh, R.P.D., Newbery, D.M. 1999. The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. *Philosophical Transactions of the Royal Society of London (Series B), **354**, 1869-1883.*

Walters, M.B., Reich, P.B. 1996. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology, **77**, 841-853.*

Walton, A.B. 1948. Some considerations for the future management and silvicultural treatment of Malayan forests. *Malayan Forester, **11**, 68-74.*

Watson, A.J., Tombleson, J.D. 2002. Toppling in juvenile pines: a comparison of the root system characteristics of direct-sown seedlings, and bare-root seedlings and cuttings. *Plant and Soil, **230**, 187-196.*

Wells, K., Bagchi, R. 2005. Eat in or take away – seed predation and removal by rats (muridae) during a fruiting event in a dipterocarp rainforest. *Raffles Bulletin of Zoology, **53**, 281-286.*

Whitmore, T.C. 1984. Tropical Rain Forests of the Far East (2nd Edition). *Clarendon Press, Oxford.*

Whitmore, T.C. 1990. An Introduction to the Tropical Rain Forests. *Clarendon Press, Oxford.*

Whitmore, T.C., Brown, N.D. 1996. Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. *Philosophical Transactions of the Royal Society of London (Series B), **351**, 1195-1203.*

Whitmore, T.C. 1998. Potential impact of climate change on tropical rain forest seedlings and forest regeneration. *Climatic Change, **39**, 429-438.*

Whitmore, T.C. 1999. Arguments on the forest frontier. *Biodiversity and Conservation, **8**, 865-868.*

Williamson, B.G., Ickes, K. 2002. Mast fruiting and ENSO cycles – does the cue betray a cause? *Oikos, **97**, 459-461.*

Wood, G.H.S. 1956. The dipterocarp flowering season in North Borneo, 1955. *Malayan Forester, **19**, 193-201.*

Wright, P.S. 1975. The Soils of Sabah. Vol. 3. Western Parts of Tawau and Lahad Datu Districts. *Ministry of Overseas Development, UK.*

Wyatt-Smith, J. 1963. Manual of Malayan Silviculture for Inland Forests. *Malayan Forest Record No. 23. Forest Research Institute, Kepong.*

Yamada, T., Suzuki, E., Yamakura, T., Tan, S. 2005. Tap-root depth of tropical seedlings in relation to species-specific edaphic preferences. *Journal of Tropical Ecology, **21**, 155-160.*

Yang, J.C., Chung, J.D., Chen, Z.Z. 1995. Vegetative propagation of adult *Eucalyptus grandis* x *uriophylla* and comparison of growth between micropropagated plants and rooted cuttings. *Plant Cell Reports, **15**, 170-173.*

Yap, S.W. 1998. Large scale enrichment planting of dipterocarps in logged-over forest in Sabah, Malaysia: potential role of fertilizer application. *PhD Thesis, Wye College, University of London.*

Zabala, N.Q. 1986. Vegetative propagation of some dipterocarp species. *Philippine Lumberman, **32**, 13-16.*

Zipperlen, S.W., Press, M.C. 1996. Photosynthesis in relation to growth and seedling ecology of two dipterocarp rain forest tree species. *Journal of Ecology, **84**, 863-876.*

Zwolinski, J.B., Bayley, A.D. 2001. Research on planting stock and forest regeneration in South Africa. *New Forests, **22**, 59-74.*

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Garcia, C. 2005. Manager, Innoprise-INIKEA Rainforest Rehabilitation Project (INIKEA), Research and Development Division, Yayasan Sabah Group, Tawau Regional Office, Sabah, Malaysia.

Hector, A. 2006. Head, Biodiversity and Ecosystems Research Group, Institute of Environmental Sciences, University of Zurich.

Philipson, C. 2006. PhD student, Biodiversity and Ecosystems Research Group, Institute of Environmental Sciences, University of Zurich.

Sinun, W. 2005. Group Manager, Research and Development Division, Yayasan Sabah Group, Kota Kinanabalu, Sabah, Malaysia.

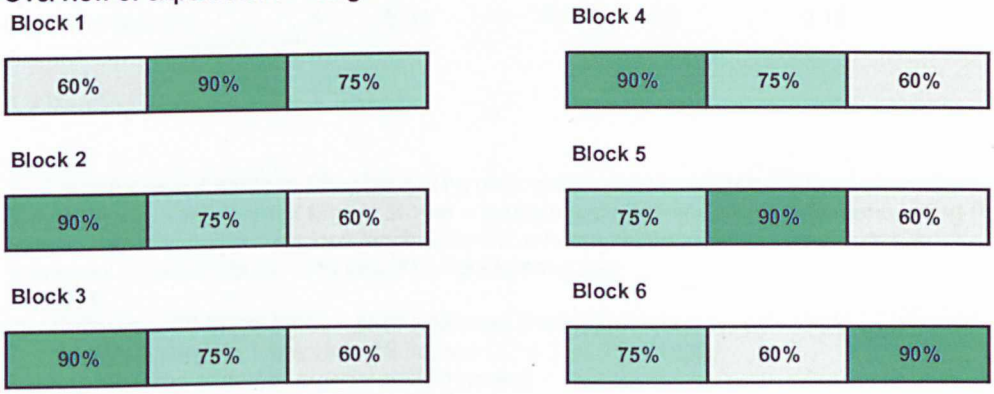
Yap, S.W. 2005. Senior Manager (Forest Rehabilitation and Plantations), Research and Development Division, Yayasan Sabah Group, Kota Kinabalu, Sabah, Malaysia.

APPENDIX 1

1.1 Survival analysis

Notes
Analyses for experiments in **Chapter 3** (The propagation phase: varying the level of irradience)
Statistical test: **Generalised Linear Model** – binary logistic regression on proportions (using R)
Species (3 levels): *Dryobalanops lanceolata, Parashorea malaanonan, Shorea leprosula*
Treatment (3 levels): 60%, 75% and 90% light interception
Blocks: 6
Shade houses: 18 (3 per block – each treatment level represented in each block)
Cuttings: 22 cuttings x 3 species x 18 houses (22 x 3 x 18 = 1,188)
Survival recorded at end of experiment (6 weeks)
Significant values (P<0.05) shown in red, marginal significance (P<0.1) shown in blue

Overview of experimental design



1: Load data into a dataframe ('light')
light<-read.table("C:\\Documents and Settings\\Glen\\My Documents\\Thesis\\Data\\Chapter 3\\light.survival.txt ", header=T), attach(light), names (light)
"block" "house" "treatment" "species" "survival" "rooting"

2: Making new collapsed dataset for analysis of proportions
dead <- survival==0
N <- as.vector(table(block, treatment, species)) ; N
P <- as.vector(tapply(survival, list(block, treatment, species), sum)) ; P
Q <- as.vector(tapply(dead, list(block, treatment, species), sum)) ; Q

3: Check that alive & dead cuttings totals 22 cuttings in each species in each house
pq.check <- P+Q ; pq.check

4: Calculate proportion of cuttings surviving
propSurv <- P / N ; propSurv

5: Shorten explanatory variables columns & convert species text to numbers using 'as.numeric' function
Block <- as.vector(tapply(block, list(block, treatment, species), mean)) ; Block
Shade <- as.vector(tapply(treatment, list(block, treatment, species), mean)) ; Shade
House <- as.vector(tapply(house,list(block,treatment,species), mean)) ; House
Species <- as.vector(tapply(as.numeric(species), list(block, treatment, species), mean)) ; Species

6: Declare factors
BLOCK <- factor(Block)
TREATMENT <- factor(Shade)
HOUSE <- factor(House)
SPECIES <- factor(Species)

7: Bind alive & dead cuttings
pq <- cbind(P, Q)

8: Collate all variables into a new, shortened dataset "shade.surv"
shade.surv <- data.frame (BLOCK, HOUSE, SPECIES, N, P, Q, propSurv) ; summary(shade.surv)

9: Analysis (Generalised Linear Model)
surv.glm <- glm(pq ~ BLOCK + TREATMENT * SPECIES, binomial, data = shade.surv) ;
summary(surv.glm)

10: Check for over-dispursion
Residual deviance: 49.756 on 40 degrees of freedom. Dispursion = 1.2439
Dispursion within parameters of test. Use of binomial distribution valid

11: Summary of the analysis
anova(surv.glm, test="Chi")

Source	***Df***	***Deviance***	***Resid. Df***	***Resid. Dev***	***P(>|Chi|)***
null			53	61.2	
block	5	2.17	48	59.03	0.83
treatment	2	0.051	46	58.98	0.98
species	2	2.64	44	56.34	0.27
treatment:species	4	6.34	40	50	0.18

1.2 Rooting analysis

Notes
Analyses for experiments in **Chapter 3** (The propagation phase: varying the level of irradience)
Statistical test: **Generalised Linear Model** – binary logistic regression of proportions (using R)
Species (3 levels): *Dryobalanops lanceolata, Parashorea malaanonan, Shorea leprosula*
Treatment (3 levels): 60%, 75% and 90% light interception
Blocks: 6
Shade houses: 18 (3 per block – each treatment level represented in each block)
Cuttings: 22 cuttings x 3 species x 18 houses (22 x 3 x 18 = 1,188)
Rooting recorded at end of experiment (10 weeks)

