Growth and acclimation responses of dipterocarp seedlings to logging disturbance

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Declaration

This thesis has been composed by myself from the results of my own work, except where stated otherwise, and has not been submitted for any other application for a degree.

Abstract

The growth and acclimation response of wild dipterocarp seedlings to environmental change caused by logging disturbance was examined in lowland dipterocarp forest in Central Kalimantan (Indonesian Borneo). The aim was to identify environmental and physiological limitations to natural regeneration after logging. The microclimate of logged forest was compared with undisturbed forest. Seedling growth and mortality after logging was described at the population level, and the physiological causes of growth limitation and mortality after logging were explored. A system for estimating daily below canopy PPFD (photosynthetic photon flux density) from hemispherical photographs was developed and calibrated against direct measurements of PPFD. Predictions from photographs were repeatable, accurate ($r^2 > 0.95$) and linearly related to measured PPFD over at least the range 5 - 50 % of above canopy daily PPFD. Photographic estimates of the diffuse proportion and above canopy PPFD were independent of canopy cover and representative of measured above canopy values over a range of seasonal conditions, thus supporting the validity of the model.

The most important effect of logging on the seedling microclimate will be the increased exposure of seedling leaves to direct sunlight. Air temperature and the vapour pressure deficit of the air were influenced more by season and site location than by canopy opening. Low wind speed was an important feature which will decouple seedling leaves from ambient conditions. It was hypothesised that low boundary layer conductance and high leaf temperatures during periods of direct sunlight would have important effects on dipterocarp seedling regeneration in logging gaps.

Logging increased patchiness and removed seedlings from disturbed areas where they were most required. Seedling mortality was lower than in undisturbed forest. Wild light hardwood seedlings (*Shorea johorensis*, *S. leprosula*, *S. parvifolia*, *S. ovalis*) reached maximum growth rates at moderate PPFDs (5 - 10 mol m^{-2} day^{-1}), and in disturbed soil growth declined with further increases in PPFD. Canopy opening after conventional logging often exceeds that required for maximum seedling release.

Seedling nutrient status, mycorrhizal infection and the capacity for photosynthetic acclimation were investigated as potential causes of limitation to growth in open sites. Seedlings of *S. leprosula* and *S. parvifolia* were tolerant of low nutrient availability when grown in high light under controlled conditions. Mycorrhizal infection was increased when nutrient availability was low and seedlings were growing fast in high light. Both species exhibited significant architectural and photosynthetic plasticity. *S. johorensis* seedlings were found to be capable of acclimation to extreme post logging conditions, including changes in leaf nutrient partitioning, but the respiratory cost of acclimation to high leaf temperatures and PPFD may contribute to limitation of seedling growth. Water availability and the response of stomata to humidity were not important limitations during the wet season. Variation in the acclimation response was attributed to soil conditions and seedling nutrient status.

It was concluded that the most important limitation to natural regeneration after logging was the direct physical impact on seedling populations and the residual stand at the time of logging. Limitations imposed by microclimate and seedling physiological characteristics will be less important if logging impacts are reduced.

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List of Abbreviations and Symbols

A	net instantaneous rate of photosynthesis (μmol CO_2 m^{-2} s^{-1})
A_{max}	maximum rate of photosynthesis, estimated from the photosynthetic response to PPFD. Expressed on an area (A_{max} area, μmol CO_2 m^{-2} s^{-1}), leaf dry mass (A_{max} mass, nmol CO_2 g^{-1} s^{-1}) or leaf nitrogen (A_{max} nitrogen, μmol CO_2 mol^{-1} s^{-1}) basis
ASEAN	Association of South East Asian Nations
B	a parameter related to shade tolerance (refer to Chapter 7)
C	parameter describing the capacity for phenotypic plasticity
D_a	the vapour pressure deficit of water vapour in the air, expressed as a mole fraction (mmol mol^{-1})
D_s	the vapour pressure deficit of water vapour at the leaf surface, expressed as a mole fraction (mmol mol^{-1})
E	rate of transpiration (mol H_2O m^{-2} s^{-1})
f_d	proportion of total above canopy PPFD that is diffuse
F_v/F_m	ratio of variable to maximum fluorescence
g_s	stomatal conductance to water vapour (mol m^{-2} s^{-i})
HN	high nutrient treatment
HQ	high PPFD treatment
IPNUE	instantaneous photosynthetic nitrogen use effciency, here equivalent to A_{max} nitrogen (μmol CO_2 mol^{-1} s^{-1})
LAR	leaf area ratio (m^2 kg^{-1})
LMR	leaf mass ratio (kg kg^{-1})
LN	low nutrient treatment
LQ	low PPFD treatment
N	nitrogen
N	net assimilation rate (g m^{-2} day^{-1})

P	phosphorus
PPFD	photosynthetic photon flux density (μmol photons $m^{-2} s^{-1}$, or mol photons $m^{-2} day^{-1}$)
$Q_{comp.}$	PPFD compensation, Q at which $A = 0$.
$Q_{sat.}$	PPFD saturation of the photosynthetic response to PPFD, Q required for A to reach 90% of A_{max}
Q	incident irradiance, photosynthetic waveband only (equivalent to PPFD; μmol $m^{-2} s^{-1}$)
Q_a	measured or modelled total above canopy PPFD (daily integrated total, mol $m^{-2} day^{-1}$)
R, r	relative growth rate
R:FR	red : far red ratio; the ratio of quanta in the 10 nm band centred on 660 nm to the 10 nm band centred on 730 nm
R_d	rate of leaf dark respiration, measured in the dark (μmol CO_2 $m^{-2} s^{-1}$)
R_i	radiant intensity for annulus i within the sky hemisphere
r_m	maximum relative growth rate of a species
R_z	radiant intensity at the zenith
SLA	specific leaf area ($m^2 kg^{-1}$)
SMS	(Malaysian) Selective Management System
T_{air}	air temperature (°C)
T_b	direct site factor, an estimate of the proportion of direct above canopy PPFD that is received below the canopy
T_d	diffuse site factor, an estimate of the proportion of diffuse above canopy PPFD that is received below the canopy
T_{leaf}	leaf temperature (°C)
TPTI	Tebang Pilih Tanam Indonesia, Indonesian Selective Cutting and Planting system

T_t	global site factor, an estimate of the proportion of total above canopy PPFD (Q_a) that is received below the canopy
v_i	weighting factor for time step i, for calculation of T_b
w_i	weighting factor for annulus i, for calculation of T_d
z	the zenith angle (radians)
ϕ	apparent quantum efficiency, the intial slope of the photosynthetic response to PPFD (mol CO_2 mol $^{-1}$ incident photons)
θ	convexity (rate of bending) of the curve describing the photosynthetic response to PPFD
τ	atmospheric transmissivity (assumed to be 0.65)

1. Introduction

1.1 *Achieving sustainable forest management*

Concerns have risen in the last decade over the rapid rate of deforestation in tropical countries (Poore *et al.* 1989). Indonesia contains approximately 10% of the world's tropical rain forest, and the rates of deforestation in Indonesia have more than doubled since the 1970s (Barbier *et al.* 1994; Sunderlin and Resosudarmo, 1996; FAO, 1997). During the same period the forest products sector in Indonesia has expanded dramatically, and since the 1980s timber from the lowland dipterocarp forests of Indonesia has dominated the international trade in tropical timber (Barbier *et al.* 1994). The causes of deforestation are complex, but it is tempting to conclude that the expansion of the timber trade is the main cause of deforestation (Sunderlin and Resosudarmo, 1996). It is clear that industrial logging plays at least an important indirect role by opening up previously inaccessible areas which are then converted to other forms of land use, especially agriculture (Burgess, 1993; Barbier *et al.* 1994). However, the exploitation of some forest in Indonesia is inevitable, and the value of sustainable extraction of timber and other products from designated production forests can help prevent their conversion to other forms of use (Burgess, 1993). Current interest is now focused on two areas: defining how to manage natural tropical forest sustainably (Poore *et al.* 1989; Putz and Viana, 1996), and creating the right social and economic conditions for the implementation of sustainable management practices (Barbier *et al.* 1994). This thesis is a contribution to the former. The process of natural tree regeneration after selective logging of lowland dipterocarp rain forest is examined from an ecological standpoint with the aim of identifying constraints and possible improvements to the methods for sustainable management.

1.2 *The Dipterocarpaceae*

The Dipterocarpaceae is a diverse family of approximately 470 tree species which dominates much of the aseasonal moist tropical forest in South East Asia (Ashton, 1982;

Ashton, 1988). Their range extends from the Indian sub-continent through the Malesian forests to the Philippines. Borneo is the centre of diversity, with 287 species in nine genera, 59% of which are endemic (Ashton, 1982; Still, 1996). All dipterocarps have seedlings that can germinate and establish in the shade and they are therefore classified as climax species (Swaine and Whitmore, 1988; Whitmore, 1984; Whitmore, 1996). The distinctively cyclic nature of dipterocarp reproduction has important implications for forest management practices. Dipterocarps are well known for irregular mast fruiting events which occur on average every 3 - 5 years (Ashton, 1989). A short period of unusually low night time temperature during the dry season is thought to be the cue for synchronised flowering of the majority of individuals over large areas (Ashton, Givnish and Appanah, 1988; Appanah, 1993). The fruits of most species are relatively heavy and are wind dispersed over short distances (usually < 100 m). The seeds lack dormancy and germinate immediately, with some species establishing a 'bank' of shade-suppressed seedlings known as advanced regeneration (Whitmore, 1984). Mortality of shade-suppressed seedlings is high and numbers decline over time (Fox, 1972; Whitmore, 1984). Large temporal fluctuations in dipterocarp seedling density are therefore normal, and reported values from different sites vary from 100 to more than 100 000 per hectare (Fox, 1972; Fox, 1973; Liew and Wong, 1973; Still, 1996). Short dispersal distances and a low density of adult trees also contribute to high spatial variability. Usually at least a few seedlings are present, but they sometimes disappear completely before the next fruiting (Appanah and Weinland, 1990; Whitmore, 1984).

The seedlings of some dipterocarp species can persist in the shade for many years, but all require at least a small amount of canopy opening for significant growth (Whitmore, 1984). It is this requirement for 'release', usually in the form of a natural disturbance, that forms the basis of silvicultural systems for the management of timber production from natural dipterocarp forest (Wyatt-Smith, 1963; Whitmore, 1984). Foresters have divided the family according to density of their timber and their seedling light requirements. Within the family there is wide variation from heavy hardwoods with slow growing, shade-tolerant seedlings through to light hardwoods with faster growing, light-demanding seedlings (Newman, Burgess and Whitmore, 1996). The length of time seedlings can survive in the shade is thought to be correlated with light requirements and growth rates upon release, with heavier hardwoods surviving for longer and requiring less light for regeneration (Wyatt-Smith, 1958; Still, 1996). However, there have been few long term comparisons (Still, 1996; Whitmore and Brown, 1996), and the mechanisms behind differential seedling shade tolerance are only just beginning to be understood for other tropical and temperate trees (Kitajima, 1994; Walters and Reich, 1996).

This study was concerned primarily with natural regeneration. The choice of species was therefore determined as the species that were most abundant in the study area. Four species were included in various aspects of this study: *Shorea johorensis* Foxw., *Shorea leprosula* Miq., *Shorea ovalis* (Korth.) Blume ssp. *ovalis* and *Shorea parvifolia* Dyer. All belong to the red meranti timber group and have light demanding, fast growing seedlings and relatively low density timber of high commercial value (Meijer and Wood, 1964; Newman, Burgess and Whitmore, 1996). All are emergent trees (> 45 m in height) of large stature. These species can be considered representative of the light demanding end of the continuum from shade tolerant to light demanding dipterocarps, and are target species for silvicultural treatments (Wyatt-Smith, 1963; Whitmore, 1984). *S. leprosula* and *S. parvifolia* are common throughout Malaysia and Indonesia and are perhaps the best known dipterocarps (Appanah and Weinland, 1993). Seedlings of both species are tolerant of open conditions and are often chosen for planting schemes. *S. johorensis* is less widespread but is also known for strong seedling and sapling growth after canopy opening (Meijer and Wood, 1964). *S. ovalis* is widespread but has a scattered distribution, and is usually found in moist places on low lying ground. *S. ovalis* is also capable of rapid growth but may be slower growing at first (Appanah and Weinland, 1993; Newman, Burgess and Whitmore, 1996).

1.3 Silvicultural systems and sustainable management

The sustainability of forest exploitation is dependent on good silvicultural practices that are well implemented (Appanah and Weinland, 1990). In this study the harvest is considered the most important component of the silvicultural system, as it has by far the biggest impact on the stand (Bertault *et al.*, 1993). Tropical forestry in the past has favoured simple systems for rapid wood production, often with emphasis on artificial regeneration (Hall, 1996). Timber production for profit remains the ultimate goal, but there is now recognition of the need to sustain other forest products and services as well (Panayotou and Ashton, 1992; Barbier *et al.* 1994). In South East Asia the result has been the wider implementation of polycylic systems and an accompanying reliance on natural regeneration (Appanah and Weinland, 1990; Hall, 1996). The task is made easier by the often copious regeneration of dipterocarps and the experience already gained from past efforts to promote natural regeneration (Wyatt-Smith, 1963). However, in depth knowledge remains restricted to a small number of species and is often based on casual field observations or studies under artificial conditions. Meanwhile, the forester is faced with the need to understand the response of complex mixed forest to management interventions (Hall, 1996). Rigorous ecological studies are now required to examine the assumptions of the silvicultural systems that are in use and provide guidance for their improvement (Appanah and Weinland, 1990; Kuusipalo *et al.* 1996; Tuomela *et al.* 1996). Field studies that are conducted in conventionally logged forest are also useful for highlighting areas for improvement in the implementation of the chosen silvicultural system.

Timber production from lowland dipterocarp forest in Indonesia is managed under the Indonesian Selective Cutting and Planting system (Tebang Pilih Tanam Indonesia, TPTI; FAO, 1990; Anonymous, 1993a). This system is heavily dependent on natural regeneration as the source of future harvests. Trees larger than a threshold size (usually 50 cm diameter breast height, dbh) are harvested while at the same time a minimum number of residual trees (diameter > 20 cm dbh) are retained to form the main crop at the next rotation in approximately 35 years time. It is a polycylic system, with only a small proportion of the stand harvested at each cut (around 5 to 15 stems per hectare) and a rotation length that is shorter than the age of the trees (Whitmore, 1984; Matthews, 1989). Harvests beyond the second cut are provided by smaller size classes which are not included in pre- or post-harvest inventories unless the larger residuals are lacking. Future rotations are therefore dependent on natural regeneration which is either present at the time of the first harvest or that will be provided by seeding of the residual trees. Artificial regeneration (planting in lines) is prescribed if the post-harvest inventory indicates a low density of residual and smaller size classes. TPTI is similar to the currently practised Malaysian Selective Management System (SMS) for hill dipterocarp forests and the Philippines Selective Logging System (PSLS) (Appanah and Weinland, 1990). All three can be contrasted with the Malaysian Uniform System, which is a monocyclic system with an absolute requirement for abundant advance regeneration at the time of felling (Wyatt-Smith, 1963; Whitmore, 1984).

1.4 Defining the problem

The selective cutting systems practised in Indonesia and Malaysia have been strongly criticised for their reliance on advanced residuals as the source of the next rotation and of much of the seedling regeneration (Appanah and Weinland, 1990). Implicit in both systems is the assumption that seedling regeneration of desired species will survive the harvesting operations or will be provided after harvesting by fruiting of residual trees (Appanah and Weinland, 1990). Natural fluctuations in seedling density between mast years means that abundant advance regeneration at the time of logging cannot be assumed. Damage is usually heavier than projected and the distribution of residuals (and hence seedlings as well) is likely to be uneven (Appanah and Weinland, 1990; Bertault *et al.*, 1993; Bertault and Sist, 1995; Pinard and Putz, 1996). The capacity of smaller trees to fruit in logged forest has also been questioned (Appanah and Manaf, 1990; Appanah and Manaf, 1994; Thomas and Appanah, 1995). Both TPTI and SMS include artificial regeneration if necessary, but guidelines for line planting are only now being developed and the method is unlikely to be economically viable for recently logged high forest (Appanah and Weinland, 1990; Appanah and Weinland, 1993; Adjers *et al.* 1995). Polycyclic systems in general have also been considered in the past to be inappropriate for dipterocarp forest because they are thought to favour the dominance of less desirable heavy hardwood species (Whitmore, 1984). All of these criticisms highlight the need to consider seriously how natural regeneration can be encouraged as a reliable source of future harvests. Some of the problems represent possible areas for improvement of the silvicultural system itself, while others are more symptomatic of the difficulties of implementing a complex harvesting system during normal everyday practice (lack of expert supervision, excessive damage, little attention paid to seedlings or residuals; Bertault *et al.*, 1993).

There is also a need to develop appropriate techniques for the artificial regeneration of areas where natural regeneration is not possible (Appanah and Weinland, 1990; Adjers *et al.* 1995; Ang and Maruyama, 1995; Korpelainen *et al.* 1995). Large areas of forest in South East Asia have already been logged over, and a significant proportion of these are now degraded as the result of repeated selective logging, burning and shifting cultivation. In Indonesia alone there are 39 million hectares of logged over forest with a remaining tree volume less than 40 m^3 ha^{-1}. This includes 20 million hectares dominated by *Imperata cylindrica* grassland (ITTO, 1990; Adjers *et al.* 1995; Sunderlin and Resosudarmo, 1996) Interest in planting and tending techniques appropriate for the rehabilitation of these areas is now increasing as the amount extracted from natural forest falls. This study concentrates on natural regeneration, but the physiological characteristics of seedlings of commonly planted species are described.

This thesis attempts to identify potential limits to the natural regeneration of desirable timber species. Dipterocarp seedlings are naturally adapted to disturbance. Regeneration after large scale logging disturbance is sometimes abundant, as testified by early successes with the Malaysian Uniform System (Whitmore, 1984). In other cases, regeneration after disturbance is absent or patchily distributed (Bertault and Sist, 1995). After disturbance has occurred it may be difficult to determine why regeneration is lacking. Was advanced regeneration absent at the time of logging, or was it removed by mechanical damage during logging? Are there aspects of the logged forest environment which will limit the growth and survival of dipterocarp seedlings? Are seedlings absent because of a limited ability to adjust (acclimate) to post logging conditions?

1.5 Dipterocarp seedlings: general characteristics and physiological factors potentially limiting to regeneration

Previous research on dipterocarp seedling physiology has concentrated on the influence of light intensity on seedling establishment and growth, often under nursery conditions.

There is now a need to consider the way seedling physiological characteristics interact with all aspects of disturbed environments (Ashton, 1994).

Light

Although canopy opening is necessary for successful regeneration, nursery and shade house studies have shown that dipterocarp seedlings benefit from partial shade during establishment and subsequent growth (Nicholson, 1960; Sasaki and Mori, 1981; Aminuddin, 1986; Ashton, 1995). Dipterocarp seeds do not germinate and establish well on exposed mineral soil in full sunlight (Tomboc and Basada, 1978), and when established seedlings are grown in full sunlight, their growth rates (height or stem diameter) are the same or less than that observed under partial shade (Nicholson, 1960; Sasaki and Mori, 1981). The cause of reduced growth in full sunlight has never been clearly established, and most earlier studies did not distinguish the effects of light from other likely interacting effects, such as pot size and water and nutrient availability. Root to shoot ratios are often higher when seedlings are grown in full sunlight (Sasaki and Mori, 1981; Aminuddin, 1986), suggesting the seedlings are responding to the more extreme environment by partitioning resources to root growth. In two recent studies of the response of wild dipterocarp seedlings to natural gap formation, growth rates were higher in the gaps, but light levels equivalent to 'full sunlight' in a nursery or large logging gap were not encountered (Turner, 1990a; Turner, 1990b; Brown and Whitmore, 1992; Whitmore and Brown, 1996).

Nutrients

Soil nutrient status is often cited as a limiting factor after shaded tree seedlings are released (Barrett and Ash, 1992; Thompson, Kriedemann and Craig, 1992). In two studies of fertilisation of wild dipterocarp seedlings no response was observed (Burslem, 1993; Turner, Brown and Newton, 1993). In both cases seedlings were growing in undisturbed sites or in natural tree fall gaps. Lack of response in these examples may be the result of shade suppression in understorey seedlings, root competition from surrounding trees, or the role of ectomycorrhizal fungi in buffering the nutrient requirements of seedlings in all but the most open, nutrient poor situations. Fertilisation of seedlings grown in the nursery or planted into severely disturbed logged areas where light levels were higher have demonstrated significant increases in growth rate with fertilisation, but the role of mycorrhizal fungi in these examples is unclear (Bruzon, 1982; Sundralingam, 1983; Sundralingam, Hotta and Osumi, 1985; Nussbaum, Anderson and Spencer, 1995). Future studies need to concentrate on the response of seedlings growing naturally in logged areas, and to separate the interacting effects of soil nutrient status, root competition and mycorrhizal fungi on the growth of advance regeneration after logging (Lee, 1994).

Mycorrhizal associations

Mycorrhizal associations formed between a dipterocarp seedling's roots and soil inhabiting fungi will influence seedling nutrient status and the response of seedlings to disturbance (Lee, 1990; Alexander, Ahmad and Lee, 1992). Dipterocarps are predominantly ectomycorrhizal, in contrast to the vesicular-arbuscular mycorrhizas formed by most other tropical trees (Alexander, 1989). The role of ectomycorrhizas in improving nutrient uptake by the host is well known for other groups of plants (Alexander, 1989; Marschner, 1995). Ectomycorrhizas may also improve the tolerance of the host to drought and other adverse soil conditions (Lee, 1994), although under natural conditions the association may not always be beneficial (Alexander, 1989). The importance of seedling mycorrhizal status for the survival and growth of dipterocarp seedlings after logging is poorly understood and the matter of some debate (Smits, 1983; Lee, 1990; Smits, 1992; Lee, 1994). Logging may adversely affect the abundance of mycorrhizal propagules in the soil (Lee, 1990; Alexander, Ahmad and Lee, 1992; Ahmad, 1996), but there are virtually no published studies of wild seedling mycorrhizal status after logging.

Soil water and drought

The role of soil water availability in dipterocarp seedling survival is poorly understood. Drought stress during the annual dry season has been proposed as the most significant cause of mortality for shade suppressed understorey seedlings (Whitmore, 1984; Turner, 1990a; Brown, 1993), and may be an important cause of low seedling densities in secondary forest (Ashton, 1982; Smits, 1983). Low root to shoot ratios and shallow root systems are likely to make shade suppressed seedlings vulnerable to even short term soil surface desiccation (Brown, 1993; Veenendaal *et al.* 1996). Disturbance of a forest canopy does not always lead to lower soil moisture in the gap (Ashton, 1992; Whitmore, 1996), but sudden increases in light intensity and temperature will increase evaporative demand from the seedlings' leaves. Thereafter seedlings may respond to higher light intensity by developing more extensive root systems, as demonstrated for nursery grown seedlings (Sasaki and Mori, 1981; Aminuddin, 1986). Well rooted dipterocarp seedlings planted into open areas have been observed to maintain high transpiration rates, even during the hottest and driest periods of the day (S. Zipperlen, pers. comm;. Hadriyanto, 1995). In summary, short term drought stress may be an important factor in the survival of dipterocarp seedlings, particularly after logging disturbance, but there is little published information on soil water status or seedling water relations in these types of environments.

Acclimation potential

Acclimation is the process by which plants adjust their physiology to a sudden change in conditions (Chazdon *et al.* 1996). For pre-existing dipterocarp seedlings, acclimation is the first stage of regeneration after disturbance. It is during this period that interactions between environmental conditions and phenotype are likely to be most critical. Water stress and poor nutrient status will exacerbate the damaging effects of high light intensity (Demmig-Adams and Adams, 1992; Long, Humphries and Falkowski, 1994). Turner and Newton (1990) recorded low stomatal conductance, high leaf temperatures, and the bleaching of *Shorea macroptera* leaves when nursery grown seedlings were transferred from the shade to full sun. Bleaching of seedling leaves in nurseries is common if shading is removed too quickly (M. Clearwater, personal observation). It is not known how important these effects are for wild seedlings during the initial period after logging, or how individual species might differ in their potential to acclimate to severe canopy disturbance.

1.6 Study site

All field measurements were conducted in or near the Wanariset Sangai research forest (01° 18' S 112° 23' E; altitude approximately 200 m a.s.l.) in Central Kalimantan (Indonesian Borneo, Figs. 1.1 & 1.2). The research forest is a 650 ha block of logged and undisturbed lowland dipterocarp rain forest, established and managed by the Indonesian Ministry of Forestry in co-operation with the United Kingdom Department for International Development (formerly the Overseas Development Administration).

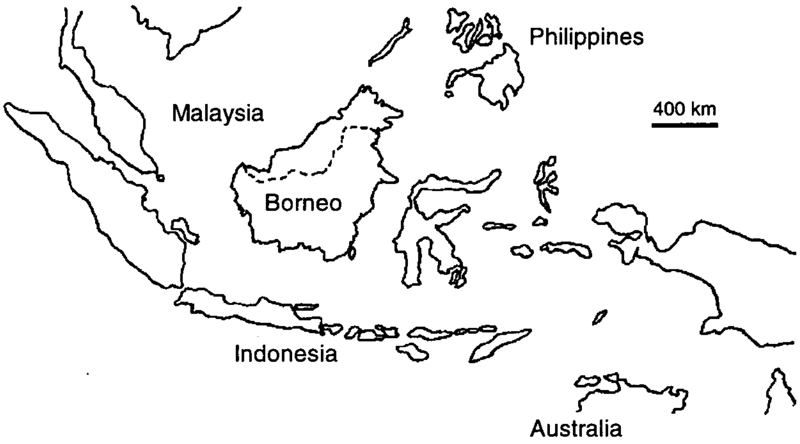


Fig. 1.1 South East Asia, Indonesia and the island of Borneo

Fig. 1.2 Study site location, Wanariset Sangai, Central Kalimantan (Indonesian Borneo)

Forest in the area is noted for its exceptional species diversity and the highly dispersed distribution of individual species (Argent *et al.*, 1997). The average density of trees above 10 cm dbh in 13 one hectare plots is 583 ha^{-1}. In the same area approximately 1300 taxa (> 10 cm dbh) from 52 families have been recorded (Argent *et al.*, 1997). In terms of density the Dipterocarpaceae (14%) and Euphorbiaceae (13%) are co-dominant, followed by a large number of other families at much lower densities (Lauraceae, Myristicaceae and Myrtaceae, next most frequent at 4% each). At least 30 species of Dipterocarpaceae belonging to 6 genera (*Anisoptera*, *Dipterocarpus*, *Hopea*, *Parashorea*, *Shorea*, *Vatica*) have been recorded (Argent *et al.*, 1997). Palms are rare and the density of lianas is low. In terms of stature the Dipterocarpaceae are dominant, with the majority of very large trees (> 1 m dbh) belonging to this family. Average canopy height is approximately 45 m, with emergent trees to 60 m. The forest at Wanariset Sangai is considered representative of lowland dipterocarp forest in Central Kalimantan, and the density and diversity of trees is similar or higher than at other sites in Borneo (Argent *et al.*, 1997). The density of trees > 30 cm in girth in Danum Valley, north-eastern Borneo, was 470 ha^{-1}; the Euphorbiaceae dominated in terms of density but the Dipterocarpaceae were again dominant in terms of stature and basal area (Newbery *et al.* 1992; Newbery *et al.* 1996; Argent *et al.*, 1997).

The climate of the area is perhumid, and is influenced by the wet north-west monsoon from November to April and the dry south-east monsoon from May to October (MacKinnon *et al.* 1996). Annual rainfall is at least 3000 mm and seasonality is low. No month has an average rainfall less than 100 mm, although averages obscure short dry periods which occur most often from July to September. From meteorological data collected in 1994 (see also Chapter 3), average daily temperature was approximately 25 °C, with an average night time minimum of 22 °C and an average day time maximum of 31 °C. Extremes ranged from 20 to 35 °C. Average daily relative humidity was approximately 94 %, usually reaching saturation at night time and declining to an average day time minimum of 68 % (1994 included an exceptionally dry period).

The topography of Wanariset Sangai research forest is highly dissected with many small streams and low hills. Slopes are up to 40 ° and altitude ranges between approximately 100 and 300 m. Soils are mainly Ultisates (USDA classification) or Acrisols (FAO classification) and are similar to those bearing large statured, species rich forests in other parts of Borneo (Proctor, 1994). There is generally a thin brown horizon (ca. 5 cm) with many roots and signs of biological activity. Below this there are increasingly firm yellow horizons. There are few roots below 60 cm. Charcoal has been observed in some areas between depths of 30 and 100 cm, and the underlying rocks are granite (Proctor, 1994).

1.7 Thesis Aim:

To identify environmental and physiological limitations to the regeneration of wild dipterocarp seedlings after logging disturbance.

1.8 Thesis structure, objectives and hypotheses

The approach of this thesis is to describe the post-logging seedling environment and examine the response of seedlings to this environment at the level of the population and individual. Emphasis is placed on the study of wild seedlings under natural conditions. The chapters are related, but each is written as an independent study. Some repetition of basic information occurs as a result.

Chapter 2

Objective: to calibrate a system of hemispherical photography for rapid characterisation of the understorey light environment. The general model for the prediction of light availability from hemispherical photographs was tested over a range of canopy and climatic conditions, and the system was used as a basic tool throughout the study.

Chapter 3

Objective: to describe the effects of logging on the understorey microclimate and identify factors which might limit seedling survival and growth. The hypothesis was that logging would have a severe effect on all aspects of the seedling microclimate, especially air temperature, light, water vapour pressure deficits and soil temperatures.

Chapter 4

The objective was to describe population structure, mortality and growth of wild seedlings in relation to canopy cover, soil disturbance and light availability after logging. The hypothesis was that in open areas seedling density and growth would be reduced, and mortality increased.

Chapter 5

The objective was to examine interactions between light, nutrients and mycorrhizal infection during seedling growth. Wild seedlings were taken from the forest and grown under controlled conditions. The hypothesis was that the growth of seedlings in high light would become limited by nutrient availability.

Chapter 6

The objective was to determine whether the potential for acclimation of a common fast growing species imposed a limitation to seedling survival and growth after logging. It was hypothesised that seedlings would be unable to acclimate beyond the microclimatic conditions associated with only moderate canopy opening.

Chapter 7

Summary and conclusions. Which factors are most likely to limit natural seedling regeneration and the long term sustainability of forest management systems?

2. Calibration of hemispherical photography and estimates of the diffuse component for predicting below canopy light climate in Bornean tropical rain forest

2.1 Introduction

An increase in light intensity is the principle driving force for tree regeneration after forest disturbance. Studies of regeneration invariably require some kind of assessment of canopy cover or light availability. Hemispherical photography is now widely used as a convenient alternative to costly and time consuming direct measurements using light sensors (e.g. Turner, 1990b; Dirzo *et al.* 1992; Oberbauer *et al.* 1993; Zipperlen and Press, 1996). A number of computerised analysis systems have been developed which predict the understorey light climate from photographs (Chazdon and Field, 1987; Becker, Erhart and Smith, 1989; Rich, 1990; Whitmore *et al.* 1993; Ter Steege, 1994; Wagner, 1996). All rely on the original assumption that above canopy light can be divided into direct beam light from the sun and diffuse light from the sky (Evans and Coombe, 1959; Anderson, 1964). The relative transmission through the canopy of each is then modelled separately and the resulting estimated transmitted proportions are expressed as 'site factors' (Anderson, 1964). Attempts have been made to predict absolute transmission from first principles and known extra terrestrial irradiance, but without knowledge of prevailing sky conditions (especially cloudiness) these predictions are unreliable and are not attempted here (Chazdon and Field, 1987; Whitmore *et al.* 1993). It is assumed in this study that researchers will retain estimates as relative site factors, or use direct measurements of above canopy irradiance to convert these to absolute totals of photosynthetic photon flux density (PPFD).

Despite widespread use of the technique, there are relatively few published comparisons of estimates from photographs and direct measurements using light sensors (Chazdon and Field, 1987; Becker, Erhart and Smith, 1989; Yahata,1991; Rich *et al.* 1993; Easter and Spies, 1994). The relationship between observed PPFD and predicted site factors is often poor, especially at low or moderate PPFDs (Whitmore *et al.* 1993; Roxburgh and

Kelly, 1995). Whitmore *et al.* (1993) tested hemispherical photography in Bornean dipterocarp forest (the same forest type as this study) and concluded that both directly measured and predicted measurements were unreliable below approximately 13 mol m^{-2} day^{-1} or 15 % projected open area on the photograph. This threshold is above most of the range of natural variation in below canopy light environments of this forest type. Other studies have reported better results, although variability at very low PPFD is usually high (Becker, Erhart and Smith, 1989; Rich *et al.* 1993; Easter and Spies, 1994; Wagner, 1996). Rich *et al.* (1993) provided the first long term study and demonstrated the importance of including measured variation in above canopy totals. They also addressed the important question of the weighting that should be given to the direct and diffuse site factors when these are combined to predict total transmission and absolute PPFD. This weighting, herein referred to as f_d (the diffuse proportion), was determined indirectly as the value which maximised the correlation between measured PPFD and the combined direct and diffuse site factors (Rich *et al.* 1993). Results from their study were good, but given the variation between studies and the scepticism of some authors, there is clearly a need for further testing of predictions and refinement of methodology.

This study compares predictions from high resolution analysis of hemispherical photographs and direct measurements of below canopy PPFD made in lowland tropical rain forest in Borneo. Measurements were part of a study of seedling regeneration after logging disturbance, and predictions were therefore required for light environments ranging from undisturbed forest to very open areas in logged forest. The aim was to extend the calibration of Rich *et al.* (1993), who demonstrated the utility of predictions over the range of 1 - 10% of above canopy fluxes. It was also considered important to determine whether site factors from photographs were linearly, rather than curvilinearly, related to above canopy fluxes. If the relationship was linear, site factors could still be used to compare sites even if predictions of absolute totals were inaccurate. The studies of Rich *et al.* (1993) and Easter and Spies (1994) were also extended by comparing modelled f_d and above canopy PPFD with the measured values of these parameters. Easter and Spies (1994) found that modelled f_d was not independent of the forest type in which it was determined. If this was the result of a weakness in the underlying model, it will be an important limitation to intersite comparisons based on photographs. The specific aims of this study were:

To calibrate the analysis of hemispherical photographs for prediction of daily PPFD beneath a wide range of canopy conditions, from undisturbed primary forest to large gaps in logged forest.

To compare modelled and direct estimates of above canopy daily PPFD and the mean proportion of total daily PPFD contributed by diffuse light, and examine the importance of day to day and seasonal variation in these parameters.

A unique test of the methodology for analysis of photographs was provided by an unusual period of bright but very diffuse conditions caused by smoke from forest fires (ASEAN, 1995) (Chapter 3).

2.2 Methods

Site description

All light measurements and hemispherical photographs were taken in the Wanariset Sangai research forest (01° 18' S 112° 23' E) in Central Kalimantan (Indonesian Borneo). Forest in the area is classified as lowland evergreen dipterocarp rain forest. The forest is dense and highly diverse; of trees > 10 cm in diameter at breast height there may be 300 to 600 stems and 200 species per hectare (Argent *et al.*, 1997). The mean height of the canopy is approximately 45 m with occasional emergents reaching 60 m. The understorey is sparse and consists of scattered shrubs and lianas. The climate is perhumid with an annual rainfall of approximately 3500 mm. A period of lower rainfall usually occurs during the south east monsoon from May to October (MacKinnon *et al.* 1996). Average light intensities and sunshine hours usually increase during dry periods (Ashton, 1992; Brown, 1993). No month has an average rainfall less than 100 mm, but long term averages conceal short periods of low rainfall which can occur at any time. Widespread wildfires or deliberate burning for agricultural purposes can occur throughout Kalimantan if a dry period is prolonged (Goldammer, Seibert and Schindele, 1996). A regional smoke haze sometimes develops, resulting in lowered air quality and visibility over much of Borneo, Singapore and the Malaysian Peninsular (ASEAN, 1995).

PPFD measurements

Direct measurements of understorey PPFD were made in three forest sites (2 logged areas and one undisturbed area). All three sites were within 2 km of each other and were part of a study of dipterocarp seedling population dynamics and growth after logging. Light measurements were taken 1.2 m above the ground in seedling plots or above individual tagged seedlings, with site locations determined by sampling procedures for the seedling study (Chapter 3). Direct measurements of PPFD were made using quantum sensors (SKP215, Skye Instruments Ltd., Powys, UK or equivalent sensors made at the University of Edinburgh; Sinclair, 1995) connected to a multiplexor, datalogger and data storage module (AM416, CR10 and CSM1, Campbell Scientific

Ltd., Leicestershire, UK). All sensors were calibrated in 1994 and again in 1995 against a single factory calibrated sensor (LI-190SA, LI-COR Instruments, Nebraska, U.S.A.). Sensors were attached to wooden stakes, levelled with a bubble level and connected to the datalogger with cables up to 70 m long. PPFD was recorded every minute; instantaneous values or 15 minute averages were stored and daily averages calculated afterwards.

Total above canopy and diffuse PPFD were recorded using two quantum sensors and a shadow band (Horowitz, 1969) mounted on the roof of a hut in a large clearing. Daily totals measured in the clearing were multiplied by 1.09 to correct for shading from the clearing edges. This correction was taken from a regression of clearing totals vs true above canopy totals measured on a tower, $y = 1.09\ x$, $r^2 = 0.88$). Each 15 minute average of diffuse component measurements was corrected for anisotropic sky conditions and geometric obstruction by the band (Turner and Mujahid, 1983; Turner, 1984). The daily diffuse proportion was calculated after excluding times when the apparatus was shaded (before 8 am and after 4 pm; this correction reduced measured f_d by 0.02). Measurement of diffuse above canopy PPFD at the same time as below canopy total PPFD measurements was only possible in 1995 during measurements in logged forest A. A further 230 days of above canopy diffuse PPFD measurements were obtained in 1996 (April - November) using a custom built automated shadow band.

The three calibration sites were:

Logged forest A. 30 days of PPFD measurements were made during wet season conditions in October 1995 above 19 wild seedlings in an area logged 10 months earlier. The seedlings were distributed over a 50 x 30 m plot which included large logging gaps and an area of closed canopy. Simultaneous measurements of above canopy PPFD and the diffuse proportion were made in the large clearing, located approximately 200 m from the study site.

Logged forest B. 132 days of PPFD measurements were made over a range of seasonal conditions (June 2 - October 17, 1994, with one 3 day gap) above the centre of 20 seedling plots. This calibration period included unusually strong seasonal variation, from heavy rain in June to no rain at all in September, and a heavy regional smoke haze which peaked around October 2 (ASEAN, 1995). Plot locations were determined after first stratifying the 1 ha study area according to canopy cover (Chapter 3), thus ensuring a range of conditions from undisturbed forest to large logging gaps. The large clearing site described above was not established at this time; daily above canopy total PPFD for the period was instead estimated from totals measured at 2 m using a weather station located in the largest logging gap. These totals were corrected for shading by dividing by the daily global site factor (average T_t = 0.57) estimated from a photograph taken at the point of measurement, with the global site factor calculated using a constant f_d of 0.6 for the whole period.

Undisturbed forest. 30 days of PPFD measurements were made during wet season conditions (April 1994) above the centre of 10 seedling plots and 9 other randomly selected sites in undisturbed primary forest. Sensors were up to 60 m apart. Daily above canopy total PPFD was estimated from totals measured using a weather station in a large clearing, as described above.