1: Load data into a dataframe ('light')
rm(list=ls(all=TRUE))
light<-read.table("C:\\Documents and Settings\\Glen\\My Documents\\Thesis\\Data\\Chapter 3\\light.survival.txt ", header=T)

2: Making new collapsed dataset for analysis of proportions
unrooted <- rooting==0
N <- as.vector(table(block, treatment, species)) ; N
R <- as.vector(tapply(rooting, list(block, treatment, species), sum)) ; R
S <- as.vector(tapply(unrooted, list(block, treatment, species), sum)) ; S

3: Check that rooted and unrooted cuttings totals 22 cuttings in each species in each house
rs.check <- R+S ; rs.check

4: Calculate proportion of cuttings rooting (propRoot)
propRoot <- R/N ; propRoot

5: Shorten explanatory variables columns & convert species text to numbers using 'as.numeric' function
Block <- as.vector(tapply(block, list(block, treatment, species), mean)) ; Block
Shade <- as.vector(tapply(treatment, list(block, treatment, species), mean)) ; Shade
House <- as.vector(tapply(house,list(block,treatment,species), mean)) ; House
Species <- as.vector(tapply(as.numeric(species), list(block, treatment, species), mean)) ; Species

6: Declare factors
BLOCK <- factor(Block)
TREATMENT <- factor(Shade)
HOUSE <- factor(House)
SPECIES <- factor(Species)

7: Bind rooted & unrooted cuttings
rs <- cbind(R, S)

8: Collate all variables into a new, shortened dataset "shade.root"
shade.root <- data.frame (BLOCK, HOUSE, SPECIES, N, R, S, propRoot) ; summary(shade.root)

9: Analysis asuming binomial distribution (Generalised Linear Model)
root.glm1 <- glm(rs ~ BLOCK + TREATMENT * SPECIES, binomial, data = shade.root)

10: Check for over-dispursion
Residual deviance: 78.157 on 40 degrees of freedom. Dispursion = 1.954
Data outside parameters of test and over-dispursed. Necessary to use quasibinomial distribution

11: Re-analysis asuming quasibinomial distribution (Generalised Linear Model)
root.glm2 <- glm(rs ~ BLOCK + TREATMENT * SPECIES, quasibinomial, data = shade.root)
summary(root.glm2)
anova(root.glm2, test="F")

Source	***Df***	***Deviance***	***Resid. Df***	***Resid. Dev***	***F***	***Pr(>F)***
null			53	216.76		
block	5	32.078	48	184.69	3.34	0.013
treatment	2	1.21	46	183.47	0.32	0.73
species	2	93.88	44	89.59	24.49	<0.0001
treatment:species	4	11.44	40	78.16	1.49	0.22

1.3 Destructive harvest

Notes
Analyses for experiments in **Chapter 3** (The propagation phase: varying the level of irradience)
Statisitical test: **Linear Mixed-Effects Model** (using R)
Species (3 levels): *Dryobalanops lanceolata, Parashorea malaanonan, Shorea leprosula*
Treatment (3 levels): 60%, 75% and 90% light interception
Blocks: 6
Shade houses: 18 (3 per block – each treatment level represented in each block)
Destructive harvest: All surviving cuttings harvested at end of experiment, measuring leaf, stem and root dry weight (546 cuttings in total)
Significant values (P<0.05) highlighted in red

1: Load data into a dataframe ('lightData')
rm(list=ls(all=TRUE))
lightData <- read.table("C:\\Documents and Settings\\Glen\\My Documents\\Thesis\\Data\\Chapter 3\\light.destructive.txt",header=T)

2: Declare factors
BLOCK <- as.factor(block)
HOUSE <- as.factor(house)
TREATMENT <- as.factor(treatment)
SPECIES <- as.factor(species)

3: Calculate response variables
shoot.mass <- leaf.mass+stem.mass
RSratio <- root.mass/shoot.mass
RLratio <- root.mass/leaf.mass

4: Load R's Mixed-Effects library
library(nlme)

5: Create group data objects for each response variable

```
light.gdata1 <- groupedData(root.mass ~ TREATMENT | BLOCK / HOUSE, inner = ~SPECIES)
light.gdata2 <- groupedData(shoot.mass ~ TREATMENT | BLOCK / HOUSE, inner = ~SPECIES)
light.gdata3 <- groupedData(leaf.mass ~ TREATMENT | BLOCK / HOUSE, inner = ~SPECIES)
light.gdata4 <- groupedData(RSratio ~ TREATMENT | BLOCK / HOUSE, inner = ~SPECIES)
light.gdata5 <- groupedData(RLratio ~ TREATMENT | BLOCK / HOUSE, inner = ~SPECIES)
```

6: Analyses

Root mass

```
root.mass.lme <- lme(log(root.mass) ~ TREATMENT*SPECIES, random = ~1 | BLOCK / HOUSE /
SPECIES, data=light.gdata1)
anova(root.mass.lme)
```

Source	*numDF*	*denDF*	*F-value*	*p-value*
intercept	1	492	2351.74	<0.0001
treatment	2	10	2.52	0.13
species	2	30	1.84	0.18
treatment:species	4	30	1.68	0.18

Shoot mass

```
shoot.mass.lme <- lme(log(shoot.mass) ~ TREATMENT*SPECIES, random = ~1 | BLOCK / HOUSE /
SPECIES, data=light.gdata2)
anova(shoot.mass.lme)
```

Source	*numDF*	*denDF*	*F-value*	*p-value*
intercept	1	492	34.24	<0.0001
treatment	2	10	4.79	0.035
species	2	30	132.63	<0.0001
treatment:species	4	30	0.55	0.7

Leaf mass

```
leaf.mass.lme <- lme(log(leaf.mass) ~ TREATMENT*SPECIES, random = ~1 | BLOCK / HOUSE /
SPECIES, data=light.gdata3)
anova(leaf.mass.lme)
```

Source	*numDF*	*denDF*	*F-value*	*p-value*
intercept	1	492	489.44	<0.0001
treatment	2	10	1.036	0.39
species	2	30	110.86	<0.0001
treatment:species	4	30	1.57	0.21

Root:shoot ratio

```
RSratio.lme <- lme(log(RSratio) ~ TREATMENT*SPECIES, random = ~1 | BLOCK / HOUSE /
SPECIES, data=light.gdata4)
anova(RSratio.lme)
```

Source	*numDF*	*denDF*	*F-value*	*p-value*
intercept	1	492	1466.086	<0.0001
treatment	2	10	1.086	0.37
species	2	30	17.52	<0.0001
treatment:species	4	30	1.43	0.25

Root:leaf ratio

```
RLratio.lme <- lme(log(RLratio) ~ TREATMENT*SPECIES, random = ~1 | BLOCK / HOUSE /
SPECIES, data=light.gdata5)
anova(RLratio.lme)
```

Source	*numDF*	*denDF*	*F-value*	*p-value*
intercept	1	492	1286	<0.0001
treatment	2	10	3.71	0.063
species	2	30	37.94	<0.0001
treatment:species	4	30	1.06	0.39

APPENDIX 2

2.1 Survival analysis

Notes
Analyses on experiments in **Chapter 4** (The propagation phase: hormone treatments)
Statistical test: **Generalised Linear Model** binary logistic regression with split-plot ANODEV (using R)
Species (3 levels): *Dryobalanops lanceolata, Parashorea malaanonan, Shorea leprosula*
Hormone concentration (5 levels): 0, 100, 300, 1000, 3000 ppm IBA
Exposure to hormone (5 levels): 1 sec, 1 hour, 12 hours, 48 hours, 120 hours
Blocks: 3 (nursery beds)
Plots within blocks (confounded with species): 3 x 3 blocks = 9
Subplots in each species plot: 25 x 9 plots = 225
Cuttings, 8 in each subplot: 225 x 8 = 1800
N = 3 x 5 x 5 x 3 x 8 = 1800
Treatment model: hormone concentration and exposure duration within species
Error model: blocks, plots, sublpots and cuttings
Significant values (P<0.05) shown in red, marginal significance (P<0.1) shown in blue

Overview of experimental design

BLOCK 3

Plot 7 *Shorea leprosula*								Plot 8 *Dryobalanops lanceolata*								Plot 9 *Parashorea malaanonan*							
155	18	160	19	165	16	170	13	175	2	180	9	185	11	190	20	195	19	200	7	205	25	210	24	215	9	220	2	225	3
154	22	159	3	164	14	169	6	174	21	179	8	184	25	189	18	194	2	199	15	204	19	209	13	214	16	219	1	224	12
153	15	158	20	163	23	168	10	173	12	178	12	183	17	188	3	193	16	198	21	203	23	208	4	213	20	218	6	223	22
152	8	157	7	162	4	167	25	172	11	177	24	182	6	187	10	192	5	197	4	202	8	207	5	212	18	217	10	222	21
151	24	156	5	161	9	166	17	171	1	176	13	181	22	186	14	191	1	196	23	201	11	206	7	211	15	216	17	221	14

BLOCK 2

Plot 4 *Shorea leprosula*								Plot 5 *Parashorea malaanonan*								Plot 6 *Dryobalanops lanceolata*							
80	20	85	1	90	24	95	2	100	11	105	10	110	8	115	16	120	12	125	5	130	5	135	17	140	19	145	18	150	12
79	7	84	6	89	12	94	22	99	8	104	3	109	25	114	23	119	19	124	21	129	13	134	9	139	23	144	11	149	16
78	21	83	13	88	25	93	16	98	3	103	13	108	17	113	20	118	22	123	2	128	24	133	8	138	1	143	14	148	20
77	14	82	19	87	17	92	10	97	9	102	6	107	24	112	14	117	15	122	4	127	6	132	10	137	25	142	22	147	21
76	5	81	4	86	18	91	23	96	15	101	7	106	18	111	1	116	11	121	9	126	4	131	3	136	2	141	7	146	15

BLOCK 1

Plot 1 *Dryobalanops lanceolata*								Plot 2 *Parashorea malaanonan*								Plot 3 *Shorea leprosula*							
5	2	10	1	15	20	20	17	25	13	30	8	35	3	40	2	45	13	50	5	55	19	60	8	65	3	70	14	75	4
4	11	9	15	14	12	19	8	24	21	29	4	34	21	39	17	44	19	49	1	54	16	59	22	64	20	69	10	74	12
3	25	8	4	13	10	18	3	23	6	28	6	33	25	38	11	43	24	48	15	53	17	58	23	63	21	68	9	73	11
2	9	7	24	12	16	17	7	22	14	27	18	32	9	37	23	42	22	47	16	52	13	57	1	62	15	67	18	72	7
1	5	6	19	11	23	16	22	21	18	26	12	31	7	36	14	41	20	46	10	51	25	56	24	61	6	66	2	71	5

Sub-plot number in green
Treatment code in blue (concentration x exposure - 5 x 5 = 25 treatments)

1: Load data into a dataframe ('hormoneData')

```
rm(list=ls(all=TRUE))
hormoneData <- read.table("C:\\Documents and Settings\\Glen\\My Documents\\Data – master\\Chapter 4\\hormone2.txt", header=T)
names(hormoneData)
```

"block" "plot" "subplot" "cutting" "species" "concentration" "exposure.secs" "survival" "rooted"

2: Make new columns

```
exposure <- exposure.secs / (60*60)
dead <- survival==0
```

3: Make new collapsed dataset for analysis of proportions

```
N <- as.vector (table(block, species, concentration, exposure) )
P <- as.vector (tapply(survival, list(block, species, concentration, exposure), sum) )
Q <- as.vector (tapply(dead, list(block, species, concentration, exposure), sum) )
```

4: Calculate proportion of cuttings surviving
propSurv <- P / N

5: Shorten explanatory variables columns & convert species text to numbers using 'as.numeric' function
Block <- as.vector (tapply(block, list(block, species, concentration, exposure), mean))
Plot <- as.vector (tapply(plot, list(block, species, concentration, exposure), mean))
Sub <- as.vector (tapply(subplot, list(block, species, concentration, exposure), mean))
Spp <- as.vector (tapply(as.numeric(species), list(block, species, concentration, exposure), mean))
Conc <- as.vector (tapply(concentration, list(block, species, concentration, exposure), mean))
Exp <- as.vector (tapply(exposure, list(block, species, concentration, exposure), mean))

6: Declare factors
BLOCK <- factor (Block)
PT <- factor (Plot)
SUB <- factor (Sub)
CONC <-factor (Conc)
EXP <- factor (Exp)
SPP <- levels(species)[Spp]

7: Bind alive & dead cuttings
pq <- cbind(P, Q)

8: Collate all variables into a new, shortened dataset "hormone.surv"
hormone.surv <- data.frame (PLOT, SUB, BLOCK, SPP, conc, exp, CONC, EXP, N, P, Q, propSurv)

9: Analysis - split-plot analysis of deviance using mean-deviance ratios for approx. F tests
surv.glm1 <- glm(pq ~ BLOCK + SPP + PLOT + SPP*CONC*EXP, binomial (link=cloglog), data = hormone.surv)
surv.glm1.tab <- anova(surv.glm1)

Source	***Df***	***Deviance***
block	2	0.65
spp	2	29.67
plot	4	1.29
concentration	4	186.83
exposure	4	167.5
spp:conc	8	24.17
spp:exp	8	37.62
conc:exp	16	167.73
spp:conc:exp	32	42.52
residual	144	155.9
total	224	813.88

10: Check for over-dispursion
Residual deviance = 155.9 on 144 degrees of freedom. Dispursion = 1.08
Dispursion within parameters of test. Use of binomial distribution valid

11: Construct a new table, calculate mean deviances, round the output to 2 dp, make column labels, do F tests & calculate P values
glm1.df <- surv.glm1.tab$Df ; glm1.df
glm1.dev <- surv.glm1.tab$Deviance ; glm1.dev
glm1.df <- c(glm1.df, 144)[-1] ; glm1.df
glm1.dev <- c(glm1.dev, 155.9)[-1] ; glm1.dev
glm1.dev <- round(glm1.dev , 2)
glm1.source <- c("Block","Species","BxS(plot)","Concentration","Exposure","SxC", "SxE", "CxE", "SxCxE","Residual") ; glm1.source
glm1.mndev <- round(glm1.dev/glm1.df , 2) ; glm1.mndev
F.vs.pt <- glm1.mndev / glm1.mndev[3] ; F.vs.pt
F.vs.res <- glm1.mndev / glm1.mndev[10] ; F.vs.res
F <- c(F.vs.pt[1:2], F.vs.res[3:10])
F <- round(F, 3)
pB <- 1 - pf(F[1], 2, 4) ; pB
pS <- 1 - pf(F[2], 2, 4) ; pS
pP <- 1 - pf(F[3], 4,144) ; pP
pC <- 1 - pf(F[4], 4,144) ; pC
pE <- 1 - pf(F[5], 4,144) ; pE
pCE <- 1 - pf(F[6], 16,144) ; pCE

```
pSC  <- 1 - pf( F[7],  8,144) ; pSC
pSE  <- 1 - pf( F[8],  8,144) ; pSE
pSCE <- 1 - pf( F[9], 32,144) ; pSCE
Prob. <- c(pB,pS,pP,pC,pE,pCE,pCE,pSC,pSE,pSCE)
Prob. <- round(Prob. , 4)
```

12: Construct final analysis table

```
glm1.results <- cbind(glm1.source, glm1.df, glm1.dev, glm1.mndev, F, Prob.) ; glm1.results
```

Source	*df*	*Dev.*	*Mean Dev.*	*F*	*P.*
block	2	0.65	0.33	1.031	0.44
species	2	29.67	14.84	46.38	0.0017
block:spp (=plot)	4	1.29	0.32	0.3	0.88
concentration	4	186.83	46.71	43.25	<0.0001
exposure	4	167.5	41.88	38.78	<0.0001
spp:conc	8	24.17	3.02	2.8	<0.0001
spp:exp	8	37.62	4.7	4.35	<0.0001
conc:exp	16	167.73	10.48	9.70	<0.0001
spp:conc:exp	32	42.52	1.33	1.23	<0.0001
residual	144	155.9	1.08		

2.2 Rooting analysis

Notes

Analyses on experiments in **Chapter 4** (The propagation phase: hormone treatments)
Statistical test: **Generalised Linear Model** binary logistic regression with split-plot ANODEV (using R)
Species (3 levels): *Dryobalanops lanceolata, Parashorea malaanonan, Shorea leprosula*
Hormone concentration (5 levels): 0, 100, 300, 1000, 3000 ppm IBA
Exposure to hormone (5 levels): 1 sec, 1 hour, 12 hours, 48 hours, 120 hours
Blocks: 3 (nursery beds)
Plots within blocks (confounded with species): 3 x 3 blocks = 9
Subplots in each species plot: 25 x 9 plots = 225
Cuttings, 8 in each subplot: 225 x 8 = 1800
N = 3 x 5 x 5 x 3 x 8 = 1800
Treatment model: hormone concentration and exposure duration within species
Error model: blocks, plots, sublpots and cuttings

1: Load data into a dataframe ('hormoneData')

```
rm(list=ls(all=TRUE))
hormoneData <- read.table("C:\\Documents and Settings\\Glen\\My Documents\\Data – master\\Chapter 4\\hormone3.txt", header=T)
names(hormoneData)
"block"  "plot"  "subplot"  "cutting"  "species"  "concentration"  "exposure.secs"  "survival"  "rooted"
```

2: Make new columns

```
exposure <- exposure.secs / (60*60)
unrooted <-rooted==0
```

3: Making new collapsed dataset for analysis of proportions

```
N <- as.vector (table(block, species, concentration, exposure) )
R <- as.vector(tapply(rooted, list(block, species, concentration, exposure), sum) )
S <- as.vector(tapply(unrooted, list(block,species, concentration, exposure), sum) )
```