Hemispherical photography

Methodology follows that of previous authors. Only the main features and important differences will be discussed here. Hemispherical photographs were taken in the same location as all quantum sensors, at the beginning of each period of direct measurements. Photographs were taken only under heavily overcast sky conditions using a Nikkor 8 mm fish-eye lens mounted on a Nikon FM2 body and MF16 data back. Kodachrome 200 ISO colour slide film was chosen for its stability and consistent processing (films are returned to the manufacturer for processing). Exposure levels were set using a photographic spot meter with a 1° field of view (Minolta Spot Meter F). Consistent exposures were obtained by sighting the spot meter through small canopy gaps and taking a reading for the sky only. The best exposure was found to be three f - stops (over exposed) below the spot meter reading, but photographs were usually bracketed one f - stop either side of this. The camera was mounted on a tripod, levelled with a bubble level and the top of the film oriented towards magnetic north. North and South were marked using yellow light emitting diodes attached to a collar around the lens.

Grey scale images were digitised directly from developed film using a slide scanner (Microtek 35T, Microtek, Taiwan) connected to an IBM compatible PC. The final image diameter was 1000 pixels. Images were processed using macros written for a commercial image analysis package (Optimas 5.2, Optimas Co., Washington) to give estimates of diffuse and daily direct site factors. While relatively expensive (ca. £3000, 1995), the commercial package offered a wide range of built in image processing functions, a C-syntax macro language and the flexibility to quickly develop customised image processing routines. Important features and assumptions of the analysis included:

- The analysis framework was positioned on the image after automatic detection of a constant feature of the data back mark (the left hyphen of the 'day of month, hour, minute' setting is always printed in the same place relative to the position of the image). User intervention was possible if the data back marks were not present or the detection failed. This routine reduced processing time and subjectivity in the choice of image position.
- Image rotation, radius, and magnetic declination were set by the user. Corrections were applied for lens distortion.
- A low grade sharpening filter (Sharpen Low, Optimas 5.2) was applied to the image before the user was requested to set the grey scale threshold (distinguish sky from leaf), and its effects were reversed before processing continued. If asked to repeat thresholding of a single image, users set the threshold more consistently after the sharpening filter was applied.
- The diffuse site factor (T_d) represents the proportion of diffuse PPFD incident on a horizontal surface above the canopy that is transmitted to the point of the photograph. The projected image of the hemisphere was divided into 20 concentric annuli representing equal areas of sky and the proportion of pixels classified as sky within each annulus extracted. All pixels were checked for estimating the proportion of sky. The diffuse site factor was then calculated as:

$$T_d = \frac{\sum_{i=1}^{20} p_i w_i}{\sum_{i=1}^{20} w_i} \qquad (2.1)$$

where p_i is the proportion of sky in annulus i and w_i is a weighting for annulus i which includes the cosine correction for a horizontal surface and the Standard Overcast Sky assumption (Anderson 1964; Appendix A for further details).

- The direct site factor (T_b) represents the proportion of total daily direct PPFD incident on a horizontal surface that is transmitted to the point of the photograph. Equations for solar geometry (Iqbal 1983) were used to draw a solar track for any day requested by the user, and the proportion of open pixels sampled at 5 minute time steps along each solar track. With an image 1000 pixels wide the diameter of the solar disk near the zenith was at least 2 pixels. For each time step a square of four pixels was therefore selected and openness between 0 and 1 returned in multiples of 0.25 (a crude penumbral effect). This feature had little effect (compared to sampling a single pixel) on the direct site factor calculated for the whole day, but may be more important for the direct site factor over shorter time intervals. The shape of the solar disk actually varies within the image (radial distortion), and more sophisticated representations would be possible at higher image resolutions. For n time steps the direct site factor was calculated as:

$$T_b = \frac{\sum_{i=1}^{n} p_i v_i}{\sum_{i=1}^{n} v_i} \qquad (2.2)$$

where p_i is the proportion of open pixels at time step i and v_i is a weighting factor for time step i which includes corrections for a horizontal surface and the optical pathlength through the atmosphere (assuming atmospheric transmissivity of 0.65; Gates, 1980; Iqbal, 1983; Appendix A for further details).

- Analysis results and image processing details were sent to a Microsoft Excel spreadsheet.
- Images were saved as TIF (Tagged Image Format) files. The user defined threshold, image radius, and *x y* location of the image origin were saved with the image as tags. These were automatically retrieved (if requested) when the image was opened for further analysis.
- Using the threshold and positioning information stored as image tags, routines were easily developed to sequentionally open batches of images and automatically

calculate site factors. This feature was useful when large numbers of images (e.g. 300) were processed and T_b calculated for many days (e.g. for logged site B, 135 days). T_d based on 20 annuli took 5 seconds to extract, and for a single solar track approximately 1.5 seconds (< 1 second during faster batch analysis).

The same model of below canopy irradiance as adopted by previous authors was used (Rich *et al.* 1993; Easter and Spies, 1994), applied on a daily time scale.

$$T_t = f_d . T_d + (1 - f_d) T_b \qquad (2.3)$$

where T_d, T_b and T_t are the diffuse site factor, direct site factor and global site factor, respectively, and f_d is the proportion of total above canopy PPFD that is diffuse. T_t represents the proportion of total daily above canopy PPFD that passes through the canopy to the site of the photograph:

$$Q = T_t . Q_a \qquad (2.4)$$

where Q is transmitted PPFD and Q_a is total daily above canopy PPFD. f_d can be found by direct measurement, or as the value which gives the maximum correlation between T_t and measured daily fluxes (solved analytically or using iterative non linear regression). If the relationship is linear, the slope of the resulting measured Q vs T_t relationship is an indirect estimate of Q_a and the intercept should be zero. In this study the value of the intercept and comparison between measured and modelled values of f_d and Q_a were used to assess the validity of the model.

2.3 Results

Global site factor vs measured PPFD

Site factors estimated from photographs were good predictors of mean daily PPFD in both logged forest sites. The diffuse and direct site factors were both highly correlated with measured fluxes ($r^2 > 0.84$), but a linear combination of the two (the global site factor) improved the relationship further (Figs. 2.1 & 2.2). Daily PPFD was linearly related to the global site factor over the full range of light environments encountered (T_t 0.01 - 0.52, PPFD 0.3 - 12.5 mol m^{-2} day^{-1}; Fig. 2.1). Modelled values of f_d and the slopes of the PPFD vs T_t relationship were comparable to corresponding measured values of f_d and above canopy PPFD (Tables 2.1 & 2.2). In both cases the intercept of the PPFD vs T_t relationship was not significantly different from zero (Table 2.2).

Daily PPFD totals below the canopy in undisturbed forest were very low, average values over all sites varying between 0.2 and 1.2 mol m^{-2} day^{-1} (Fig. 2.3). Global site factors estimated for the same time period varied between 0.008 and 0.051. Mean daily PPFD was still significantly related to site factors predicted from photographs (Fig. 2.3, $p < 0.0001$), but modelled site factors accounted for less of the variation between sites (max $r^2 = 0.68$) than in either of the logged forests. Variation was greatest for sites with moderate fluxes (0.8 mol m^{-2} day^{-1}) and site factors (0.05; Fig. 2.3). Modelled f_d was higher than the value estimated from measurements in a clearing, but was still a reasonable value given wet season conditions (Table 2.1). Modelled average above canopy PPFD (the regression slope) was lower than the expected value and was considered a poor estimate (Table 2.2).

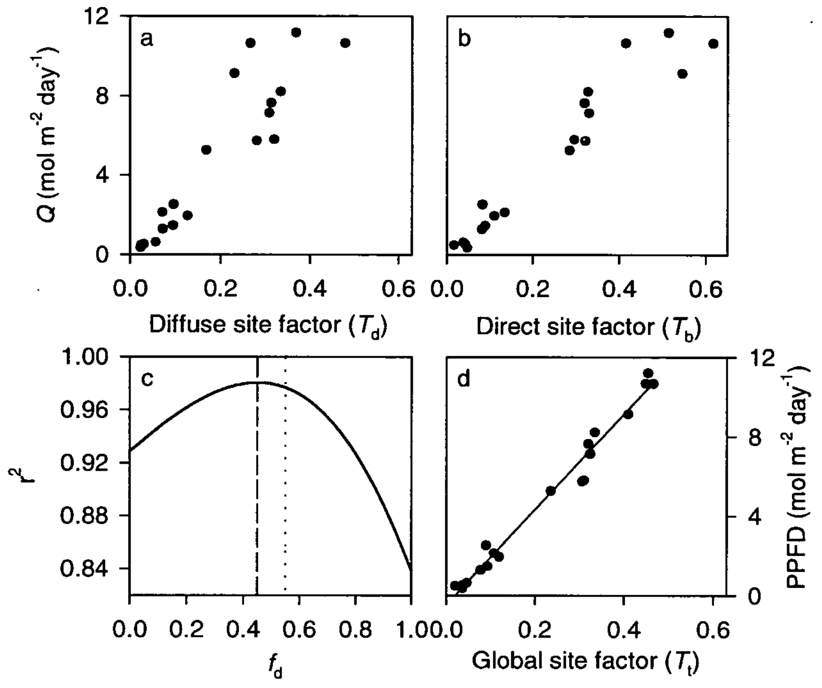


Fig. 2.1. Measured below canopy PPFD (Q), site factors and determination of f_d for logged forest A. Q is shown as a function of the diffuse (a) and direct (b) site factors. Each point represents the mean of the daily PPFD and site factor for the calibration period. Modelled f_d is determined as the value which maximises the r^2 (c) of the Q vs T_t regression (d). The vertical dashed line in (c) indicates the modelled value of f_d, and the dotted line is the measured value (Table 2.1). Modelled Q_a is the slope of the linear regression in (d) (Table 2.2).

Table 2.1. Summary of measured and modelled values of f_d for the three calibration sites, and the number of days on which the values are based (the length of the calibration period). Standard errors are given for the measured values. 'Measured' values for logged B and undisturbed forest (*) were estimated from the regression relationship presented in Figure 2.5.

	f_d		
Site	measured	modelled	days
logged A	0.55 ± 0.03	0.45	30
logged B	0.48 ± 0.02 *	0.60	132
undisturbed	0.38 ± 0.04 *	0.54	30
average	0.47	0.53	-

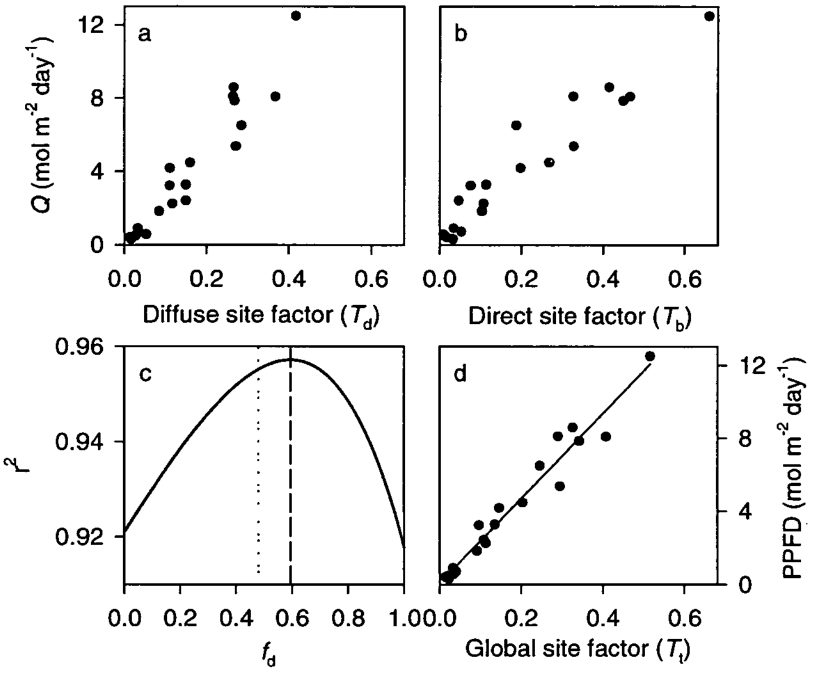


Fig. 2.2. Measured below canopy PPFD (Q), site factors and determination of f_d for logged forest B. For explanation refer to Fig. 2.1.

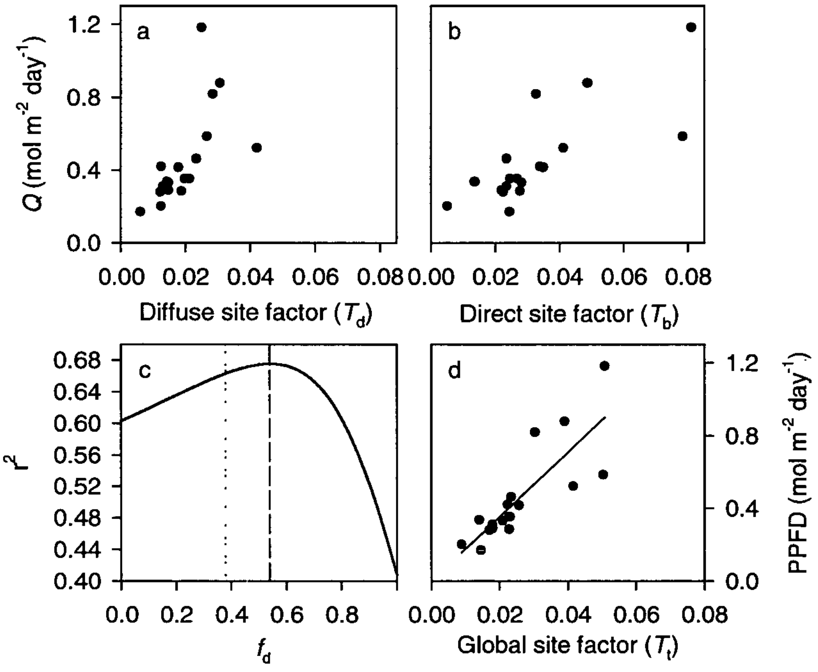


Fig. 2.3. Measured below canopy PPFD (Q), site factors and determination of f_d for the undisturbed forest site. For explanation refer to Fig. 2.1. Note the difference in horizontal scale for T_t between this figure and figs. 2.1 and 2.2.

Table 2.2. Summary of regression results for the Q vs T_t relationships presented in Figures 2.1 - 2.3 and 2.8. Measured Q_a is above canopy PPFD measured in large clearing and corrected for shading. Modelled Q_a and the intercept are the slope and intercept, respectively, of the Q vs T_t regressions. Modelled Q_a is significantly different from zero in all cases ($p < 0.001$). Intercept values are not significantly different from zero ($p > 0.05$). Units for Q_a are mol m^{-2} day^{-1}; n is the number of photo sites.

Site	n	measured Q_a	modelled Q_a	intercept	r^2
logged A	19	23.4 ± 1.1	24.0	-0.50	0.98
logged B	20	23.2 ± 0.7	23.4	0.03	0.96
undisturbed	19	27.1 ± 1.5	17.8	-0.01	0.68
combined	58	-	23.5	-0.16	0.98

Daily variation in f_d and Q_a - measured and modelled values

Model estimates of f_d and Q_a for logged area A were compared to the directly measured values of the same parameters (Tables 2.1 & 2.2). Modelled f_d was lower than the corresponding measured value (Table 2.1), while modelled Q_a corresponded closely with the measured value (Table 2.2). To further test the relationship between measured and modelled parameters, estimates from photographs and below canopy PPFD measurements were made on a daily basis and compared with daily measured values (Fig. 2.4). Daily estimates of f_d were again significantly different from measured values, but the relationship is good considering the potential errors introduced by hourly variation in cloudiness and the uncertainty of predicting the T_b for single days (Fig. 2.4).

Day to day variation in above canopy f_d was directly related to variation in above canopy total PPFD (Fig. 2.5). The proportion of diffuse light was high on cloudy days with low total fluxes. All light was measured as diffuse ($f_d = 1$) on days with a total flux below 8 mol m^{-2}. The regression relationship presented in Figure 2.5 was used to predict the mean above canopy f_d for the logged forest B and undisturbed forest calibration periods (Table 2.2).

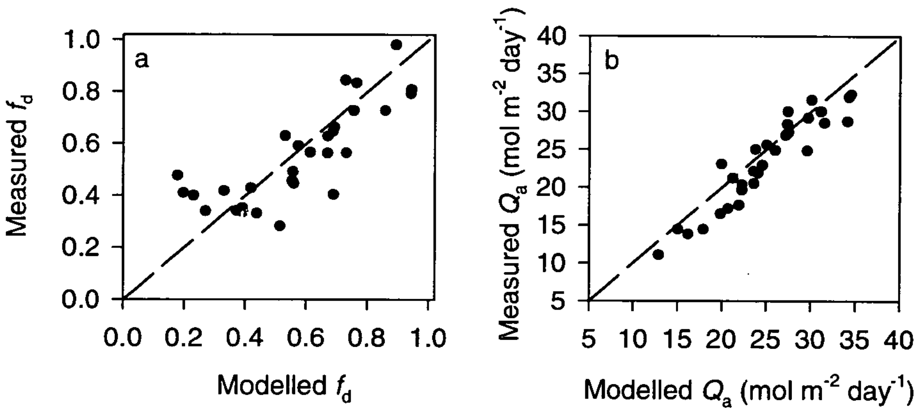


Fig. 2.4. Measured f_d (a) and Q_a (b) as a function of their modelled values, on a daily basis for the 30 day calibration period in logged forest A. Each point is based on below canopy measurements and site factors for a single day. Dashed lines indicate 1:1 correspondence. Linear regressions: (a) $y = 0.69x + 0.16$, $r^2 = 0.65$; (b) $y = 0.99x - 1.14$, $r^2 = 0.88$. In (a) the regression slope and intercept are significantly different from the 1:1 line ($p < 0.05$); in (b) they are not significantly different ($p > 0.05$). There was no significant autocorrelation between days in either case (Durbin Watson statistic, SAS Institute Inc.).

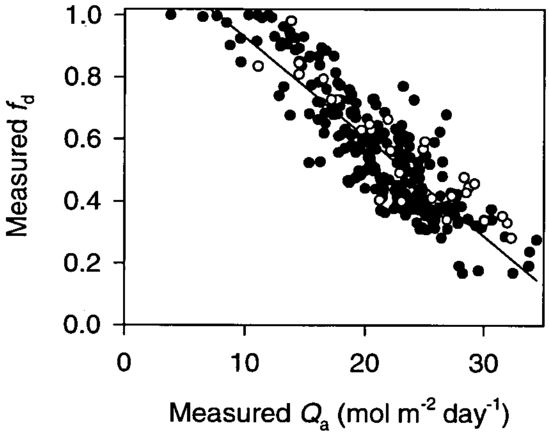


Fig. 2.5. Measured f_d as a function of measured Q_a, for 30 days in 1995 (open circles) and 230 days in 1996 (closed circles). f_d was measured with quantum sensor and shadow band in a large clearing. Linear regression, all data, $y = -0.03x + 1.25$, $r^2 = 0.75$.

Seasonal variation in f_d and Q_a

The 135 day calibration period in logged forest B included a rainy period, a drought, and a period of heavy regional haze when daily maximum fluxes and daily total PPFD were significantly reduced (Fig. 2.6; see also chapter 3). f_d and Q_a were again estimated from site factors and measured fluxes on a daily basis (Fig. 2.6). f_d showed more obvious seasonal changes than Q_a, although day to day variation for both parameters was large.

Modelled f_d was close to 1.0 on cloudy (usually rainy) days with low maximum fluxes, and close to 0.2 on sunny days with long periods of sunshine (Fig. 2.6 b). Modelled f_d was low during the first month of the drought, but increased gradually towards 1.0 at the peak of the regional haze (Fig. 2.6b). Regression analysis using the means for ten days centred on the hazy period clearly demonstrated the shift towards completely diffuse conditions (Fig. 2.7).

Modelled Q_a (the T_t vs PPFD regression slope) did not show clear seasonal changes, except for a decline at the peak of the hazy period. Ten day means of modelled Q_a were closely matched by ten day means of actual above canopy PPFD (Fig. 2.6c, thick line). The 'actual' above canopy PPFD totals were estimated from measurements in a large gap (see methods and Chapter 3), and are independent of the data used for calibration of the hemispherical analysis.

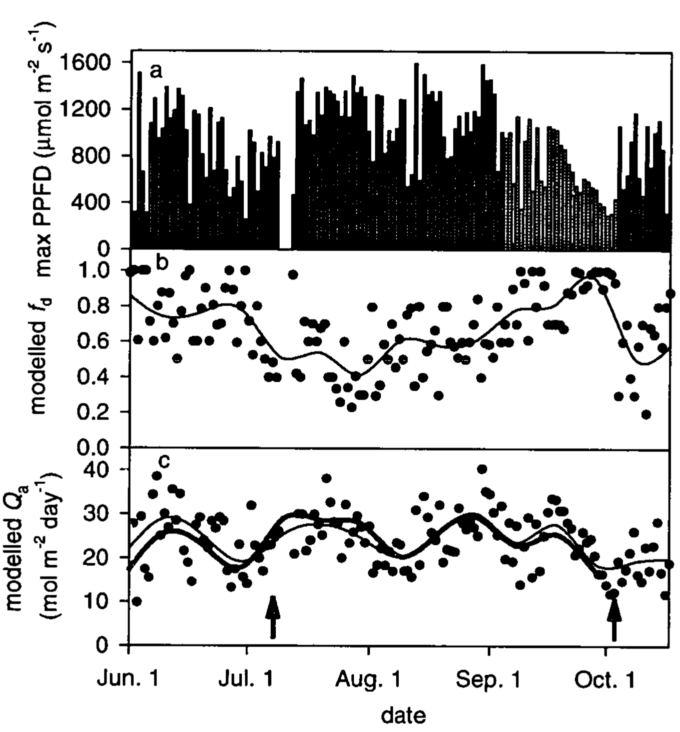


Fig. 2.6. Daily maximum PPFD (a), modelled f_d (b) and modelled Q_a (the regression slope; c) for a 135 day period during 1996 in logged forest B. Maximum PPFD illustrates the effects of the regional haze and is for a single quantum sensor located in a logging gap. f_d and Q_a were modelled on a daily basis; each point is based on below canopy measurements and site factors for a single day. Thin lines are drawn through the ten day averages. The thick line in (c) is for ten day averages of Q_a measured independently in a large gap (see methods). Arrows indicate the end of significant rainfall (left) and the peak of the hazy period (right). Meteorological conditions during this period are described in more detail in Chapter 3.

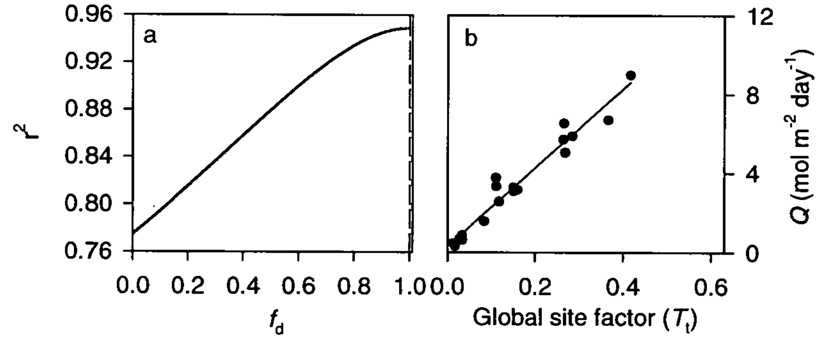


Fig. 2.7. Determination of f_d (a) and the Q vs T_t (b) relationship for logged forest B using ten days centred on the hazy period. During this period modelled f_d is 1 and T_t is equivalent to the diffuse site factor. For explanation refer to Fig. 2.1. Linear regression in (b), $Q = 20.0T_t + 0.3$, $r^2 = 0.95$, intercept not significantly different from zero.

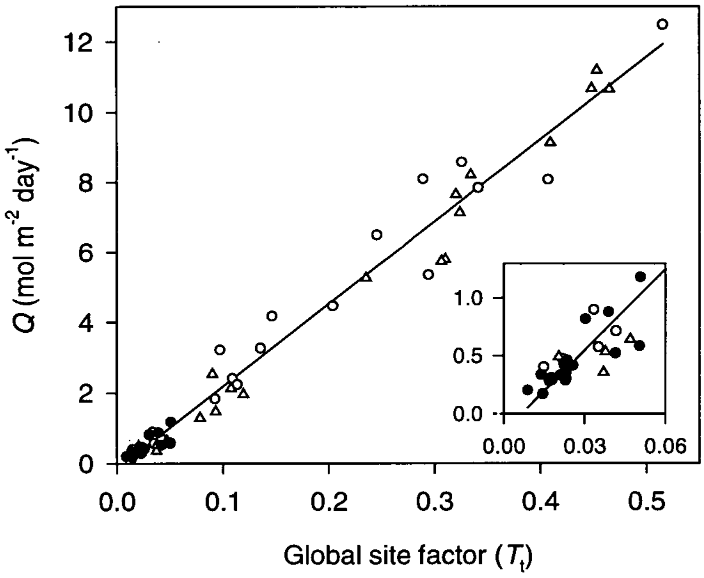


Fig. 2.8. Q vs T_t for the logged forest A (triangles; Fig. 2.1d), logged forest B (open circles; Fig. 2.2d) and undisturbed forest (closed circles; Fig. 2.3d) sites, drawn together on a single set of axes. The inset shows detail of scatter near the origin. Regression results are given in Table 2.2.

Combined results

The PPFD vs T_t relationship did not differ significantly between either of the two logged areas or the undisturbed forest site (Analysis of Covariance, T_t as the covariate, $p > 0.22$). There was no apparent difference between the data sets when all three were plotted together (Fig. 2.8). Variation at low light levels (below $T_t = 0.05$) was large relative to measured fluxes, but was small compared to absolute variation at high light levels (Fig. 2.8). There was no evidence for non linearity at low light levels and the intercept of the overall regression was not significantly different from zero (Table 2.2; $t = -1.5$, $p = 0.13$).

2.4 Discussion

Estimates of the global site factor from hemispherical photographs can provide reliable predictions of the understorey light climate in tropical broadleaf forest. This study demonstrates that with careful methodology, intersite comparisons can be made using photographs over the range of at least 5 - 50% of above canopy daily PPFD. Predictions below 5 % were still useful but errors may be larger than any intersite differences in plant growth response. Predictions above 50% were found to be reliable for individual sites (data not shown), but a full set of calibration data was not available for this range. The relationship was linear over the tested range of light environments (cf. Whitmore *et al.* 1993). The global site factor (T_t) was also a good estimate of the actual proportion of above canopy PPFD that penetrated to the point of the photograph (i.e. modelled Q_a = measured Q_a). T_t can therefore be used as a direct substitute for daily PPFD if no estimates of above canopy PPFD are available. If the researcher has access to quantum sensors, T_t can be converted to PPFD using measurements of total daily PPFD above the canopy or by calibrating the relationship against measurements made below the canopy at a number of photosites. The diffuse proportion and measured or estimated above canopy totals that are used should then be reported (Rich *et al.* 1993).

Agreement between modelled and measured values of f_d and above canopy PPFD indicates that the current model for analysis of hemispherical photographs is valid. Fitted model parameters agreed with real above canopy conditions, and the model was robust over the full range of seasonal variation. Smoke haze during the drought provided a useful test in the form of consistently diffuse conditions without confounding variation in cloudiness, rain or solar geometry (cf. temperate winter conditions when f_d is high and solar elevation is low). Model parameters indicated 100% diffuse conditions and a decline in above canopy totals during the period of maximum regional haze reported in Malaysia and Singapore (ASEAN, 1995). During normal wet or dry season conditions, day to day variation was usually greater than longer term trends. Measured and modelled values of f_d did not always correspond exactly, but variation within ± 0.15 had little effect on estimated PPFD and was unlikely to change the ranking between photo-sites. Exact correspondence cannot be expected when it is considered that the division between direct and diffuse irradiance is a simplification, and that shadow band estimates of f_d are subject to errors which depend on sky condition and the type of sensors used (Drummond, 1964; Turner and Mujahid, 1983; Michalsky *et al.* 1991).

If calibration is not possible and above canopy measurements are not available, an f_d of 0.5 could be assumed when calculating long term averages for below canopy global site factors in Borneo (Table 2.1). Good estimates of f_d will be more important when calculating average T_t for short time periods (one month or less), and for higher latitudes where seasonal variation in sky condition and solar position is greater. Where there is pronounced seasonal variation, inclusion of monthly averages of f_d will substantially improve predictions. Predictions of absolute PPFD will be dependent on the estimate of total above canopy PPFD that is used (Table 2.2), and true values will vary between sites and with season (Rich *et al.* 1993). Mean daily above canopy totals for tropical regions are usually between 20 and 35 mol m^{-2} day^{-1} (Yoda, 1974; Torquebiau, 1988; Oberbauer *et al.* 1989; Raich, 1989; Ashton, 1992; Bellingham *et al.* 1996; Chazdon *et al.* 1996) with maximum daily values of approximately 45 mol m^{-2}. The mean measured value reported here for Wanariset Sangai (24.6 mol m^{-2} day^{-1}) is much lower than the 38 mol m^{-2} day^{-1} reported by Whitmore *et al.* (1993) for Danum valley in north-eastern Borneo. Although Wanariset Sangai is at a higher altitude and has fewer sunshine hours (Chapter 3), the maximum daily fluxes reported for Danum valley were exceptionally high (ca. 53 mols m^{-2}, Fig. 8 in Brown, 1993); equivalent to approximately 70% of the extra-terrestrial total). Fluxes of this magnitude are normally only measured in temperate locations with a clear atmosphere and longer day-lengths, suggesting that the average totals reported for Danum Valley may be over-estimates. Overestimation of PPFD by these authors would also explain why the PPFD value they considered a minimum for reliable predictions (13 mol m^{-2} day^{-1}) was set at such a high level.

The predictions from photographs in this study were as good or better than those reported previously (Rich *et al.* 1993; Easter and Spies, 1994), even though the underlying model and algorithms were the same. The improvement is thought to be largely the effect of the increased resolution of the computerised image capture and sampling procedures. Image diameter in this study was 1000 pixels, compared to the usual 500 achieved with earlier systems. All pixels in the image were included in T_d calculations, and solar tracks were drawn for every day at 5 minute intervals. Pixel width at low resolutions approaches the size of the solar disk and exceeds the size of individual canopy elements and small gaps. Image resolution will be most critical beneath canopies with small leaves, such as temperate coniferous forests. Easter and Spies (1994) achieved high correlations between site factors and measured fluxes in coniferous forest of the pacific north west, but modelled f_d was unusually low and dependent on canopy structure. They concluded that the image processing system was failing to adequately resolve the many small but important gaps in the canopy. This limitation does not invalidate the underlying model (separate direct and diffuse components), as demonstrated here for a coarser broad leaf canopy. Low digitised image resolution also explains why in some studies the site factor vs PPFD relationship becomes non linear under very dense canopies (Whitmore *et al.* 1993; Roxburgh and Kelly, 1995). Small canopy holes are not detected even though a significant proportion of available light is entering through them (Wagner, 1996). With currently available hardware the resolution of the scanning and analysis procedures should be increased to as high a level as possible without exceeding the resolving power of the film and hemispherical lens (van Gardingen, Jeffree, Clearwater and Sharp, 1997).

The two other important features of the system described here were the use of a spot meter to set photograph exposure times and the automated detection of camera data back marks for positioning of the analysis framework. The spot meter had a narrow field of view which was aimed through small canopy holes. If a wider angled meter is used, exposure settings will not be independent of canopy cover. Automated detection of camera data back marks was found to be more reliable than indicator lamps viewed through the lens. Reliable detection of image location on the film is particularly important for photographs taken beneath very dense canopies. Under these conditions the resulting image was a collection of small gaps on otherwise blank film, with no edges visible to indicate the position of the hemisphere.

Inaccuracies in daily predictions presented here are thought to be the result of hourly variation in the diffuse component, as well as errors in the measurement of actual fluxes (Whitmore *et al.* 1993). Temporal variation in sunshine was more important for undisturbed forest sites where contributions from short sunflecks were large relative to daily totals. At one closed forest site a single intense sunfleck lasting less than 15 minutes on one day was found to change the measured monthly average by 5%. The simplistic daily model used in the analysis cannot capture this scale of temporal variability. Some previous systems have combined hourly site factors with monthly averages of hourly totals (Becker, Erhart and Smith, 1989), but even averaging over a month may fail to predict the large contribution of a small number of events (the size distribution of sunfleck contributions will be skewed). Improved predictions for closed sites may therefore require combining site factors with the measured daily time courses of above canopy PPFD for the period in question (Yahata, 1991). This approach would have to include testing the accuracy of camera orientation and solar track positioning, and will be limited by the system's ability to resolve canopy holes.

Conclusions

A high resolution system of analysis for hemispherical photographs was successfully calibrated for use in Bornean broadleaf rain forest and provided reliable linear predictions of daily site factors and PPFD over at least 5 - 50 % of above canopy values.

Provided calibration was conducted over a wide range of light environments, the values of the fitted parameters f_d (the diffuse proportion) and Q_a (above canopy PPFD) were independent of canopy cover and representative of above canopy conditions, thus supporting the validity of the underlying model.

Seasonal variation in f_d and Q_a was significant for Wanariset Sangai but was usually unimportant compared to day to day variation. Uncalibrated long term predictions of below canopy PPFD will be insensitive to the value of f_d, but the magnitude of Q_a will be more important.

Careful attention to methodology has been stressed by previous authors (Rich *et al.* 1993; Whitmore *et al.* 1993) and cannot be over emphasised. High digitised image resolution is considered essential for reliable predictions beneath dense canopies.

3. Effects of logging and drought on the understorey microclimate of lowland dipterocarp rain forest

3.1 Introduction

The severity of forest disturbance influences the pattern of regeneration that occurs afterwards. Part of this effect is exerted through the changes in the forest microclimate, with more severe disturbances creating a wider range of conditions (Bazzaz and Pickett, 1980; Brown, 1993). Selective logging of dipterocarp forest in Indonesia causes disruption to the canopy, understorey and soil. The aim of the silvicultural system used in Indonesia is to create a microclimate suitable for the regeneration of commercial dipterocarp species (Appanah and Weinland, 1990; Anonymous, 1993a). However, logging damage is usually severe and the regeneration of dipterocarp species in open areas is not always good (Appanah and Weinland, 1990; Adjers *et al.* 1995; Tuomela *et al.* 1996; Chapter 4). Part of the problem may be that the microclimate of logged forest is not suitable for the optimal growth of surviving dipterocarp seedlings. A recent study has even suggested that the commonly applied post-harvest silvicultural treatment of liberation thinning may actually prolong succession by maintaining conditions which favour the dominance of secondary species (Kuusipalo *et al.* 1996). There is clearly a need for a more quantitative approach to the problems of managing such complex natural forests. Few studies have examined the microclimate of logged tropical forest and its interaction with seedling growth. More information exists on the microclimate of undisturbed forest (Richards, 1952; Whitmore, 1984) and the effects of smaller scale natural disturbances on forest microclimate (Raich, 1989; Ashton, 1992; Brown, 1993; Chazdon *et al.* 1996). This study compares the microclimate of logged and unlogged forest in Borneo and attempts to determine which aspects of the logged forest environment could potentially be most limiting to dipterocarp seedling regeneration. It was hypothesised that logging would have a severe effect on all aspects of the seedling microclimate, especially air temperature, light, water vapour pressure deficits and soil temperatures.

The lowland dipterocarp forest of Borneo is noted for its low seasonality and high rainfall. There are normally only weak seasonal differences between the wetter north-west monsoon which occurs from November to April and the drier south-east monsoon from May to October (MacKinnon *et al.* 1996). Average monthly rainfall at the study site in Central Kalimantan is lower during the south-east monsoon, but no month has an average rainfall less than 100mm (BMG, 1993; Asdak, 1997). Averages obscure short dry periods (rainfall < 100 mm in a month) which can occur at any time of the year but which are more likely from July to September. Dry periods are unpredictable and do not occur every year, but they have important effects on forest phenology and understorey populations of shade suppressed seedlings (Appanah, 1993; Brown, 1993; MacKinnon *et al.* 1996; Walsh, 1996). Drought is sometimes prolonged and widespread forest fires can occur (Leighton and Wirawan, 1986; Goldammer, Seibert and Schindele, 1996). This study reports changes in forest microclimate during the transition from a relatively wet period in May 1994 until near the end of a prolonged dry period in October 1994. Widespread burning for shifting cultivation and traditional agriculture occurred near the end of this period (Goldammer, Seibert and Schindele, 1996), resulting in a regional haze and poor air quality over much of Borneo, Sumatra, Singapore and the Malaysian Peninsular (ASEAN, 1995).

Continuous measurements of forest microclimate were made over a wide range of climatic conditions using automatic weather stations, and comparable measurements were made above the canopy. The interactions between regional climate, topography and canopy opening in determining seedling microclimate are clearly demonstrated. A disadvantage of this approach was that the automatic weather stations were relatively large and were fixed at a single point. Microclimatic variation within and between logging gaps of different size is therefore not considered. Spatial variation in light availability is reported elsewhere (Chapter 4). The conditions described here can be considered the extremes of variation between closed, undisturbed forest and the centre of a large gap in selectively logged forest. Even more extreme conditions should be expected in completely cleared areas such as log landings and logging roads.

The aims of this study were:

To compare the microclimate of undisturbed and logged forest over a range of seasonal conditions.

To identify which aspects of the logged forest microclimate are most likely to limit dipterocarp seedling growth and survival.

To provide a 'baseline' for future studies of the effects of logging disturbance on seedling regeneration (Chapters 4 - 6) and the dipterocarp forest environment in general.

3.2 Methods

Site description

The study was conducted in the Wanariset Sangai research forest (01° 18’ S 112° 23’ E) in Central Kalimantan (Indonesian Borneo). The area is hilly with altitude ranging between approximately 100 and 300 m above sea level and slopes up to 40 °. Forest in the area is classified as lowland evergreen dipterocarp rain forest. The climate is perhumid with an annual rainfall of approximately 3500 mm (Whitmore, 1984; Asdak, 1997).

Meteorological measurements

Automatic weather stations (CM10/2 tripod, Campbell Scientific Ltd., Leicestershire, UK) were used to take microclimatic measurements at three sites: on a tower above undisturbed forest, beneath the canopy in undisturbed forest, and in a gap in logged forest. Measurements were part of a larger study and the choice of sites was dictated by the location of permanent forest sample plots and logging activities. The three sites were within 2 km of each other, but they differ in elevation and aspect. The above canopy site was located on the windward (south) side of a steep east-west ridge approximately 150 m above the undisturbed site. A 56 m tower was built from tripole masting guyed with wire rope. The tower was built with only minor disturbance to the surrounding forest (2 large branches were cut) and a weather station assembled on top, approximately 10 m above the surrounding canopy. Results suggest that because of its location on the windward side of a prominent ridge, the above canopy station was ‘sampling’ air that was normally higher above the canopy than the weather station itself. The below canopy site in undisturbed forest was located on a lower, flatter (ca. 80 m wide), south facing ridge top approximately 30 m above the valley floor. The below canopy site in logged forest was on a terrace 5 m above the river bed, with the weather station built at the intersection of three skid trails approximately 15 m from the nearest undisturbed canopy. Total annual canopy transmittance of PPFD at the site of each weather station (global site factor, Chapter 2), estimated from hemispherical photographs, was 2.6% for the undisturbed site, 51% for the logged site and 99.9% for the above canopy site.