4: Calculate proportion of rooting cuttings

```
propRoot <- R/N ; propRoot
```

5: Shorten explanatory variables columns & convert species text to numbers using 'as.numeric' function

```
Block <- as.vector( tapply(block, list(block, species, concentration, exposure), mean) ) ; Block
Plot <- as.vector( tapply(plot, list(block, species, concentration, exposure), mean) ) ; Plot
Sub <- as.vector( tapply(subplot, list(block, species, concentration, exposure), mean) ) ; Sub
Spp <- as.vector( tapply( as.numeric(species), list(block, species, concentration, exposure), mean) ) ; Spp
Conc <- as.vector( tapply(concentration, list(block, species, concentration, exposure), mean) ) ; Conc
Exp <- as.vector( tapply(exposure, list(block, species, concentration, exposure), mean) ) ; Exp
```

6: Declare factors

```
BLOCK <- factor (Block)
```

```
PLOT <- factor (Plot)
SUB <- factor (Sub)
CONC <-factor (Conc)
EXP <- factor (Exp)
SPP <- levels(species)[Spp]
```

7: Bind rooted and unrooted cuttings

```
rs <- cbind(R, S)
```

8: Collate all variables into a new, shortened dataset "hormone.root"

```
hormone.root <- data.frame(PLOT, SUB, BLOCK, SPP, CONC, EXP, N, R, S, propRoot) ; hormone.root
```

9: Analysis - split-plot analysis of deviance using mean-deviance ratios for approx. F tests

```
root.glm1 <- glm(rs ~ BLOCK + SPP + PLOT + SPP*CONC*EXP, binomial (link=cloglog), data =
hormone.root)
root.glm1.tab <- anova(root.glm1)
```

Source	***Df***	***Deviance***
block	2	1.26
species	2	133.82
plot	4	1.99
concentration	4	68.05
exposure	4	68.68
spp:conc	8	7.33
spp:exp	8	12.33
conc:exp	16	131.78
spp:conc:exp	32	75.76
residual	144	186.60
total	224	687.60

10: Check for over-dispursion

Residual deviance = 188.6 on 144 degrees of freedom. Dispursion = 1.31

Dispursion within parameters of test. Use of binomial distribution valid

11: Construct a new table, calculate mean deviances, round the output to 2 dp, make column labels, do F tests & calculate P values

```
glm1.df <- root.glm1.tab$Df ; glm1.df
glm1.dev <- root.glm1.tab$Deviance ; glm1.dev
glm1.df <- c(glm1.df, 144)[-1] ; glm1.df
glm1.dev <- c(glm1.dev, 186.6)[-1] ; glm1.dev
glm1.dev <- round( glm1.dev , 2)
glm1.source <- c("Block","Species","BxS(plot)","Concentration","Exposure","SxC", "SxE", "CxE",
"SxCxE","Residual" ) ; glm1.source
glm1.mndev <- round( glm1.dev/glm1.df , 2) ; glm1.mndev
F.vs.pt <- glm1.mndev / glm1.mndev[3] ; F.vs.pt
F.vs.res <- glm1.mndev / glm1.mndev[10] ; F.vs.res
F.vs.res
F <- c(F.vs.pt[1:2], F.vs.res[3:10])
F <- round( F, 3) ; F
pB  <- 1 - pf( F[1],  2,  4) ; pB
pS  <- 1 - pf( F[2],  2,  4) ; pS
pP  <- 1 - pf( F[3],  4,144) ; pP
pC  <- 1 - pf( F[4],  4,144) ; pC
pE  <- 1 - pf( F[5],  4,144) ; pE
pCE  <- 1 - pf( F[6], 16,144) ; pCE
pSC  <- 1 - pf( F[7],  8,144) ; pSC
pSE  <- 1 - pf( F[8],  8,144) ; pSE
pSCE <- 1 - pf( F[9], 32,144) ; pSCE
Prob. <- c(pB,pS,pP,pC,pE,pCE,pCE,pSC,pSE,pSCE)
Prob. <- round(Prob. , 4)
```

12: Construct final analysis table

```
glm1.results <- cbind(glm1.source, glm1.df, glm1.dev, glm1.mndev, F, Prob.) ; glm1.results
```

Source	***df***	***Dev.***	***Mean Dev.***	***F***	***P.***
block	2	1.26	0.63	1.26	0.38
species	2	133.82	66.91	133.82	<0.0001
block:spp (=plot)	4	1.99	0.5	0.39	0.82
concentration	4	68.05	17.01	13.085	<0.0001

exposure	4	68.68	17.17	13.21	<0.0001
spp:conc	8	7.33	0.92	0.71	0.78
spp:exp	8	12.33	1.54	1.19	0.78
conc:exp	16	131.78	8.24	6.34	0.31
spp:conc:exp	32	75.76	2.37	1.82	<0.0001
residual	144	186.6	1.3		

2.3 Destructive harvest

Notes
Analyses on experiments in **Chapter 4** (The propagation phase: hormone treatments)
Statistical test: **Linear Model** (using R)
Species (3 levels): *Dryobalanops lanceolata, Parashorea malaanonan, Shorea leprosula*
Hormone concentration (5 levels): 0, 100, 300, 1000, 3000 ppm IBA
Exposure to hormone (5 levels): 1 sec, 1 hour, 12 hours, 48 hours, 120 hours
Destructive harvest: Sub-sample measuring leaf, stem and root dry weight, height and diameter
Significant values (P<0.05) highlighted in red, marginal significance (P<0.1) highlighted in blue

1: Group treatments (amend source dataset)
Treatments grouped to improve replication (*only limited destructive harvest possible as cuttings required for outplanting experiment – see Chapter 5*).

	0 ppm IBA	*100 ppm IBA*	*300 ppm IBA*	*1,000 ppm IBA*	*3,000 ppm IBA*
1 sec	1	2	3	4	5
1 hour	6	7	8	9	10
12 hours	11	12	13	14	15
48 hours	16	17	18	19	20
120 hours	21	22	23	24	25

Group 1	24 cuttings
Group 2	48 cuttings
Group 3	46 cuttings

2: Load data into a dataframe ('destructive')

```
rm(list=ls(all=TRUE))
destructive <- read.table("C:\\Documents and Settings\\Glen\\My Documents\\Thesis\\Data\\Chapter 4\\destructive.group5.txt", header=T) ;
attach(destructive)
names(destructive)
"plant.ident" "species" "source" "pre.treat" "group" "height" "diameter" "leaf.no" "leaf.mass" "stem.mass" "rootmass"
```

3: Declare factors and make new columns

```
GROUP <- as.factor(group)
total.shoot <- stem.mass+leaf.mass
total.plant <- stem.mass+rootmass
RS.ratio <- rootmass/total.shoot
RTP.ratio <- rootmass/total.plant
RL.ratio <- rootmass/leaf.mass
```

4: Analyses

Total root mass

```
root.mass.lm <- lm(rootmass ~ species * GROUP)
anova(root.mass.lm)
```

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
species	2	0.079	0.04	2.74	0.069
GROUP	2	0.028	0.014	0.97	0.38
species:GROUP	4	0.019	0.0048	0.33	0.86
Residuals	109	1.57	0.014		

Total shoot mass

```
total.shoot.lm <- lm(total.shoot ~ species * GROUP)
anova(total.shoot.lm)
```

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
species	2	10.58	5.29	17.93	<0.0001
GROUP	2	1.52	0.76	2.58	0.08
species:GROUP	4	0.44	0.11	0.37	0.83
Residuals	109	32.16	0.3		

Leaf mass

leaf.mass.lm <- lm(leaf.mass ~ species * GROUP)
anova(leaf.mass.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
species	2	4.32	2.16	16.5	<0.0001
GROUP	2	0.71	0.35	2.7	0.072
species:GROUP	4	0.34	0.085	0.65	0.63
Residuals	109	14.27	0.13		

Root:shoot ratio

RS.ratio.lm <- lm(RS.ratio ~ species * GROUP)
anova(RS.ratio.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
species	2	0.018	0.0088	2.48	0.089
GROUP	2	0.002	0.001	0.28	0.76
species:GROUP	4	0.012	0.0031	0.87	0.48
Residuals	109	0.39	0.0036		

Root:leaf mass ratio

RL.ratio.lm <- lm(RL.ratio ~ species * GROUP)
anova(RL.ratio.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
species	2	0.34	0.17	7.9	0.00063
GROUP	2	0.0021	0.0011	0.05	0.95
species:GROUP	4	0.062	0.016	0.73	0.58
Residuals	109	2.33	0.021		