Microclimatic variables recorded at each site included air temperature, relative humidity, wind speed, wind direction, photosynthetic photon flux density (PPFD) and rainfall. Temperature and humidity were measured using a thermistor and a capacitive relative humidity sensor combined together in a single probe (HMP35AC, Campbell Scientific Ltd., Leicestershire, UK) and housed in a stacked-plate radiation shield. Absolute humidity and the vapour pressure deficit (D_a) were calculated from temperature and relative humidity and expressed on a mole fraction basis, assuming a standard atmospheric pressure of 101.3 kPa (Monteith and Unsworth, 1990). Wind speed and wind direction were measured with a cup anemometer and potentiometer wind vane (A100R and W200P, Vector Instruments, Clwyd, U.K.), PPFD with a quantum sensor (SKP215, Skye Instruments Ltd., Powys, UK) and rainfall with a tipping bucket rain gauge (ARG100, Campbell Scientific Ltd., Leicestershire, UK). All sensors were connected to a data logger and data card storage module (CR10 and CSM1, Campbell Scientific Ltd., Leicestershire, UK) set to record every 20 s and save averages every 15 minutes. The non-linear response of the anemometer at low wind speeds was corrected for using calibration tables provided by the manufacturer. Measurements at wind speeds below 1 m s^{-1} were accurate to approximately ± 0.2 m s^{-1}; when the rotor was stalled the recorded windspeed was 0.09 m s^{-1}. Continuous measurements were made in the logged and below canopy undisturbed site between May 16 and October 2, 1994 (140 days). The above canopy station was not installed until August 1994. Above canopy measurements for 25 days in the dry season of 1994 (August 13 - September 6) and 30 days during a wet period in 1996 (March 16 - April 14) were used for comparison with results from the below canopy sites.

Sunshine hours

Sunshine hours were estimated from measurements of global and diffuse PPFD made in a large clearing in 1996 using a shade band (Chapter 2). Sunshine was defined as periods when the direct normal solar irradiance exceeded a threshold of 120 W m^{-2} (Anonymous, 1995), with PPFD converted to short wave solar radiation using a conversion factor of 0.49 W s μmol^{-1} (Anderson, 1971; McCree, 1972; Jones, 1992). The results were used to define the relationship between sunshine duration and total daily PPFD, and the diurnal distribution of sunshine hours.

Soil surface temperatures

Soil temperatures were measured at a depth of 3 cm at twelve locations in the logged area for 40 days in June and July 1994. Temperature probes were constructed from thermistor beads (100K6AX, Betatherm Thermistors UK Ltd., Fleet, Hampshire, UK) inserted into 100 mm x 5 mm diameter stainless steel tubes and connected via cables to a datalogger (Delta-T Devices Ltd., Burwell, Cambridge, UK) set to record every 5 minutes and save averages every 30 minutes. Probes were inserted at an angle close to horizontal near the centre of 2 x 2 m seedling plots that were part of a separate study of dipterocarp seedling population dynamics (Chapter 4). Air temperature was recorded simultaneously near the datalogger at a height of 50 cm using a fine wire (0.08 mm) copper constantan thermocouple. Measurements were made in 12 seedling plots selected to provide a range of canopy densities from closed, undisturbed forest to sites with no remaining overhead canopy (near the site of the automatic weather station). Mean daily PPFD over the measurement period was estimated from hemispherical photographs taken 1.2 m above the centre of each soil temperature probe (Chapter 2).

3.3 Results

Rainfall was high for the first two months of the study period, but a drought occurred during the final three months (Fig. 3.1). No rain fell during September, and the regional haze caused by burning peaked on October 2, the final day of the study period (ASEAN, 1995). No weather station data was available for the following month.

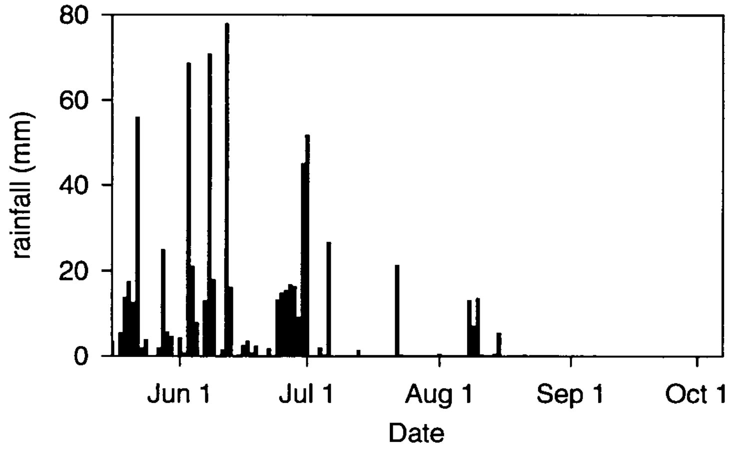


Fig. 3.1. Daily rain fall measured in the open from May 16 to October 2, 1994. Total rain fall for the period was 731 mm; monthly totals: May (the whole month), 265 mm; June, 439 mm; July, 103; August, 40; September, 0 mm.

Logged versus undisturbed forest

Mean daily PPFD was 13.8 mol m^{-2} day^{-1} in the logging gap and 0.6 mol m^{-2} day^{-1} in undisturbed forest. Apart from the large increase in irradiance, logging disturbance had a relatively small effect on other aspects of the below canopy microclimate (Figs. 3.2 & 3.3). Differences in temperature, humidity and wind speed between the logged and unlogged site were small compared to day to day variations within each site (Fig. 3.2). Mean and maximum air temperatures were approximately 2 °C higher in the logging gap, but there were no clear differences in the daytime mean vapour pressure deficits (Figs. 3.2 & 3.3). Wind speeds were usually higher at the undisturbed forest site (Fig. 3.2).

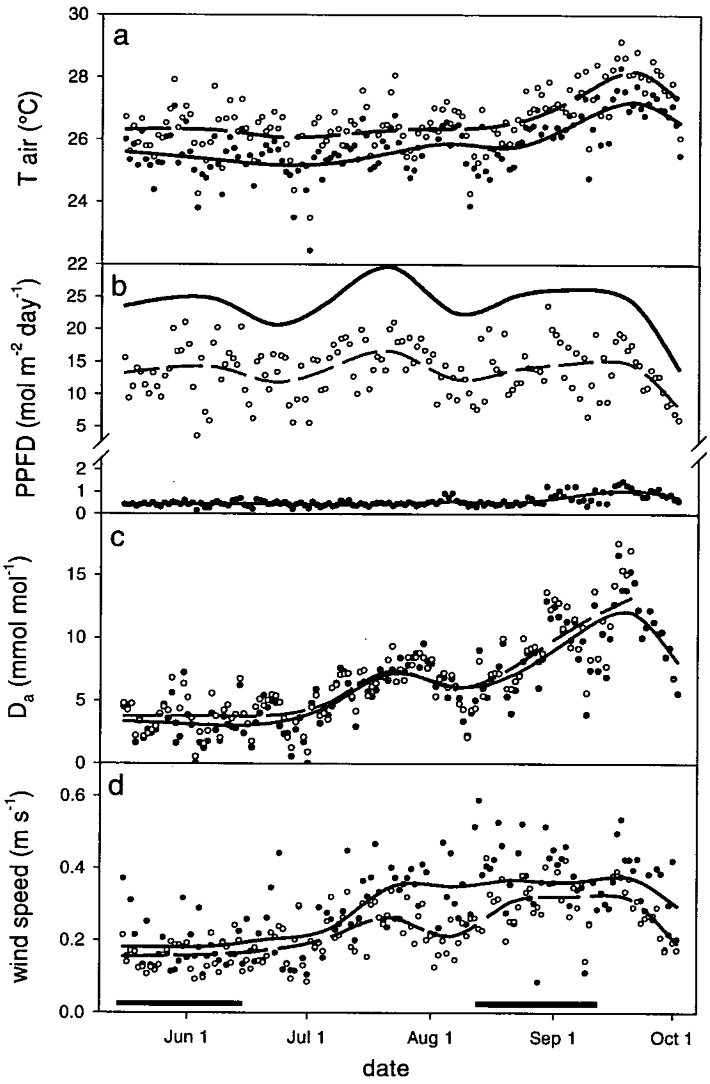


Fig. 3.2. Daily mean air temperature (a), total PPFD (b), mean vapour pressure deficit (c) and mean wind speed (d) in undisturbed forest (closed circles, solid line) and logged forest (open circles, dashed line) from May 16 to October 2, 1994. Values are the means for day time only, 6 am to 6 pm (solar time). The lines are drawn through the 15 day averages for each parameter. The upper solid line in (b) indicates estimated above canopy PPFD (PPFD measured in the gap divided by the daily global site factor from a hemispherical photograph). Note the break and change in scale of the vertical axis for PPFD. Horizontal bars show averaging period for the daily time courses shown in Fig. 3.4.

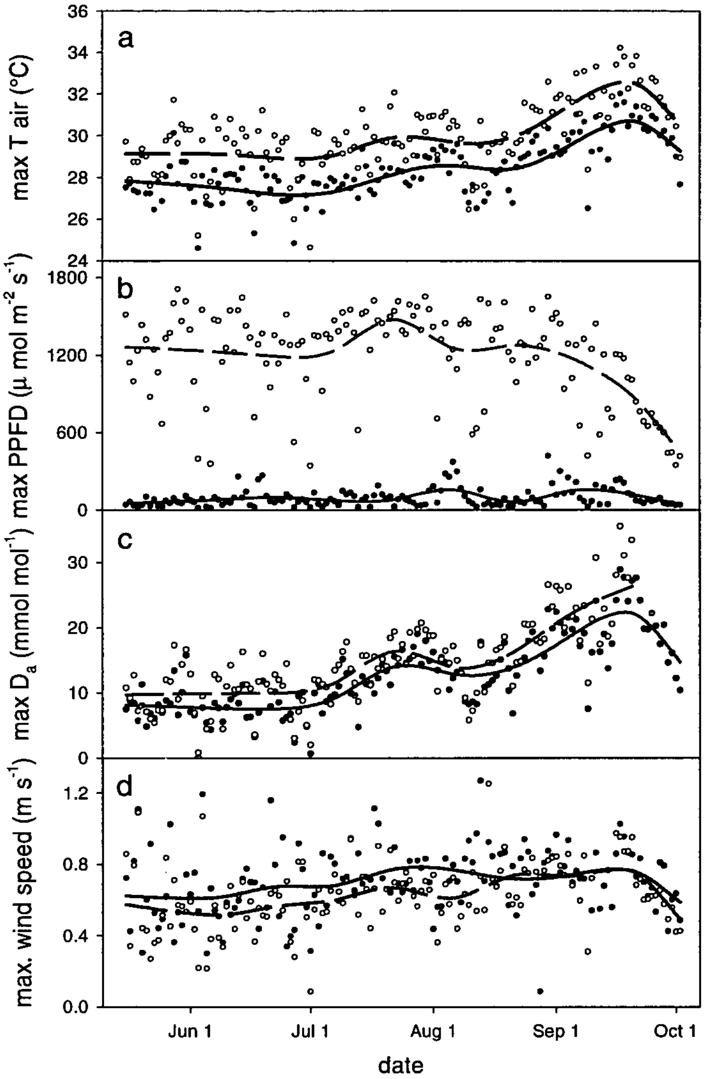


Fig. 3.3. Daytime maxima of air temperature (a), instantaneous PPFD (b), vapour pressure deficit (c) and wind speed (d) in undisturbed forest (closed circles, solid line) and logged forest (open circles, dashed line) from May 16 to October 2, 1994. Values are maxima for day time only, 6 am to 6 pm (solar time). The lines are drawn through the 15 day averages for each parameter.

Daily versus seasonal variation

Day to day variation in PPFD and temperature was usually larger than longer term seasonal trends, except after a prolonged period of low rainfall (Figs. 3.2 & 3.3). Daily variation during the wet season was associated with rainfall events and variation in cloudiness. Above canopy PPFD totals were not available for the 1994 wet period, but comparison with wet season values for 1996 show lower totals during the wet period (Fig. 3.4). Indirect estimates of above canopy PPFD from measurements in the logging gap show an initial increase after the end of rain, but over the whole of the dry period there was no clear increase (Fig. 3.2 b). Average wind speed and the vapour pressure deficit (D_a) increased soon after daily rainfall ended, but average temperature increased more slowly (Fig. 3.2). PPFD, temperature, D_a and windspeed all declined sharply after two months of low rainfall, the decline coinciding with the peak in regional haziness caused by biomass burning (2 October,ASEAN, 1995). Other measurements taken at the site show that the haze cleared and PPFD fluxes returned to normal on day 277, 2 days after the end of measurements reported here (Chapter 2).

Daily time courses

Average daily time courses of microclimatic conditions at 15 minute intervals were calculated for 30 day periods during each of the wet and dry seasons (Fig. 3.4). The raw data were checked visually to ensure the average time courses were representative of conditions occurring on single days. This approach tends to smooth out the extremes and variation over short time periods. Hourly changes in the micro-climate of logged and undisturbed forest could only be interpreted when they were compared to conditions occurring above the canopy. Wind speeds were usually lower in the more sheltered logged site, and air temperature and water vapour concentrations tended to follow levels of irradiance (Fig. 3.4). Although absolute humidity in the logged site was usually higher than in the undisturbed forest, temperature effects were more important and the vapour pressure deficit was higher in the logged site until the mid afternoon (Fig. 3.4). In the undisturbed site wind speeds were higher and conditions were less influenced by irradiance and more closely coupled to those occurring above the canopy (Fig. 3.4). Air temperatures increased more slowly and reached a maximum later, and in the late afternoon average water vapour deficits in the undisturbed site were higher than in the logged site (Fig. 3.4).

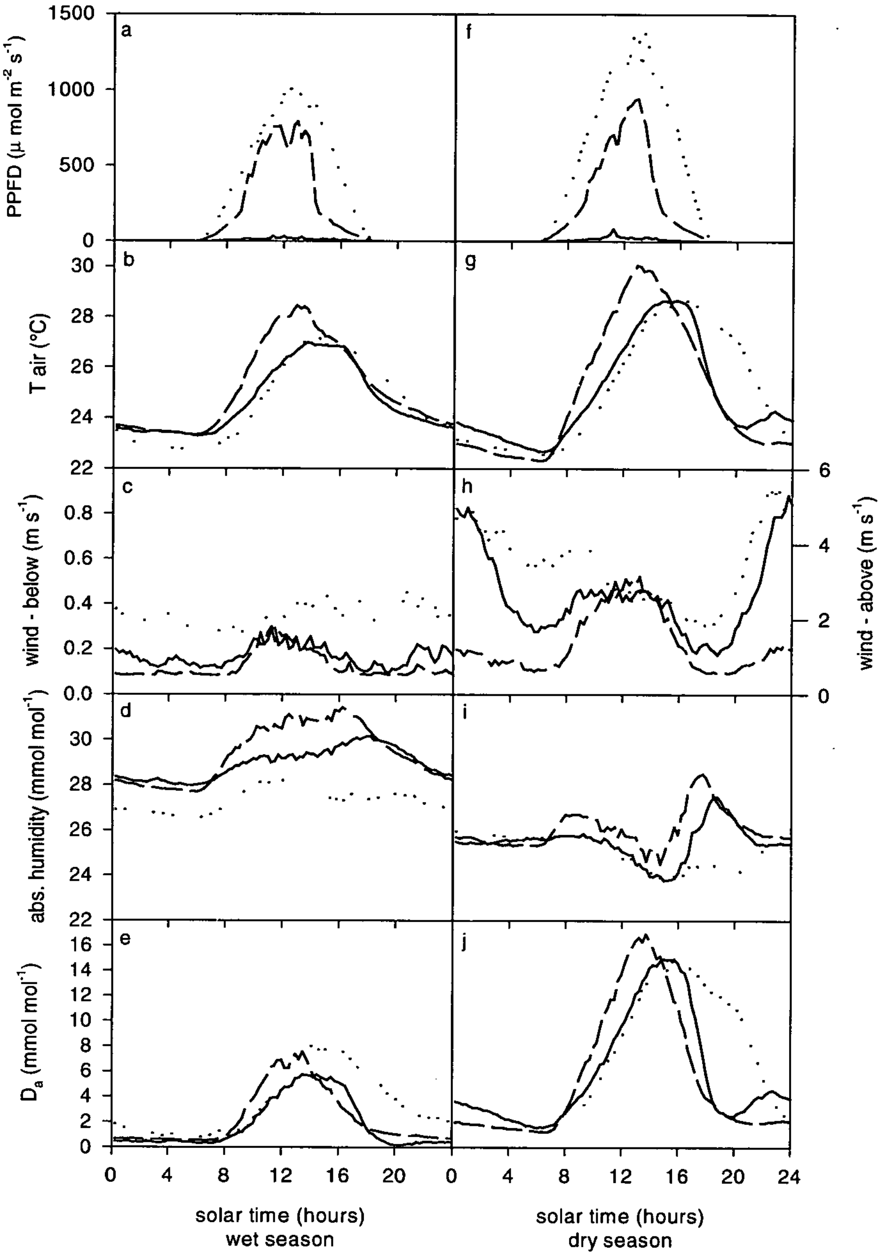


Fig. 3.4. Average daily time courses for PPFD (a,f), air temperature (b,g), wind speed (c,h), absolute humidity (d,i), and vapour pressure deficit (e,j) in undisturbed forest (solid line), logged forest (dashed line) and above the canopy (dotted line). Time courses are shown for 30 days during the wet (a - e) and dry (f - j) seasons. Above canopy means for wind speed are plotted on a different scale to below canopy means, and the scale for absolute humidity is exaggerated compared to that for D_a. Below canopy wet season means are for May 16 - June 14, 1994 (30 days); dry season means are for August 13 - September 11, 1994 (30 days). Above canopy wet season means are for March 16 - April 14, 1996 (30 days); dry season means are for August 13 - September 6, 1994 (25 days). Note that wet season above canopy means are for a different year.

Daily time courses were most consistent during the dry season when there were no rain storm events. The diurnal range of conditions and the differences between undisturbed and logged forest were also greater than in the wet season (Fig. 3.4). Air movement in the logged area during the dry season appeared to be driven by radiation inputs and local heating; wind speed was maximal during the day (Fig. 3.4). Wind speed in the undisturbed area also reached a maximum during the day, but during the night the wind speed peaked a second time at twice the daytime level (Fig. 3.4). Nocturnal air movements were caused by changes above the canopy, where wind speeds consistently increased suddenly to an average maximum of 6 m s^{-1} at approximately 8 p.m. each evening, then declined gradually throughout the night and the following day (Fig. 3.4). Rapid changes in air temperature and absolute humidity accompanied the changes in windspeed (Figs. 3.4 & 3.5). Below canopy humidity was higher and temperatures lower during stable periods of low windspeed (sunrise and sunset). When wind speed increased suddenly in the evening, above canopy temperature decreased and humidity increased (Figs. 3.4 & 3.5), while below the canopy the opposite changes occurred (Fig. 3.4).

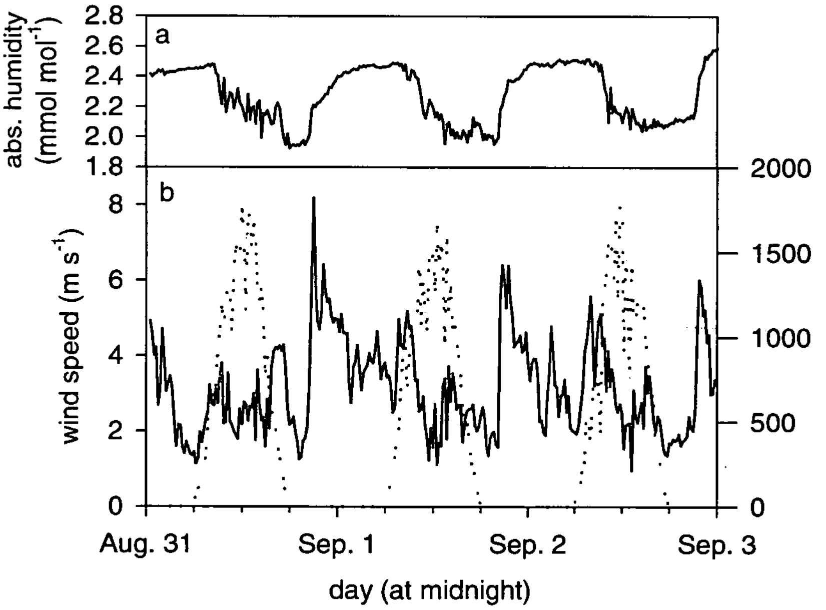


Fig. 3.5. A sample of above canopy absolute humidity (a) wind speed (b, solid line) and PPFD (b, dotted line) for three days during the dry season, 1994. This period was chosen to illustrate the coincident sudden rise in absolute humidity and windspeed between sunset and midnight. Based on 15 minute averages.

Above canopy wind directions illustrate the differences in stability between the wet and dry seasons (Fig. 3.6). During the wet season (data for 1996) wind directions were variable but were predominantly from the north. During the dry season the wind was consistently from the south or south east, with little variation except during the mid to late afternoon (Fig. 3.6).

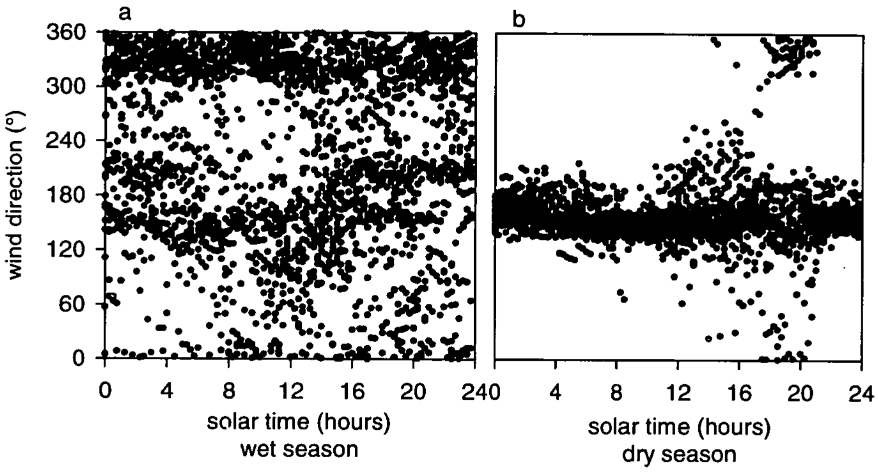


Fig. 3.6. Above canopy wind directions for all 15 minute intervals over 30 and 25 day periods during the wet (a) and dry (b) season, respectively, plotted as a function of solar time. See Fig. 3.4 legend for dates of measurement. Times when wind speed < 0.6 ms^{-1} (the threshold for the windvane) have been excluded.

Variation in cloudiness and sunshine hours

Total daily PPFD was linearly related to the number of sunshine hours and the relative contribution of the direct component (Fig. 3.7a; see also chapter 2). On days with heavy cloud cover, no sunshine and often high rainfall, total PPFD in a large clearing was approximately 10 mol m^{-2} day^{-1} (Fig. 3.7a). Daily PPFD was at least doubled on days with more than 6 hours of sunshine. At Wanariset Sangai cloudy mornings are common. Over an eight month period of mostly high rainfall, sunshine occurred more frequently around solar noon and the early afternoon (Fig. 3.7 b).

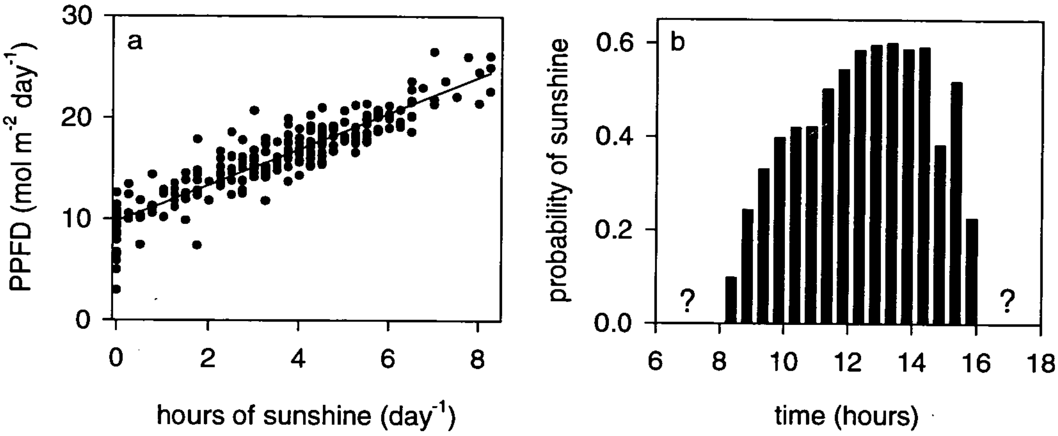


Fig. 3.7. Daily total PPFD as a function of estimated hours of sunshine (a) and the diurnal distribution of sunshine (b). Sunshine was estimated from measurements of diffuse and global PPFD in a large clearing over a 231 day period in 1996 (see methods for details). The sensors were shaded before 8 am and after 4 pm. Equation for least squares regression shown in (a): PPFD = 1.8 sunshine hours + 9.8, $r^2 = 0.82$. This figure can be directly compared with Figs. 8 & 13, Brown 1993, for north eastern Borneo.

Soil temperatures

Soil temperature in undisturbed and disturbed forest followed a similar diurnal time course to air temperature (Fig. 3.8), but the range of variation in soil temperature was strongly dependent on canopy cover and season (Fig. 3.9). Soil temperature below closed or partially open canopy varied less than 2 °C between the nocturnal minimum and the early afternoon maximum. With increasing openness the average temperature and the range of variation increased (Fig. 3.9). Temperature fluctuations were larger in the dry season and were closely related to the amount of ground cover (living or dead plant material) near the ground. Over wet and dry periods the average daily maximum soil temperature recorded for a 2 x 2 m seedling plot containing seedlings and receiving 12 mol m^{-2} day^{-1} PPFD was 31.5 °C, and the highest recorded temperature was 35.2 °C.

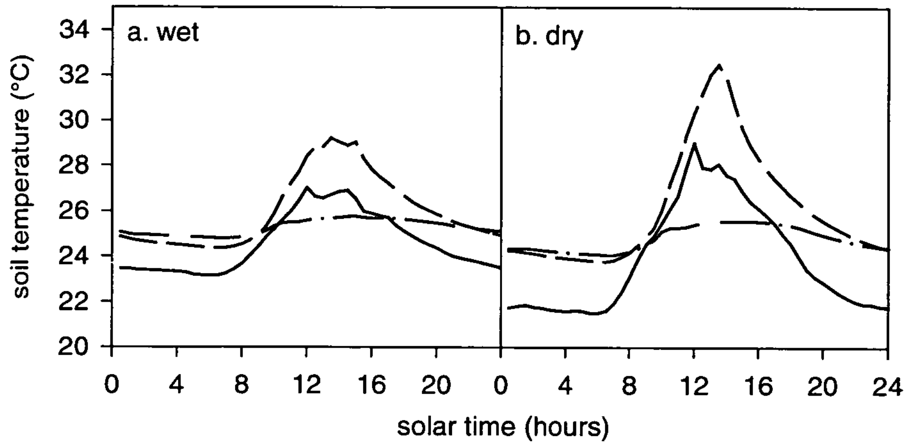


Fig. 3.8. Average daily time courses for soil surface temperature beneath closed canopy (dot dash line) and open canopy (dashed line) in the logged area during a wet (a) and dry (b) period. Air temperature in the logging gap at a height of 0.5 m is shown for comparison (solid line). The wet period was June 25 - July 4, 1994, and the dry period July 23 - August 4, 1994. Average daily PPFD above the undisturbed and open sites were 1.2 mol m^{-2} day^{-1} and 12.0 mol m^{-2} day^{-1}, respectively.

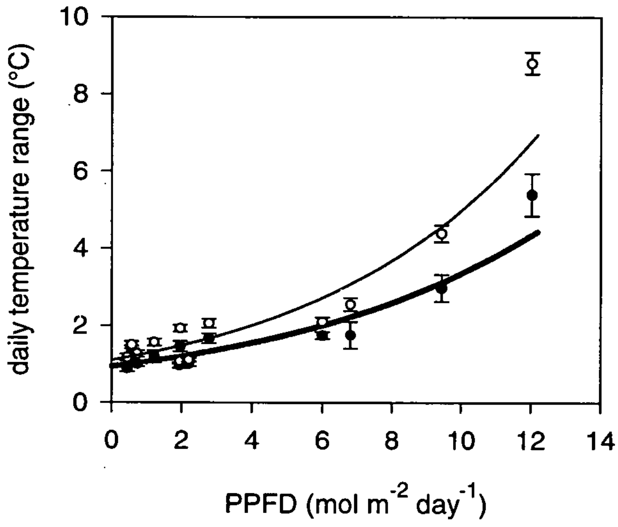


Fig. 3.9. Daily ranges of soil surface temperature variation in the logged area as a function of average daily PPFD incident above the point of measurement. The average ranges are shown for 10 days during a wet period (closed circles, thick line) and 10 days during a dry period (open circles, thin line) period. See Fig. 3.8 legend for dates of measurement. Error bars = ± 1SE.

3.4 Discussion

Effects of logging

The most obvious feature of the post logging environment is the increase in light intensity and accompanying rise in midday air temperatures. Dipterocarp seedlings in large gaps are exposed to long periods of bright sunshine around the middle of the day. It is well known that seedling growth rates are increased by moderate increases in light intensity (e.g. Nicholson, 1960; Sasaki and Mori, 1981; Whitmore and Brown, 1996; Chapter 4), but direct sunlight can saturate the photosynthetic apparatus and is probably in excess of requirements for maximum growth. The final impact of prolonged exposure on any regenerating seedlings is partly determined by other aspects of the physical environment determine. Wind speed in particular determines boundary layer thickness and the degree of coupling between seedling leaves and the bulk air (Jarvis and McNaughton, 1986; Grace, Fasehun and Dixon, 1980; Meinzer *et al.* 1995). An open canopy should lead to increased air movements, but in this study the undisturbed site was elevated and more exposed to prevailing above canopy winds, while the logged site was more sheltered. In both sites wind speeds were low and often below the stalling speed of the anemometers (ca. 0.2 m s^{-1}). Measurements 2 m above the ground and away from obstructing vegetation will also over estimate the true values closer to sites of regeneration (Meinzer *et al.* 1995). When wind speeds are very low, leaves can become strongly decoupled and transpirational cooling is reduced (Meinzer *et al.* 1993; Meinzer *et al.* 1995). Low wind speed may therefore be an important general feature of the seedling environment in these forests.

Low boundary layer conductance and low D_a during periods of direct sunlight will lead to high leaf temperatures and increase the probability of photoinhibitory damage to the leaves of seedlings in logging gaps (Long, Humphries and Falkowski, 1994; Valladares and Pearcy, 1997). Humidification of the boundary layer will decrease evaporation, while elevated leaf temperatures will have the opposing effect of increasing the driving force for evaporation. If dipterocarp seedlings are sensitive to high vapour pressure gradients the net effect may be stomatal closure and a further increase in resistance to evaporation and carbon gain (Chapter 6). Average wind speeds increase during the dry season, but lower soil moisture content and higher vapour pressure deficits are likely to induce increased stomatal limitation of gas exchange (Meinzer *et al.* 1995). While it is difficult to predict the true balance under any set of conditions, it can be hypothesised that tolerance of prolonged periods of simultaneously high irradiance and high leaf temperature will be an important determinant of a dipterocarp species' ability to regenerate well after logging disturbance (Chapter 6). Any consideration of dipterocarp seedling behaviour, especially those based on measurements of single leaf gas exchange in a stirred cuvette, should account for the effects of low wind speed before results are extrapolated to the whole plant (Leuning, 1989; McDermitt, 1990; Meinzer *et al.* 1993; Meinzer *et al.* 1995).

The other effects of logging on the seedling microclimate were correlated with the increase in intensity and duration of exposure to full sun. Site location and higher wind speeds in the undisturbed site reduced the size of differences and make direct comparison more difficult. However, air temperatures and vapour pressure deficits in the logging gap were not extreme and are considered less important than the potential effects of direct sunlight and low wind speed on leaf temperature and boundary layer conditions. Increases in air temperature were the main cause of increased vapour pressure deficit in the logged area. During the wet season water was abundant and absolute humidity actually increased during the day, especially in the logging gap where rates of evaporation were likely to be higher. The small day time rise in D_a was therefore entirely the effect of increased air temperature (Fig. 3.4 e). During the dry season air temperature was higher and ambient humidity tended to decline during the day, leading to a much larger diurnal increase in D_a. Significant stomatal closure can be expected above a D_a of 15 mmol mol^{-1} if wind speeds are moderate or high and leaves are well coupled to ambient conditions (Chapter 6).

Maximum soil surface temperature and the range of variation in soil temperature were directly correlated with spatial variation in irradiance within the logged area (Majid and Jusoff, 1987). Similar relationships have been found between gap size and soil temperatures in single tree fall gaps (Kennedy, 1991; Ashton, 1992; Whitmore, 1996).

While canopy cover was important, when a site was exposed to direct sunlight the amount of cover near the soil surface also had a strong influence on soil temperatures (Kennedy, 1991). Scraping and denuding of the soil surface tends to be correlated with reductions in canopy cover, and the result was an exponential rise in daily temperature variation with increased canopy opening (Fig. 3.9). High soil surface temperatures may be an important limitation to seedling colonisation of denuded areas. Apart from direct effects on seedling roots, high temperatures may also reduce the abundance of mycorrhizal inocula in disturbed soil (Alexander, Ahmad and Lee, 1992; Ahmad, 1996), further reducing seedling nutrient status and growth potential. Mulching of bare sites with bark or leaf litter will reduce soil temperatures and has been shown to enhance pioneer seedling establishment (Pinard, Howlett and Davidson, 1996). However, Nussbaum *et al.* (1995) planted seedlings into bare soil and found that mulching had little effect on dipterocarp seedling growth when compared to fertilisation or the addition of forest top soil. Their results suggest that nutrient availability or the abundance of mycorrhizal inocula in exposed soil will remain as limitations even after soil temperatures are reduced (Nussbaum and Hoe, 1996).

The microclimate of the logging gap examined in this study did not differ strongly from conditions reported by Ashton (1992) and Brown (1993) for natural or simulated natural tree fall gaps in Sri Lanka and Sabah, respectively. These studies give a better indication of the effects of gap size on microclimate and spatial variation in conditions within single gaps. While measures of gap size and openness differ, the logging gap examined here is at least as large as the largest gaps examined by these authors. Air temperatures and daily PPFD in the logging gap examined here were actually lower than those reported for the smaller gaps in Sabah, also on the island of Borneo (Brown, 1993). Comparison of the two studies suggest that the present site in Kalimantan receives fewer sunshine hours (is cloudier) and that sunshine is more likely in the early afternoon rather than in the morning (cf. Fig. 3.7, this study, with Figs. 8 & 13, Brown, 1993). Higher daily PPFDs should therefore be expected in Sabah, but the maximum fluxes reported by Brown (1993) are exceptionally high, suggesting they may be over-estimates (Chapter 2). Overall, comparison with these studies suggests that large gap microclimate is strongly dependent on regional climatic conditions and gap location relative to topographic features. The most consistent differences between logging gaps, natural gaps, and undisturbed forest will therefore be the higher probability of direct sunshine and soil disturbance near the centre of logging gaps, rather than more minor differences in temperature and humidity.

Seasonal changes in forest microclimate

The most important features of the seasonal dry period were the reduced rainfall and increased temperatures, vapour pressure deficits and wind speed. Although reductions in cloudiness were expected, above canopy irradiance did not clearly increase, possibly because of the opposing effect of increased atmospheric haze. Increased midday temperatures and vapour pressure deficits may therefore be mostly the result of reduced evaporative cooling. Conditions during the dry period were also more stable and the average daily time course was more strongly influenced by meso-scale climatic events. Wind speed began to increase at sunrise and absolute humidity increased slightly in the logging gap, presumably as the result of stomatal opening and evaporation from surrounding vegetation (Fig. 3.4). Absolute humidity in all sites then declined until mid afternoon as temperatures and wind speed increased further. The decrease in absolute humidity is thought to represent increased entrainment of dry air from higher altitudes as the height of the convective boundary layer increases during the day (Stull, 1988). In the late afternoon temperatures and windspeed declined rapidly and absolute humidity below the canopy increased (Fig. 3.4), presumably as a new boundary layer formed and entrainment of drier above canopy air ceased.

Depending on its timing relative to canopy opening, a dry period may have a severe impact on dipterocarp seedling regeneration after disturbance (Brown, 1993). Changes in absolute humidity during the dry season were small, but combined with temperature increases they resulted in midday vapour pressure deficits which were at least twice the maximum values observed during normal wet season conditions (Richards, 1952). Evaporative demand in logging gaps will be further increased by high leaf temperatures and increased wind speed (all other things being equal). Logging during a dry period can cause high mortality of newly exposed dipterocarp seedlings (Whitmore, 1984), but in this study logging occurred six months earlier and exposed seedlings were already

1 m high and well established (Chapter 4). Wilting and death of shade suppressed seedlings was observed at the undisturbed site. Shade suppressed tropical tree seedlings have low root mass ratios and may be more vulnerable to low soil moisture and high vapour pressure deficits than seedlings growing in gaps (Veenendaal *et al.* 1996).

Regional haze caused by biomass burning during the drought had a strong influence on microclimate within the forest. At the peak of the hazy period, daily PPFD in the open was halved and the proportion that was direct sunlight declined to zero (Fig. 3.2; Chapter 2). Daytime temperature, vapour pressure deficits and wind speed all declined to wet season levels, even though rainfall had not occurred (Fig. 3.2). High altitude haze almost certainly reduced direct heating of the forest, and therefore also reduced convective turbulence and entrainment of drier above canopy air. Ironically, dry season burning reduced the severity of dry season effects in both undisturbed and logged forest.

Nocturnal wind - a sea breeze front?

High nocturnal wind speeds were an unexpected but consistent feature of both the above canopy and undisturbed sites during the dry season (Fig. 3.4). Both of these sites are south facing and elevated compared to the logged site. Wind speed was usually minimal at sunset, followed by a sudden increase in wind from a south-south easterly direction between 2 and 4 hours later (Fig. 3.5). A sharp increase in absolute humidity and decline in temperature were usually coincident with the increase in wind speed above the canopy. The below canopy site was already cooler and the increase in wind speed brought a sudden decrease in humidity and increase in temperature, presumably as the trunk space was flushed with warmer, drier air from above the canopy (Fig. 3.4).

It is proposed that this sudden nocturnal change represents the arrival of a 'sea breeze front' of cool, moist air which has travelled from the coast some 250 km to the south (Stull, 1988). Most studies of sea breezes are for mid latitudes where inland penetration is usually limited to less than 100 km (Garratt and Physick, 1985). Sea breeze activity at lower latitudes is thought to be possible up to at least 280 km inland (Garratt and Physick, 1985; Lohar, Pal and Chakravarty, 1994). Conditions which favour deeper penetration include stronger day time heating, a synoptic background flow in the same direction as the sea breeze and the lack of obstacles such as mountains which will obstruct flow (Stull, 1988). All of these conditions are met in Kalimantan during the dry season: insolation is high, the monsoon winds are from the south east and land to the south of the study site is dominated by flat alluvial plains. The putative sea breeze appears to persist until at least the next morning. Conditions suitable for sea breeze activity may only occur for a small proportion of each year, and without longer term records it is difficult to speculate how it might influence dry season conditions below the canopy. Richards (1952) discussed influence of sea breezes on coastal tropical forest formations. This study suggests that a deep-penetrating sea breeze front may have a significant effect on forest microclimate over large areas of Kalimantan.