APPENDIX 3

3.1 Survival analyses

Notes
Analyses on experiments in **Chapter 5** (The establishment phase: initial survival & growth)
Statistical test: **Generalised Linear Model** – binary logistic regression (using R)
Outplanting experiment comparing survival in cuttings and seedlings up to 20 months after planting
Cutting material derived from hormone experiment (Chapter 4)
Species (3 levels): *Dryobalanops lanceolata, Parashorea malaanonan, Shorea leprosula*
Treatments: Cuttings vs Seedlings
Pre-treatments (cuttings only): Hormone treatments from previous experiment
Plots: 3 (100 m x 100 m)
Lines: 11 planting lines within each plot (100 m long at 10 m centres)
Cuttings/seedlings: 250 per plot (125 cuttings, 125 seedlings). Total = 750 (375 cuttings, 375 seedlings)
Survival & growth measurements recorded every 4 months
Canopy openness at each planting point recorded every 4 months
Int.height = cutting/seedling height at planting
Significant values (P<0.05) shown in red, marginal significance (P<0.1) shown in blue

1: Load data into a dataframe ('outplant')
```
rm(list=ls(all=TRUE))
outplant <- read.table("C:\\Documents and Settings\\Glen\\My Documents\\Thesis\\Data\\Chapter 5\\outplant2.txt", header=T)
names(outplant)
"plant.id" "spp" "treat" "pretreat" "plot" "line" "point" "time" "survival" "int.height" "int.diam" "height" "diameter" "leaf" "canopy"
```

2: Declare & check factors
```
PRETREAT<-as.factor(pretreat)
PLOT<-as.factor(plot)
LINE<-as.factor(line)
POINT<-as.factor(point)
```

3: Fit a saturated model as a baseline for comparison (survival after 4 months) NOT including hormone pre-treatments
```
surv4.fullmodel <- glm(survival ~ PLOT + LINE + treat * spp * int.height*canopy, binomial, subset=(time == 4), data=outplant)
```

4: Analysis of the saturated model
```
anova(surv4.fullmodel, test="Chi")
```

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
null			749	437.41	
plot	2	1.71	747	435.70	0.43
line	30	29.22	717	406.48	0.51
treat	1	1.65	716	404.83	0.20
spp	2	1.07	714	403.76	0.59
int.height	1	0.88	713	402.88	0.35
canopy	1	0.59	712	402.29	0.44
treat:spp	2	1.69	710	400.59	0.43
treat:int.height	1	0.01	709	400.59	0.94
spp:int.height	2	0.62	707	399.97	0.73
treat:canopy	1	1.26	706	398.71	0.26
spp:canopy	2	1.51	704	397.20	0.47
int.height:canopy	1	4.00	703	393.20	0.05
treat:spp:int.height	2	0.25	701	392.95	0.88
treat:spp:canopy	2	1.90	699	391.05	0.39
treat:int.height:canopy	1	3.14	698	387.91	0.08
spp:int.height:canopy	2	8.40	696	379.51	0.01
treat:spp:int.height:canopy	2	0.35	694	379.16	0.84

5: Remove non-significant interactions (through stepwise backwards deletion) & test new model against saturated model using Akaike Information Criterion (AIC)
Start by removing "line" from the model
```
surv4.model1 <- update(surv4.fullmodel, ~. –LINE)
```

6: Analysis of the new model (Surv4.model1)

anova(surv4.model1, test="Chi")

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
null			749	437.41	
plot	2	1.71	747	435.70	0.43
treatment	1	1.72	746	433.98	0.19
species	2	1.62	744	432.36	0.44
int.height	1	1.62	743	430.74	0.20
canopy	1	2.08	742	428.65	0.15
treat:spp	2	1.06	740	427.59	0.59
treat:int.height	1	0.01	739	427.58	0.92
spp:int.height	2	1.62	737	425.96	0.44
treat:canopy	1	1.33	736	424.63	0.25
spp:canopy	2	1.55	734	423.08	0.46
int.height:canopy	1	3.07	733	420.01	0.08
treat:spp:int.height	2	0.18	731	419.83	0.92
treat:spp:canopy	2	2.18	729	417.65	0.34
treat:int.height:canopy	1	2.60	728	415.05	0.11
spp:int.height:canopy	2	9.98	726	405.07	0.01
treat:spp:int.height:canopy	2	0.71	724	404.36	0.70

7: Test the new model against the original saturated model using AIC

AIC(surv4.fullmodel, surv4.model1)

Source	*df*	*AIC*
surv4.fullmodel	56	491.1556
surv4.model1	26	456.3639

AIC for new model is lower than for saturated model, indicating new model is better

8: Removing non-significant 4-way interaction

surv4.model2 <- update(surv4.model1, ~. -treat:spp:int.height:canopy)

9: Analysis of new model (Surv4.model2)

anova(surv4.model2, test="Chi")

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
null			749	437.41	
plot	2	1.71	747	435.70	0.43
treatment	1	1.72	746	433.98	0.19
species	2	1.62	744	432.36	0.44
int.height	1	1.62	743	430.74	0.20
canopy	1	2.08	742	428.65	0.15
treat:spp	2	1.06	740	427.59	0.59
treat:int.height	1	0.01	739	427.58	0.92
spp:int.height	2	1.62	737	425.96	0.44
treat:canopy	1	1.33	736	424.63	0.25
spp:canopy	2	1.55	734	423.08	0.46
int.height:canopy	1	3.07	733	420.01	0.08
treat:spp:int.height	2	0.18	731	419.83	0.92
treat:spp:canopy	2	2.18	729	417.65	0.34
treat:int.height:canopy	1	2.60	728	415.05	0.11
spp:int.height:canopy	2	9.98	726	405.07	0.01

10: Test the new model

AIC(surv4.model1, surv4.model2)

Source	*df*	*AIC*
surv4.model1	26	456.3639
surv4.model2	24	453.0690

AIC for new model is lower, indicating a better model. No more deletions possible as 3-way interaction is significant – Surv4.model2 is therefore the final model

11: Fit a saturated model as a baseline for comparison (survival after 8 months)

surv8.fullmodel <- glm(survival ~ PLOT + LINE + treat * spp * int.height*canopy, binomial, subset=(time == 8), data=outplant)

12: Analysis of the saturated model

anova(surv8.fullmodel, test="Chi")

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
null			748	632.00	
plot	2	0.60	746	631.40	0.74
line	30	30.45	716	600.95	0.44
treatment	1	7.26	715	593.69	0.01
species	2	3.72	713	589.97	0.16
int.height	1	0.000045	712	589.97	0.99
canopy	1	1.00	711	588.96	0.32
treat:spp	2	5.88	709	583.08	0.05
treat:int.height	1	1.13	708	581.95	0.29
spp:int.height	2	2.53	706	579.42	0.28
treat:canopy	1	0.19	705	579.23	0.66
spp:canopy	2	1.69	703	577.53	0.43
int.height:canopy	1	2.11	702	575.43	0.15
treat:spp:int.height	2	1.39	700	574.04	0.50
treat:spp:canopy	2	0.93	698	573.11	0.63
treat:int.height:canopy	1	0.0049	697	573.11	0.94
spp:int.height:canopy	2	10.02	695	563.09	0.01
treat:spp:int.height:canopy	2	2.11	693	560.97	0.35

13: Remove 'Line' from the model

surv8.model1 <- update(surv8.fullmodel, ~. –LINE)

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
null			748	632.00	
plot	2	0.60	746	631.40	0.74
treatment	1	7.24	745	624.16	0.01
species	2	4.02	743	620.14	0.13
int.height	1	0.13	742	620.01	0.72
canopy	1	0.80	741	619.21	0.37
treat:spp	2	5.62	739	613.59	0.06
treat:int.height	1	0.79	738	612.80	0.37
spp:int.height	2	2.00	736	610.81	0.37
treat:canopy	1	0.16	735	610.64	0.69
spp:canopy	2	0.77	733	609.88	0.68
int.height:canopy	1	1.16	732	608.72	0.28
treat:spp:int.height	2	1.15	730	607.57	0.56
treat:spp:canopy	2	0.52	728	607.05	0.77
treat:int.height:canopy	1	0.05	727	607.01	0.83
spp:int.height:canopy	2	10.98	725	596.03	0.0041
treat:spp:int.height:canopy	2	1.53	723	594.49	0.46

14: Test the new model

AIC(surv8.fullmodel, surv8.model1)

Source	*df*	*AIC*
surv8.fullmodel	56	672.9719
surv8.model1	26	646.4936

15: Remove non-significant 4-way interaction

surv8.model2 <- update(surv8.model1, ~. -treat:spp:int.height:canopy)

16: Analysis of new model (Surv8.model2)

anova(surv8.model2, test="Chi")

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
null			748	632.00	
plot	2	0.60	746	631.40	0.74
treatment	1	7.24	745	624.16	0.01
species	2	4.02	743	620.14	0.13
int.height	1	0.13	742	620.01	0.72
canopy	1	0.80	741	619.21	0.37
treat:spp	2	5.62	739	613.59	0.06
treat:int.height	1	0.79	738	612.80	0.37
spp:int.height	2	2.00	736	610.81	0.37
treat:canopy	1	0.16	735	610.64	0.69
spp:canopy	2	0.77	733	609.88	0.68
int.height:canopy	1	1.16	732	608.72	0.28
treat:spp:int.height	2	1.15	730	607.57	0.56
treat:spp:canopy	2	0.52	728	607.05	0.77
treat:int.height:canopy	1	0.05	727	607.01	0.83
spp:int.height:canopy	2	10.98	725	596.03	0.0041

17: Test the new model

AIC(surv8.model1, surv8.model2)

Source	*df*	*AIC*
surv8.model1	26	646.4936
surv8.model2	24	644.0255

AIC for new model is lower, indicating a better model. No more deletions possible as 3-way interaction is significant – Surv8.model2 is therefore the final model

18: Fit a saturated model as a baseline for comparison (survival after 20 months)

surv20.fullmodel <- glm(survival ~ PLOT + LINE + treat * spp * int.height*canopy, binomial, subset=(time == 20), data=outplant)

19: Analysis of the saturated model

anova(surv20.fullmodel, test="Chi")

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
null			749	954.77	
plot	2	5.45	747	949.32	0.07
line	30	39.14	717	910.18	0.12
treatment	1	5.89	716	904.29	0.02
species	2	10.86	714	893.42	0.0004
int.height	1	1.614e-05	713	893.42	1.00
canopy	1	0.49	712	892.93	0.48
treat:spp	2	5.58	710	887.35	0.06
treat:int.height	1	2.55	709	884.80	0.11
spp:int.height	2	1.33	707	883.48	0.51
treat:canopy	1	0.03	706	883.45	0.86
spp:canopy	2	7.11	704	876.33	0.03
int.height:canopy	1	2.17	703	874.16	0.14
treat:spp:int.height	2	5.08	701	869.08	0.08
treat:spp:canopy	2	2.05	699	867.04	0.36
treat:int.height:canopy	1	0.05	698	866.99	0.82
spp:int.height:canopy	2	0.44	696	866.55	0.80
treat:spp:int.height:canopy	2	3.03	694	863.52	0.22

20: Remove lines from the model

surv20.model1 <- update(surv20.fullmodel, ~. –LINE)

21: Test the new model

AIC(surv20.fullmodel, surv20.model1)

Source	*df*	*AIC*
surv20.fullmodel	56	975.5168
surv20.model1	26	955.1914

22: Remove non-significant 4-way interaction
surv20.model2 <- update(surv20.model1, ~. -treat:spp:int.height:canopy)

23: Remove the 4-way interaction from the model
anova(surv20.model2, test="Chi")

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
null			749	954.77	
plot	2	5.45	747	949.32	0.07
treatment	1	6.20	746	943.12	0.01
species	2	11.35	744	931.77	0.0034
int.height	1	0.02	743	931.75	0.88
canopy	1	0.13	742	931.62	0.72
treat:spp	2	4.67	740	926.95	0.10
treat:int.height	1	2.30	739	924.65	0.13
spp:int.height	2	1.75	737	922.91	0.42
treat:canopy	1	0.02	736	922.89	0.89
spp:canopy	2	7.26	734	915.63	0.03
int.height:canopy	1	1.40	733	914.23	0.24
treat:spp:int.height	2	4.98	731	909.25	0.08
treat:spp:canopy	2	2.55	729	906.70	0.28
treat:int.height:canopy	1	0.08	728	906.62	0.77
spp:int.height:canopy	2	0.77	726	905.84	0.68

24: Test model
AIC(surv20.model1, surv20.model2)

Source	*df*	*AIC*
surv20.model1	26	955.1914
surv20.model2	24	953.8417

25: Removing non-significant 3-way interaction
surv20.model3 <- update(surv20.model2, ~. - spp:int.height:canopy)

26: Test model
AIC(surv20.model2, surv20.model3)

Source	*df*	*AIC*
surv20.model2	24	953.8417
surv20.model3	22	950.6163

27: Remove next non-significant 3-way interaction
surv20.model4 <- update(surv20.model2, ~. - treat:int.height:canopy)

28: Test model
AIC(surv20.model2, surv20.model4)

Source	*df*	*AIC*
surv20.model2	24	953.8417
surv20.model4	23	952.0064

29: Remove next non-significant 3-way interaction
surv20.model5 <- update(surv20.model2, ~. - treat:spp:canopy)

30: Test model
AIC(surv20.model2, surv20.model5)

Source	*df*	*AIC*
surv20.model2	24	953.8417
surv20.model5	22	950.5415

31: Removing next non-significant 3-way interaction
surv20.model6 <- update(surv20.model2, ~. - treat:spp:int.height)

32: Test model
AIC(surv20.model2, surv20.model6)

Source	*df*	*AIC*
surv20.model2	24	953.8417
surv20.model6	22	955.3357

AIC indicates that removing treat:spp:int.height interaction does not improve model

33: Final amendments to model
surv20.model7 <- update(surv20.model2, ~. - spp:int.height:canopy - treat:spp:canopy – treat:int.height:canopy)

34: Test model
AIC(surv20.model2, surv20.model7)

Source	*df*	*AIC*
surv20.model2	24	953.8417
surv20.model7	19	947.2495

35: Summary of final model
anova(surv20.model7, test="Chi")

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
null			749	954.77	
plot	2	5.45	747	949.32	0.07
treatment	1	6.20	746	943.12	0.01
species	2	11.35	744	931.77	0.0034
int.height	1	0.02	743	931.75	0.88
canopy	1	0.13	742	931.62	0.72
treat:spp	2	4.67	740	926.95	0.10
treat:int.height	1	2.30	739	924.65	0.13
spp:int.height	2	1.75	737	922.91	0.42
treat:canopy	1	0.02	736	922.89	0.89
spp:canopy	2	7.26	734	915.63	0.03
int.height:canopy	1	1.40	733	914.23	0.24
treat:spp:int.height	2	4.98	731	909.25	0.08

3.2 Survival analyses – with cutting pre-treatments (from hormone experiment – Chapter 4)

Notes
Analyses on experiments in **Chapter 5** (The establishment phase: initial survival & growth)
Statistical test: **Generalised Linear Model** – binary logistic regression (using R)
Testing effect previous cutting pre-treatments (hormone concentration and duration of exposure – see Chapter 4) on survival

Treatment groupings

	0 ppm IBA	*100 ppm IBA*	*300 ppm IBA*	*1,000 ppm IBA*	*3,000 ppm IBA*
1 sec	1	2	3	4	5
1 hour	6	7	8	9	10
12 hours	11	12	13	14	15
48 hours	16	17	18	19	20
120 hours	21	22	23	24	25

Treatment group 1	87 cuttings
Treatment group 2	139 cuttings
Treatment group 3	149 cuttings

1: Load data into a dataframe ('outplant')
rm(list=ls(all=TRUE))
outplant <- read.table("C:\\Documents and Settings\\Glen\\My Documents\\Thesis\\Data\\Chapter 5\\outplant3new.txt", header=T)
attach(outplant)
names(outplant)
summary(outplant)

2: Set factors

```
PLOT <- as.factor(plot)
LINE <- as.factor(line)
GROUP <- as.factor(group)
```

3: Effects of cutting pre-treatments (by treatment group) on survival

4 months

```
surv4PT.model <- glm(survival ~ PLOT + LINE + GROUP * spp, binomial, subset=(time == 4 & treat == "c"), data=outplant)
anova(surv4PT.model, test="Chi")
```

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
NULL		374	241.61		
PLOT	2	1.74	372	239.87	0.42
LINE	30	30.45	342	209.42	0.44
GROUP	2	5.96	340	203.47	0.051
spp	2	0.42	338	203.048	0.81
GROUP:spp	4	10.081	334	192.97	0.039

8 months

```
surv8PT.model <- glm(survival ~ PLOT + LINE + GROUP * spp, binomial, subset=(time == 8 & treat == "c"), data=outplant)
anova(surv8PT.model, test="Chi")
```

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
NULL		374	361.02		
PLOT	2	1.00	372	360.02	0.61
LINE	30	33.75	342	326.26	0.29
GROUP	2	6.63	340	319.64	0.04
spp	2	1.79	338	317.84	0.41
GROUP:spp	4	6.71	334	311.13	0.15

12 months

```
surv12PT.model <- glm(survival ~ PLOT + LINE + GROUP * spp, binomial, subset=(time == 12 & treat == "c"), data=outplant)
anova(surv12PT.model, test="Chi")
```

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
NULL		374	410.99		
PLOT	2	0.12	372	410.87	0.94
LINE	30	30.65	342	380.22	0.43
GROUP	2	5.48	340	374.75	0.06
spp	2	1.34	338	373.40	0.51
GROUP:spp	4	8.86	334	364.54	0.06

16 months

```
surv16PT.model <- glm(survival ~ PLOT + LINE + GROUP * spp, binomial, subset=(time == 16 & treat == "c"), data=outplant)
anova(surv16PT.model, test="Chi")
```

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
NULL		374	455.58		
PLOT	2	2.77	372	452.80	0.25
LINE	30	30.61	342	422.20	0.43
GROUP	2	4.23	340	417.97	0.12
spp	2	0.22	338	417.74	0.89
GROUP:spp	4	6.15	334	411.59	0.19