Conclusions

Canopy opening by logging causes an obvious increase in exposure to direct sunlight, but the understorey microclimate of undisturbed and logged forest in Kalimantan was also strongly influenced by topography and seasonal changes. A shaded, undisturbed site on a low ridge could sometimes be hotter and less humid than an open, logged site on a river terrace. Low wind speed was an important feature, and windiness (or the lack of it) had strong effects on below canopy humidity and temperature. Site elevation and aspect influenced below canopy wind speed and the degree of coupling between above and below canopy conditions.

Low wind speed will decouple seedling leaves from ambient conditions. It is hypothesised that low boundary layer conductance and high leaf temperatures during periods of the direct sunlight will have important effects on dipterocarp seedlings regenerating in logging gaps.

The microclimate of undisturbed and logged forest were both strongly influenced by the dry season decrease in rainfall and increases in insolation and wind speed. The dry season climate itself was strongly influenced by a regular nocturnal front of cool moist air, and later in the season by reductions in atmospheric transmissivity caused by biomass burning and regional haze.

4. Population dynamics and growth of dipterocarp seedlings after logging in Central Kalimantan, Indonesia

4.1 Introduction

Timber from the natural dipterocarp forests of Indonesia and Malaysia dominates the international trade in tropical timber. The silvicultural systems used in dipterocarp forest rely primarily on natural regeneration as the source of trees for future rotations (Appanah and Weinland, 1990; Anonymous, 1993a). Guidelines for sustainable practice state that sufficient advance regeneration should be present before logging, that a minimum number of residual or seed trees should be left, and that if regeneration after logging is inadequate, that enrichment planting should be undertaken (Anonymous, 1993a; Dykstra and Heinrich, 1996). In reality, stocks of dipterocarp seedlings are highly variable in space and time and are usually ignored during pre- or post-harvest inventories. Instead it is assumed that sufficient seedlings will have survived the logging, or that residual trees will fruit and restock the damaged areas (Appanah and Manaf, 1994). Dipterocarp seedlings can respond well to canopy disturbance (Fox, 1973; Whitmore, 1984; Chapter 6), but regeneration is often patchy or inadequate and after the event it may be difficult to determine why regeneration is lacking (Appanah and Weinland, 1990). Further quantitative studies of seedling ecology and the impact of logging on seedling populations are required (Kuusipalo *et al.* 1996; Tuomela *et al.* 1996). The results of these studies can be used improve management techniques and our understanding of the ecology of these forests. If forest growth models are used to predict long term sustainable yields, they should also include the effects of logging on the seedling population (Vanclay, 1994; Kuerpick, Kuerpick and Huth, 1997).

Poor regeneration after logging may be the result of either low seedling density or the slow growth of the seedlings that are present. Low seedling density in turn may be the result of insufficient advance regeneration before logging or the death of seedlings during and after logging. Despite its potential economic importance, there are few published studies which quantify the impact of logging on seedling density and distribution (Fox, 1973; Liew and Wong, 1973; Appanah and Manaf, 1994; Kuusipalo *et al.* 1996). Similarly, the growth response of *wild* seedlings after natural or logging disturbance has rarely been described (Fox, 1973; Whitmore and Brown, 1996). Research in nurseries has often shown the benefit of partial shade during early growth (Nicholson, 1960; Sasaki and Mori, 1981; Aminuddin, 1986; Ashton, 1995). Early nursery studies usually reported the relative degree of shading applied (e.g. 70 % of full sunlight), a measure which is relevant for nursery management but which may vary between studies and is difficult to compare with the light environment of logged forest.

Lowland dipterocarp forest is also characterised by its diversity. At least thirty dipterocarp species co-occur in the area where this study was conducted (Argent *et al.*, 1997). Comparisons between species are needed to improve our ability to predict the response of mixtures of species to disturbance and improve the selection of species for planting programs (Adjers *et al.* 1995; Hall, 1996). A number of studies of wild dipterocarp seedling survival and growth after disturbance are now underway (Tuomela *et al.* 1996; Whitmore and Brown, 1996). This study examines the effects of conventional logging on the distribution and growth of wild dipterocarp seedlings in Central Kalimantan (Indonesian Borneo).

The aims of this study were:

To describe the spatial distribution of dipterocarp seedlings in relation to canopy and soil conditions after logging, and use this information to design a sampling strategy for the study of seedling growth in response to available light.

To describe seedling growth and mortality in response to the range of light environments occurring in logged forest, with emphasis placed on absolute measurements of light availability. The hypothesis was that in open areas seedling density and growth would be reduced, and mortality increased.

To compare the dipterocarp species that were encountered, and determine their optimum light requirements for growth.

4.2 Methods

Site description

Measurements were made in unlogged and recently logged lowland dipterocarp tropical rain forest in Central Kalimantan (Indonesian Borneo) between April 1994 and December 1995. The study area was part of the Wanariset Sangai research forest (01° 18' S 112° 23' E). Annual rainfall is high (approximately 3500 mm), but a drier season usually occurs from July - October. Part of the study area had been logged 6 months before the study began using conventional methods in accordance with the Indonesian Selective Cutting and Planting (TPTI) system. Approximately 10 trees per ha are removed, but up to 50 % of the trees left remaining in the stand may be damaged or destroyed during extraction, leaving behind a mosaic of undisturbed and disturbed patches of forest (Torquebiau, 1986; Cannon *et al.* 1994; Bertault and Sist, 1995).

Mapping of logged forest and location of seedling plots

Seedling density in dipterocarp forest is highly variable. Purely random sampling will provide many sites with few or no seedlings. A simple technique for mapping canopy cover, seedling density and soil disturbance was developed so that sampling could be restricted to areas where seedlings were present and stratified according to canopy cover. One hectare (100 x 100 m) permanent sample plots had already been established as part of a larger study, and string arranged at 10 m intervals in a grid pattern across the plots. Over each 5 m interval (25 m^2), using the string for location, the condition of the canopy, soil and seedling population was assessed. Canopy cover was assessed as open space, partially open, or closed. Soil disturbance was assessed as undisturbed forest soil, moderately disturbed (some erosion or disturbance over part of the 5 m interval), very disturbed (most of the interval bladed or compacted by tractor activity) or logging debris (the ground covered by crowns of felled trees, stems or foliage). Dipterocarp seedling density was assessed as many seedlings (> 5 seedlings), few seedlings (1 - 5 seedlings), or no seedlings. The presence or absence of seedlings was more reliably determined than the density of seedlings. The survey of a plot was done quickly (one day) and is not intended to provide quantitative data on seedling density and logging impacts, but the results were useful for illustrating spatial correlations between seedling densities and canopy and soil conditions.

Seedling plots (2 m x 2 m) were established within two one hectare permanent sample plots. One of the one hectare plots was located in forest logged six months earlier, and the other was in unlogged forest 2 km from the logged area. The logged area was mostly flat (< 10°) and lay next to a river. In the logged area, 30 2 x 2 m square seedling plots were distributed within areas that were classified as containing dipterocarp seedlings, with ten seedling plots located in randomly selected 5 m grid squares from each of the three canopy classes. A further 5 seedling plots were located on skid trails to follow the development of pioneer vegetation. The unlogged area was located on gently sloping ground on a low ridge, where 10 seedling plots were established in sites containing dipterocarp seedlings (canopy cover was uniformly high).

Seedling tagging and measurement

All dipterocarp and pioneer seedlings within each seedling plot were identified and tagged with water proof plastic labels (Tyvek, Dupont, Bristol, UK). Common dipterocarp taxa were *Shorea johorensis* Foxw., *Shorea leprosula* Miq., *Shorea ovalis* (Korth.) Blume ssp. *ovalis* and *Shorea parvifolia* Dyer. All are fast growing species belonging to the commercially important light red meranti timber group. The important pioneers were *Macaranga* (Euphorbiaceae) species (*Macaranga gigantea* (Reichb. F. & Zoll.) M.A., *Macaranga hypoleuca* M.A., and *Macaranga triloba* (Bl.) M.A.) and *Anthocephalus chinensis* (Lam.) A. Rich. ex Walp. (Rubiaceae). Other taxonomic groups occurred only occasionally in some plots.

A seedling was defined as a plant below 1.2 m in height. In the logged plot all regenerating seedlings were included even though some were between 1.2 and 2.0 m by the time of the first measurement. Seedling height (vertical distance between the base of the stem and the heighest shoot apex) and the number of leaves were recorded. In the logged area, if more than 10 seedlings of a given taxa were present within a seedling plot, height and leaf number were recorded for a subsample of 10 randomly selected seedlings only. All of the seedlings in the logged area were present before logging (no new seedlings established after logging). The seedling plots were re-visited twice and surviving seedlings remeasured and new recruits tagged. Dates for measurements were: in the logged area, June 1994 (6 months after logging), October 1994 (10 months after logging) and June 1995 (18 months after logging); in the unlogged area, April 1994, July 1994 and July 1995. In total, 1638 dipterocarp seedlings and 154 pioneer seedlings were tagged. Many more pioneer seedlings are likely to have germinated and died between measurements in the logged area.

Annual mortality (m) was calculated as:

$$m = 1 - (n_1 / n_0)^{1/t_2 - t_1} \qquad (4.1)$$

where n_0 and n_1 are the numbers surviving at the beginning and end of the interval, respectively, and $t_2 - t_1$ is the time interval in years (Sheil, Burslem and Alder, 1995). Annual relative height growth (R) was calculated as:

$$R = (\log_e h_2 - \log_e h_1) / (t_2 - t_1) \qquad (4.2)$$

where h_1 and h_2 are the heights at the beginning and end of the measurement interval (Hunt, 1982).

Seedling light climate

Quantum sensors and hemispherical photographs were used to characterise the light climate above each seedling plot. Hemispherical photographs were taken at a height of 1.2 m above the centre of all seedling plots at the time of the first seedling measurements, and direct (T_b) and diffuse (T_d) site factors calculated according to the methods described in Chapter 2. Photographs were also taken at 20 m intervals in a grid pattern over the entire 1 ha logged plot. Site factors from a subset of 20 seedling plots in the logged area were calibrated against daily total photosynthetic photon flux density (PPFD) measured for 137 days at the same sites using quantum sensors (Chapter 2). The final relationship between measured PPFD and site factors ($r^2 > 0.95$) was then used to predict mean absolute daily PPFD for all seedling plots (Chapter 2). In the unlogged area it was possible to measure daily fluxes above all plots using quantum sensors.

The results of the first measurements of seedlings in the logged area were compared with PPFD predicted from the photographs for the two month period (62 days) before the measurements were made. Solar tracks and direct site factors were calculated on a daily basis, and the mean values used to predict mean daily PPFD. The second and third measurements were compared with PPFD predicted for the four month period (125 days) between the first and second measurements. Average fluxes up until the third measurement were not predicted because significant canopy closure and seedling growth was occurring and the photographs would no longer have been representative of seedling microsite conditions. It was assumed that the photographs were still indicative of the relative differences between seedling plots. Seedling measurements in the unlogged area were compared with measured fluxes for April 1994 (31 days).

An alternative approach - light climate estimates for individual seedlings

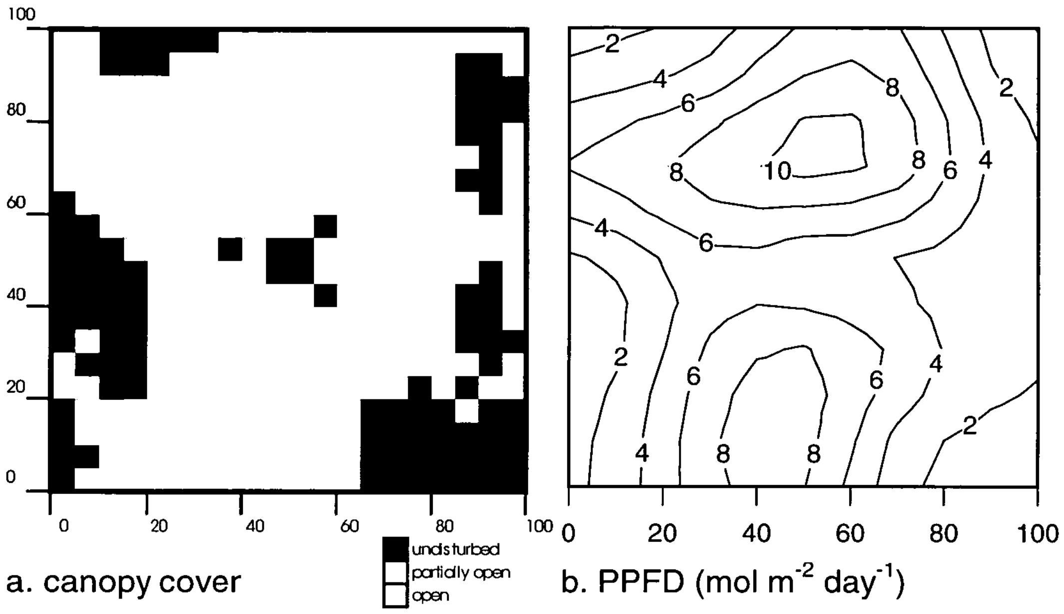
A difficulty encountered with the seedling plot approach was the variable numbers of seedlings of each taxa in each plot. In this study only two dipterocarp species (*S. johorensis* and *S. parvifolia*) were well represented across the full range of light environments. It was also thought that a single estimate of mean PPFD above a seedling plot may not have been representative of the light climate of all seedlings within that plot. An alternative method was tested in which individual seedings were located and tagged, and a hemispherical photograph taken at the shoot apex of each seedling. A new study site (50 m x 30 m) was established in July 1995 in forest logged 7 months earlier. This area was systematically searched for dipterocarp seedlings, and at least 20 seedlings of each dipterocarp species (285 in total) were tagged and measured beneath each canopy environment (closed, partially open or open). The grid co-ordinates of each seedling were recorded to the nearest 0.5 m. Seedlings in this area were of variable age; some were present before logging, and some had clearly established from new seed falling into disturbed areas since logging. Only one remeasurement of these seedlings was possible, in December 1995 (12 months after logging), and the results are only briefly discussed here.

4.3 Results

Logging damage and seedling densities

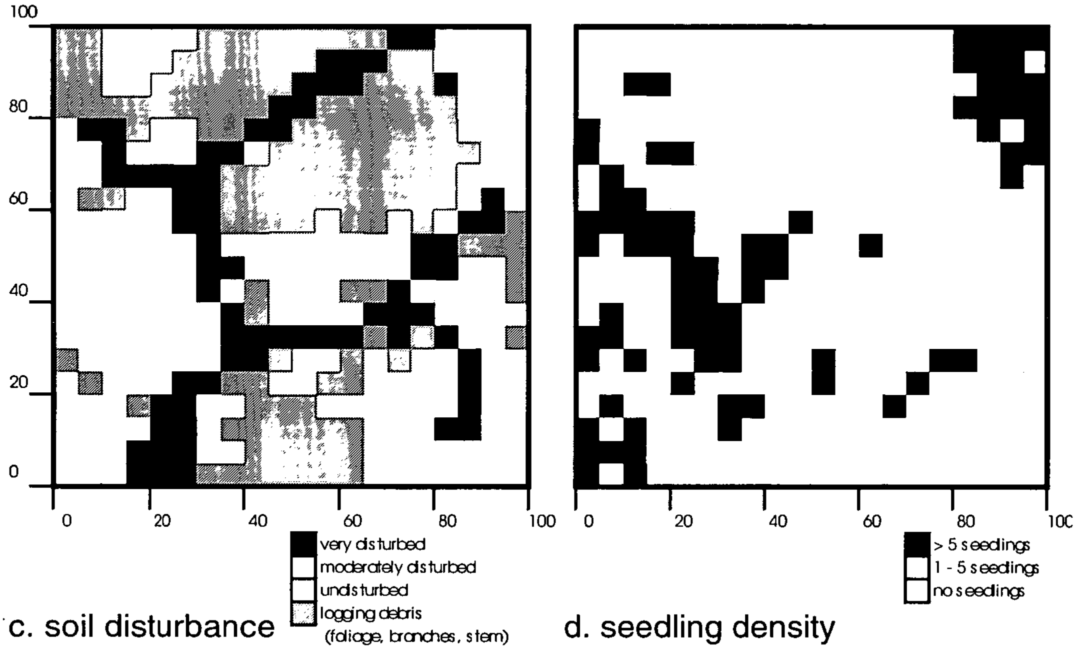
Canopy cover in unlogged forest was uniformly high, and dipterocarp seedlings were present over 73 % of the 1 ha unlogged area. Logging caused increased spatial variation in canopy cover and seedling density. Within the 1 ha logged area, 38 % of the canopy had been completely removed, and 52 % of the ground was covered by logging debris or skid trail (Tables 4.1 & 4.2; Fig. 4.1). Where there were debris or skid trails, there were few seedlings (Table 4.2). Remaining dipterocarp seedlings were concentrated along the margins of skid trails and felling gaps in areas with undisturbed soil and partially open canopy (Fig. 4.1). Areas with intact canopy had similar or lower seedling density than partially open areas (Fig. 4.1).

Spatial variation in understorey light availability in the logged area matched the distribution of canopy disturbance (Fig. 4.1b), with more than 50 fold variation in daily fluxes of PPFD between undisturbed areas and the centre of skid trails and felling gaps (0.2 - 13 mol m^{-2} day^{-1}). Mean daily PPFDs (mol m^{-2} day^{-1}) for the period 4 - 6 months after logging were: closed canopy = 1.0 ± 0.2; partially open = 3.4 ± 0.5; open = 7.5 ± 0.7. The maximum average daily PPFD in the 1 ha logged area was 12.9 mol m^{-2} day^{-1}, or 56 % of that incident above the canopy. Daily PPFD varied only 10 fold between sites in unlogged forest. Average daily PPFD above 10 seedling plots, for April 1994, was 0.4 mol m^{-2} day^{-1}, the maximum was 1.2 mol m^{-2} day^{-1}, or 4 % of that incident above the canopy.



a. canopy cover

b. PPFD (mol m^{-2} day^{-1})



c. soil disturbance

d. seedling density

Fig. 4.1. Canopy cover (a), mean daily below canopy PPFD for the period 4 - 6 months after logging (b), soil disturbance (c) and dipterocarp seedling density (d), over one hectare of logged forest. Canopy cover, soil disturbance and seedling density were surveyed at 5 m intervals. Skid trails are visible in (c) as areas of very disturbed soil. PPFD was estimated from hemispherical photographs taken at a height of 1.2 m and at 20 m intervals; contour intervals were drawn after a smoothed interpolation between points (G3GRID procedure, SAS Institute Inc.) and are not representative of small scale temporal and spatial variation in light availability. North is at the top and all axes represent horizontal distance (m).

Table 4.1. Dipterocarp seedling density relative to canopy cover after logging, for 1 ha. Values correspond to the proportion (%) of 5 m grid squares allocated to each class.

	Seedling density			
Canopy cover	no seedlings	1 - 5 seedlings	> 5 seedlings	Totals
open	28	7	2	37
partially open	14	12	12	38
undisturbed	7	12	6	25
Totals	49	31	20	100

Table 4.2. Dipterocarp seedlings density relative to soil disturbance after logging, for 1 ha. Values correspond to the proportion (%) of 5 m grid squares allocated to each class.

	Seedling density			
Soil disturbance	no seedlings	1 - 5 seedlings	> 5 seedlings	Totals
undisturbed	5	15	12	32
moderately disturbed	5	5	6	16
very disturbed	14	3	1	18
logging debris	25	8	1	34
Totals	49	31	20	100

Population structure

Seedlings of *S. parvifolia* and *S. johorensis* were common in the unlogged forest. *Shorea multiflora* and a *Dipterocarpus* species were also present, but in lower densities. The distribution of dipterocarp seedling heights was unimodal at the time of the first measurement, suggesting most of the seedlings had established at the time of the last major seeding event 1 - 3 years before measurements (Fig. 4.2). Seedlings of both species were usually short (below 0.4 m) and had few leaves (Fig. 4.2), and there was only a small increase in mean height during the measurement period (Fig. 4.2). A fruiting event occurred and new *S. johorensis* seedlings established in the unlogged area between the second and third measurements. After establishment the new seedlings were on average 10 cm shorter than the cohort which had established at least 2 years earlier (Fig. 4.2).

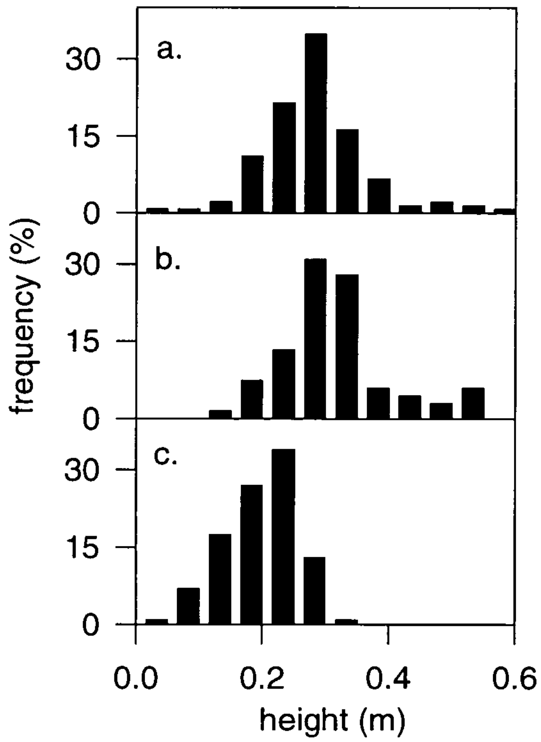


Fig. 4.2. Height frequency distributions for *S. johorensis* seedlings in unlogged, closed canopy forest. A. At the beginning of measurements (n = 135). B. surviving seedlings after 15 months (n = 68). C. new seedlings which established after a fruiting event around month 10 (measured at the same time as B.; n = 115). The population structure for *S. parvifolia* was similar, but there were no new seedlings (mean initial height and leaf number, *S. johorensis* = 0.28 ± 0.1 m and 5.4 ± 0.2 leaves, n = 135; *S. parvifolia* = 0.27 ± 0.01 m and 7.1 ± 0.3 leaves, n = 280).

Seedlings of *S. johorensis* and *S. parvifolia* were also found in the logged area, as well as smaller numbers of *S. leprosula* and *S. ovalis*. Dipterocarp seedlings were already growing rapidly in disturbed areas at the time of the initial measurement (6 months after logging), and the mean seedling height and range of heights was higher than in areas with undisturbed canopy (Fig. 4.3). Initially there was no clear difference between seedlings in areas with partially open or open canopy, but one year later (18 months after logging) the heighest seedlings were found in the most open areas (Fig. 4.3). Fruiting occurred near the logged area, but there were no fertile trees close enough for new seedlings to establish in disturbed areas.

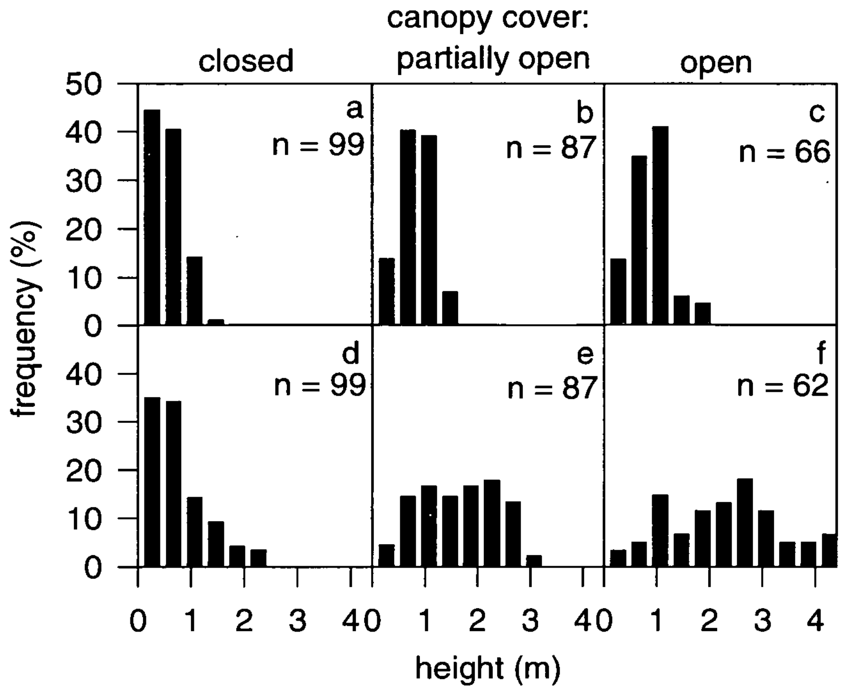


Fig. 4.3. Height frequency distribution for *S. johorensis* seedlings in logged forest, 6 months (a - c) and 18 months (d - f) after logging. Results are pooled according to estimates of canopy cover remaining above the seedling plots (undisturbed, partially open and open). Similar results were obtained for *S. leprosula*, *S. parvifolia* and *S. ovalis*. Sample sizes are shown; measured seedlings were a sub-sample of all seedlings (see methods).

Pioneer species (*A. chinensis*, *M. gigantea*, *M. triloba*, *M. hypoleuca*) had begun germinating in disturbed parts of the logged area by six months after logging, but they were still shorter than the dipterocarp seedlings (for partially open and open canopy, mean height ± SE, *A. chinensis* = 0.21 ± 0.05 m, n = 9; *M. gigantea* = 0.15 ± 0.03 m, n = 32). By 18 months after logging the tallest *A. chinensis* and *M. gigantea* seedlings were higher than the dipterocarp seedlings, reaching 8.5 m and 4.3 m respectively (for partially open and open canopy, mean height ± SE, *A. chinensis* = 4.5 ± 1.5 m, n = 6; *M. gigantea* = 1.9 ± 0.5 m, n = 12). Few pioneer seedlings (12, all species) were recorded in plots beneath closed canopy in logged forest, and none were found in the unlogged forest.

Mortality

The annual mortality of dipterocarp seedlings was higher in unlogged forest, with 30 - 50 % of all *S. parvifolia* and *S. johorensis* seedlings dying within one year of tagging (Table 4.3). Mortality was also higher in undisturbed than disturbed parts of logged forest (Table 4.4). In all areas smaller seedlings had higher mortality than larger seedlings, but this trend was strongest in disturbed parts of logged forest (Fig. 4.4). *S. parvifolia* had a higher mortality rate than *S. johorensis* in the unlogged area (Table 4.3), but there were no significant differences between dipterocarp species in the logged area. *Macaranga* seedlings had the highest morality rate of all species in the logged area (Table 4.4). Small *Macaranga* seedlings were also more likely to die, with 70 % of seedlings below 10 cm dying within one year, compared with 25 % of seedlings above 20 cm.

Table 4.3. Annual mortality of dipterocarp seedlings in unlogged forest. Values are calculated from the pooled data from all seedling plots, ± 95% confidence limit.

Species	Annual mortality, unlogged forest	n
S. johorensis	0.31 ± 0.08	135
S. parvifolia	0.54 ± 0.06	284

Table 4.4. Annual mortality of dipterocarp and *Macaranga* seedlings beneath undisturbed and disturbed canopy in logged forest. Disturbed canopy includes seedling plots in partially open and open areas. Values are calculated from the pooled data from all seedling plots, ± 95% confidence limit.

	Annual mortality, logged forest			
Species	undisturbed canopy	n	disturbed canopy	n
Macaranga sp.	0.67 ± 0.31	12	0.64 ± 0.09	132
S. johorensis	0.17 ± 0.05	241	0.13 ± 0.03	410
S. leprosula	0.15 ± 0.14	33	0.11 ± 0.06	113
S. ovalis	0.25 ± 0.17	32	0.16 ± 0.09	80
S. parvifolia	0.32 ± 0.18	31	0.18 ± 0.07	147

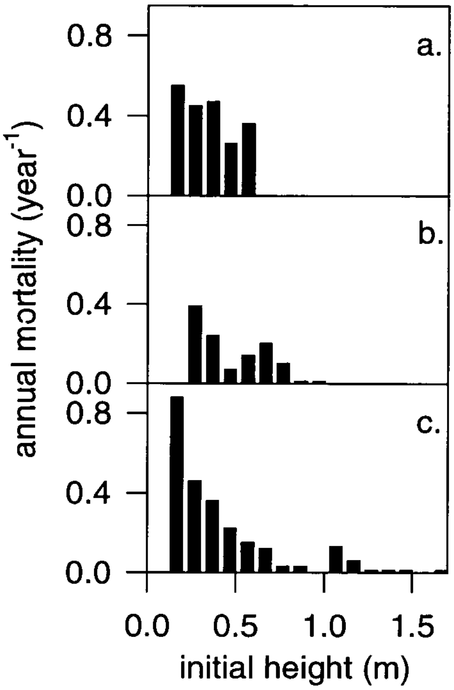


Fig. 4.4. Annual mortality for all dipterocarp seedlings as a function of initial height for unlogged forest (a), undisturbed sites in logged forest (b), and disturbed sites (pooled partially open and open canopy) in logged forest (c). Mortality is for the interval between the first and last measurement, and heights are from the first measurement.

Growth

In undisturbed forest there was no relationship between light availability and seedling size or growth (in height or leaf number) of either *S. johorensis* or *S. parvifolia*. Growth of individual seedlings was variable, with shoot damage causing negative height growth in some individuals while others achieved positive growth. Both species grew slowly in mean height at a similar rate (surviving seedlings only, mean relative height growth ± SE, *S. johorensis* = 0.052 ± 0.011 m m^{-1} year^{-1}, n = 60; *S. parvifolia* = 0.066 ± 0.010 m m^{-1} year^{-1}, n = 36), and had a net loss of leaves (mean relative leaf gain ± SE, *S. johorensis* = -0.15 ± 0.05 year^{-1}, n = 60; *S. parvifolia* = -0.18 ± 0.05 year^{-1}, n = 36). New leaf production accompanied height growth, but old leaves were lost at a faster rate than new leaves were produced.

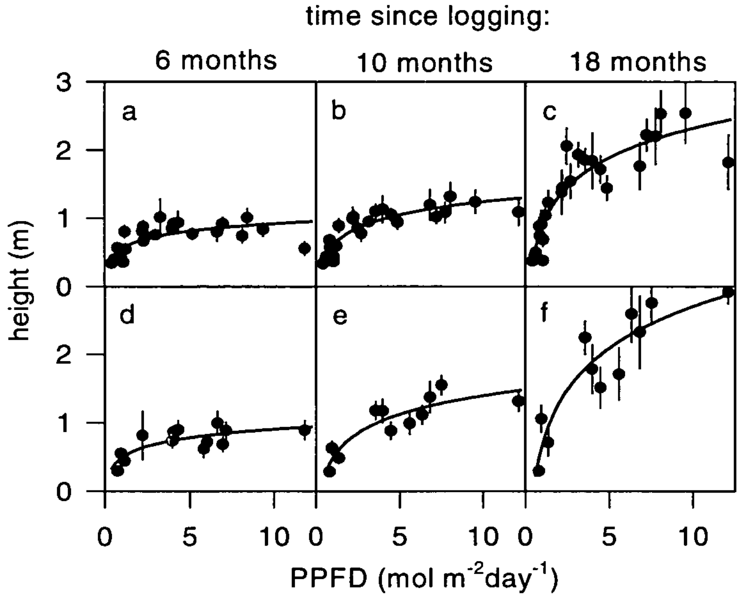


Fig. 4.5. Mean seedling height as a function of mean daily PPFD for *S. johorensis* (a - c) and *S. parvifolia* (d - f), 6 months, 10 months and 18 months after logging. Each point represents the mean height for a seedling plot, ± SE. Only plots with 4 or more seedlings and only seedlings that survived the entire period are included. Lines represent a linear regression between the natural logarithm of PPFD and height (Table 4.5).

Dipterocarp seedling height and leaf totals increased rapidly with small increases in light availability after logging, but above 5 mol m^{-2} day^{-1} PPFD there was little further increase in seedling size (Figs. 4.5 & 4.6). Seedling size and relative growth rates were therefore best described as a function of the logarithm of daily PPFD (Figs. 4.5 - 4.7, Table 4.5). The same pattern was observed for the heighest dipterocarp seedling in each seedling plot (all species; Fig. 4.8), and individually for all four dipterocarp species. The relationship was more variable in the less common species (*S. leprosula* and *S. ovalis*; data not shown). Variable seedling numbers growth rates within each seedling plot made interspecific comparisons difficult, but growth rates for a given PPFD were similar and the maximum height of all four species had exceeded 4 m by 18 months after logging (Fig. 4.8).

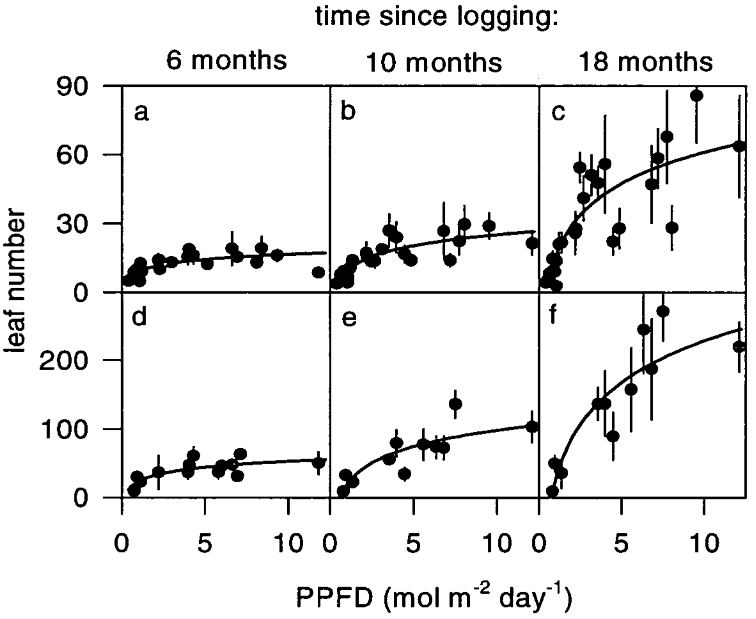


Fig. 4.6. Mean leaf number as a function of mean daily PPFD for *S. johorensis* (a - c) and *S. parvifolia* (d - f), 6 months, 10 months and 18 months after logging. Each point represents the mean leaf number for a seedling plot, ± SE. Only plots with 4 or more seedlings and only seedlings that survived the entire period are included. Note the difference in vertical scale between *S. johorensis* and *S. parvifolia* - *S. johorensis* has fewer, larger leaves than *S. parvifolia*. Lines represent a linear regression between the natural logarithm of PPFD and leaf number (Table 4.5).

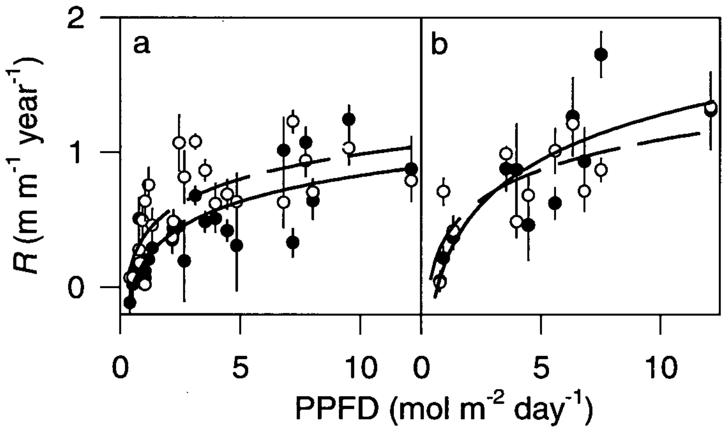


Fig. 4.7. Annual relative height growth (*R*) as a function of mean daily PPFD for *S. johorensis* (a) and *S. parvifolia* (b). Closed symbols and solid lines are for relative growth over the first measurement interval (6 - 10 months after logging), open symbols and dashed lines for the second measurement interval (10 - 18 months after logging). Each point represents the mean growth for a seedling plot, ± SE. Only seedling plots with 4 or more seedlings and only seedlings that survived the entire period are included. Logarithmic functions are fitted for comparison with Fig. 4.5 (Table 4.5). For *S. parvifolia* the relationship can also be approximated with a straight line.

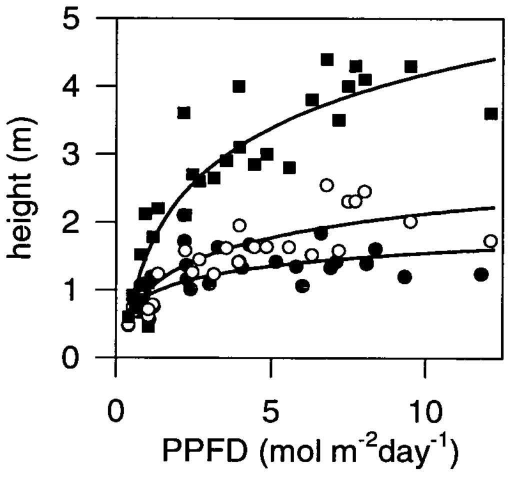


Fig. 4.8. Height of the highest dipterocarp seedling in each seedling plot as a function of mean daily PPFD, for 6 months (closed circles), 10 months (open circles) and 18 months (squares) after logging. Lines represent a linear regression between the natural logarithm of PPFD and height (Table 4.5).

Table 4.5. Regression coefficients for the curves describing seedling height, leaf number and relative growth (R) after logging as a function of the natural logarithm of PPFD (Figures 4.5 - 4.8). Equations are of the form y = a.ln(Q) + b and all regressions are significant ($p < 0.01$).

		6 months			10 months			18 months		
Species	y	a	b	r^2	a	b	r^2	a	b	r^2
S. johorensis	height	0.16	0.56	0.53	0.28	0.60	0.83	0.62	0.89	0.83
S. parvifolia	height	0.18	0.50	0.59	0.39	0.50	0.80	0.88	0.68	0.85
S. johorensis	leaf no.	3.3	9.2	0.55	6.9	9.4	0.73	19.6	15.9	0.70
S. parvifolia	leaf no.	12.6	23.7	0.55	34.7	18.8	0.69	87.6	27.5	0.81
S. johorensis	R	-	-	-	0.28	0.19	0.65	0.27	0.37	0.58
S. parvifolia	R	-	-	-	0.48	0.18	0.70	0.32	0.36	0.59
all dipterocarps	max height	0.28	0.9	0.56	0.50	0.97	0.71	1.15	1.53	0.84

Dipterocarp seedling relative growth rates in the second logged area were again found to reach a maximum at approximately 5 mol m^{-2} day^{-1} PPFD (Fig. 4.9). The growth of individual seedlings was variable, and there were no clear differences between species. Seedlings that established on disturbed soil after logging grew as fast as pre-existing seedlings that had survived the logging operations, except in the most open sites (above 10 mol m^{-2} day^{-1} PPFD; Fig. 4.9). Soil disturbance and light intensity were spatially correlated, leading to higher seedling growth rates in moderately open areas (within 10 m of intact canopy) than in the centre of large logging gaps (Fig. 4.10).

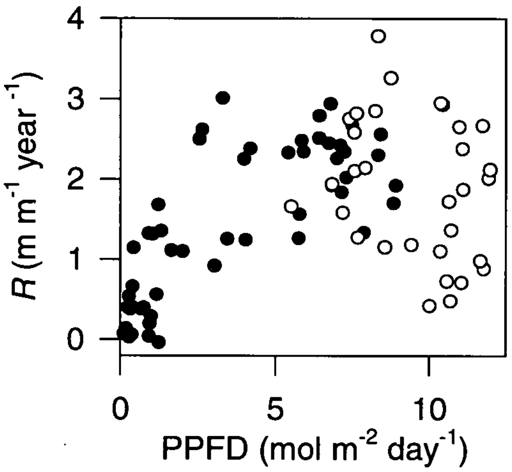


Fig. 4.9. Annual relative height growth (*R*) as a function of mean daily PPFD for *S. johorensis* seedlings in undisturbed (closed symbols) and disturbed (open symbols) soil in the second logged area. Each point represents the growth of an individual seedling over the period 7 - 12 months after logging. Initial seedling heights were lower than for the other logged area and relative growth rates are higher (compare with Fig. 4.7).