20 months

```
surv20PT.model <- glm(survival ~ PLOT + LINE + GROUP * spp, binomial, subset=(time == 20 & treat == "c"), data=outplant)
anova(surv20PT.model, test="Chi")
```

Source	*Df*	*Deviance*	*Resid. Df*	*Resid. Dev*	*P(>|Chi|)*
NULL		374	496.55		
PLOT	2	4.12	372	492.43	0.13
LINE	30	44.24	342	448.20	0.05
GROUP	2	2.85	340	445.34	0.24
spp	2	0.82	338	444.53	0.67
GROUP:spp	4	3.11	334	441.42	0.54

3.3 Destructive harvest at planting & after 20 months

Notes
Analyses on experiments in **Chapter 5** (The establishment phase: initial survival & growth)
Statistical test: **Linear Model** (using R)
Outplanting experiment comparing cuttings and seedlings 20 months after planting
Cutting material derived from hormone experiment (Chapter 4)
Species (3 levels): *Dryobalanops lanceolata, Parashorea malaanonan, Shorea leprosula*
Treatments: Cuttings vs Seedlings
Pre-planting sub-sample: 164 plants harvested (45 seedlings, 121 cuttings)
End of experiment sub-sample: 44 plants harvested (22 cuttings, 22 seedlings)
Destructive sub sample measuring dry weights of fine root mass (<2mm diam), main root mass (> 2 mm diameter), stem mass, leaf mass.
Significant values (P<0.05) shown in red, marginal significance (P<0.1) shown in blue

1: Load data into a dataframe ('destructive')

```
rm(list=ls(all=TRUE))
pre.post.destructive <- read.table("C:\\Documents and Settings\\Glen\\My
Documents\\Thesis\\Data\\Chapter 5\\destructive.pre.post.txt", header=T) ;
names(pre.post.destructive)
[1] "plant.ident"  "species"     "source"      "time"
 [5] "pre.treat"   "height"      "diameter"    "leaf.no"
 [9] "leaf.mass"   "stem.mass"   "rootmass.main" "rootmass.fine"
```

2: Declare factors & define response variables

```
spp <- as.factor(species)
treatment <- as.factor(source)
TIME <- as.factor(time)
total.roots <- rootmass.main + rootmass.fine
total.shoots <- leaf.mass + stem.mass
total.plant <- total.roots + total.shoots
rs.ratio <- total.roots/total.shoots
```

3: Analyses

Fine root mass

```
rootmass.fine.lm <- lm(log(rootmass.fine) ~ spp * treatment * TIME)
anova(rootmass.fine.lm)
```

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
spp	2	3.66	1.83	2.99	0.053
treatment	1	0.40	0.40	0.65	0.42
TIME	1	62.87	62.87	102.62	<0.0001
spp:treatment	2	2.47	1.23	2.012	0.14
spp:TIME	2	0.067	0.033	0.054	0.95
treatment:TIME	1	0.15	0.15	0.24	0.62
spp:treatment:TIME	2	1.25	0.62	1.017	0.36
Residuals	195	119.47	0.61		

Total root mass

```
total.roots.lm <- lm(log(total.roots) ~ spp * treatment * TIME)
anova(total.roots.lm)
```

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
spp	2	6.42	3.21	5.95	0.0031
treatment	1	145.1	145.1	268.89	<0.0001
TIME	1	123.73	123.73	229.29	<0.0001
spp:treatment	2	0.45	0.22	0.41	0.66
spp:TIME	2	0.046	0.023	0.043	0.96
treatment:TIME	1	20.47	20.47	37.94	<0.0001
spp:treatment:TIME	2	1.25	0.62	1.15	0.32
Residuals	195	105.23	0.54		

Leaf mass

leaf.mass.lm <- lm(log(leaf.mass) ~ spp * treatment * TIME)
anova(leaf.mass.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
spp	2	27.97	13.99	25.28	<0.0001
treatment	1	15.36	15.36	27.76	<0.0001
TIME	1	113.063	113.063	204.33	<0.0001
spp:treatment	2	2.13	1.066	1.93	0.15
spp:TIME	2	0.58	0.29	0.52	0.59
treatment:TIME	1	1.53	1.53	2.76	0.098
spp:treatment:TIME	2	0.67	0.34	0.61	0.55
Residuals	195	107.9	0.55		

Stem mass

stem.mass.lm <- lm(stem.mass ~ spp * treatment *TIME)
anova(stem.mass.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
spp	2	2.38	1.19	0.11	0.9
treatment	1	215.4	215.4	19.073	<0.0001
TIME	1	1522.33	1522.33	134.79	<0.0001
spp:treatment	2	1.41	0.71	0.062	0.94
spp:TIME	2	24.65	12.33	1.092	0.34
treatment:TIME	1	11.31	11.31	1.0012	0.32
spp:treatment:TIME	2	0.54	0.27	0.024	0.98
Residuals	195	2202.31	11.29		

Total shoot mass

total.shoots.lm <- lm(log(total.shoots) ~ spp * treatment * TIME)
anova(total.shoots.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
spp	2	7.84	3.92	13.089	<0.0001
treatment	1	27.61	27.61	92.15	<0.0001
TIME	1	117.29	117.29	391.44	<0.0001
spp:treatment	2	1.33	0.67	2.22	0.11
spp:TIME	2	0.041	0.02	0.068	0.93
treatment:TIME	1	1.33	1.33	4.43	0.037
spp:treatment:TIME	2	0.21	0.1	0.34	0.71
Residuals	195	58.43	0.3		

Total plant mass

total.plant.lm <- lm(log(total.plant) ~ spp * treatment * TIME)
anova(total.plant.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
spp	2	7.3	3.65	12.24	<0.0001
treatment	1	41.38	41.38	138.72	<0.0001
TIME	1	114.7	114.7	384.52	<0.0001
spp:treatment	2	1.12	0.56	1.88	0.16
spp:TIME	2	0.034	0.017	0.056	0.95
treatment:TIME	1	3.13	3.13	10.48	0.0014
spp:treatment:TIME	2	0.24	0.12	0.41	0.67
Residuals	195	58.17	0.3		

Root:shoot ratio

rs.ratio.lm <- lm(rs.ratio ~ spp * treatment * TIME)
anova(rs.ratio.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
spp	2	0.086	0.043	6.48	<0.0001
treatment	1	2.23	2.23	338.36	<0.0001
TIME	1	0.038	0.038	5.71	0.018
spp:treatment	2	0.02701	0.01351	2.0458	0.13
spp:TIME	2	0.0014	0.00069	0.11	0.9
treatment:TIME	1	0.63	0.63	95.26	<0.0001
spp:treatment:TIME	2	0.079	0.04	6.018	0.0029
Residuals	195	1.29	0.0066		

Height

height.lm <- lm(height ~ spp * treatment * TIME)
anova(height.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
spp	2	2964	1482	15.79	<0.0001
treatment	1	21331	21331	227.27	<0.0001
TIME	1	32897	32897	350.49	<0.0001
spp:treatment	2	2413	1207	12.85	<0.0001
spp:TIME	2	394	197	2.1	0.13
treatment:TIME	1	3066	3066	32.67	<0.0001
spp:treatment:TIME	2	302	151	1.61	0.2
Residuals	195	18303	94		

Diameter

diameter.lm <- lm(diameter ~ spp * treatment * TIME)
anova(diameter.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
spp	2	9.44	4.72	6.81	0.0014
treatment	1	110.741	110.741	159.7135	<0.0001
TIME	1	233.106	233.106	336.1932	<0.0001
spp:treatment	2	1.907	0.953	1.3749	0.26
spp:TIME	2	0.390	0.195	0.2816	0.75
treatment:TIME	1	2.931	2.931	4.2270	0.041
spp:treatment:TIME	2	1.212	0.606	0.8743	0.42
Residuals	195	135.207	0.693		

3.4 Destructive harvest (sub-analysis of 20 month harvest)

Notes
Analyses on experiments in **Chapter 5** (The establishment phase: initial survival & growth)
Statistical test: **Linear Model** (using R)
Outplanting experiment comparing cuttings and seedlings 20 months after planting
Cutting material derived from hormone experiment (Chapter 4)
Species (3 levels): *Dryobalanops lanceolata, Parashorea malaanonan, Shorea leprosula*
Treatments: Cuttings vs Seedlings
Cuttings/seedlings: 44 harvested (22 cuttings, 22 seedlings)
Destructive sub sample measuring dry weights of fine root mass (<2mm diam), main root mass (> 2 mm diameter), stem mass, leaf mass.
Significant values (P<0.05) shown in red, marginal significance (P<0.1) shown in blue

1: Load data into a dataframe ('destructive')

rm(list=ls(all=TRUE))
destructive <- read.table("C:\\Documents and Settings\\Glen\\My Documents\\Thesis\\Data\\Chapter 5\\destructive2.20.txt", header=T) ;
attach(destructive)
names(destructive)
"plant.ident" "species" "source" "height" "diameter" "leaf.no" "leaf.mass" "stem.mass" "rootmass.main" "rootmass.fine"