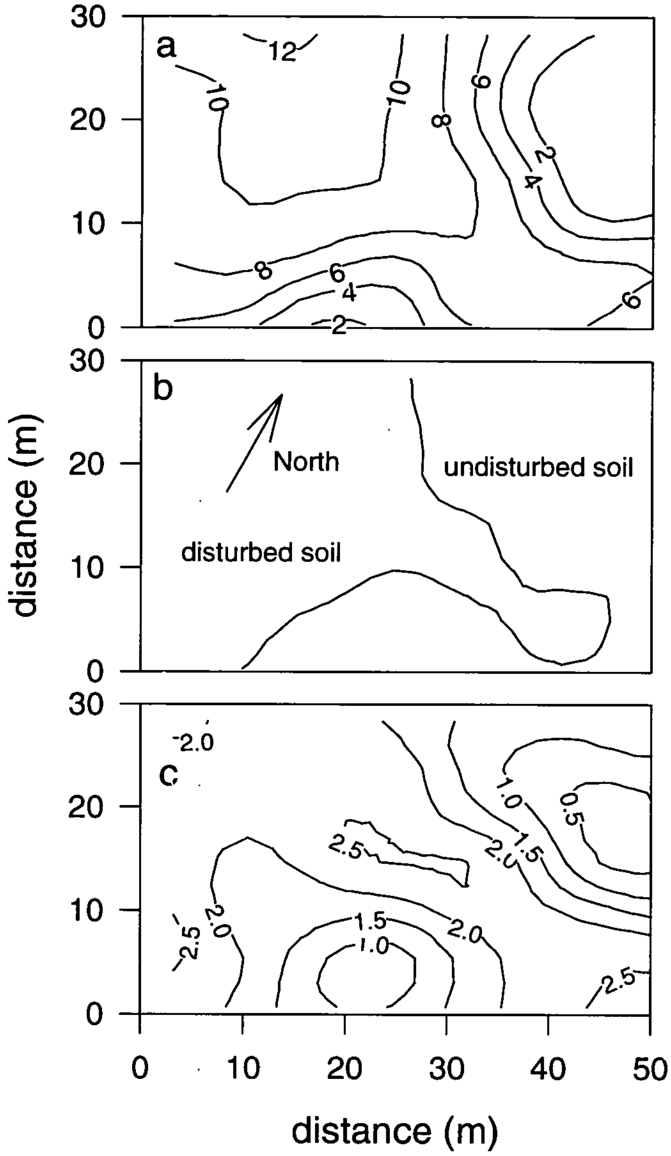


Fig. 4.10. Mean daily below canopy PPFD for the period 7 - 12 months after logging (a), soil disturbance (b) and dipterocarp seedling annual relative height growth (c) for the second logged area. Contour plots are based on measurements of height and PPFD for 285 seedlings (*S. johorensis*, *S. leprosula*, *S. ovalis* and S. *parvifolia*) randomly distributed across the plot. PPFD contours of 4 mol m^{-2} day^{-1} and below are roughly equivalent to areas with undisturbed canopy.

4.4 Discussion

Spatial heterogeneity after logging

Logging operations remove pre-existing dipterocarp regeneration from areas where regeneration is most required. In addition to the obvious damage caused by tractor skidding and blading, dipterocarp seedling density is low in areas smothered by logging debris. Regeneration in large logging gaps will therefore require the establishment of new dipterocarp seedlings. This cannot be guaranteed in more intensively logged areas where the nearest surviving mother tree may be some distance from the denuded area. Harvesting techniques that reduce the severity and extent of damage (Bertault and Sist, 1995; Pinard *et al.* 1995; Dykstra and Heinrich, 1996) will increase the probability that surviving seedlings are left near the centre of gaps and that new seedlings will establish in the gaps. If canopy openings are small, regeneration along the margins may be sufficient to fill the gap (Fox, 1972). The uneven distribution of seedlings after logging means that an inventory of seedlings on the scale of a stand may indicate abundant regeneration, even though there are few seedlings left remaining in the larger open areas. Knowledge of the spatial distribution of seedling damage and recruitment patterns may therefore be crucial for accurate predictions from forest growth and yield simulations, while the population structure and changes in absolute numbers of small seedlings on the scale of a whole stand will be less important.

Growth response to light

Wild seedling height and leaf area growth reached a maximum at moderate PPFDs that were roughly equivalent to those reported for the centre of natural tree fall gaps (5 mol m^{-2} day^{-1}; Chazdon and Fetcher, 1984; Ashton, 1992; Rich *et al.* 1993; Bellingham *et al.* 1996). This observation is consistent with their ecological classification as climax species which require gap formation for regeneration (Whitmore and Brown, 1996). Turner (1990b) hypothesised that wild *S. multiflora* seedlings would have constant growth rates above an intermediate PPFD. Castro *et al.* (1995) noted that a limited increase in growth rate above a threshold irradiance is common to many climax tree species. The causes of growth limitation at higher PPFD and its importance during the regeneration of wild seedlings after logging are not known. It is possible that dipterocarp seedlings growing in undisturbed soil and high PPFD are not limited by any single external factor, but are instead growing at their inherent maximum rate (Saverimuttu and Westoby, 1996a). Even when limited with respect to light availability, the growth observed in this study was fast (at least a doubling in height per year for seedlings between 0.3 and 2 m tall, Figs. 4.7 and 4.9).

If growth limitation is occurring, potential causes include competition with other seedlings, increased partitioning to roots (not captured by height or leaf number measurements), nutrient limitation, or the inability of dipterocarp seedlings to acclimate to the microclimate of large logging gaps. Limitation occurred even in the highest dipterocarp seedling, with or without competing pioneer species (large pioneers were not present in all seedling plots). Competition for light is therefore unlikely to be the cause, although it will become more important once a canopy of pioneer species develops and begins shading the regenerating dipterocarp seedlings (Tuomela *et al.* 1996). Partitioning of growth to roots does increase in exposed seedlings (Chapter 6; Sasaki and Mori, 1981; Aminuddin, 1986), but this change is unlikely to be large enough to account entirely for the limitation of above ground growth. Nutrient limitation remains an important area for further investigation, but recent studies suggest that dipterocarp seedlings are relatively tolerant of low nutrient availability (Chapter 5). Nutrient availability probably limits seedling growth in the most disturbed soil and exposed conditions (Fig. 4.9; Nussbaum, Anderson and Spencer, 1995). It has been proposed that dipterocarp seedlings may be unable to acclimate to post logging environmental conditions (Turner and Newton, 1990; Tuomela *et al.* 1996). In Chapter 6 it is shown that light demanding dipterocarp seedlings can acclimate to open post logging conditions, but the respiratory costs of acclimation may contribute to growth limitation.

For management purposes it may be possible to alleviate the cause of growth limitation in high PPFD, or avoid limitation by reducing logging damage. Examples of the potential for treatment of nutrient limitation are fertilisation, mulching or mycorrhizal inoculation. Treatment is unlikely to be economically viable for wild seedlings in logged natural forest, but intensive management is possible for enrichment planting schemes and plantations of dipterocarps where growth limitation may also occur (Adjers *et al.* 1995; Otsamo *et al.* 1995). For natural forests it may be better to reduce damage intensity and canopy opening at the time of logging. A reduction in gap size and understorey light intensity from high (above 10 mol m^{-2} day^{-1} PPFD) to moderate (5 - 10 mol m^{-2} day^{-1} PPFD) levels will reduce competition from pioneer trees and vines, but is unlikely to reduce dipterocarp seedling growth significantly. These results provide a physiological explanation for the observation of Kuusipalo *et al.* (1996) that post-logging crown liberation (cutting of competing non-commercial trees) tended to promote further recruitment of pioneers and prolong the pioneer phase, rather than achieving the desired effect of promoting dipterocarp regeneration. It can be hypothesised that the growth response of pioneer species does not saturate at moderate light intensities and that their growth rate continues to increase with increasing canopy opening. Tuomela *et al.* (1996) found that even large dipterocarp saplings grew fastest in small gaps, probably because of reduced competition from pioneer species. At present, understorey light is likely to exceed that required for maximum seedling growth over large areas of conventionally logged forest (Figs. 4.1 and 4.10). Larger gaps may favour later growth as the seedlings become larger and their tolerance of high light intensities increases (the relationships presented in Figs. 4.5 - 4.9 will become more linear with time), but larger gaps are usually correlated with soil disturbance and hence the complete loss of advance regeneration.

Mortality

High mortality and slow growth of shade-suppressed dipterocarp seedlings is an important feature of dipterocarp regeneration ecology (Fox, 1972; Whitmore, 1984; Still, 1996). From year to year there are large changes in seedling density, and seedlings can sometimes disappear completely before the next seeding event (Appanah and Weinland, 1990). However, there will usually be some seedlings which survive until the next fruiting or until canopy opening and release occurs. It is for this reason that spatial variation in seedling density and logging damage is considered at least as important as variation in total numbers of seedlings. Overall mortality was lower in logged forest, supporting the conclusion that low seedling density in logging gaps was the result of mechanical damage during logging rather than increased mortality after logging in response to a harsher microclimate (see also Chapter 6).

The causes of seedling death in logged and unlogged forest are different. Seedlings in undisturbed forest may die from herbivory, drought (Turner, 1990a), or branch and leaf fall (Still, 1996). Smaller seedlings were more likely to die from these causes (Fig. 4.4; Turner, 1990b; Still, 1996), but competition with other seedlings was probably negligible because individuals were widely spaced relative to their height. In deep shade the carbon balance of individual seedlings can be negative (Chapter 6; Chazdon *et al.* 1996), and the net loss of leaves which accompanied height growth may further increase rates of respiratory loss (increased stem biomass and declining photosynthetic area). In disturbed forest the decline in mortality with height was more pronounced, reflecting increased competition between seedlings and the death of shorter seedlings. Seedlings were tall but had few leaves in seedling plots where competition and crowding was most intense (Figs. 4.5 and 4.6). That 'small seedlings die young' is true for other taxa (Walters and Reich, 1996) and was particularly important for new *Macaranga* seedlings which were smaller than dipterocarp seedlings and had the highest mortality of all.

Interspecific comparisons

Variation between individuals, high mortality and the difficulty of obtaining an adequate sample size over a range of light environments prevented useful comparisons between the species included in this study. Whitmore and Brown (1996) were more successful when comparing a broader range of shade tolerant and light demanding dipterocarp species. The species encountered in this study were all from the same timber group, and actual differences are probably small. Variability was high even when individual seedlings were mapped and their light environments characterised using hemispherical photographs. Studies of planted or potted seedlings under more controlled conditions provide a useful alternative, but for ecological purposes it will always be necessary to test the results of such studies on wild seedlings under natural conditions. The accuracy and resolution of light climate estimates from hemispherical photographs now exceeds variability in the growth response (cf. Whitmore *et al.* 1993). Large numbers of seedlings should be included in a study, and the limiting factor then becomes the ability to tag and easily relocate individual seedlings distributed over wide areas (> 0.25 ha). Electronic methods of tagging and positioning may provide a useful alternative to disruptive permanent plots and large visible labels.

Conclusions

Conventional logging increases patchiness and removes dipterocarp regeneration from the most disturbed areas. Seedling density was reduced in open areas, but mortality after logging was lower than in undisturbed forest. Abundant dipterocarp regeneration may occur in logged forest, but it will often be unevenly distributed and lacking in the gaps where it is most required.

Wild light hardwood dipterocarp seedlings reach maximum growth rates at only moderate light intensities (5 mol m^{-2} day^{-1}). Canopy opening during conventional logging often exceeds that required for maximum dipterocarp seedling release. In disturbed soil growth rates may even decline with increasing light intensity. Future research will focus on factors which limit dipterocarp seedling growth at high light intensities (Chapters 5 & 6).

For comparisons between similar dipterocarp species, efforts should be concentrated on large sample sizes and determination of the causes of variability in the growth response (e.g. light environment, herbivory, drought, nutrient availability).

The most important impact of logging may be soil disturbance and the loss of seedlings during harvesting; seedlings that survive in open areas may initially be over-topped by pioneers but will probably outlive the pioneer phase (Kuusipalo *et al.* 1996). This study shows how soil disturbance and open conditions are correlated. Reducing soil disturbance by reducing over all disturbance intensity will result in lower below canopy light intensity, but may not significantly decrease dipterocarp seedling growth rates. Logging techniques that reduce the degree of canopy opening will therefore increase the likelihood that commercial species survive or establish to fill canopy gaps, and decrease competition from pioneer species.

5. Effects of light and nutrient supply on the growth, mycorrhizal infection and photosynthesis of Shorea seedlings

5.1 Introduction

The ability to promote regeneration after disturbance of tropical forest depends on our knowledge of the physiological characteristics of individual species and the way they respond to contrasting environmental conditions. Disturbance of tropical forest exposes tree seedlings to high light intensities and soil conditions which vary from undisturbed forest soil to bare, nutrient poor mineral soil. In Indonesia, harvesting of timber from dipterocarp rain-forest usually causes greater soil disturbance and higher light intensities than natural disturbances (Chapter 4). Dipterocarp seedling growth in large logging gaps is therefore unlikely to be limited by light levels (Chapter 4), but seedling nutrient status may be poor. Mycorrhizal associations between soil inhabiting fungi and seedling roots may enhance their nutrient status (Lee, 1990), but the abundance of fungal inocula may also be adversely affected by logging (Alexander, Ahmad and Lee, 1992; Ahmad, 1996). This study examines how interactions between light intensity, nutrient availability and mycorrhizal infection influence dipterocarp seedling growth and photosynthesis under controlled conditions. Two fast growing species, *Shorea leprosula* Miq. and *Shorea parvifolia* Dyer, are compared to determine how these relationships differ between closely related taxa.

The moist tropical forests of South East Asia and the international trade in tropical timber are dominated by the Dipterocarpaceae, a diverse family of approximately 470 tree species (Ashton, 1988; Barbier *et al.* 1994). Management of these forests for timber production relies primarily on natural regeneration as the source of future harvests. Current silvicultural systems aim to promote the natural regeneration of timber species, or supplement with enrichment planting if natural regeneration is inadequate (Whitmore, 1984; Adjers *et al.* 1995; Kuusipalo *et al.* 1996). A broader knowledge of the ecological and physiological characteristics of dipterocarp seedlings is needed to refine these management techniques and improve their long term sustainability. Areas of greatest interest include factors which limit the growth of naturally established or planted seedlings under open conditions, and the ranking of dipterocarp species according to shade tolerance, growth rates and site requirements. Previous studies have examined the role of individual environmental factors, particularly light intensity (Nicholson, 1960; Sasaki and Mori, 1981; Ashton, 1995; Whitmore and Brown, 1996), but there is now an urgent need to consider the interacting effects of combinations of environmental conditions (Ashton, 1994).

The importance of seedling mycorrhizal status for the survival and growth of dipterocarps seedlings after logging is poorly understood (Lee, 1994). Ectomycorrhizal infection can enhance growth in dipterocarp seedlings and cuttings (Lee and Alexander, 1994; Supriyanto *et al.*, 1994; Yazid, Lee and Lapeyrie, 1994), but it is not known how often soil disturbance and the death of adult trees might limit the abundance of inoculating fungi in logged forest (Alexander, Ahmad and Lee, 1992). Inadequate infection may only be a problem for seedlings planted or establishing naturally in exposed mineral soil after logging. It is also not known to what extent nutrient availability *per se* might limit the growth of dipterocarp seedlings in logged forest, except again for seedlings growing in exposed mineral soil (Nussbaum, Anderson and Spencer, 1995). Fertilisation can lead to a reduction in mycorrhizal infection for temperate tree species (Newton and Pigott, 1991), hence it may not be a useful silvicultural treatment for dipterocarp seedlings (Turner, Brown and Newton, 1993). Ensuring adequate mycorrhizal infection with appropriate fungal partners may be better approach (Smits, 1992; Turner, Brown and Newton, 1993). There is now an urgent need for further research examining the relationship between dipterocarp seedling mineral nutrition, mycorrhizal status and other aspects of growth and survival (Lee, 1994).

In this study seedlings of *S. leprosula* and *S. parvifolia* were grown in high and low light and with two rates of nutrient supply. These two closely related species are perhaps the commonest and best known dipterocarps, widely distributed across Thailand, Malaysia, Sumatra and Borneo (Ashton, 1982; Newman, Burgess and Whitmore, 1996). Both are members of the fast growing, light red meranti timber group, with light demanding seedlings that are suitable for planting in open situations (Appanah and Weinland, 1993). The hypotheses were that (1) at high light intensities seedling growth would become limited by nutrient availability, and (2) that mycorrhizal infection would increase in response to low nutrient availability. A second aim was to describe the capacity of these seedlings for adjustment of shoot architecture and leaf physiology (plasticity) in response to the contrasting growing conditions, and to compare their plasticity with that of other tropical tree species. A third aim was to compare the two species and determine which types of measurement will be most useful for ranking a larger range of dipterocarp species according to light and nutrient requirements. Recent studies have concluded that measurements of leaf physiology are only useful for predicting dipterocarp seedling ecology when combined with information on patterns of carbon partitioning (Ashton and Berlyn, 1992; Ashton, 1995; Zipperlen and Press, 1996). *S. parvifolia* and *S. leprosula* are more similar than the species compared in these studies, although *S. leprosula* is sometimes classified by foresters as more light demanding than *S. parvifolia* (Appanah and Weinland, 1993; Adjers *et al.* 1995). Can comparisons of shoot architecture and leaf physiology be used to rank closely related dipterocarp species?

5.2 Methods

Plant material

Seedlings of *S. parvifolia* and *S. leprosula* were collected from undisturbed lowland dipterocarp forest near the Wanariset Sangai research station in Central Kalimantan, (Indonesian Borneo; 01° 18' S 112° 23' E) and transported to Edinburgh, Scotland, without soil. The seedlings were estimated to be 1 - 2 years old when collected, based on the time since the last mast seeding. Average height was approximately 0.3 m and most had at least three leaves at the time of removal from the forest. Roots and leaves were trimmed before transport. Seedlings were planted in groups of ten in large pots filled with clean river sand and kept under mist in a heated glass-house enclosure (day time temperature ca. 20 °C). After two months, surviving seedlings were transplanted individually to free draining plastic pots (21 cm high x 7 cm diameter) filled with equal volumes of vermiculite and perlite. At this stage most seedlings had one or two leaves and root development was poor. The seedlings were transferred to controlled environment rooms, set to a 12 hour, 27 °C day and 12 hour, 23 °C night at constant 85 % relative humidity. Lighting was provided by banks of metal halide discharge lamps (Thorn Kolararc 400W MBIF/BU) interspersed with incandescent spotlights (General Electric 120 W PAR spotlight). The photosynthetic photon flux density (PPFD) at the top of the canopy during day time was approximately 200 μmol m^{-2} s^{-1}. Seedlings were watered daily with a nutrient solution modified from Ingestad and Lund (1986) to give a low pH by supplying a greater proportion of N as HNO_3 rather than NH_4NO_3. The ratio NH_4^- / NO_3^- was 1.9, and the proportions of N, P, and K were 100 : 13 : 65 by weight. Concentrations used in the stock solutions were (in g dm^{-3}): Solution A, NH_4NO_3 200.1, KNO_3 49.5, KH_2PO_4 31.3, K_2HPO_4 33.1, K_2SO_4 48.8, HNO_3 31.5; Solution B, $Ca(NO_3)_2$ 40.1, $Mg(NO_3)_2$ 89.7, HNO_3 3.2, $Fe(NO_3)_3$ 5.1, $Mn(NO_3)_2$ 1.8, H_2BO_3 1.1, $Zn(NO_3)_2$ 0.27, $CuCl_2$ 0.080, Na_2MoO_4 0.018. The stock solutions were diluted in equal proportions to give a final N concentration of 80 g m^{-3}, and pH ca. 4.2. The nutrient solution pH was intended to approximate the conditions occurring at the seedling collection site in Central Kalimantan (J. Proctor, personal communication).

After three months growth in the controlled environment room, sufficient leaf area had developed to allow experimental treatments to begin.

Experimental treatments

The seedlings were grown for 78 days in high (HQ) and low (LQ) PPFD and with high (HN) and low (LN) concentrations of nutrient solution. Forty seedlings of each species were randomly allocated to high or low PPFD by placing seedlings inside 1 m x 0.3 m x 0.3 m frames constructed from 18 mm PVC piping. The frames were partially covered with either clear Mylar polyester film (HQ treatment, DuPont Electronics, UK) or pigmented polyester filter (LQ treatment, Strand Chromatic 211, Strand Lighting Ltd, Middlesex, UK). Five frames of each light treatment were allocated to each of two growth rooms, with temperature, relative humidity and day length set as described above. The intensity and spectral quality of light within the frames was measured using a portable spectroradiometer (LI-1800, LI-COR Inc., Lincoln, Nebraska). R:FR ratios were calculated as the ratio of quanta in the 10 nm band centred on 660 nm to the 10 nm band centred on 730 nm. Mean PPFDs and R:FR ratios, respectively, were 450 μmol m^{-2} s^{-1} and 1.4 (HQ); 30 μmol m^{-2} s^{-1} and 0.2 (LQ). These treatments gave a total daily PPFD (HQ treatment, 19.4 mol m^{-2} day^{-1}; LQ treatment, 1.3 mol m^{-2} day^{-1}) and R:FR ratio roughly equivalent to the centre of a logging gap and a bright undisturbed forest site, respectively, as measured at the seedling collection site (Chapter 3 and unpublished data).

Within each frame, a seedling of each species was allocated to high or low nutrient treatment (four seedlings per frame) and pots flushed three times daily with nutrient solution, diluted to give a final N concentration of 80 g m^{-3} (HN) or 15 g m^{-3} (LN). The low nutrient treatment was known to be low enough to induce nutrient stress in seedlings of other tropical species (Riddoch, Lehto and Grace, 1991). Frequent, automated watering with nutrient solution, using 5 mm irrigation piping and solenoid valves connected to a control device (CR10 datalogger, Campbell Scientific, UK), allows the assumption that the nutrient concentration in the root zone was maintained near the stated concentration.

The final arrangement of four seedlings per frame, ten frames per room, gave a sample size of ten seedlings for each combination of light, nutrient and species. Overall treatment effects were tested for using a replicated (two growth rooms) split plot ANOVA with light as main-plot factor and species x nutrients as sub-plot factors. Additional pre-planned contrasts were used to test for significant nutrient treatment effects within species x light treatment groups e.g. compare high and low nutrients within high light grown *S. leprosula* (SAS GLM procedure, SAS Institute Inc.; Appendix B for further details). If necessary, the data were log transformed before analysis to improve normality and homogeneity of variance.

Seedling growth and biomass partitioning

For estimates of initial biomass, an additional 20 seedlings of each species were randomly selected at the beginning of the treatment period and measured (height, root collar diameter, length of lateral stems, leaf length and area), then harvested and their mass recorded after drying at 80 °C for 24 hours. Similar morphological measurements were made for the shoots of the treatment seedlings and the newest fully expanded leaf on all shoots was marked. Linear regressions of organ dry mass against size were used to predict the initial mass of the constituent parts of the treatment plants. Trimming of the roots at the time of removal from the forest meant that the initial length of the tap root was still distinguishable at the end of treatments. This length, combined with root collar diameter at the beginning of treatments, was used to predict a minimum initial root mass using a regression developed from the harvested plants.

At the end of the treatment period the seedlings were remeasured, dried, and the mass of the tap root, fine roots, stems and leaves recorded separately. Fine root mass was defined as total root mass minus the mass of the woody tap root. The mass and area of leaves developing before and after the treatments began were recorded separately. Stomatal counts were made for each plant from an impression of the under-surface of a recently matured leaf made from dental impression compound (Kerr Extrude Wash, Petersborough, UK) and nail polish. Leaf area was measured using a LI-3000 leaf area meter (LI-COR Inc., Lincoln, Nebraska). The lengths of all lateral branches and the lengths and diameters (taken half way between each node) of the three internodes beneath the uppermost fully expanded leaf on the main stem were recorded.

Relative growth rate (R) and the Net Assimilation Rate (N) were calculated as:

$$R = (\log_e(W_2) - \log_e(W_1)) / t \qquad (5.1)$$

$$N = 2(W_2 - W_1) / ((A_2 - A_1)t) \qquad (5.2)$$

(Chiariello, Mooney and Williams, 1989), where W_1 and A_1 are the initial mass and leaf area, respectively, W_2 and A_2 the final mass and area, and t the length of the treatment period in days. Other calculations were: Specific leaf area (SLA) = leaf area / leaf mass; leaf area ratio (LAR) = leaf area / total plant mass; organ mass ratios (e.g. leaf mass ratio, LMR) = mass of organ / total plant mass; branch frequency = number of first order branches (those arising directly from the main stem) / total length of the main stem; total branch length = sum of the lengths of all first order branches; leaf area : stem length ratio = total leaf area / total stem length (main stem + first order branches).

Mycorrhizal infection

At the end of the treatment period the roots of all treatment seedlings were assessed for percent mycorrhizal infection by counting the numbers of mycorrhizal and non-mycorrhizal root tips. The mycorrhizal types occurring on each seedling were noted and samples taken for later identification. Values for mycorrhizal infection were arcsine transformed before comparison between treatments and species using the ANOVA design described above.

Leaf chlorophyll and nutrient concentrations

At the end of the treatment period the uppermost fully expanded leaf was taken from five randomly selected plants per treatment and total concentrations of chlorophyll, nitrogen and phosphorus determined. Two 12 mm discs were cut from each sample, weighed and the chlorophyll extracted over three days in 3 ml of N,N-dimethylformamide (Moran and Porath, 1980). The absorbance of the resulting solution at 647 nm and 664 nm was measured using a spectrophotometer (Cecil Instruments, Cambridge) and chlorophyll a and b concentrations calculated after Porra *et al.* (1989). The remainder of the sample leaves were dried at 80 °C, ground, and 0.1 g samples wet digested in a mixture of conc. H_2SO_4 and H_2O_2 (Grimshaw, Allen and Parkinson, 1989). Total nitrogen content of the digest was determined by gas diffusion using a flow injection analyser (Fiaster, Tecator, Wilsonville, Oregon) and total phosphorus by a molybdenum blue method and the flow injection analyser.

Photosynthetic light response curves

The response of photosynthesis to light was investigated at the end of the treatment period using a portable, open photosynthesis system (LI-6400, LI-COR Instruments, Nebraska) fitted with an electronically controlled LED light source (LI-6400-02; Tennessen, Singsaas and Sharkey, 1994). Measurements were made on the uppermost fully expanded leaf of three of the five plants from each treatment group that were randomly selected for chlorophyll and nutrient determinations. Air temperature was held at a constant 25 °C. Average CO_2 concentration, relative humidity and leaf temperature were 360 μmol mol^{-1} (range 338 - 389 μmol mol^{-1}) and 75 % (range 72 - 80 %), 26 °C (25 - 29 °C) respectively. The water vapour mole fraction deficit at the leaf surface varied between 6.0 and 17.2 mmol mol^{-1} (average 8.3 mmol mol^{-1}). Each leaf was allowed to reach a constant rate of photosynthesis at 250 μmol m^{-2} s^{-1} PPFD, then stepped up to light saturation and back down to darkness over a period of at least 120 minutes, allowing photosynthesis and stomatal conductance to reach a steady state at each intermediate PPFD. Dark respiration was measured after the leaf was darkened for at least 15 minutes. Final values were the average of at least three measurements after a steady state had been reached.

A non-rectangular hyperbola was fitted to the photosynthesis data for each plant:

$$\theta A^2 - (\phi\, Q + A_{\max})A + \phi\, QA_{\max} = 0 \qquad (5.3)$$

(Ogren and Evans, 1993), where A is the net rate of photosynthesis (μmol CO_2 m^{-2} s^{-1}), $A_{\max}$ is light-saturated photosynthesis, ϕ is the apparent quantum efficiency (mol CO_2 mol incident photons $^{-1}$), Q is incident PPFD (μmol m^{-2} s^{-1}) and θ is the convexity (rate of bending). Convexity is related in complex manner to the transition from light limitation to light saturation. This model is a good approximation to the photosynthetic light response curve (Prioul and Chartier, 1977; Ogren and Evans, 1993), and gave a better fit to the experimental data than a simple rectangular hyperbola (Long and Hällgren, 1985). To avoid correlation between ϕ and θ during curve fitting (especially when θ is low), ϕ was first found by least squares regression of the initial linear portion of the curve (Leverenz, 1988). After solving for A and the addition of a dark respiration term (Zipperlen and Press, 1996), the model was fitted to the experimental data and A_{max} and θ estimated using non-linear regression (NLIN Marquardt procedure, SAS Institute Inc.). The light compensation point (PPFD at which $A = 0$) was found as the x intercept of a linear regression of photosynthesis for the three lowest light intensities, including darkness. The light saturation point (PPFD at which $A = 90\%\ A_{\text{max}}$) was found after solving equation 5.3 for Q (Zipperlen and Press, 1996).

5.3 Results

Growth

The seedlings of *S. leprosula* were taller at the beginning of the treatments and had a higher relative growth rate than *S. parvifolia* in both high and low light (Tables 5.1 & 5.2). Both species grew faster in high light. The net assimilation rate was also higher in high light and higher for *S. leprosula.* Both species had a higher proportion of their biomass partitioned to leaves and lower SLA in high light (Tables 5.2 & 5.3, Fig. 5.1). The effects of light on SLA were strongest in leaves which developed after treatments began, but there were also significant effects on the SLA of pre-existing leaves (for pre-existing leaves, overall mean SLA after HQ treatment = 23.1 ± 0.4 m^2 kg^{-1}, after LQ treatment = 25.4 ± 0.4 m^2 kg^{-1}, $F = 19.1$, $p<0.01$).

Table 5.1. Initial and final heights and final dry mass for *S. leprosula* and *S. parvifolia* seedlings. There were no differences in estimated initial mass between species or treatment groups (mean initial mass 1.9 ± 0.1 g, $F = 0.59$, $p = 0.92$). Treatments were high light and high nutrients (HQ HN), high light and low nutrients (HQ LN), low light and high nutrients (LQ HN), low light and low nutrients (LQ LN). All values are means ± 1 SE (n = 10). Significant treatment effects are indicated (ANOVA; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). F ratios and significance values are presented in detail in Appendix B.

Treatment	initial height (m)	final height (m)	final dry mass (g)
S. leprosula			
HQ HN	0.35 ± 0.03	0.70 ± 0.05	12.7 ± 3.1
HQ LN	0.39 ± 0.02	0.73 ± 0.02	12.8 ± 1.3
LQ HN	0.38 ± 0.01	0.56 ± 0.04	3.4 ± 0.7
LQ LN	0.37 ± 0.02	0.57 ± 0.04	3.4 ± 0.7
S. parvifolia			
HQ HN	0.33 ± 0.02	0.65 ± 0.03	9.1 ± 1.7
HQ LN	0.31 ± 0.02	0.59 ± 0.03	6.3 ± 0.9
LQ HN	0.32 ± 0.02	0.48 ± 0.05	2.6 ± 0.4
LQ LN	0.33 ± 0.02	0.47 ± 0.04	2.8 ± 0.6
Source of variation			
Species	**	***	*
Light (Q)	ns	***	***
Nutrients (N)	ns	ns	ns
Interactions	ns	ns	ns

Table 5.2. Relative growth (*R*) and net assimilation rate (*N*) during the treatment period, and the leaf area ratio (LAR) and specific leaf area (SLA) at the end of the treatment period. SLA is for leaves developing after the treatments began. Leaf loss is the percent loss of leaves that were already present at the beginning of the treatments. All values are means ± 1 SE (n = 10). For explanation of treatments and sources of variation, see Table 5.1.

Treatment	*R* (mg g^{-1} d^{-1})	*N* (g m^{-2} day^{-1})	LAR (m^2 kg^{-1})	SLA (m^2 kg^{-1})	leaf loss (%)
S. leprosula					
HQ HN	21.1 ± 1.6	1.47 ± 0.12	12.5 ± 1.0	25.5 ± 1.0	11 ± 4
HQ LN	22.3 ± 0.5	1.83 ± 0.14	10.5 ± 0.8	24.9 ± 0.6	19 ± 9
LQ HN	6.0 ± 0.6	0.57 ± 0.07	12.1 ± 0.8	32.0 ± 1.1	13 ± 3
LQ LN	6.5 ± 0.9	0.62 ± 0.10	11.8 ± 0.7	30.3 ± 1.6	14 ± 3
S. parvifolia					
HQ HN	19.9 ± 1.5	1.44 ± 0.08	11.8 ± 0.7	24.7 ± 1.0	2 ± 1
HQ LN	18.7 ± 1.1	1.30 ± 0.08	13.0 ± 0.6	26.2 ± 0.8	1 ± 1
LQ HN	4.3 ± 0.8	0.37 ± 0.07	12.5 ± 0.5	31.4 ± 1.1	2 ± 3
LQ LN	3.6 ± 0.9	0.31 ± 0.07	12.0 ± 0.3	29.3 ± 0.9	5 ± 4
source of variation					
Species	***	***	ns	ns	***
light (Q)	***	***	ns	***	ns
Nutrients (N)	ns	ns	ns	ns	ns
Interactions	ns	species x N *	ns	ns	ns

Nutrient effects on growth and final mass were weak, and there was considerable variation between plants. The effects of nutrients on growth and biomass partitioning can be related to the developmental stage achieved by each treatment group. *S. leprosula* seedlings were taller at the beginning, had a higher *RGR*, and achieved an even greater size advantage by the end of the experiment (Tables 5.1 & 5.2). A small increase in fine root mass ratio and a decrease in leaf mass ratio suggests that low nutrients had begun to affect the growth of the larger *S. leprosula* seedlings at the time of harvest (Table 5.3, Fig. 5.1). These changes were reflected in a small apparent increase in net assimilation rate (*N*) for high light, low nutrient treated *S. leprosula* (significant Q x N interaction; Table 5.2). A single high light, high nutrient *S. leprosula* seedling grew at less than half the rate of the next slowest plant, and was excluded from the growth analysis. Variation in the response of growth to light and nutrient treatment is thought to be the result of variation in the age and condition of these seedlings at the time of collection.

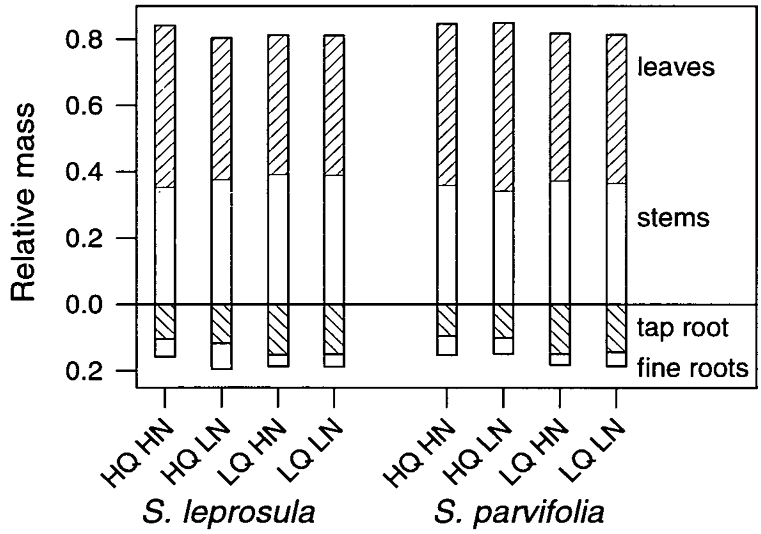


Fig. 5.1. Proportions of total biomass partitioned to leaves, stems, the tap root and fine roots, for each treatment group. The results of ANOVA comparisons between treatments for each organ type are presented in Table 5.3.

Table 5.3. Results of ANOVA comparisons for the effects of species and treatment on the biomass ratios presented in Figure 1. For explanation of sources of variation and significance levels, see Table 5.1.

source of variation	leaf mass ratio	stem mass ratio	tap root mass ratio	fine root mass ratio
species	*	ns	ns	ns
light (Q)	*	ns	***	***
nutrients (N)	ns	ns	ns	ns
interactions	ns	ns	ns	species x Q x N *

Shoot architecture

While the two species did not differ in LAR, they did differ strongly in the way their leaves were arranged (Table 5.4). In both light environments *S. leprosula* produced a denser canopy (higher leaf area / stem length ratio) with leaves arranged on shorter, thicker internodes (Table 5.4). *S. parvifolia* branched more frequently and had leaves arranged more sparsely on longer branches. Only *S. leprosula* increased its branch frequency in response to high light (significant species x Q interaction; Table 5.4). For both species total branch length was greater in high light, but internodes were shorter and leaf area more densely arranged (Table 5.4).

Table 5.4. Shoot architecture at the end of the treatment period. All values are means ± 1 SE (n = 20). For explanation of treatments and sources of variation, see Table 5.1.

Treatment	branch frequency (branches m^{-1})	total branch length (m)	leaf area : stem length ratio (m^2 cm^{-1})	internode length / diameter (m m^{-1})
S. leprosula				
HQ	5.2 ± 0.4	0.63 ± 0.08	9.8 ± 0.6	27.6 ± 1.7
LQ	1.5 ± 0.3	0.11 ± 0.04	5.5 ± 0.4	36.0 ± 2.7
S. parvifolia				
HQ	6.3 ± 0.6	0.74 ± 0.11	6.7 ± 0.4	38.0 ± 2.4
LQ	6.8 ± 0.7	0.37 ± 0.07	4.1 ± 0.3	56.1 ± 7.4
source of variation †				
species	***	*	***	***
light (Q)	***	***	***	*
interactions	species x Q ***	Ns	ns	ns

† No significant nutrient effects. Means calculated from pooled data.

Mycorrhizal associations

For 13 of the 80 plants no mycorrhizas were found. Mycorrhiza free plants were homogeneously distributed with respect to species and treatments (Chi square, between species, light or nutrient treatments, $\chi^2 < 0.7$, n = 2, $p > 0.25$), allowing the assumption that these plants were not infected at the beginning of the experiment. Non-mycorrhizal plants were excluded from analysis of treatment effects on mycorrhizal associations.

In plants with mycorrhizas, light and nutrient treatments significantly influenced mycorrhizal infection rates, and the two species differed both in degree of infection and types of fungal associates present (Table 5.5). Overall, mycorrhizal infection rates were significantly higher for low nutrient treatments. While variable, nutrient effects were stronger for high light treatments and for *S. parvifolia* than *S. leprosula*. Mycorrhizal infection was significantly higher in high light treated plants, and higher in *S. leprosula* than *S. parvifolia* for all combinations of light and nutrient supply (Table 5.5).

Sixteen mycorrhizal types were found on the seedling roots; 9 on roots of *S. leprosula* and 13 on *S. parvifolia*, 6 were common to both species of seedling. The majority of mycorrhizal types encountered were typical of those already recorded on wild seedling roots in Kalimantan (Effendi *et al.*, 1997), with *Riessiella* sp. the most common type.

Table 5.5. Root mycorrhizal infection, leaf chlorophyll concentrations and chlorophyll a/b ratios at the end of the treatment period. (means ± 1 SE , n = 7 - 9 for mycorrhizal infection - uninfected plants excluded; n = 5 for chlorophyll values). For explanation of treatments and sources of variation, see Table 5.1. Curly brackets next to a pair of means indicates a significant difference (contrast) between high and low nutrient treatments within that species and light combination.

Treatment	mycorrhizal infection (%)	Chlorophyll a+b / fresh mass (mg g^{-1})	Chlorophyll a+b / area (mg m^{-2})	Chlorophyll a/b ratio
S. leprosula				
HQ HN	73 ± 9	5.0 ± 0.6 } ***	500 ± 66 } **	2.5 ± 0.2
HQ LN	89 ± 8	2.8 ± 0.4	300 ± 41	2.7 ± 0.3
LQ HN	61 ± 12	5.5 ± 0.4	403 ± 21	2.4 ± 0.1
LQ LN	47 ± 8	6.2 ± 0.3	478 ± 47	2.1 ± 0.1
S. parvifolia				
HQ HN	61 ± 10 } *	2.7 ± 0.2	315 ± 31	2.4 ± 0.1
HQ LN	83 ± 10	3.0 ± 0.3	320 ± 26	2.3 ± 0.2
LQ HN	8 ± 1	3.7 ± 0.5	378 ± 21	2.0 ± 0.1
LQ LN	36 ± 10	4.3 ± 0.4	426 ± 38	2.1 ± 0.1
source of variation				
species	**	***	*	ns
light (Q)	***	***	*	**
nutrients (N)	*	Ns	ns	ns
interactions	ns	species x Q x N *	species x Q x N *	ns

Foliar chlorophyll and nutrient content

Leaf chlorophyll per unit mass was reduced and the chlorophyll a:b ratio increased in high light (Table 5.5). *S. leprosula* had higher leaf chlorophyll concentrations than *S. parvifolia* (Table 5.5). Low nutrient treatment reduced extracted leaf chlorophyll content in high light treated *S. leprosula* plants (significant species x Q x N interactions, Table 5.5), but had no effect on chlorophyll content of *S. parvifolia* leaves. Indirect measurements of chlorophyll content on intact leaves using a Minolta Chlorophyll meter (SPAD-502, Minolta Camera Co., Osaka) confirmed a reduced chlorophyll content in low nutrient, high light treated *S. leprosula* (data not shown).

Treatment effects on foliar nutrient concentrations were very different for the two macro-nutrients examined. Foliar nitrogen per unit mass was insensitive to nutrient supply, while phosphorus content varied strongly in response to nutrient supply, especially for *S. parvifolia* (Table 5.6). Overall light treatment effects on nitrogen and phosphorus per unit mass were not significant, but there were differences which influenced the calculation of photosynthetic rates on a nitrogen basis (Table 5.7). There was a small increase in nitrogen per unit mass of *S. parvifolia* leaves in high light, while the nitrogen per unit mass of *S. leprosula* leaves was not related to light treatment. Average foliar N (mg g $^{-1}$) of *S. leprosula* was 15 % greater than *S. parvifolia*, but foliar P (mg g $^{-1}$) of *S. leprosula* was 40 % lower than *S. parvifolia* (Table 5.6). Low nutrient treated plants of *S. parvifolia* had roughly half the foliar P content of high nutrient plants, while for *S. leprosula* nutrient treatment effects on foliar P were smaller and non-significant (significant interactions; Table 5.6).

Table 5.6. Foliar nitrogen and phosphorus at the end of the treatment period. (means ± 1 SE, n = 5). For explanation of treatments and sources of variation, see Table 5.1. Curly brackets next to a pair of means indicates a significant difference (contrast) between high and low nutrient treatments within that species and light combination.

Treatment	Foliar N area (g m^{-2})	Foliar N dry mass (mg g^{-1})	Foliar P area (g m^{-2})	Foliar P dry mass (mg g^{-1})
S. leprosula				
HQ HN	1.10 ± 0.14	23.8 ± 1.9	0.116 ± 0.012	2.5 ± 0.1
HQ LN	0.97 ± 0.06	20.2 ± 0.7	0.094 ± 0.010	2.0 ± 0.2
LQ HN	0.70 ± 0.07	20.3 ± 1.9	0.054 ± 0.006	1.6 ± 0.2
LQ LN	0.82 ± 0.07	22.6 ± 1.2	0.066 ± 0.006	1.8 ± 0.2
S. parvifolia				
HQ HN	0.99 ± 0.13	19.9 ± 2.3	0.200 ± 0.010 } ***	4.1 ± 0.3 } **
HQ LN	0.80 ± 0.08	18.9 ± 1.4	0.089 ± 0.005 }	2.1 ± 0.1 }
LQ HN	0.63 ± 0.03	18.1 ± 0.8	0.147 ± 0.023	4.4 ± 0.8
LQ LN	0.67 ± 0.04	18.6 ± 1.2	0.108 ± 0.037	3.2 ± 1.1
source of variation				
species	ns	*	***	***
light (Q)	***	ns	**	ns
nutrients (N)	ns	ns	***	**
interactions	ns	ns	species x N ** Q x N *	species x N * species x Q *

Nitrogen and phosphorus per unit leaf area were usually higher in high light (Table 5.6), the indirect result of reduced SLA (Table 5.2). N per unit area was higher for *S. leprosula* than *S. parvifolia* for each treatment combination, but this difference was marginally non-significant (Table 5.6; $F = 3.7, p = 0.06$).

Photosynthetic response to light

Light saturated rates of photosynthesis per unit area doubled when plants were grown in high light, but were unaffected by nutrient supply. In both light treatments, *S. leprosula* had higher rates than *S. parvifolia* (Table 5.7, Fig. 5.2). Differences between light treatments and species were smaller when $A_{\max}$ was expressed per unit leaf mass, and were not significant when $A_{\max}$ was expressed per unit nitrogen, although $A_{\max}$ per unit nitrogen was marginally higher for *S. leprosula* (species effect, $F = 3.4$, $p = 0.07$, Table 5.7). This suggests that differences in photosynthetic capacity between species and light treatment were mostly related to reduced SLA in high light and slightly higher leaf nitrogen per unit area in *S. leprosula* (Tables 5.2 & 5.6). In *S. leprosula* there were no clear changes in nitrogen per unit mass with light treatment (Table 5.6), and there was therefore a small but non-significant increase in $A_{\max}$ per unit nitrogen (Table 5.7). In *S. parvifolia* there were small increases in nitrogen per unit mass in high light (Table 5.6), and no change in $A_{\max}$ per unit nitrogen (Table 5.7). Photosynthetic capacity was unrelated to leaf phosphorus content (Tables 5.6). The rate of dark respiration was higher in high light plants on an area, mass and nitrogen basis (Table 5.7, R_d per unit mass and nitrogen not shown).

Light and species effects on other photosynthetic parameters matched their effects on photosynthetic capacity. Parameters describing photosynthesis at low PPFD differed significantly between light treatments but not between species (Table 5.8, Fig. 5.2). Apparent quantum efficiency was lower and the light compensation point higher in high light. Parameters describing photosynthesis at saturating PPFD differed between light treatments and species (Table 5.8, Fig. 5.2). Maximum conductance and the light saturation point were higher for high light plants and higher for *S. leprosula* than *S. parvifolia* (the light treatment effect on Q_{sat} was non significant, $F = 3.5$, $p = 0.08$). Stomatal density was higher for high light plants, but did not differ between species (HQ mean = 358 ± 8 pores mm^{-2}, LQ mean 270 ± 9 pores mm^{-2}, F = 45, p<0.001). The convexity of the light response curve varied between 0 and 0.87 (mean = 0.49, SEM = 0.06) but no relationship between convexity and treatment or species could be detected (F = 1.0, p = 0.46). Variability in Q_{sat} and convexity reflects variability in the goodness of fit of the photosynthetic model. Model predictions were better for low light treated plants and for photosynthesis at lower PPFDs (Fig. 5.2).

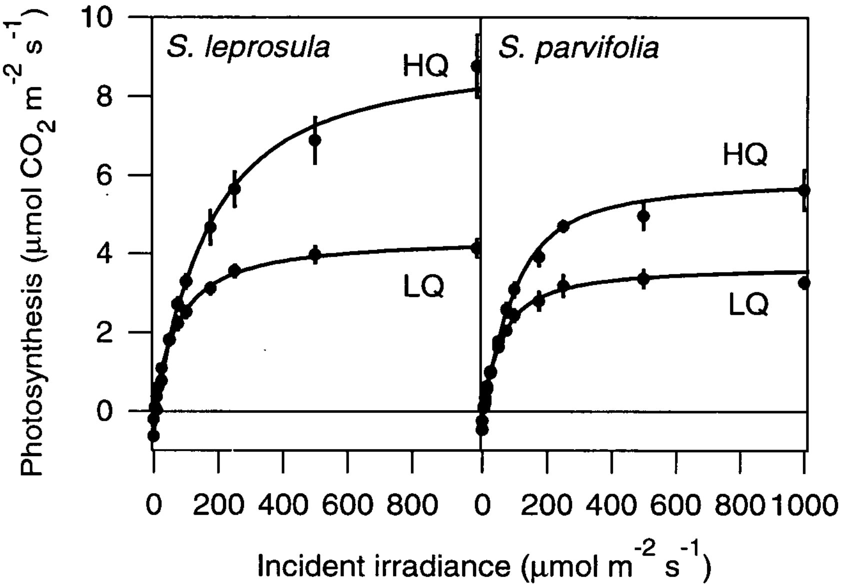


Fig. 5.2. Observed and modelled photosynthetic response to light for leaves of *S. leprosula* and *S. parvifolia* seedlings grown at high (HQ) and low PPFD (LQ). Points indicate means ± 1 SE for the observed values. There was no significant nutrient effect on photosynthesis; values for high and low nutrient treatments were pooled (n = 6). Lines indicate the modelled response, using the parameter values given in Tables 5.7 & 5.8.

Table 5.7. Maximum photosynthesis (A_{max}) on an area, mass and nitrogen basis, and dark respiration (R_d) on an area basis. For explanation of treatments and sources of variation, see Table 5.1. (means ± 1 SE, n = 6).

Treatment	A_{max} area (μmol CO_2 m^{-2} s^{-1})	A_{max} mass (nmol CO_2 g^{-1} s^{-1})	A_{max} Nitrogen (μmol CO_2 mol^{-1} s^{-1})	R_d area (μmol CO_2 m^{-2} s^{-1})
S. leprosula				
HQ	9.1 ± 0.9	185 ± 17	112 ± 11	-0.65 ± 0.08
LQ	4.4 ± 0.3	132 ± 6	85 ± 6	-0.21 ± 0.02
S. parvifolia				
HQ	5.9 ± 0.6	130 ± 16	83 ± 7	-0.48 ± 0.08
LQ	3.7 ± 0.3	110 ± 10	81 ± 4	-0.25 ± 0.02
source of variation †				
species	**	*	ns	ns
light (Q)	***	*	ns	***
interactions	ns	ns	ns	ns

† No significant nutrient effects. Means calculated from pooled data.

Table 5.8. Apparent quantum efficiency (ϕ), maximum conductance, and the light compensation and saturation points of photosynthesis (*Q* compensation and *Q* saturation) after treatments. (means ± 1 SE, n = 6).

Treatment	ϕ (mol mol^{-1})	Maximum conductance (mol H_2O m^{-2} s^{-1})	*Q* compensation (μmol m^{-2} s^{-1})	*Q* saturation (μmol m^{-2} s^{-1})
S. leprosula				
HQ	0.042 ± 0.002	0.160 ± 0.029	10.6 ± 1.3	1100 ± 192
LQ	0.050 ± 0.002	0.080 ± 0.014	3.8 ± 0.6	614 ± 132
S. parvifolia				
HQ	0.040 ± 0.003	0.093 ± 0.009	7.1 ± 1.1	503 ± 128
LQ	0.046 ± 0.002	0.065 ± 0.012	3.9 ± 0.4	424 ± 116
source of variation †				
species	ns	*	ns	*
light (Q)	**	*	***	ns
interactions	ns	ns	ns	ns

† No significant nutrient effects. Means calculated from pooled data.

5.4 Discussion

Response to nutrients: interactions with light and mycorrhizas

S. leprosula and *S. parvifolia* seedlings were tolerant of low nutrient availability, at least at the levels tested in this experiment. The use of wild seedlings and a constant nutrient addition rate makes it difficult to exclude the effects of initial seedling size on the degree of nutrient limitation achieved (Ingestad and Ågren, 1992). It is possible that nutrient addition rates were not low enough to achieve significant nutrient limitation, but similar low nutrient treatments have caused large reductions in the growth of other tropical tree species (Riddoch, Lehto and Grace, 1991; Lehto and Grace, 1994). Low nutrient supply only affected these *Shorea* seedlings when they were growing fast in response to high light. Reductions in the leaf chlorophyll concentrations of *S. leprosula* suggests nutrient limitation had at least begun (Table 5.5), but there was no overall nutrient effect on growth. Increased mycorrhizal infection and fine root partitioning suggest that compensatory increases in nutrient uptake capacity occur when nutrient supply is low and demand high (Marschner, 1995).

Mycorrhizal infection increases in response to low nutrient supply in temperate ectomycorrhizal species (Marx, Hatch and Mendecino, 1977; Holopainen and Heinonentanski, 1993; Wallander, 1995), but it has not previously been clearly documented for the Dipterocarpaceae (Turner, Brown and Newton, 1993). A similar effect is known to nursery workers who have observed reduced dipterocarp mycorrhizal infection after excessive fertiliser addition (Aldrianto Priadjati, personal communication). For *S. leprosula*, infection rates have been correlated with seedling size (Becker, 1983b) and leaf phosphorus contents in wild seedlings when soil P availability was low (Lee and Lim, 1989). Mycorrhizal infection is thought to increase the volume of soil exploited and enhance the nutritional status and growth of the host plant when soil nutrients are limiting, especially through increased rates of phosphorus uptake (Alexander, 1989; Koide, 1991).

Mycorrhizal infection was also enhanced in plants growing in high light, an effect already reported for wild *S. leprosula* and *S. parvifolia* seedlings growing in disturbed areas (Becker, 1983b; Lee, 1988; Effendi *et al.*, 1997). Lower nutrient availability *per se* or faster growth in response to high light both increase the potential deficit between rates of nutrient supply and demand for a given plant (Koide, 1991). The mechanisms leading to greater infection under either condition may therefore be the same. Accumulation of photosynthate in high light may also enhance root exudation and hence microbial activity (Grayston, Vaughan and Jones, 1997).

It can be hypothesised that *S. leprosula* and *S. parvifolia* will be relatively unresponsive to fertilisation except under extreme conditions when the demand for nutrients is high and soil nutrient status low. Fertilisation of wild seedlings of other dipterocarp species has usually had no effect, suggesting that soil nutrients may already have been adequate or that growth rates were limited by light availability rather than nutrients (Burslem, 1993; Turner, Brown and Newton, 1993). Experiments demonstrating faster growth after nutrient addition have usually been for seedlings growing in high light in poor soils, for example seedlings growing in pots in the nursery (Bruzon, 1982; Sundralingam, 1983; Sundralingam, Hotta and Osumi, 1985) or in disturbed soils after logging (Kustiawan, 1991; Nussbaum, Anderson and Spencer, 1995). In an extreme example, Nussbaum *et al.* (1995) found that mycorrhizal *S. leprosula* and *Dryobalanops lanceolata* seedlings planted into compacted mineral soil on open log landings responded strongly to fertilisation or the addition of forest topsoil. It can be concluded that fast growing dipterocarp species are unlikely to be strongly nutrient limited when naturally established in undisturbed forest soil under open or closed canopy, but they may respond to fertilisation when planted into disturbed soils under open conditions.

Physiological characteristics of fast growing dipterocarps

The phenotypic plasticity of these dipterocarp seedlings was high in comparison with other tropical climax species (Chazdon *et al.* 1996). This plasticity may be an important component of their ability to tolerate shade suppression and to grow rapidly under very open conditions (Brown and Whitmore, 1992; Tuomela *et al.* 1996; Whitmore, 1996). Doubling of $A_{\max}$area between low and high light represents a high acclimation potential (Chazdon *et al.* 1996), and maximum rates in high light were high compared to the seedlings of other tropical climax species (Riddoch *et al.* 1991; Poorter and Oberbauer, 1993; Strauss-Debenedetti and Bazzaz, 1996). Branch frequency and leaf area density were increased in high light, and at the leaf level there were decreases in SLA (Table 5.4). Low leaf area density will reduce self shading in low light, while high leaf area density will increase light interception when light availability is high (Canham, 1988; Bonser and Aarssen, 1994).

Increased photosynthetic capacity in high light was achieved through both increased tissue mass per unit leaf area and increased photosynthetic capacity per unit leaf mass (decreased SLA and increased A_{max} mass; Tables 5.2 & 5.7). Nitrogen content per unit area increased with decreasing SLA in high light and was therefore correlated with increases in photosynthetic capacity. Photosynthetic capacity is usually correlated with nitrogen content, and photosynthetic acclimation of leaves within canopies or between plants growing in contrasting environments is normally achieved through changes in leaf nitrogen content (Field and Mooney, 1986; Anten *et al.*, 1996). In this example, increases in nitrogen concentration were probably achieved mostly through changes in the quantity of photosynthetic tissue per unit area, rather than an increase in nitrogen content per unit leaf mass (light effect strong for A_{max} per unit area, but weak for A_{max} per unit mass). Variation in A_{max} per unit mass with light environment is characteristic of light demanding species (Chazdon and Kaufmann, 1993; Chazdon *et al.* 1996). Although the results for the nitrogen versus photosynthetic capacity relationship were inconclusive, there may have been subtle differences between *S. leprosula* and *S. parvifolia* in the way nitrogen was allocated in response to irradiance (discussed below). If the two species are considered together, values of A_{max} per unit mass and per unit nitrogen were more similar to those reported for light demanding early or mid-successional species than to truly shade tolerant climax species (Field and Mooney, 1986; Reich, Ellsworth and Uhl, 1995; Raaimakers *et al.* 1995, Walters and Reich, 1996).

Infrequent seeding and the lack of seed dormancy means that the survival of seedlings for long periods in the shade is also an important feature of the regeneration ecology of the Dipterocarpaceae (Fox, 1972; Whitmore, 1984). Both species exhibited typical acclimatory responses to shade, including reductions in dark respiration rates and a shift in emphasis from high maximum rates of photosynthesis towards increased light harvesting capacity: higher SLA, higher chlorophyll concentrations, lower chlorophyll a:b ratio (Boardman, 1977; Chazdon, 1992). Higher apparent quantum efficiencies in the shade also suggest greater absorption of incident light. The reduction in respiration rate is greater than the corresponding changes in SLA and nitrogen per unit area, indicating acclimation at the metabolic level which goes beyond a simple reduction in the size of the photosynthetic apparatus. A low respiration rate is thought to be an important component of shade adaptation in other tropical species (Turnbull, Doley and Yates, 1993; Chazdon *et al.* 1996; Chapter 6).

Comparing closely related dipterocarp species

Canopy architecture and photosynthetic capacity in high light were the most useful indicators of species differences in growth rates and ecological preferences. *S. leprosula* can be classified as more light demanding than *S. parvifolia* on the basis of light demanding architectural traits alone. These include increased branching in response to high light, shorter, thicker internodes and more densely arranged leaves in both light treatments (Givnish, 1988; Canham, 1988; Bonser and Aarssen, 1994). *S. parvifolia* branched frequently in both light environments and had leaves arranged more sparsely on longer, thinner axes. This growth form is thought to be more favourable in shaded environments, where a spreading architecture may better exploit a spatially variable light environment (Kohyama, 1991). Zipperlen and Press (1996) reached similar conclusions after comparing *S. leprosula* with *Dryobalanops lanceolata*, a shade tolerant dipterocarp species which also has lower photosynthetic rates and a more spreading architecture.

Photosynthetic traits also distinguish *S. leprosula* as more demanding of light and nutrients than *S. parvifolia*. The higher net assimilation rate and A_{max} per unit area of *S. leprosula* was associated with higher leaf nitrogen and chlorophyll contents. The two species may have differed in the total amount of nitrogen partitioned to the photosynthetic apparatus, and in the partitioning of nitrogen within the photosynthetic apparatus. In *S. leprosula* there was a small increase in A_{max} per unit nitrogen in high light, while in *S. parvifolia* there was a small increase in nitrogen concentrations and no change in A_{max} per unit nitrogen. While these changes were marginally non-significant, they are in agreement with earlier studies which have shown that more light demanding species are more likely to show decreases in nitrogen use efficiency during acclimation to low light (Evans, 1989; Reich *et al.* 1994; Reich, Ellsworth and Uhl, 1995). Light demanding species generally show greater capacity for increased partitioning of nitrogen to carbon fixing compounds, and reduced capacity for partitioning to the light harvesting (thylakoid membranes) components (Evans, 1989; Press *et al.*, 1996). In shade tolerant species, increased partitioning of nitrogen to the thylakoid membranes in low light tends to compensate for lower rates of carbon fixation per unit chlorophyll. Photosynthetic capacity per total leaf nitrogen therefore remains more constant (Evans, 1989), as was observed for *S. parvifolia.* Overall, the results suggest marginally higher and more variable photosynthetic rates per unit nitrogen for *S. leprosula*, a finding which warrants further investigation given the important links between nutrient use and growth rates. Photosynthetic nitrogen use and whole plant nitrogen use efficiency are correlated (Garnier, Gobin and Poorter, 1995), and nitrogen concentrations and nitrogen use efficiencies are normally both higher in true pioneer species (Field and Mooney, 1986). Faster growth rates and higher foliar nitrogen concentrations mean that if *S. leprosula* and *S. parvifolia* seedlings were compared at the same plant size, *S. leprosula* would have higher rates of nutrient uptake and may be more susceptible to nutrient limitation.

Species differences in foliar phosphorus concentration (Table 5.6) also suggest inherent differences in patterns of nutrient use. Phosphorus concentrations were not related to photosynthetic capacity or growth rates, suggesting the nutrient treatment effect on *S. parvifolia* foliar phosphorus concentration was the result of 'luxury' phosphorus uptake in the high nutrient treatment rather than a nutrient deficiency in the low nutrient treatment. Luxury consumption when nutrient availability is high is characteristic of slower growing plants adapted to low nutrient environments (Marschner, 1995).

Growth rates alone were a less reliable indicator of species light requirements than architectural and photosynthetic traits. *S. leprosula* had the most light demanding architectural and photosynthetic characteristics, but grew faster in both the high light *and* shade (Table 5.2). Walters and Reich (Walters and Reich, 1996) argued that survival in the shade should be positively related to growth - species that maintained the highest RGR should also have the highest survival rates. It is possible that *S. parvifolia* would have grown faster than *S. leprosula* if the seedlings were grown at light levels that more closely approximated deep shade (Walters and Reich, 1996), but Lee *et al.* (1996) used lower controlled light levels and also found that shade-intolerant species (non dipterocarp) grew at least as fast as shade tolerant *S. singkawang* and *Dryobalanops aromatica.* In two studies which compared forest understorey growth and survival of *S. leprosula* seedlings with more shade tolerant dipterocarp species, *S. leprosula* again had faster height growth but lower rates of survival (Becker, 1983a; Zipperlen and Press, 1996). Becker (1983a) found that *S. leprosula* suffered higher rates of herbivory than *S. maxwelliana*, but partial artificial defoliation had no effect on seedling survival. Zipperlen and Press (1996) proposed that lower investment in leaf defence and maintenance by *S. leprosula* may have contributed to its lower survival when compared with *Dryobalanops lanceolata.*

The arguments used above to explain contradictions between growth rates and shade tolerance are similar to those used to explain plant responses to nutrients. In short experiments with low nutrient levels, inherently fast growing species from productive habitats often have higher growth rates than slower growing species from less productive habitats (Vanderwerf *et al.* 1993). The competitive advantage of fast growing species over the long term is thought to be reduced in the low nutrient environment by higher rates of biomass turnover (Vanderwerf *et al.* 1993; Ryser and Lambers, 1995). Here it is proposed that similar processes occur when tree seedlings with inherently different light requirements and growth rates are shaded. Faster initial growth is accompanied by the production of shorter lived leaves with higher foliar nutrient concentrations. Over the long term the resulting increased susceptibility to herbivory and faster rates of biomass turnover will reduce the competitive advantage of the fast growing species. More shade tolerant species will grow more slowly and produce fewer longer lived leaves (Kitajima, 1994). In this study, *S. leprosula* lost old leaves and developed new ones faster than *S. parvifolia*, even in the low light environment (Table 5.2). A study of wild dipterocarp seedling demography in undisturbed forest confirmed that shade intolerant species had faster height growth and higher mortality than more shade tolerant species, but there were no clear differences between *S. leprosula* and *S. parvifolia* (Still, 1996).

Conclusions

Seedlings of *S. leprosula* and *S. parvifolia* can be considered well adapted to low nutrient availability. The hypothesis that growth would become nutrient limited at high light intensities was not confirmed - signs of nutrient deficiency were only beginning to occur at the end of the experiment. Tolerance of low nutrients was possibly enhanced by increased mycorrhizal infection when nutrient availability is low and demand is high. Results from this experiment do not exclude a rôle for nutrient limitation when seedlings are planted under open conditions in the field, but they indicate nutrient availability may only be limiting when soil conditions are very poor and nutrient demand is high. If fertiliser application is to be considered as part of a management program, it should be managed to avoid undue suppression of mycorrhizal activity, and field trials should be conducted to determine when fertiliser application will be of benefit.

S. leprosula and *S. parvifolia* demonstrated extensive architectural and photosynthetic plasticity and can be considered light demanding opportunists when compared with other climax species. This implies that they will demonstrate architectural and photosynthetic adjustment across a wide range of light environments, and provides a partial explanation of their ability to tolerate shade and grow well in exposed locations (Whitmore, 1996).

These two closely related species could be clearly contrasted on the basis of their growth, architectural and physiological responses to variation in light and nutrient availability. The results from all three classes of measurement reinforced the classification of *S. leprosula* as more demanding of light and nutrient resources. *S. leprosula* may therefore be more suitable for planting when soil conditions are better and is more likely to respond to fertilisation or mycorrhizal inoculation when soil conditions are poor. A combination of simple growth, architectural and physiological measurements may be the best method of ranking a larger selection of dipterocarp species for ecological and management purposes. Differences between species are likely to be greater in high light, but further species comparisons of long term survival and growth under natural shaded conditions are also required.

6. Rapid photosynthetic acclimation of *Shorea johorensis* seedlings after logging disturbance

6.1 Introduction

Tree regeneration after disturbance can occur from seed or from pre-existing seedlings. In the dipterocarp family of South-east Asia, there is no seed dormancy and most regeneration occurs from pre-existing, shade suppressed seedlings which survive the disturbance event (Ashton, 1989). The ability of seedlings to physiologically adjust or 'acclimate' to the dramatic changes in conditions which occur at the time of disturbance is therefore of central importance to the regeneration ecology of dipterocarps. Logging of dipterocarp rain forest is now widespread and the effects of logging on the seedling environment are severe (Chapter 3). Dipterocarps are sometimes poorly represented in logged over forest and growth in seedling height tends to reach a maximum at only moderate levels of canopy opening (Chapter 4; Adjers *et al.* 1995; Whitmore and Brown, 1996), suggesting that dipterocarp seedlings might be limited by their ability to acclimate to post logging conditions. This is supported by the common observation that seedlings grow faster in nurseries under partial shade (Nicholson, 1960; Sasaki and Mori, 1981; Aminuddin, 1986; Ashton, 1995). However, there are also examples of good regeneration after logging disturbance (Whitmore, 1984; Kuusipalo *et al.* 1996). This study examined the acclimation of a fast growing dipterocarp species after normal logging operations to determine whether seedling acclimation potential was a limiting factor for natural regeneration.

The central hypothesis of this study was that seedlings left in the most exposed sites would be unable to acclimate beyond the level achieved with more moderate canopy opening. Most rain forest plants exhibit at least some plasticity over the range of light environments encountered in natural forests (around 1 - 20% of above canopy light) and many are capable of significant acclimation within this range (Chazdon *et al.* 1996). Plasticity here refers to the total possible range of phenotypic variation, whereas acclimation is the response of an individual to a change in conditions (Chazdon *et al.*

1996). Normal logging operations in dipterocarp forest are more severe than most forms of natural disturbance (Chapter 3), and seedlings are exposed to a wider range of light environments. The hypothesis implies that new leaves which develop in open areas will have the same photosynthetic characteristics as leaves in areas with more moderate canopy opening (equivalent to natural treefall gaps). It also suggests that exposed seedlings will be more likely to suffer from long term photoinhibition (a reduction in photosynthetic efficiency caused by damage to photosystem II), because they are exposed to higher light intensities for longer periods without an increased capacity for photochemical dissipation of the excess absorbed energy (Long, Humphries and Falkowski, 1994; Skillman, Strain and Osmond, 1996). A study of potted central American tree seedlings concluded that long term photoinhibition was uncommon in canopy tree seedlings, except perhaps when nutrient availability was limiting (Castro, Fetcher and Fernandez, 1995). The photochemical tolerance of wild dipterocarp seedlings after logging disturbance has not been examined (Scholes, Press and Zipperlen, 1997), and the role of seedling nutrient status during dipterocarp regeneration is poorly understood (Lee, 1994).

A second hypothesis of this study was that dipterocarp seedlings are sensitive to the higher temperatures and lower humidities which occurs in logged areas. This hypothesis was prompted by the comparison of meteorological conditions in logged and unlogged areas (Chapter 3), and the observation that stomatal conductance was sometimes very low in newly exposed seedlings (M. Clearwater, unpublished data; Turner and Newton, 1990). It was proposed that closure of stomata in response to high vapour pressure gradients between the leaf and the air would limit seedling carbon gain and growth, and increase the susceptibility of seedlings to photoinhibitory damage. This effect of low humidity on stomatal conductance and carbon gain is well known for other species, and stomatal sensitivity sometimes increases with acclimation to a disturbed environment (Ellsworth and Reich, 1992; Tinocoojanguren and Pearcy, 1993). It was not know if conditions in logged over dipterocarp forest would be severe enough to have the same affect on dipterocarp seedlings.

A third hypothesis relates to the initial impact of canopy opening on shade suppressed seedlings. It was proposed that sudden exposure to high light intensities would cause severe photoinhibition and water stress, even when soil moisture content was high. Lovelock *et al.* (1994) showed that photoinhibition was common in rain forest tree seedlings after disturbance but that on its own it was unlikely to cause seedling death. Leaf bleaching and necrosis are common in nursery grown dipterocarp seedlings upon transfer to high light (Turner and Newton, 1990). In wild seedlings other stresses may co-occur with this type of damage (Lovelock *et al.*, 1994), causing slower seedling recovery or death. Water stress was considered likely for newly exposed dipterocarp seedlings because the root mass of shade suppressed seedlings is often dominated by a woody taproot, with very little fine root material. Poor rooting could impose a hydraulic limitation on seedling water use that was independent of soil moisture content. Transplanted dipterocarp wildlings are known to be susceptible to short term water stress (Palmiotto, 1993), and Veenendaal *et al.* (1996) have shown for the African species *Terminalia superba* and *Entandrophragma utile*, shaded seedlings with lower root to shoot ratios were more susceptible to drought than nearby seedlings growing in gaps.

To test these hypotheses, the photosynthetic properties, chlorophyll fluorescence and leaf water potentials of *Shorea johorensis* Foxw. seedlings were compared between recently logged and unlogged environments. Measurements were taken 3 months after logging, and at another site they were repeated for a smaller number of seedlings that had been exposed for only 2 weeks. *S. johorensis* is a common member of the commercially important red meranti timber group (Newman, Burgess and Whitmore, 1996). Its seedlings are fast growing and light demanding compared to other dipterocarp species (Seibert, 1990; Brown and Whitmore, 1992; Adjers *et al.* 1995; Brown, 1996; Otsamo *et al.* 1996; Still, 1996), and adult trees reach a large size (> 50 m in height, at least 1.6 m in diameter). Small *S. johorensis* seedlings were common in unlogged forest within the study area.

6.2 Methods

Site description

Measurements were made in logged tropical rain-forest in Central Kalimantan (Indonesian Borneo) between March 15 and April 13, 1996. The study area was located within the Kayu Tribuana Rama timber concession operated by PT Kayu Mas, approximately 10 km east of the Wanariset Sangai research station (01° 18' S 112° 23' E). The forest in the area is perhumid lowland dipterocarp rain forest. Annual rainfall is high (approximately 3500 mm), but a drier season usually occurs from July - October. Forest within the study area is designated a permanent production forest, and is managed for timber according to the Indonesian Selective Cutting and Planting (TPTI) system. Approximately 10 trees per ha are removed, but up to 50 % of the trees left remaining in the stand may be damaged or destroyed during extraction, leaving behind a mosaic of undisturbed and disturbed patches of forest (Bertault and Sist, 1995; Pinard and Putz, 1996).

Seedling selection and biomass measurements

The main study site had been logged approximately 90 days before measurements for this study began. The aim was to select *S. johorensis* seedlings that were initially of the same age and size, but that had been exposed to a range of different conditions since disturbance. Seedlings in disturbed environments had grown in height since logging, but the height of each seedling at the time of felling could be determined from the height of transition from distinctively shaped shade leaves to sun leaves. Using this approach, only seedlings under 1 m in height were included in the study, and it is assumed that they all originate from the same mast seeding event which occurred at least one 1 year earlier. Ten seedlings were selected from each of three subjectively defined environments - forest with undisturbed canopy, forest with partially open canopy (e.g. on the margin of an undisturbed area) and sites with no remaining overhead canopy (open).

The second study site was 5 km from the main site and had been logged 14 days prior to the taking of physiological measurements. To assess the initial impact of canopy opening on shade suppressed seedlings, ten seedlings were selected from a single large canopy gap. Seedlings in this area had not begun growing since disturbance, but were larger than seedlings in the undisturbed area of the main study site. It is therefore assumed that they originate from an earlier mast seeding.

All seedlings were individually tagged and their height and stem diameter at the root collar recorded. Physiological measurements were taken over one month at the main study site, and for 4 days in the middle of the same month at the second study site. At the end of the study period, all seedlings were harvested, separated into roots, stems and leaves, dried at 80 °C for 24 hours and the mass of each component recorded. Fine root mass was defined as total root mass minus the mass of the woody taproot. All leaves were photographed before drying, and leaf area estimated using a computer based image analysis package (Optimas 5.2, Optimas Corporation, Washington).

Meteorological measurements and hemispherical photography

Air temperature, relative humidity and photosynthetic photon flux density (PPFD) were recorded continuously near seedlings growing under open conditions, using a copper-constantan thermocouple, a relative humidity probe (HMP35AC, Campbell Scientific Ltd., Leicestershire, UK) and a quantum sensor (SKP215, Skye Instruments Ltd., Powys, UK), all connected to a datalogger (Delta-T Devices Ltd., Burwell, Cambridge, UK) set to record every minute and store average values every 10 minutes. An identical set of equipment was used to record conditions in the undisturbed area. Hemispherical photographs were taken at the shoot apex of each seedling under overcast conditions using a Nikkor 8 mm fish eye lens (Nikon Corporation, Tokyo), Kodachrome 200 ISO slide film, and exposure times set using a photographic spot meter (Minolta Spotmeter F). The photographs were digitised and analysed according to standard methodology (Chapter 2) to provide estimates of the mean diffuse (T_d) and direct (T_b) site factors for the study period. The global site factor (T_t) was calculated as 0.6 T_d + 0.4 T_b, with the weightings representing the average proportions of indirect and direct PPFD incident above the canopy (Chapter 2).

Leaf temperatures, water potentials and pre-dawn chlorophyll fluorescence.

The temperature of the uppermost leaves of all seedlings in the main study site was recorded every 2 -3 hours on 6 days between 20 March and 12 April using an infra-red thermometer (AGA Thermopoint 80, AGEMA Infrared Systems Ltd, Bedfordshire, UK). For each temperature measurement it was noted whether the leaf was receiving direct sunlight at the time. The ratio of variable to maximum fluorescence (F_v/F_m) was measured at dawn (i.e. 12 hour dark relaxation period) on 5 days between 20 March and 12 April using a portable fluorimeter (PSM II, Biomonitor SCI, Umeå, Sweden). Two measurements were made on the uppermost fully expanded leaves of each seedling. Leaf water potentials were measured at dawn, mid morning and mid afternoon on four days between 20 March and 12 April using a pressure chamber (Skye SKPM 1400). Leaves were taken from adjacent *S. johorensis* seedlings to avoid affects on the seedlings selected for detailed study. Identical leaf temperature, chlorophyll fluorescence and water potential measurements were made between 5 and 8 April in the area logged two weeks before measurements.

Photosynthetic response to light and vapour pressure deficit

The response of leaf photosynthesis to light and the vapour pressure deficit was investigated using a portable, closed photosynthesis system (LI-6200, LI-COR Instruments, Nebraska), with light provided by a red light emitting diode light source (Q-Beam 2001-A, Quantum Devices Inc., Barneveld, Wisconsin; Tennessen, Singsaas and Sharkey, 1994). The CO_2 concentration and humidity of the incoming air stream was controlled using a gas mixing system (CIRAS, PP Systems, Hitchin, Herts., U.K.). Average leaf chamber CO_2 concentration, air temperature and leaf temperature during measurements were 342 μmol mol^{-1} (range 300 - 365 μmol mol^{-1}), 31 °C (range 27 - 37 °C) and 32 °C (range 27 - 38 °C), respectively. Mean leaf temperature during measurements within each environment varied from 30.7 °C in the undisturbed environment to 32.5 °C in the open environment. The leaf to air vapour pressure deficit at the leaf surface (D_s) was calculated from temperature and relative humidity and expressed on a mole fraction basis by dividing by atmospheric pressure (Monteith and Unsworth, 1990). For the light response, the average D_s was 12 mmol mol^{-1} (range 8 -

18 mmol mol^{-1}) and the PPFD incident on the leaf was varied from 0 - 1200 μmol m^{-2} s^{-1}. Leaves were first allowed to reach a constant rate of photosynthesis at a PPFD of 250 - 500 μmol m^{-2} s^{-1}, then stepped up to light saturation and back down to darkness over a period of approximately 2 hours, allowing photosynthesis and stomatal conductance to reach a steady state at each intermediate PPFD. A dark respiration value was obtained after the leaf was darkened for at least 15 minutes. For the D_s response, PPFD was held at a constant 750 μmol m^{-2} s^{-1} (assumed to be saturating) and D_s gradually increased in steps of 4 mmol mol^{-1} from approximately 8 to 45 mmol mol^{-1} by diverting a proportion of the incoming air-stream through desiccant (W.A. Hammond Drierite Co., Xenia, Ohio). The range of D_s achieved for each leaf varied with ambient conditions.

The response of photosynthesis to light was measured on the uppermost fully expanded leaf of a random subsample of five seedlings in each environment at the main site, and four seedlings at the recently disturbed site. The response to D_s was measured on three of the leaves used for light response, excluding seedlings in the partially open site. Where possible, measurements on open growing seedlings were conducted in the morning before they had been exposed to direct sunlight.

A non-rectangular hyperbola was fitted to the photosynthetic light response for each plant:

$$\theta A^2 - (\phi Q + A_{\max})A + \phi Q A_{\max} = 0 \qquad (6.1)$$

(Ogren and Evans, 1993), where A is rate of assimilation of CO_2 (μmol CO_2 m^{-2} s^{-1}), A_{max} is the rate of assimilation at light saturation, ϕ is the apparent quantum efficiency (mol CO_2 mol incident photons $^{-1}$), Q is incident PPFD (μmol m^{-2} s^{-1}) and θ is the convexity (rate of bending). To avoid correlation between ϕ and θ during curve fitting (especially when θ is low), ϕ was first found by least squares regression of the initial linear portion of the curve, including darkness (Leverenz, 1988). After solving for A and adding a dark respiration term (Zipperlen and Press, 1996), the model was fitted to the experimental data and values of A_{max} and θ estimated using non-linear regression (NLIN Marquardt procedure, SAS Institute Inc.). The light compensation point (PPFD at which $A = 0$) was found as the x intercept of the initial linear portion of the curve, including darkness. The light saturation point (PPFD at which $A = 90\% A_{\max}$) was found after solving equation 6.1 for Q (Zipperlen and Press, 1996).