2: Declare factors & define response variables

spp <- as.factor(species)
treatment <- as.factor(source)
total.roots <- rootmass.main + rootmass.fine
total.shoots <- leaf.mass + stem.mass
total.plant <- total.roots + total.shoots
rs.ratio <- total.roots/total.shoots
rtp.ratio <- total.roots/total.plant
fine.main.ratio <- rootmass.fine/rootmass.main
fine.shoot.ratio <- rootmass.fine/total.shoots

3: Analyses

Root:shoot ratio

rs.ratio.lm <- lm(log(rs.ratio) ~ spp * treatment)
anova(rs.ratio.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
species	2	0.11	0.054	0.46	0.63
treatment	1	0.17	0.16	1.43	0.24
species:treatment	2	1.47	0.73	6.27	0.0044
residuals	38	4.44	0.12		

Total root mass

total.roots.lm <- lm(log(total.roots) ~ spp * treatment)
anova(total.roots.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
species	2	1.4	0.7	0.9	0.41
treatment	1	0.72	0.72	0.93	0.34
species:treatment	2	1.38	0.69	0.89	0.42
residuals	38	29.46	0.78		

Fine root mass

rootmass.fine.lm <- lm(log(rootmass.fine) ~ spp * treatment)
anova(rootmass.fine.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
species	2	0.3	0.15	0.23	0.8
treatment	1	0.75	0.75	1.13	0.29
species:treatment	2	0.085	0.043	0.065	0.94
residuals	38	25.092	0.66		

Main root mass

rootmass.main.lm <- lm(log(rootmass.main) ~ spp * treatment)
anova(rootmass.main.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
species	2	1.7	0.85	0.94	0.4
treatment	1	1.88	1.88	2.076	0.16
species:treatment	2	2.052	1.026	1.13	0.33
residuals	38	34.37	0.9		

Total plant mass

total.plant.lm <- lm(log(total.plant) ~ spp * treatment)
anova(total.plant.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
species	2	1.094	0.55	0.61	0.55
treatment	1	0.26	0.26	0.28	0.6
species:treatment	2	0.061	0.03	0.0338	0.97
residuals	38	34.16	0.9		

Leaf mass

leaf.mass.lm <- lm(log(leaf.mass) ~ spp * treatment)
anova(leaf.mass.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
species	2	8.97	4.49	3.46	0.042
treatment	1	0.07	0.07	0.054	0.82
species:treatment	2	0.025	0.013	0.0098	0.99
residuals	38	49.25	1.3		

Total shoot mass

total.shoots.lm <- lm(log(total.shoots) ~ spp * treatment)
anova(total.shoots.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
species	2	1.083	0.54	0.57	0.57
treatment	1	0.2	0.2	0.2	0.65
species:treatment	2	0.027	0.014	0.014	0.99
residuals	38	36.23	0.95		

Stem diameter

diameter.lm <- lm((diameter) ~ spp * treatment)
anova(diameter.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
spp	2	2.43	1.22	0.47	0.63
treatment	1	4.51	4.51	1.76	0.19
spp:treatment	2	1.63	0.82	0.32	0.73
Residuals	38	97.32	2.56		

Height

height.lm <- lm((height) ~ spp * treatment)
anova(height.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
spp	2	2388.1	1194	3.2	0.052
treatment	1	18.1	18.1	0.048	0.83
spp:treatment	2	118.3	59.2	0.16	0.85
Residuals	38	14187.1	373.3		

APPENDIX 4

Notes
Analyses for experiments in **Chapter 6** (The post-establishment phase: performance after 8 years)
Statistical test: **Linear Model** (using R)
Species: *Dryobalanops lanceolata*
28 trees harvested: 16 trees at 5 years after planting (8 cuttings, 8 seedlings), 12 trees at 8 years (6 cuttings, 6 seedlings)
Fine roots = < 2 mm diameter
Medium roots = 2 -5 mm diameter
Large roots = > 5 mm diameter
z1 = roots in zone 1 (0 – 30 cm below ground)
z2 = roots in zone 2 (30 – 60 cm below ground)
z3 = roots in zone 3 (60 – 90 cm below ground)
Significant values (P<0.05) highlighted in red, marginal significance (P<0.1) highlighted in blue

1: Load data into a dataframe ('bigtrees')

```
bigtrees <- read.table("C:\\Documents and Settings\\Glen\\My Documents\\Thesis\\Data\\Chapter 6\\bigtrees.txt", header=T) names(bigtrees)
"plant.ident" "source" "sample.date" "height" "base.diam" "dbh" "leaf.no" "branch.mass" "leaf.mass" "root.depth" "lrg.root.mass" "med.root.mass" "fine.root.mass" "lrg.root.z1" "med.root.z1" "fine.root.z1" "lrg.root.z2" "med.root.z2" "fine.root.z2" "lrg.root.z3" "med.root.z3" "fine.root.z3"
```

2: Declare factors & define new response variables

```
TIME <- factor(sample.date)
total.shoots <- branch.mass + leaf.mass
total.roots <- lrg.root.mass + med.root.mass + fine.root.mass
total.plant <- total.shoots + total.roots
rs.ratio <- total.roots / total.shoots
depth.height.ratio <- root.depth / height
total.root.z1 <- fine.root.z1 + med.root.z1 + lrg.root.z1
total.root.z2 <- fine.root.z2 + med.root.z2 + lrg.root.z2
total.root.z3 <- fine.root.z3 + med.root.z3 + lrg.root.z3
```

3: Analyses

Total root mass

```
total.roots.lm <- lm(log(total.roots) ~ source * DATE)
anova(total.roots.lm)
```

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
source	1	0.63	0.63	1.74	0.20
TIME	1	6.60	6.60	18.072	0.00028
source:TIME	1	1.45	1.45	3.98	0.058
Residuals	24	8.77	0.37		

Total shoot mass

```
total.shoots.lm <- lm(log(total.shoots) ~ source * DATE)
anova(total.shoots.lm)
```

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
source	1	0.22	0.22	0.84	0.37
TIME	1	8.83	8.83	34.065	<0.0001
source:TIME	1	0.064	0.064	0.25	0.62
Residuals	24	6.22	0.26		

Leaf mass

```
leaf.mass.lm <- lm(log(leaf.mass) ~ source * DATE)
anova(leaf.mass.lm)
```

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
source	1	0.15	0.15	0.75	0.39
TIME	1	6.87	6.87	35.018	<0.0001
source:TIME	1	0.022	0.022	0.11	0.74
Residuals	24	4.71	0.20		

Total plant mass

```
total.plant.lm <- lm(log(total.plant) ~ source * DATE)
anova(total.plant.lm)
```

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
source	1	0.27	0.27	1.011	0.32
TIME	1	8.56	8.56	32.19	<0.0001
source:TIME	1	0.16	0.16	0.59	0.45
Residuals	24	6.38	0.27		

Fine root mass

fine.root.lm <- lm(log(fine.root.mass) ~ source * DATE)
anova(fine.root.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
source	1	0.41	0.41	0.80	0.38
TIME	1	22.93	22.93	44.93	<0.0001
source:TIME	1	0.85	0.85	1.67	0.21
Residuals	24	12.25	0.51		

Medium root mass

med.root.lm <- lm(log(med.root.mass) ~ source * DATE)
anova(med.root.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
source	1	2.70	2.70	4.94	0.036
TIME	1	3.53	3.53	6.47	0.018
source:TIME	1	1.53	1.53	2.80	0.11
Residuals	24	13.085	0.55		

Large root mass

lrg.root.lm <- lm(log(lrg.root.mass) ~ source * DATE)
anova(lrg.root.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
source	1	0.45	0.45	1.18	0.29
TIME	1	6.40	6.40	16.71	0.00042
source:TIME	1	1.56	1.56	4.063	0.055
Residuals	24	9.19	0.38		

Root:Shoot ratio

rs.ratio.lm <- lm(log(rs.ratio) ~ source * DATE)
anova(rs.ratio.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
source	1	0.11	0.11	1.39	0.25
TIME	1	0.16	0.16	2.085	0.16
source:TIME	1	0.91	0.91	11.68	0.0022
Residuals	24	1.86	0.078		

Root depth

root.depth.lm <- lm(sqrt(root.depth) ~ source * DATE)
anova(root.depth.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
source	1	4.77	4.77	0.34	0.57
TIME	1	81.89	81.89	5.83	0.024
source:TIME	1	0.68	0.68	0.049	0.83
Residuals	24	337.02	14.04		

Root depth:Plant height ratio

depth.height.ratio.lm <- lm(log(depth.height.ratio) ~ source * DATE)
anova(depth.height.ratio.lm

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
source	1	0.26	0.26	1.72	0.20
TIME	1	0.83	0.83	5.53	0.027
source:TIME	1	0.011	0.011	0.071	0.79
Residuals	24	3.62	0.15		

Height

height.lm <- lm(sqrt(height) ~ source * DATE)
anova(height.lm)

Source	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
source	1	102.88	102.88	2.58	0.12
TIME	1	1737.32	1737.32	43.37	<0.0001
source:TIME	1	40.48	40.48	1.011	0.32
Residuals	24	961.37	40.06		