Stomatal sensitivity to D_s was examined by taking the natural logarithm of stomatal conductance to water vapour (g_s) (Comstock and Ehleringer, 1993), and comparing the slopes of the $\ln(g_s)$ vs D_s relationship for each environment (Analysis of Covariance, SAS Institute Inc.). This approach is equivalent to assuming that stomatal conductance declines as a negative exponential function of D_s. Two common empirical descriptions of the relationship between g_s, A and D_s (the Ball, Woodrow and Berry (1987) model, as modified by Leuning (1995), and the Lambda function, Lloyd and Farquhar, 1994) were also successfully fitted to the data, but the parameters for these models were more difficult to interpret in terms of stomatal sensitivity to D_s and did not provide any further insight.

Total nitrogen and phosphorus content was determined for all leaves used in gas exchange measurements. Leaves were harvested, dried at 80 °C, ground, and 0.1 g samples wet digested in a mixture of concentrated H_2SO_4 and H_2O_2 (Grimshaw, Allen and Parkinson, 1989). Total nitrogen content of the digest was determined by gas diffusion using a flow injection analyser (Fiaster, Tecator Ltd., Wilsonville, Oregon) and total phosphorus with a molybdenum blue method and the flow injection analyser.

Daily carbon gain

A simple model of daily carbon gain was used to test the significance of photosynthetic acclimation responses for long term growth and survival. Carbon gain was predicted from equation 6.1 and continuous measurements of PPFD, assuming an instantaneous response of photosynthesis to changes in PPFD. This approach served to integrate the effect of environment and phenotype on seedling performance. Carbon gain was estimated on a leaf area basis and does not include respiration by other plant parts or photosynthetic induction responses to fluctuating light. Both of these effects will reduce whole plant carbon gain below that predicted in this study. Three simulations were used to test the sensitivity of daily carbon gain to a) variation in the parameters of the photosynthetic light response, b) stomatal closure in response to humidity deficits and c) variation in total daily PPFD.

A. The sensitivity of daily carbon gain to variation in dark respiration (R_d), ϕ, and A_{max} was examined using measurements from the two light sensors located in the undisturbed and open environments. Carbon assimilation of seedlings growing in each environment was predicted at ten minute intervals over a week long period using equation 6.1, with all parameters held at their observed mean value, and then with each parameter allowed to vary while the other two were held at their mean values. The mean assimilation rate for the week was used to calculate average daily carbon gain for each set of photosynthetic parameters. The effect of temperature on respiration (night time respiration was likely to be lower than R_d measured during the day) was accounted for by calculating R_d during darkness as an exponential function of air temperature, assuming a Q_{10} value of 2 and using the measured R_d and leaf temperature at the time of measurement as the reference point (Hagihara and Hozumi, 1991). During the day R_d was held fixed at the measured value.

B. A simple linear regression describing the relative decline in A_{max} with increasing D_s was used to quantify the potential effect of stomatal closure in response to D_s on daily carbon gain (Results, Fig. 6.5d). Two estimates of D_s were made for each ten minute interval, with leaf temperature (T_{leaf}) assumed to be either equivalent to T_{air} (no leaf temperature effect on D_s) or with T_{leaf} calculated as a simple linear function of PPFD (Q):

$$T_{leaf} = T_{air} + 12(Q / 2000) \qquad (6.2)$$

where the values 12 °C and 2000 μmol m^{-2} s^{-1} represent the observed maximum increase in T_{leaf} above T_{air} (Fig. 6.2) and the maximum recorded PPFD, respectively. The reduction in A_{max} caused by D_s (if any) was calculated for each ten minute interval before carbon gain was estimated for undisturbed and open areas as described above. This approach ignores interactions between wind speed, leaf temperature, the evaporation rate and D_s, and assumes that stomatal closure will influence carbon assimilation most when light is saturating.

C. PPFD measurements from undisturbed forest and another logged forest site were used to test the interacting effect of light microclimate and photosynthetic acclimation on daily carbon gain. As part of another study in forest 10 km from the present study, 30 quantum sensors were distributed beneath a wide range of canopy conditions in logged and unlogged forest and used to record instantaneous PPFD values at 1 minute intervals (Chapters 2 - 4). One week of PPFD and temperature measurements from these sites (temperature was measured at a single point), and the mean photosynthetic parameters observed for undisturbed, partially open and open environments were used to calculate daily carbon gain as described above. The result is a light response curve for carbon assimilation on a daily total basis, for seedlings from each environment.

6.3 Results

Seedling microclimate

Site factors and daily total PPFD increased by almost two orders of magnitude from undisturbed to severely disturbed areas (Table 6.1, Fig. 6.1). Seedlings beneath undisturbed canopy received less than 2% of the PPFD incident above the canopy, while seedlings in open sites near skid trails and logging roads received more than 50 % of that incident above the canopy (Table 6.1). Average above canopy daily PPFD measured during the study period at a site 10 Km to the east was 23.5 mol m^{-2} (range 11.5 - 33.8). The maximum instantaneous flux measured in an open area was 1974 μmol m^{-2} s^{-1}. Site factors above seedlings in the area logged two weeks before measurements were intermediate between those for partially open and open sites in the main study area (Table 6.1). Canopy opening also had significant effects on air temperature and the vapour pressure deficit of the ambient air (D_a). Air temperature was consistently 1 - 2 °C higher in the open area by mid afternoon, and D_a peaked at levels rarely observed in undisturbed forest (Table 6.1, Fig. 6.1).

High leaf temperatures occurred frequently when seedlings were exposed to long periods of direct sunlight (Fig. 6.2). Maximum leaf temperatures of seedlings growing in open areas exceeded 40 °C and were up to 12 °C above air temperatures (Fig. 6.2c). Leaf temperatures in areas with undisturbed or partially open canopy were usually closer to air temperature (Fig. 6.2a & b). Leaf temperatures in the area that had been exposed for two weeks were similar to those in disturbed areas of the main study site (Fig. 6.2d).

Table 6.1. Microclimatic conditions and seedling size measurements for seedlings in areas logged 14 and 90 days before measurements were made. Microclimatic variables are the daytime (6am - 6pm) means and daily ranges (in brackets) for 15 days during the study period. The global site factor and seedling measurements are the means ± 1SE for 10 seedlings beneath each canopy class. The area logged 14 days before measurements was 5 km from the other sites; seedlings in this site were older and larger at the time of logging. T_{air}, air temperature; D_a, vapour pressure deficit, SLA, specific leaf area; LAR, leaf area ratio. Means with the same letter are not significantly different ($p > 0.05$, Tukey's HSD).

	disturbance intensity and time since disturbance			
	fully open	undisturbed	partially open	fully open
Variable	14 days	-	90 days	90 days
T_{air} (°C)	-	25 (22-29)	-	26 (22-31)
D_a (mmol mol^{-1})	-	2.2 (0.0-10.8)	-	4.6 (0.0-16.8)
PPFD (mol m^{-2} day^{-1})	-	0.2 (0.1-0.3)	-	14.7 (9.2-18.8)
Global site factor (%)	26.9 (16-36)	1.5 (0.7-2.4)	11.9 (6-20)	52.1 (40-65)
Height (m)	0.47 ± 0.02 b	0.25 ± 0.02 a	0.49 ± 0.03 b	0.62 ± 0.06 c
Total dry mass (g)	5.3 ± 0.5 b	0.9 ± 0.1 a	5.9 ± 0.7 b	10.9 ± 1.9 c
SLA (m^2 kg^{-1})	16.5 ± 0.3 c	21.7 ± 0.3 a	17.7 ± 0.3 b	16.5 ± 0.3 c
LAR (m^2 kg^{-1})	5.4 ± 0.6 c	10.0 ± 0.6 a	7.9 ± 0.4 b	6.8 ± 0.3 bc

Biomass partitioning

Three months after disturbance, seedlings in disturbed areas were taller and heavier and had produced many new leaves (Table 6.1). Seedlings in partially open sites were 6 times heavier than seedlings in the shade. Seedlings in the most open site were heavier than in the partially open site, but the difference was small relative to the differences in light availability (Table 6.1). Variation in seedling size was greatest in the most open area, and some seedlings had grown little since disturbance. Seedlings growing in disturbed areas had more biomass partitioned to fine roots and stems and less to leaves (Fig. 6.3), and lower specific leaf area (leaf area per unit mass, SLA; Table 6.1).

Seedlings in the newly disturbed area were distinct from those at the other site. Higher proportions of total biomass were allocated to woody stem and root, and less to leaves and fine roots (Table 6.1, Fig. 6.3). Leaf loss at the time of logging may have exaggerated this trend. Two weeks after logging, no new leaves had been produced, but there were visible signs of new leaf emergence at the shoot apex.

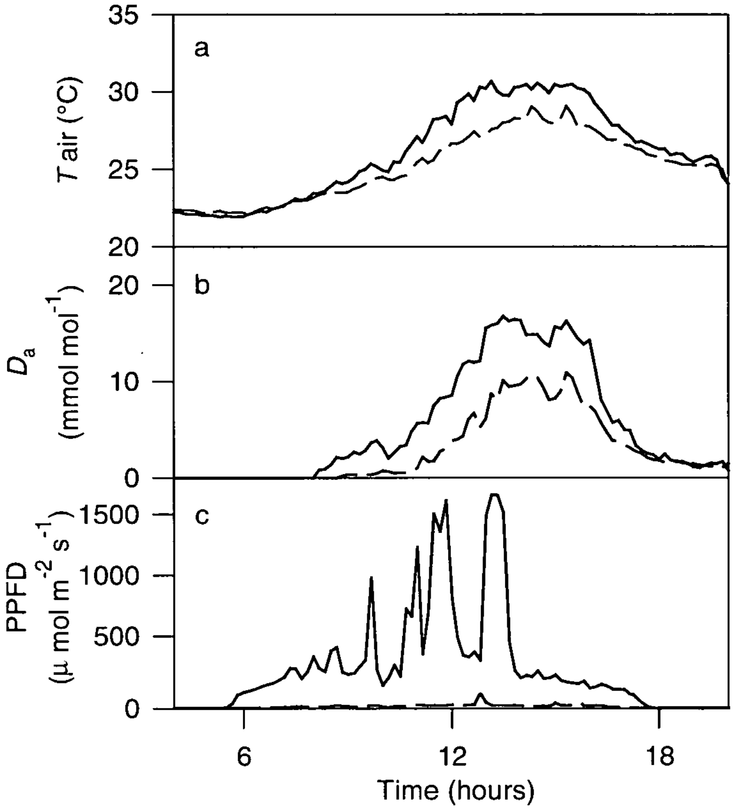


Fig. 6.1. Time course of air temperature (a), vapour pressure deficit (b), and PPFD beneath undisturbed canopy (dotted line) and in an open area, over a single day in the area logged 90 days before measurements. Data are 10 minute averages, for 20 March, 1996.

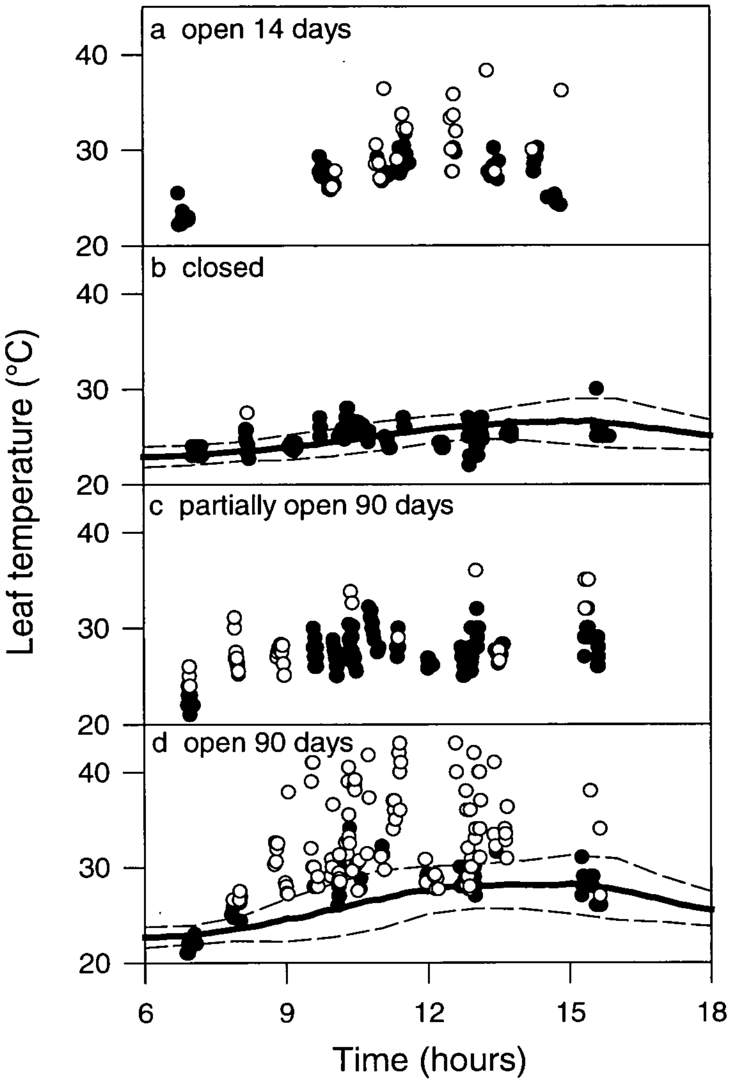


Fig. 6.2. Spot measurements of seedling leaf temperature in the areas logged 14 days (a, open canopy) and 90 days (b, undisturbed canopy; c, partially open canopy; d, open canopy) before measurements began. Temperatures were recorded with an infrared thermometer. Closed symbols are for leaves in shade, open symbols, leaves in direct sunlight. Lines represent average air temperature (± 2 SD) measured beneath undisturbed and open canopy over the same period.

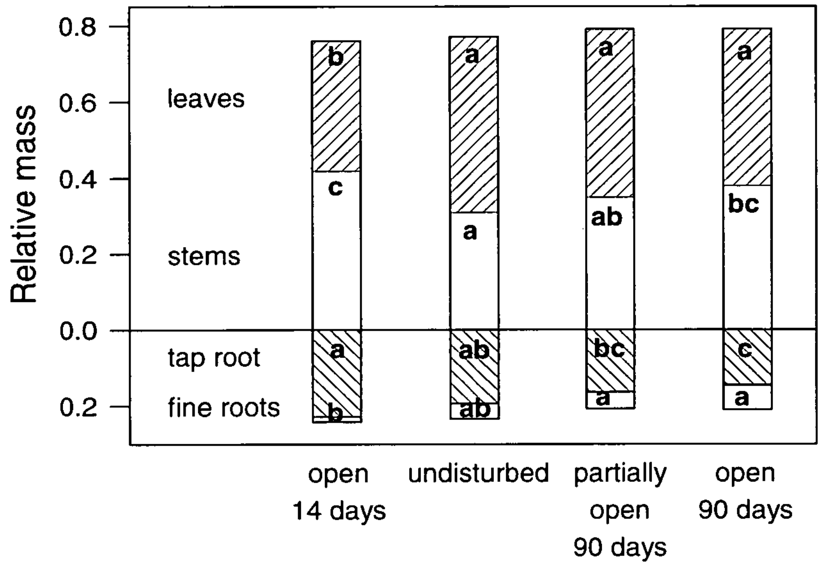


Fig. 6.3. Partitioning of seedling total dry mass between fine roots, tap root, stems and leaves. Note that seedlings in the site logged 14 days before measurements were older and larger at the time of logging. Sections of the same organ type with the same letter are not significantly different ($p > 0.05$, Tukey's HSD; $n = 10$ seedlings for each bar).

Seedling chlorophyll fluorescence and water status

Large reductions in pre-dawn F_v/F_m were measured for seedlings growing in the recently disturbed area, indicating chronic photoinhibition or photo-oxidation (Table 6.2). The uppermost leaves of some seedlings displayed obvious patches of yellowing and necrosis. No yellowing or browning of exposed leaves was observed in the area logged three months previously, and there were only small reductions in pre-dawn F_v/F_m with increased openness.

Rain fell on 28 of 31 days during the study period, with a total of 360 mm recorded at the above canopy station 10 km to the east. Pre-dawn leaf water potentials were consistently high, regardless of canopy cover or time since disturbance (Table 6.2). There were no consistent reductions in leaf water potential during the day, and no differences between sites in the diurnal pattern. For all sites, leaf water potential was never below -0.27 MPa.

Table 6.2. Mean pre-dawn leaf water potential and F_v / F_m for seedlings in areas logged 14 and 90 days before measurements were made. Means with the same letter are not significantly different ($p > 0.05$, Tukey's HSD); n = 3 - 5 days.

	Disturbance intensity and time since disturbance			
	fully open	undisturbed	partially open	fully open
Variable	14 days	-	90 days	90 days
leaf water potential (MPa)	-0.14 ± 0.06 a	-0.06 ± 0.01 a	-0.08 ± 0.02 a	-0.08 ± 0.02 a
F_v / F_m	0.63 ± 0.02 c	0.80 ± 0.01 a	0.79 ± 0.01 ab	0.77 ± 0.01 b

Foliar nutrients and photosynthetic acclimation to light

Two weeks after disturbance, quantum efficiencies and light saturated rates of photosynthesis for newly exposed seedlings were similar or slightly reduced when compared to seedlings in undisturbed areas, but SLA was lower and leaf nitrogen concentrations were higher (Table 6.3, Fig. 6.4). Photosynthetic rates expressed on a leaf mass or nitrogen basis were therefore lowest for these seedlings (Table 6.3).

Photosynthetic capacity, dark respiration rates and quantum efficiencies in disturbed areas were at least doubled in leaves which had developed after disturbance (Tables 6.3 & 6.4, Fig. 6.4). Average photosynthetic capacity was highest in the most exposed seedlings, but they were also the most variable, with A_{max} area (fitted using equation 6.1) varying from 7 to 18 μmol CO_2 m^{-2} s^{-1}. Dark respiration of leaves in the most exposed areas was 2 - 5 times greater than those in partially open or undisturbed sites (Table 6.4).

Table 6.3. Leaf nitrogen, phosphorus, and maximum photosynthesis (A_{max}) expressed per unit leaf area, per unit leaf dry mass, and for A_{max}, per unit leaf nitrogen. Means with the same letter are not significantly different ($p > 0.05$, Tukey's HSD). ± 1SE; n = 5 leaves for each site in the area logged 90 days before measurements, and 4 leaves in the area logged 14 days before measurements.

	Disturbance intensity and time since disturbance			
	fully open	undisturbed	partially open	fully open
Variable	14 days	-	90 days	90 days
N area	1.22 ± 009	0.78 ± 0.02	1.05 ± 0.07	1.35 ± 0.06
(g m^{-2})	bc	a	b	c
N dry mass	18.2 ± 0.4	16.0 ± 0.6	16.0 ± 1.0	21.4 ± 0.7
(mg g^{-1})	a	a	a	b
P area	0.068 ± 0.006	0.042 ± 0.005	0.041 ± 0.005	0.080 ± 0.003
(g m^{-2})	b	a	a	b
P dry mass	1.01 ± 0.03	0.86 ± 0.06	0.63 ± 0.07	1.27 ± 0.08
(mg g^{-1})	b	b	a	c
A_{max} area	3.8 ± 0.3	4.0 ± 0.2	9.3 ± 0.6	12.8 ± 2.4
(μmol CO_2 m^{-2} s^{-1})	a	a	b	b
A_{max} mass	56 ± 3	81 ± 4	141 ± 11	201 ± 34
(nmol CO_2 g^{-1} s^{-1})	a	a	b	c
A_{max} Nitrogen	43 ± 3	71 ± 4	126 ± 13	135 ± 25
(μmol CO_2 mol^{-1} s^{-1})	a	a	b	b

Partial canopy opening brought about increased rates of photosynthesis per unit nitrogen (instantaneous photosynthetic nitrogen use efficiency, IPNUE; Table 6.3), but no absolute increase in leaf nitrogen concentrations. Further increases in canopy openness led to increases in total nitrogen concentrations and photosynthetic rate, but no further increase in IPNUE (Table 6.3). Leaf phosphorus concentrations were also highest in the most exposed seedlings, but where not related to photosynthetic capacity when compared across all sites (Table 6.3).

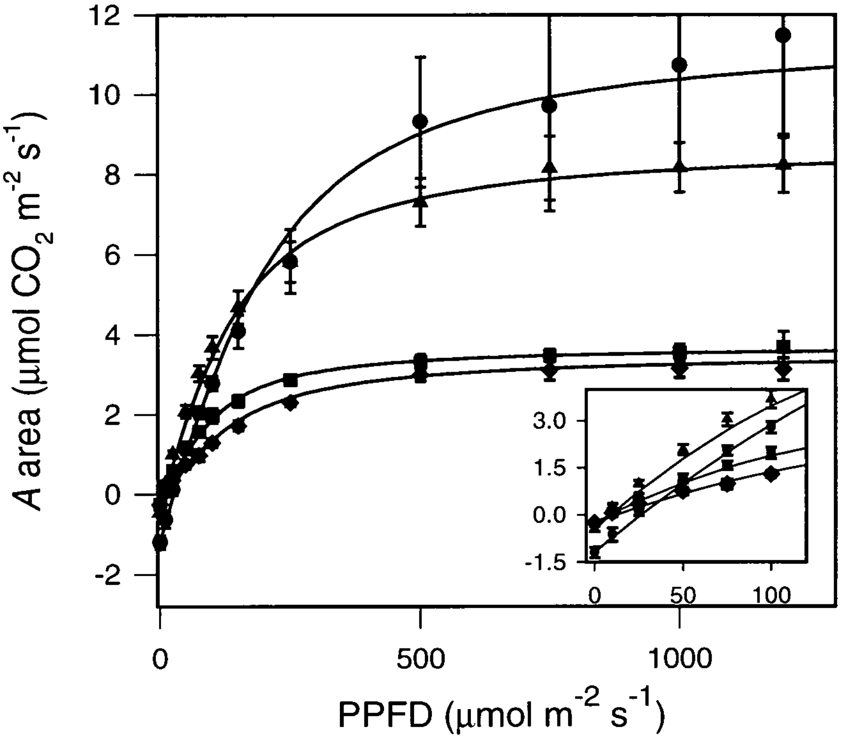


Fig. 6.4. The photosynthetic response to light for seedling leaves beneath undisturbed canopy (squares), partially open canopy (triangles) and open canopy (circles), 90 days after logging. The fourth curve (diamonds) is for seedling leaves beneath open canopy, 14 days after logging. Lines represent the modelled response and points indicate means ± 1 SE for the measured values, n = 4 for 14 day site, 5 for 90 day site. The inset shows detail for PPFD < 100.

Table 6.4. Dark respiration (R_d), apparent quantum efficiency(ϕ), and the light saturation and compensation points of photosynthesis. For sample sizes and explanation of statistical comparisons, see Table 6.3.

	disturbance intensity and time since disturbance			
	undisturbed	partially open	fully open	fully open
Variable	-	90 days	90 days	14 days
R_d area	-0.25 ± 0.02	-0.46 ± 0.08	-1.20 ± 0.17	-0.25 ± 0.04
(μmol CO_2 m^{-2} s^{-1})	a	a	b	a
ϕ	0.028 ± 0.003	0.050 ± 0.002	0.048 ± 0.003	0.021 ± 0.003
(mol mol^{-1})	a	b	b	a
Q compensation	6.9 ± 0.4	7.4 ± 1.8	24.0 ± 3.7	11.3 ± 2.5
(μmol m^{-2} s^{-1})	a	a	b	a
Q saturation	481 ± 60	757 ± 99	912 ± 86	805 ± 155
(μmol m^{-2} s^{-1})	a	ab	b	b

Stomatal response to vapour pressure deficit

Stomatal conductance and photosynthesis declined by approximately 50% when D_s was increased to 40 mmol mol^{-1} (Fig. 6.5 a & c). The relative decline in g_s and A was faster in leaves from disturbed environments, suggesting that the stomata were more sensitive to D_s in open environments (Fig. 6.5 b & d). However, log transformation of g_s and comparison of the slopes for each environment could not confirm a significant difference in sensitivity between environments (environment x D_s interaction, $F = 1.78$, $p = 0.18$). The decline in A with D_s was more linear than the decline in g_s; simple linear regression was used to describe the relationship for modelling of daily carbon gain (Fig. 6.5 d). Transpiration increased significantly with increasing D_s in shaded leaves (Fig. 6.5 e & f). Faster stomatal closure tended to limit evaporation in plants from open environments, but for individual leaves there was usually at least an initial increase in transpiration rate with increasing D_s (Fig. 6.5 f).

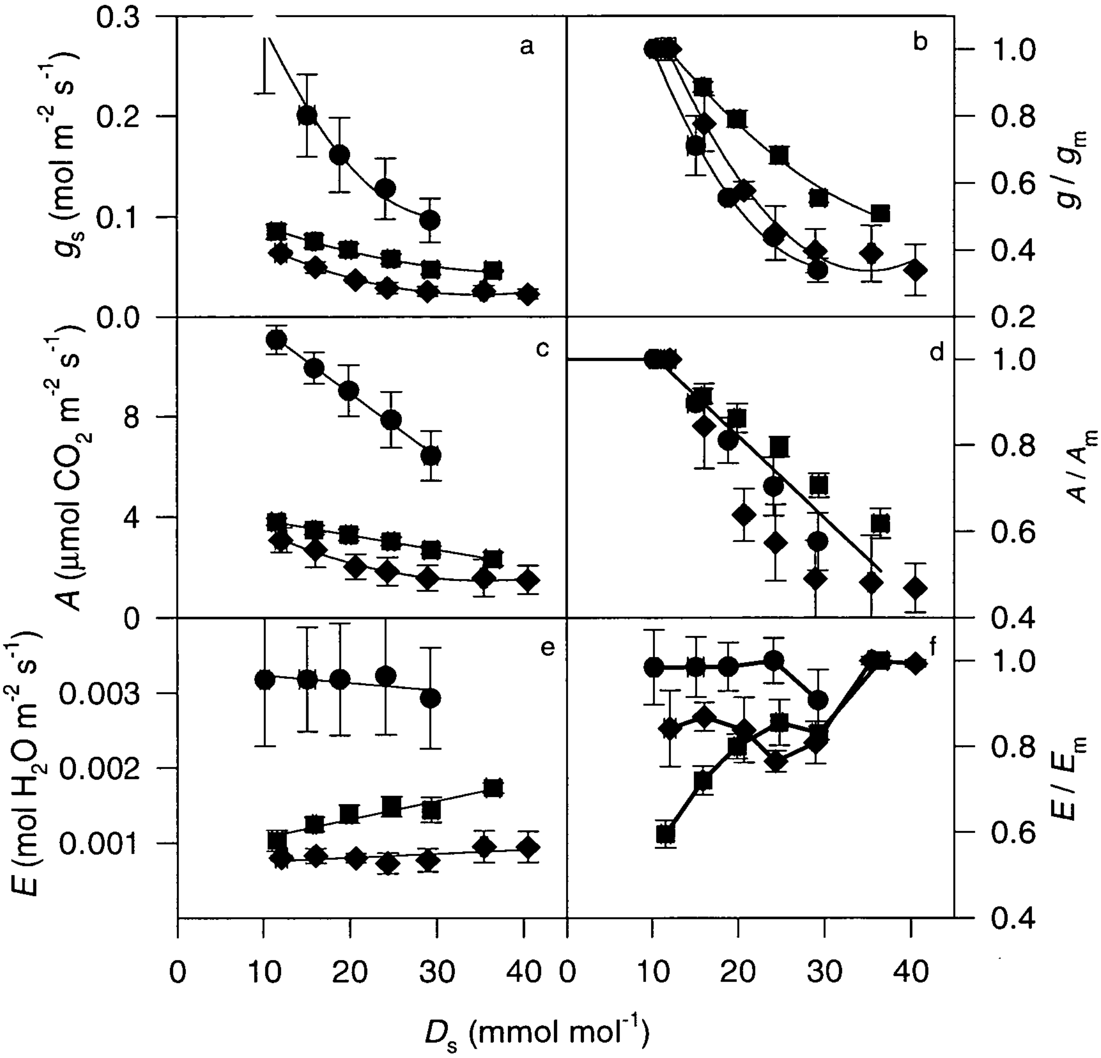


Fig. 6.5. Response of stomatal conductance (a), carbon assimilation (c) and transpiration (e) to the vapour pressure deficit at the leaf surface (D_S). Curves are for seedlings beneath open canopy 14 days after logging (diamonds), open canopy 90 days after logging (circles) and undisturbed canopy. For comparison between environments the same data are shown expressed as a proportion of their maximum (b,d,f). Points indicate means ± 1 SE, n = 3 leaves. The least squares regression line shown in (d) is for open and undisturbed environments 90 days after logging, and was used for modelling the effect of D_S on daily carbon gain (see methods).

Daily carbon balance

Modelled daily respiration for an average leaf in the undisturbed site was greater than daily photosynthesis, leading to a net loss of carbon (-13.9 mmol CO_2 m^{-2} day^{-1}) which was little affected by variation in quantum efficiency and A_{max} (Fig. 6.6). Variation in dark respiration rate caused large relative changes in the daily balance (Fig. 6.6). Modelled carbon gain in the open site was positive (184.1 mmol CO_2 m^{-2} day^{-1}) and more sensitive to variation in quantum efficiency and A_{max} (Fig. 6.6). High leaf temperatures and low humidity caused a 10% reduction in modelled carbon for the open site when the photosynthetic response to D_s was included in the model (Fig. 6.6 c). Leaf temperature accounted for the majority of this effect; the response to the water vapour concentration of ambient air alone (i.e. $T_{leaf} = T_{air}$) caused only a 1% reduction in carbon gain. D_s had no significant effect on modelled carbon gain for the undisturbed site (<0.1% reduction for either leaf temperature scenario).

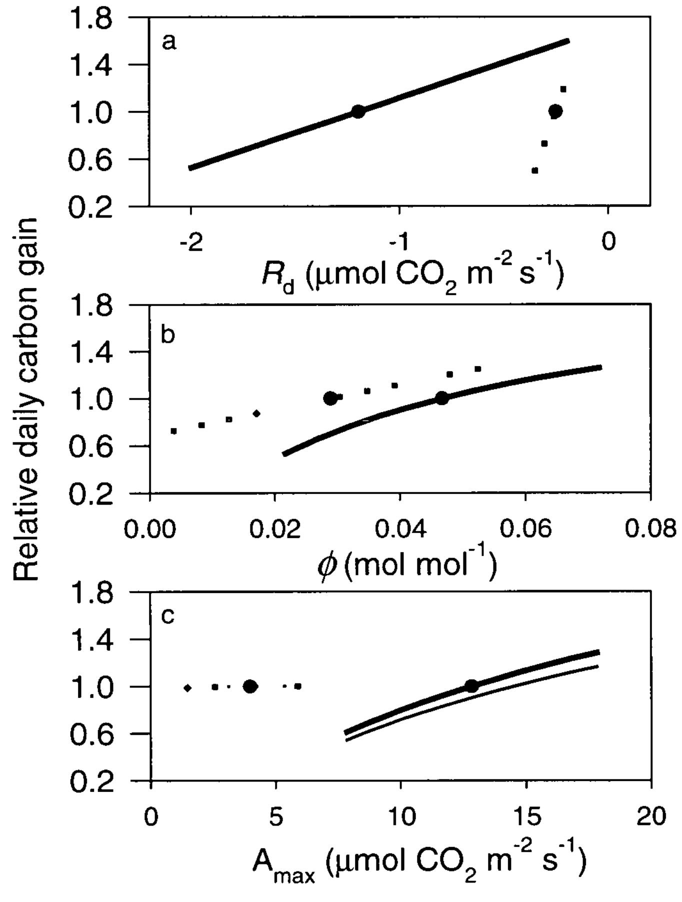


Fig. 6.6. Sensitivity of modelled daily carbon gain to variation in dark respiration (a), apparent quantum efficiency (b) and maximum photosynthesis (c), for an average leaf beneath undisturbed (dotted line) and open (solid line) canopy, 90 days after logging. Carbon gain is expressed relative to its value when all parameters are equal to their measured values (Tables 6.3 and 6.4, marked by circles). Thin lines in (c) indicate carbon gain when the modelled effect of D_s is included (see methods for explanation).

Leaves acclimated to open conditions had lower predicted carbon gain than leaves acclimated to partially shaded conditions, even at high PPFDs characteristic of the open environment (Fig. 6.7). Dark respiration offset the benefit of increased photosynthetic capacity when light availability was high, and caused a large negative balance at low PPFD (below 2 mol m^{-2} day^{-1}, Fig. 6.7). Leaves acclimated to partially open conditions had the highest rates of carbon gain under all light conditions, except when light levels were below the daily light compensation point of leaves from all environments (Fig. 6.7). Under such shaded conditions (below 1 mol m^{-2} day^{-1}), shade acclimated seedling leaves had the lowest rate of carbon loss (Fig. 6.7).

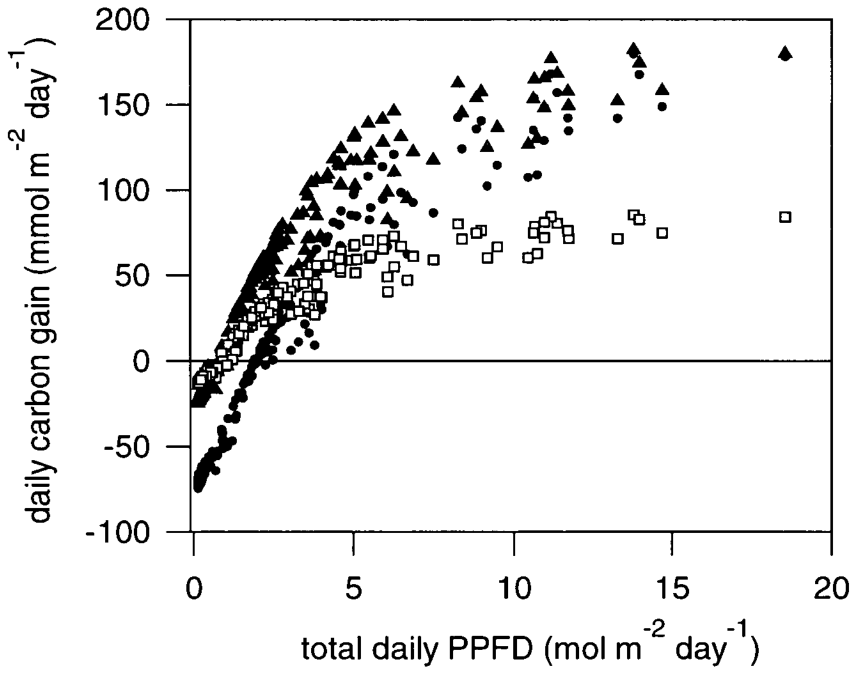


Fig. 6.7. Modelled daily carbon gain as a function of daily PPFD for an average seedling leaf beneath undisturbed (squares), partially open (triangles) and open canopy (circles), 90 days after logging. Measured parameters for the instantaneous photosynthetic light response (Tables 6.3 and 6.4) were used to predict daily carbon gain, using PPFD measured in a range of sites at one minute intervals. Each point represents carbon gain for a single day (see methods for explanation).

6.4 Discussion

Acclimation, photoprotection and respiration

These climax tree seedlings exhibited significant photosynthetic acclimation to a wide range of light environments, including conditions more extreme than those normally encountered in undisturbed forest or natural forest gaps. Shade adapted leaves were damaged by exposure to high light intensities at the time of logging, but new leaves produced after disturbance had at least double the maximum rates of photosynthesis and showed no signs of long term damage by high light intensities or leaf temperatures. Although acclimation was significant, trade offs between increased photosynthetic capacity and even greater increases in dark respiration rate mean carbon gain and growth are unlikely to increase linearly with canopy openness. It is hypothesised that a high rate of dark respiration reflects the higher cost of maintaining the photosynthetic apparatus and increased investment in photo-protective mechanisms, both of which act to dissipate excess energy and enable *S. johorensis* to grow under open conditions.

Sun leaves of other species often demonstrate an increased capacity for dissipation of the excess energy absorbed during periods of light saturation (Long, Humphries and Falkowski, 1994). The most important pathway is now thought to be thermal dissipation of energy from PSII via the xanthophyll cycle (Demmig-Adams and Adams, 1992), leading to a reversible decline in photosynthetic efficiency during periods of high PPFD (photoinhibition; Mulkey and Pearcy, 1992; Lovelock, Jebb and Osmond, 1994; Castro, Fetcher and Fernandez, 1995; Krause, Virgo and Winter, 1995; Scholes, Press and Zipperlen, 1997). Pools of xanthophyll cycle components are generally higher in sun leaves (Demmig-Adams and Adams, 1992). If absorbed energy exceeds the total capacity for photosynthetic electron transport and thermal dissipation, slowly reversible inactivation (chronic photoinhibition; Castro, Fetcher and Fernandez, 1995) or permanent damage to PSII and other components (photooxidation) may occur (Lovelock and Winter, 1996; Scholes, Press and Zipperlen, 1997). Three months after logging, predawn measurements of F_v/F_m on the leaves of exposed *S. johorensis* seedlings demonstrated that neither chronic photoinhibition nor photooxidation was occurring in leaves which had developed in the new environment (Table 6.2), despite high midday PPFDs and leaf temperatures. This provides strong indirect evidence that the capacity for thermal or other forms of non-photosynthetic energy dissipation was increased, in addition to increases in photosynthetic capacity.

Large increases in dark respiration rates accompanied acclimation to the most open sites. Increased respiration effectively negated the benefits of higher photosynthetic capacity when leaf carbon gain was integrated over a 24 hour period. The relative increase in dark respiration was greater than the corresponding changes in SLA, nitrogen concentrations and photosynthetic capacity, supporting the conclusion that there were other biochemical changes beyond a simple increase in carboxylation capacity. It is concluded that increased rates of dark respiration represent the inevitable metabolic 'cost' of acclimation to the most exposed environments (Turnbull, Doley and Yates, 1993; Chazdon *et al.* 1996). Enzyme kinetics predict that rates of enzyme degradation and turnover will be higher at higher leaf temperatures and PPFDs, and the requirement for repair may lead to higher rates of maintenance respiration even when leaf temperatures return to levels similar to those in shaded sites (Penning De Vries, 1975; Johnson and Thornley, 1985; Hagihara and Hozumi, 1991). The consequences of increased photoprotection for dark respiration are not known, but a large xanthophyll cycle pool is generally associated with a higher metabolic rate (Demmig-Adams and Adams, 1992). Dark respiration may also be enhanced by increased carbohydrate concentrations in exposed plants (Sims and Pearcy, 1991).

Nutrient use and variability in the seedling acclimation response

Changes in patterns of nitrogen use were an important component of seedling acclimation after canopy disturbance. Variation in soil conditions and nutrient availability within open areas may help to explain variation in the seedling acclimation response(Scholes, Press and Zipperlen, 1997). $A_{\max}$ mass and IPNUE were higher in leaves produced after moderate canopy disturbance, suggesting greater partitioning of existing nitrogen to the photosynthetic apparatus, or an increase in electron transport and carboxylation capacity relative to light harvesting components (Field and Mooney, 1986; Chazdon, 1992; Press *et al.* 1996). Leaf nitrogen and phosphorus concentrations increased in the most open sites, but there was no further increase in the mean IPNUE. Faster growth, higher nitrogen and phosphorus concentrations and greater investment in photoprotection will all increase nutrient demand (Koide, 1991; Ingestad and Agren, 1992). Nitrogen deficiency can limit photosynthetic capacity and increase susceptibility to photoinhibition in other species (Castro, Fetcher and Fernandez, 1995), but dipterocarp seedlings are generally tolerant of low nutrient availability (Chapter 5) and are usually unresponsive to fertilisation when growing in undisturbed forest soil (Burslem, 1993; Turner, Brown and Newton, 1993; Nussbaum, Anderson and Spencer, 1995). Seedling nutrient status is thought to be closely linked to the degree of infection of the root system by mycorrhizal fungi (Lee, 1990; Lee, 1994). In logged areas, soil disturbance and high surface temperatures (Chapters 3 and 4; Majid and Jusoff, 1987) may reduce microbial activity and the number of mycorrhizal propagules (Alexander, Ahmad and Lee, 1992; Ahmad, 1996), and it is in these areas that the growth and photosynthetic capacity of dipterocarp seedlings is most variable.

Initial acclimation of shaded seedlings after disturbance

The combined effects of long periods of direct sunlight and high leaf temperatures are the most likely cause of browning and reductions in pre-dawn F_v/F_m of newly exposed seedling leaves (Mulkey and Pearcy, 1992). Air temperatures and humidity differed moderately between adjacent undisturbed and disturbed areas, but they remained within a range considered favourable for plant growth (Chapter 3). The fact that recently exposed leaves had photosynthetic rates similar to shaded seedling leaves suggests that remaining unbleached tissue had acclimated to the new environment and was photosynthesising faster (on an area basis) than shaded leaves. Values for pre-dawn F_v/F_m and quantum efficiency were also spatial averages of bleached and more healthy tissue, and their reduction may only be important for carbon gain when light levels are below saturation (Long, Humphries and Falkowski, 1994; Stirling *et al.* 1994). The lower SLA of recently exposed compared to shade suppressed seedlings seems to confirm that acclimation of pre-existing leaves had occurred. Transfer experiments on other species have also demonstrated that previously mature leaves can undergo physiological and anatomical changes in response to the new environment (Kamaluddin and Grace, 1992; Mulkey and Pearcy, 1992; Turnbull, Doley and Yates, 1993). These results suggest that pre-existing, shade adapted leaves will have a significant contribution to the whole plant carbon budget during acclimation (Mulkey and Pearcy, 1992).

These results do not support the hypothesis that a small root mass will lead to water stress in newly exposed seedlings even when soil water moisture content is high. Water stress may still be an important limitation to seedling acclimation during short periods of low rainfall which occur during the dry season and occasionally throughout the year (Chapter 3; Brown, 1993). Higher mortality of shade suppressed seedlings occurs during these periods (Turner, 1990a), while seedlings which have already acclimated to open conditions are more tolerant (Chapter 4). Dryer periods are also favoured for logging, thus increasing the probability that seedlings will be exposed when soil water availability is limiting.

Stomatal response to post-logging conditions

No evidence was found to support the hypothesis that dipterocarp seedlings were unusually sensitive to water vapour deficits between the internal leaf spaces and the ambient air, or that the stomatal response might strongly limit whole plant acclimation after disturbance. Stomatal sensitivity to D_s was similar to that reported for species from less humid habitats (Comstock and Ehleringer, 1993; Wilson and Bunce, 1997). Although vapour pressure deficits were increased in open areas, the reduction was not large enough to significantly limit predicted carbon gain without the added effect of increases in leaf temperature. The temperature of exposed single leaves was often high enough to reduce g_s and limit carbon gain (Fig. 6.6 c), and stomatal closure itself may have contributed to higher leaf temperatures. However, the average heat load on individual leaves will decline as seedlings grow larger and develop a deeper canopy. Canopy development and low wind speed will also increase boundary layer resistance and tend to decouple conditions at the leaf surface from the ambient air (Meinzer *et al.* 1995). Carbon gain is therefore likely to be most affected when seedlings are small and exposed to long periods of direct sunshine, and the effects of stomatal conductance may be minor compared to more the direct effects of low wind speed and high leaf temperature on carbon gain and protein chemistry.

Shade tolerance

Modelling of the daily carbon balance also highlighted the importance of dark respiration for seedling survival in the shade (Turnbull, Doley and Yates, 1993; Chazdon *et al.* 1996). PPFD beneath undisturbed dipterocarp forest was so low that daily losses to respiration exceeded total gains during daylight hours, and variation in the efficiency of the photosynthetic response to light had little effect on the long term carbon balance of the leaves (Fig. 6.6). Root and stem respiration will further increase losses of carbon, but the whole-plant carbon budget is likely to be dominated by the leaves (Lehto and Grace, 1994). Results suggest that for this species, daily leaf carbon balance will always be negative below a daily PPFD of 1 mol m^{-2}, thus providing a lower limit below which the gradual death of all seedlings can be expected. More detailed modelling of the whole-plant carbon balance (Pearcy and Yang, 1996) would be a useful approach to understanding the mechanisms of shade tolerance by dipterocarp seedlings. Potential applications include the effects of herbivory and the importance of interconnection between plants via mycorrhizal bridges of fungal hyphae (Alexander, 1989). Becker (1983a) found that artificial defoliation of two other *Shorea* species had little effect on their survival in the shade. One hypothesis advanced to explain this observation was that net carbon gain by the leaves may have been so low that removal of leaf area had little effect on the whole plant carbon balance (Becker, 1983a). The results of this study support this hypothesis, and even suggest that the loss of leaf area in the most shaded sites would represent the removal of a respiratory burden.

Conclusions

Seedlings of the fast growing dipterocarp species *S. johorensis* are capable of significant acclimation to extreme post-logging conditions, but the respiratory cost of leaf acclimation to high temperatures and PPFD may limit early seedling growth.

Water availability and the stomatal response to humidity did not have a large impact during the wet season, but it was hypothesised that soil conditions and seedling nutrient status will influence the acclimation response in severely disturbed areas.

It may be possible to generalise these findings to other light demanding, fast growing dipterocarp species (e.g. *Shorea leprosula* and *S. parvifolia*). A wide acclimation potential helps explain why members of this group are sometimes observed to grow well under very exposed conditions. It is the opinion of the author that poor dipterocarp regeneration after logging does not reflect a limited acclimation potential, but is instead the result of excessive damage at the time of logging, a low density of seedlings before logging, or competition with even more vigorous pioneer species.

7. Discussion

7.1 Dipterocarp seedling ecology

This study aimed to examine the physiological characteristics of fast growing dipterocarp species and use these observations to explain the observed response of seedling populations to logging disturbance and the environment of logged forest. The first part of this chapter examines the relationship between the physiology and ecology of dipterocarp seedlings, and the second part discusses the implications of these findings for the management of natural dipterocarp forests for timber production. The ecological species groupings of Swaine and Whitmore (1988) provide a starting point: all members of the *Dipterocarpaceae* have seeds that can germinate and establish as seedlings in the shade beneath a closed canopy, and they are therefore classified as climax tree species. Climax species are contrasted with pioneers, which require canopy opening before their seedlings can establish. Although useful, these qualitative groupings represent an artificial division of the continuous range of variation in seedling shade tolerance that exists for forest tree species. A simple model of the relationship between seedling growth and mortality is suggested as a more quantitative approach to understanding the subtle differences that occur within and between broad ecological groupings (Fig. 7.1).

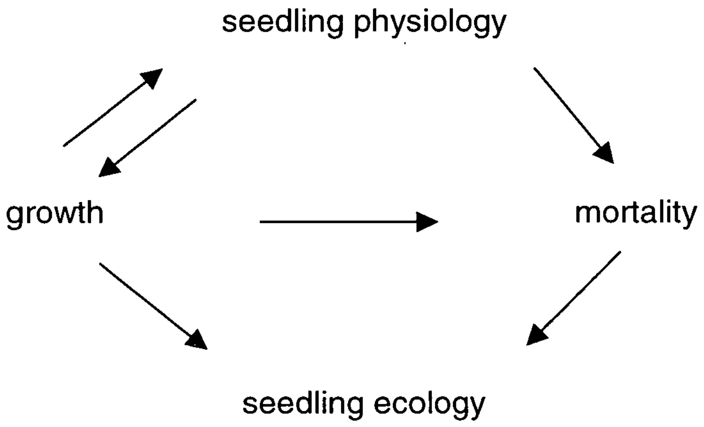


Fig. 7.1. Relationships between seedling physiology, growth, mortality and ecology.

The most important driving variable for regeneration is considered to be light availability and the two key processes are seedling relative growth rate (r) and mortality (m). Seedling photosynthetic characteristics and patterns of biomass partitioning determine the shape of the growth response curve to PPFD, and other aspects of the seedling environment, particularly nutrients, water and herbivory, interact with PPFD and modify the response. Mortality is principally a function of seedling size and growth rate and therefore is also strongly dependent on PPFD (Fig. 7.1). Walters and Reich (1996) argued that the survival of tree seedlings in deep shade was positively related to r. In terms of mortality (m):

$$m \propto -r \qquad (7.1)$$

Within a species, individuals receiving higher PPFD accumulate more carbon and have lower mortality. Walters and Reich proposed that the same relationship would hold for comparisons between species – when grown at the same low PPFD, species with the higher growth rates have lower mortality and were therefore more shade tolerant than species with low growth rates. However, r of tree seedlings and herbaceous plants under controlled conditions of limiting light or nutrients is often higher for inherently fast growing species from resource rich environments, even though their distribution implies that they are less able to survive when resources are limiting (Chapter 5). The relationship between growth and mortality is more likely to differ between species. Kobe (1996) and Kobe and Coates (1997) fitted negative exponential functions to mortality versus growth data for a range of temperate species:

$$m = e^{-Br} \qquad (7.2)$$

The fitted parameter B was then correlated to qualitative shade tolerance rankings that had previously been defined for the same group of species (Kobe and Coates, 1997). Qualitative ranking of species according to shade tolerance is normally based on the observation of species behaviour in both high and low PPFD environments. Species that are tolerant of shade are usually found to be slower growing in high PPFD than less shade tolerant species (Whitmore, 1996). It is therefore proposed that the shade tolerance of a species is related to its growth rate under non-limiting PPFD:

$$m = e^{-C\frac{r}{r_m}} \qquad (7.3)$$

where r_m is the maximum relative growth rate under non-limiting PPFD and C is a parameter that describes the capacity for phenotypic variation in response to the growth environment (plasticity). Shade tolerance is a balance between the capacity for rapid growth in high PPFD (r_m) and the potential for adjustment when PPFD is limiting (C). To survive for the same length of time in the shade, a species that is fast growing in high PPFD must either physiologically 'down-regulate' or achieve a higher r than a species that is slow growing in high PPFD. A less shade tolerant species can have a higher m in the shade even if r is higher. According to (7.3), the physiological characteristics that determine growth rate in high PPFD can be used to characterise the shade tolerance of a species, and the extent to which a species deviates from the expected r/r_m relationship is a measure of its physiological plasticity. This model serves as a useful framework for examining the physiological properties of dipterocarp seedlings and identifying priorities for future research. Emphasis is placed on the link between physiological characteristics and resource dependent rates of mortality and survival, rather than development of the model in explicit algebraic detail (for a more detailed treatment refer to Kobe and Coates, 1997).

Fast growing dipterocarps as climax species

The wild seedlings of fast growing dipterocarp species such as *S. leprosula*, *S. parvifolia* and *S. johorensis* are well known for vigorous, light demanding growth. This study shows that despite this rapid growth the response to increasing light availability saturates at PPFDs between 5 and 10 mol m^{-2} day^{-1}, at least while the seedlings are below a height of approximately 2 m. Even the most light demanding dipterocarp species are therefore well adapted for initial growth in relatively small canopy gaps up to 400 m $^{-2}$, where PPFD levels usually do not exceed 10 mol m^{-2} day^{-1} (Bellingham *et al.*, 1996). Canopy gaps of this size are created by single tree-falls and are common in lowland dipterocarp forest (Torquebiau, 1986). In contrast, pioneer species require at least 8 mol m^{-2} day^{-1} PPFD to establish and grow successfully (Chapter 4; Torquebiau, 1988; Fernandez and Fetcher, 1991). The common pioneer genera encountered in this study, *Macaranga* and *Anthocephalus*, were found in the most open seedling plots after logging and under natural conditions are expected to establish only in relatively large gaps (> 400 m^2), provided there are nearby seed sources. Under very open conditions (PPFD > 10 mol m^{-2} day^{-1}) the growth of these pioneer species exceeded that of the dipterocarps (Fig. 7.2).

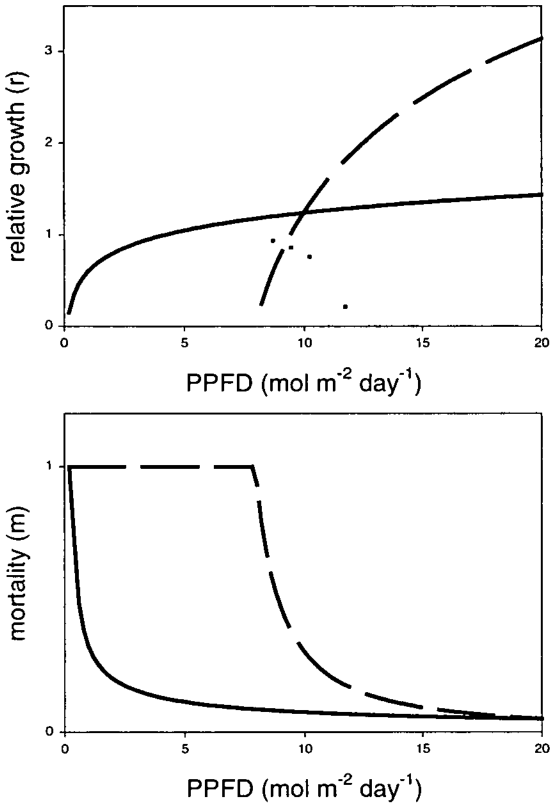


Fig. 7.2. Growth and mortality of a fast growing dipterocarp species (solid line) and a hypothetical pioneer species (dashed line) as a function of PPFD. The dotted line is growth for dipterocarp seedlings in disturbed soil (see text). Mortality is predicted from growth according to equation 7.3, with $C = 3$.

The physiological characteristics of the pioneer species encountered in this study have not been examined, but likely differences between the fast growing dipterocarps and even faster growing pioneers provide an explanation for the association between growth and mortality predicted by equation 7.3 (Fig. 7.2). The traits most consistently associated with high maximum growth rates are high specific leaf areas (SLA), high leaf mass ratios (LMR) and high leaf area ratios (LAR) (Vanderwerf *et al.*, 1993;

Saverimuttu and Westoby, 1996a). Associated with the production of a larger area of thinner or less dense leaves are higher rates of leaf turn over, and hence shorter leaf life spans (Ryser and Lambers, 1995, Ryser, 1996). Inherently fast growing plants have higher leaf nitrogen concentrations, higher nitrogen use efficiencies (instantaneous and whole plant), and higher maximum rates of photosynthesis expressed on a leaf mass basis (Vanderwerf *et al.*, 1993; Reich *et al.*, 1994). Fast growing woody plants have lower wood density (Whitmore, 1996). These traits tend to be conserved, regardless of the environment within which comparisons are made. All of these traits will increase rates of biomass turnover and susceptibility to herbivory, disease and physical damage (e.g. from branch falls or scouring during heavy rain; Still, 1996; Pinard *et al.*, 1996). When compared to the pioneers, fast growing dipterocarps achieve high growth rates and lower mortality at a much lower PPFD threshold, but are limited in their capacity for growth at higher PPFDs (Fig. 7.2). Pioneers have higher growth rates at higher PPFDs, but their characteristic patterns of carbon and nutrient partitioning result in higher rates of mortality at lower PPFDs. At a PPFD of 10 mol m^{-2} day^{-1}, dipterocarp and pioneer growth rates are predicted to be the same, but r/r_{m} (dipterocarp) > r/r_{m} (pioneer) (Fig. 7.2).

The effects of seedling size on rates of mortality are an important component of dipterocarp seedling regeneration dynamics. During initial germination and establishment, size effects may operate independently of seedling growth and the relationship expressed in equation (7.3) (Saverimuttu and Westoby, 1996b). Larger seed size favours establishment in leaf litter or unstable substrates and generally results in larger seedlings immediately after germination (Seiwa and Kikuzawa, 1996). Species with larger seeds may also persist for longer and be more tolerant of tissue loss through herbivory or physical damage in very low PPFD environments (Metcalfe and Grubb, 1997). Dipterocarps therefore have an obvious initial advantage over small seeded pioneer species. However, Grubb and Metcalfe (1996) found that correlations between seed size and shade tolerance (i.e. long term mortality) were reduced when comparisons were independent of phylogenetic associations between species within ecological groups. The modelled daily carbon balance for a shade suppressed *S. johorensis* seedling presented in Chapter 6 suggests a net annual loss of 1.4 g of carbohydrate equivalents per year from the leaves alone (based on average seedling mass and LAR). This simple carbon balance is probably inaccurate but it at least suggests that annual fluxes of assimilated and respired carbon are up to an order of magnitude larger than initial seed mass (ca. 0.1 g). Patterns of carbon assimilation and partitioning quickly become more important determinants of dipterocarp seedling mortality than seed size.

After establishment, seedling size influences rates of mortality primarily through the relationship between growth rates and the seedling PPFD environment (Fig. 7.2). The negative correlation between size and mortality was weak during shade suppression, and may be the result of variation in PPFD between seedling plots within the undisturbed sites (Fig. 4.4). After disturbance there was strong competition for light between dipterocarp seedlings. Large seedlings received higher PPFDs, had faster growth rates and consequently lower mortality (Figs. 4.4 & 7.2). Pioneer seedlings that germinate in sites occupied by pre-existing dipterocarps will also experience strong competition. These relationships highlight the importance of initial seedling size in determining competitive relationships following disturbance (Whitmore and Brown, 1996). Provided they survive the disturbance event, dipterocarp seedlings dominate afterwards. Pioneer species will dominate only if PPFDs are high enough for their growth rate to exceed that of the dipterocarps (Fig. 7.2) and if they germinate in a site free of direct competition (because of their small initial size). The spatial distribution of surviving dipterocarp seedlings in relation to available PPFD and germinating pioneer seedlings will therefore be in important determinant of the outcome of regeneration after disturbance (Chapter 4).

In Chapters 5 and 6 it was concluded that nutrient availability does not strongly limit the growth of regenerating dipterocarp seedlings if they are mycorrhizal and growing in undisturbed forest soil. Saturation of the growth response of wild seedlings to light was instead attributed to the inherent physiological characteristics of the seedlings (Fig. 6.7). The maintenance of high rates of photosynthesis and growth in high PPFD was shown to involve significant photosynthetic acclimation at the leaf level. Changes in the partitioning and concentration of nitrogen in the leaf suggest that seedling nutrient status will influence the capacity for acclimation to open conditions (Long *et al.*, 1994). In very disturbed areas where soil around a seedling is exposed to high light intensities, or a seedling establishes from seed into bare mineral soil, acclimation may be limited by poor soil nutrient status and mycorrhizal infection. Because poor soil condition is associated with more open sites, nutrient limitation to dipterocarp seedling growth is evidenced by a decline in the growth of wild seedlings receiving high daily PPFD (Fig. 7.2; based on Fig. 4.9). Equation 7.3 predicts that increased rates of mortality will also occur. Little is known about the nutrient requirements of the common pioneer species but evidence from other studies suggest that they are also only likely to be limited by nutrient availability in disturbed soils after severe disturbance. In less disturbed areas their growth will instead be limited by light (Turner, 1991; Nussbaum *et al.* 1995). The response of pioneer growth and mortality to nutrients is likely to differ from that of the dipterocarps. For example, the onset of nutrient limitation may occur at higher PPFD, and the decline in growth rate with further increasing PPFD may be less pronounced. Disturbed soils will therefore alter the competitive relationships between the two groups.

It is hypothesised that soil water status and seedling water use characteristics exert their strongest effects during discrete drought events. Press *et al.* (1996) found differences in stomatal conductance and diurnal patterns of stomatal opening between dipterocarp species, and proposed that differences in water use efficiency may influence which species survive following logging. Turner (1990a) and Brown and Whitmore (1992) observed high seedling mortality during drought, but in both examples mortality was highest for shade suppressed seedlings beneath closed canopy or in newly formed gaps. During this study, shade suppressed seedlings were observed to wilt during drought while seedlings in gaps were unaffected. Seedling death in these examples was the result of rapid desiccation and wilting of poorly rooted seedlings, rather than an inability to fix carbon and compete effectively during drought. Adaptations for tolerance or avoidance of short-term drought may be more important than long-term water use efficiencies and the maintenance of growth during drought. Stomatal control of transpiration during the wet season is also likely to be reduced by low wind speed and leaf boundary layer conductance, making it difficult to assess water use efficiency on the basis of stomatal conductance alone (Chapter 3; Meinzer *et al.*, 1995). Even less is known about the water use of the common pioneer species, but traits which contribute to their high growth rates almost certainly increase the susceptibility of their small seedlings to drought.

Variation within the Dipterocarpaceae

Dipterocarp species are known to vary in the length of time that their seedlings can persist in the shade (Whitmore, 1984). Previous authors have suggested a link between the length of time a species persists in the shade and growth rates upon release (Ashton, 1994), but there have been no attempts to quantify the relationship. Within the Dipterocarpaceae there exists a more continuous range of variation in shade tolerance than the clear disjunction between the dipterocarps and pioneers. It is correspondingly more difficult to predict differences in seedling ecology between closely related dipterocarp species. Recent reviews have emphasised that the adaptation of forest plants to their environment cannot be considered in terms of the response of only one or a few variables (Chazdon *et al.* 1996; Press *et al.*, 1996). Many studies of tree seedling ecology, including those on the Dipterocarpaceae, have concluded that patterns of carbon partitioning and seedling architecture are at least as important as the seedling photosynthetic response to shade (Walters *et al.* 1993; Kitajima, 1994; Zipperlen and Press, 1996). In Chapter 5 it was concluded that a combination of growth, architectural and photosynthetic characters would be the best predictor for species differences in ecology. Other researchers have found that patterns of carbon partitioning are correlated with maximum growth rates in a number of plant groups (Vanderwerf *et al.*, 1993; Saverimuttu and Westoby, 1996a). Equation 7.3 provides a method for quantifying the relationship between growth, mortality, and physiological characters and integrates the whole plant response over a range of environments (Fig. 7.3). Maximum growth r_m is easily measured and correlates of growth in high PPFD can be more easily distinguished than subtle, long-term differences between slow growing, shade suppressed seedlings. Traits correlated with high growth rates that are retained during shade suppression contribute to higher mortality, while modification of traits in response to suppression may prolong survival in the shade (the C parameter, Fig. 7.3).

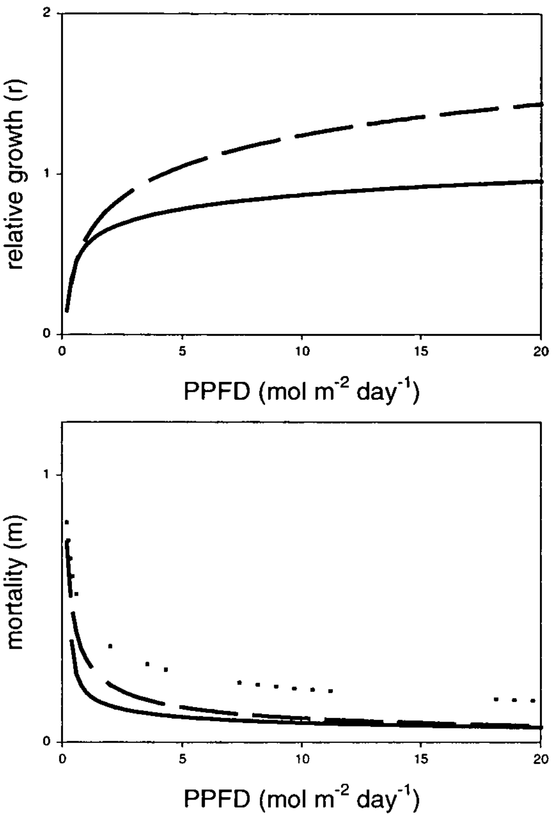


Fig. 7.3. Growth and mortality as a function of PPFD for seedlings of two dipterocarp species that differ in shade tolerance. The solid line if for the more shade tolerant species, and the dashed line is for the less shade tolerant species. Mortality is predicted from growth according to equation 7.3, with $C = 3$. The dotted line is mortality for the less shade tolerant species if $C = 2$ (a lower acclimation potential, mortality is higher at high and low PPFD).

The physiological traits associated with high growth rates in faster growing, light demanding species have already been listed above. It is predicted that species that partition proportionately more carbon to vertical growth and shorter lived, thinner or less dense leaves (high leaf area ratio and SLA) will have higher rates of morality in the shade (King, 1994; Kitajima 1994). When compared under controlled conditions, *S. leprosula* was found to have faster growth, higher rates of leaf turnover and a more orthotropic architecture than *S. parvifolia*, but leaf area was influenced by leaf loss during transplanting and there were no significant differences in LAR and SLA (Chapter 5). Both species are considered intolerant of shade and had higher mortality when compared to other dipterocarps (Still, 1996). To truly compare shade tolerance, measurements of seedling physiological response (photosynthesis and biomass partitioning) should be combined with monitoring of rates of growth and mortality in the field. The difficulty is that the sample sizes required for useful comparisons of mortality are large and difficult to achieve. Many interspecific comparisons of seedling ecology have correlated measured physiological data with anecdotal, occasionally erroneous evidence for differences in shade tolerance (Whitmore 1996). For example, Strugnell (1936) is often cited as finding *S. parvifolia* more shade tolerant than *S. leprosula* (Appanah and Weinland, 1993, Adjers *et al.*, 1995), but he in fact made the opposite conclusion on the basis of 11 surviving saplings. More emphasis should now be placed on studies of seedling population ecology combined with quantitative measurements of the seedling microenvironment (e.g. using hemispherical photography) that can be directly related to the physiological information already gathered.

It is important to note that differences between species varying in shade tolerance may not be the same as the phenotypic variation exhibited by a species in response to shade (Kitajima, 1994). *S. johorensis* had increased LAR and SLA in response to shade (Chapter 6), but species that are intolerant of shade tend to have higher LAR and SLA than shade tolerant species when both are grown in the shade. Contrasting responses within and between species suggest differences in life history 'strategy' between shade tolerant and intolerant species (King 1991; Kohyama, 1991; Kitajima 1994). Tolerance of shade may be a matter of balancing persistence in the shade against growth (Kohyama, 1987; King 1994). Kitajima (1994) hypothesised that more shade tolerant species invest more in longer-lived structural and defensive components (higher root: shoot ratios, fewer, heavier leaves) and as a result have lower overall rates of carbon gain and growth. There are several important consequences for our understanding of dipterocarp seedling ecology. Growth alone may not be directly related to rates of mortality in a given environment, while growth expressed relative to maximum potential growth may be more useful (equation 7.3). Assessment of rates of mortality in the wild will be at least as important as rates of growth. Shade tolerant species grow more slowly in the shade, and may require multiple disturbance events before they reach canopy height, but live longer and may even have a height advantage over shade intolerant species at the time of release (Whitmore, 1996). If allocation to defence is an important component of shade tolerance, species comparisons under controlled conditions with low rates of herbivory will yield different species rankings to comparisons based on wild seedlings. The choice of variable used to characterise seedling growth will also influence the outcome of the comparison – seedling height will exaggerate the growth of shade intolerant species. Seedling mass will better reflect investment in structural components and storage (Kobe, 1997), but is difficult to measure non-destructively.

This discussion has concentrated on the relationship between growth and mortality and its role in determining dipterocarp seedling ecology. To complete our understanding we need to better define how individual physiological traits interact to determine growth rates and susceptibility to death (Fig. 7.1). A model of individual seedling growth could be used to quantify the relationships between seedling architecture, light interception, the carbon balance, and nutrient and water use (Pearcy and Yang, 1996). In Chapter 5 it was concluded that a high rate of respiration and a less favourable leaf carbon balance limited the growth rate of *S. johorensis* seedlings growing in exposed sites. The importance of the carbon balance of isolated leaves will rapidly diminish as the seedling develops a canopy and the light response of the plant diverges from that of single leaves. A whole plant approach is needed to capture the changing relationship between PPFD, growth, and mortality as seedlings grow larger. A whole plant model could also be used to further explore the carbon balance of shaded seedlings. How important is photosynthetic carbon gain compared to respiratory carbon loss by the leaves and other organs? Is there really an unexplained deficit in the modelled carbon balance of suppressed seedlings, and could this deficit result from the transfer of carbon between plants via mycorrhizal symbionts (Simard *et al.*, 1997)? Is hydraulic conductance between the soil and leaves in balance with total leaf area, nitrogen content and photosynthetic capacity? Does the spreading canopy of more shade tolerant species such as *S. parvifolia* (Chapter 5) and *D. lanceolata* (Zipperlen and Press, 1996) result in increased hydraulic limitation to transpiration and vulnerability to drought?

7.2 Implications for management

This study examined three important determinants of the success or failure of natural regeneration after logging: the direct physical impacts of logging on the stand, the microclimate of logged forest compared with undisturbed forest, and the physiological characteristics of dipterocarp timber tree seedlings. The impacts of logging on the stand and its below canopy microclimate were described and related to the growth and mortality response of dipterocarp seedlings at the population level. A pronounced limitation to further increases in seedling growth rate was observed in open areas, and the potential physiological causes of growth limitation and its implications for management were explored.

Reducing logging impacts

The direct physical impact of logging on the residual stand was clearly a key limitation to the success of natural regeneration and the long-term sustainability of the silvicultural system. Damage was measured indirectly in this study as the area of open canopy and disturbed soil, and only over small areas (Chapter 4). Results were in agreement with other studies which have shown that conventional selective logging, usually damages between 40 and 60 % of the residual trees (Appanah and Weinland, 1990; Bertault and Sist, 1995; Pinard and Putz, 1996) and a similar proportion of the ground area (Bertault *et al.*, 1993). Conventional logging is here considered to be logging with low levels of supervision and some unplanned skidding and felling. Strong spatial correlations were demonstrated between canopy opening, soil conditions and seedling density. Seedling regeneration was concentrated around the margin of large open areas, and was usually absent in the most open areas where timber tree regeneration is most desirable.

Despite these simple observations, the Indonesian and Malaysian selective silvicultural systems (TPTI and SMS) are still reliant on natural regeneration. Remedial planting of open areas would be difficult and expensive (Appanah and Manaf, 1994). Natural restocking of large logging gaps by fruiting of residual trees can sometimes occur (Chapter 4), but is an unreliable way to guarantee future harvests (Appanah and Manaf, 1994; Thomas and Appanah, 1995). Reducing damage intensity and the size of open areas will have the dual benefits of increasing the probability that advance regenerants survive near the centre of gaps, and that residual trees are able to restock areas of logging debris and bare soil (Chapter 4). The growth response of light hardwood seedlings to PPFD suggests that they are unlikely to be adversely affected by moderate reductions in light intensity. Guidelines for TPTI include strong emphasis on minimising impacts and retaining an even stock of residuals or seed trees (Anonymous, 1993b; Dykstra and Heinrich, 1996). The problem is therefore clearly one of implementing these guidelines in the field. More research is required on the capacity of residual trees to fruit after logging (Thomas and Appanah, 1995), and on cost effective ways of implementing reduced impact logging techniques into normal logging concessions (Putz and Pinard, 1993; Pinard *et al.* 1995).

The microclimate of logged forest

It is proposed that the most significant effect of logging on the seedling microclimate is the exposure of seedlings to increased direct sunlight (Chapter 3). Logging effects on air temperatures and vapour pressure deficits were only of similar magnitude to diurnal variation, variation between days and seasons, and variation between sites of different elevation and aspect. Changes in air temperature and humidity are not therefore considered important limitations to natural regeneration after logging. Exposure of seedlings to long periods of direct sunlight, combined with generally low wind speeds, will decouple seedling leaves from ambient conditions and result in high leaf temperatures (Chapter 6) and low rates of transpiration (Jarvis and McNaughton, 1986). The capacity for acclimation to high leaf temperatures and PPFD is therefore important, and in the most disturbed areas this may in turn be influenced by seedling nutrient status. Field trials are required to test the importance of nutrient availability and mycorrhizal status for wild seedlings growing in high PPFD.

A second aspect of the seedling microclimate that requires attention is the effect of dry periods on seedling survival and growth. Casual observations have often indicated the importance of short dry periods in causing high mortality in shade suppressed seedlings (Whitmore, 1984; Turner, 1990a; Brown, 1993; Chapter 4). The majority of all deaths may occur during dry periods, but there have been no short-term studies of seedling water relations and mortality during these periods. Seedlings that have already been released by disturbance can survive prolonged periods of negative water balance (Chapter 4). Drought may therefore be most important in determining seedling densities before logging, or increasing mortality during logging.

Dipterocarp seedling physiological characteristics

The growth rates of light hardwood dipterocarp seedlings reached a maximum at only moderate levels of daily PPFD and canopy opening (5 - 10 mol m^{-2} day^{-1} PPFD; Chapter 4). Most other dipterocarp species are likely to have similar or lower light requirements. Reduced canopy opening at the time of logging is unlikely to inhibit the growth of dipterocarp seedlings, but it is likely to reduce competition from pioneer trees and vines (discussed above; Appanah and Putz, 1984; Putz, Lee and Goh, 1984; Yap *et al.* 1995; Kuusipalo *et al.* 1996). A similar conclusion was reached by Kuusipalo *et al.* (1996), who found that liberation thinning did not have the desired effect of speeding recruitment of dipterocarp saplings, but instead prolonged the dominance of pioneer species. Further research is required to determine the optimum light requirements of a wider range of dipterocarp and pioneer species, and on the relationship between logging damage intensity and understorey light environments (Nifinluri, 1996).

The conclusion that a reduction in disturbance intensity will not reduce seedling growth rates differs from that of Whitmore (1984), who stated that a monocyclic silvicultural system with more canopy opening was the only viable method for encouraging light hardwood species. Some shade bearing dipterocarp species will recruit after reduced impact logging, but the levels of disturbance caused by logging will always be greater than natural disturbance and the balance will still be shifted towards light demanding species. Increased canopy opening will also always be associated with higher levels of damage to advance regeneration and residual trees. The end result may therefore be to favour recruitment of vines and pioneers rather than light or heavy hardwood dipterocarps. Polycyclic systems and reduced impact logging are also more compatible with other criteria for sustainable forest management, such as maintaining levels of diversity, production of non timber forest products, and protection of forest hydrological function (Newman, Burgess and Whitmore, 1996; Putz and Viana, 1996; Kiker and Putz, 1997).

Despite the possible consequences for growth, *S. johorensis* seedlings were shown to be tolerant of sudden canopy opening. Seedlings suffer from severe photoinhibition and photo-oxidation during logging, but are capable of rapid recovery (Chapter 6). It is likely that the result for *S. johorensis* can be generalised to other fast growing red meranti species (e.g. *S. parvifolia*, *S. leprosula*). A limited acclimation potential therefore cannot explain a low density of seedlings after logging, thus reinforcing the conclusion that poor regeneration after logging is the consequence of excessive damage or a low density of seedlings before logging. There is, however, an urgent need to examine the response of seedlings to canopy opening during the dry season, and to characterise the acclimation response of a range of dipterocarp species.

A combination of simple growth, architectural and physiological measurements was found to be the best method for ranking dipterocarp species and prediction of species growth responses to disturbance or planting conditions (Chapter 5). On the basis of the model of seedling growth and mortality presented above it was predicted that differences in shade tolerance between species will be most apparent when seedlings are grown in high PPFD. Further interspecific comparisons are required to assist in the selection of species for rehabilitation programmes (Appanah and Weinland, 1993; Nussbaum and Hoe, 1996).

Conclusion

The physical impacts of logging, the logged forest microclimate, and the physiological characteristics of light hardwood dipterocarp seedlings were all found to impose limitations to natural regeneration after logging. If logging impacts are reduced, limitations imposed by microclimate and seedling physiology will become less important. *Reduce logging impacts and more dipterocarp seedlings will survive and grow in an environment that is more favourable for their growth than non-timber species.* If logging is to continue in these forests, the challenge now is to find cost-effective ways to reduce damage, while still maintaining the profits and economic sustainability of the timber company.

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9. Appendix A – Calculation of site factors

The methodology for calculation of site factors from hemispherical photographs follows that of previous authors (Chazdon and Field 1987; Pearcy, 1989; Rich et al. 1993).

Diffuse site factor (T_d)

To calculate T_d for the whole image, the proportion of open (sky) pixels from each annulus was weighted according to the cosine correction for a horizontal surface and for the standard overcast sky assumption. For the standard overcast sky assumption (assumes a higher proportion of total skylight is received from near the zenith):

$$R_i = R_z(1+2\cos z_i)/3 \qquad (9.1)$$

where R_i is the radiant intensity for annulus i, R_z is the radiant intensity at the zenith, and z_i is the zenith angle for the midpoint of annulus i (Anderson, 1964). For the cosine correction:

$$I_i = I_{o(i)} \cos z_i \qquad (9.2)$$

where I_i is the flux density received from annulus i that is incident on a horizontal surface and $I_{o(i)}$ is the flux density received from annulus i by a surface normal to the flux. If each annulus represents an equal area of sky then $I_{o(i)} \propto R_i$ and (1) and (2) can be combined to give the weighting for skylight received from each annulus relative to that from the zenith:

$$w_i = \frac{R_i \cos z_i}{R_z} = \cos z_i (1+2\cos z_i)/3 \qquad (9.3)$$

Direct site factor (T_b)

The weighting for each time step along the solar track accounts for variation in transmittance of the atmosphere and the cosine correction. Transmission of solar radiation through the atmosphere varies with atmospheric clarity and the pathlength:

$$l = 1/\cos z_i \qquad (9.4)$$

$$\tau_i = \tau^l \qquad (9.5)$$

where l is the relative pathlength through the atmosphere, z_i is the zenith angle for timestep i, τ_i is transmittance for timestep i and τ is atmospheric transmissivity (assumed to be 0.65; Gates, 1980; Iqbal, 1983). Equation (9.5) is combined with the cosine correction for a horizontal surface to give the weighting for each time step (v_i):

$$v_i = \cos z_i . \tau_i \qquad (9.6)$$

10. Appendix B - ANOVA design and analysis results

The experimental design used in Chapter 5 (Effects of irradiance and nutrient supply on growth, mycorrhizal infection and photosynthesis of *Shorea* seedlings) was a replicated (two controlled environment rooms) split plot design with light as the main plot factor and species x nutrients as sub-plot factors. Shaded and unshaded frames were paired within growth rooms (blocks), and within each frame two seedlings of each species were grown, one with high nutrients and one with low nutrients (sub-plots). The corresponding ANOVA design and SAS (SAS Institute Inc., Cary, USA) code are given below. The SAS Contrast statement provides a mechanism for custom hypothesis tests. Pre-planned contrasts were used to test for significant nutrient treatment effects within species x light treatment groups e.g. compare high and low nutrients within high light grown *S. leprosula*.

Level	**Source of variation**		**df**
main plot factors	growth rooms	r-1	1
	light	p-1	1
	light x growth rooms	(r-1)(p-1)	1
	blocks	r(q-1)	8
	error (light x blocks)	r(p-1)(q-1)	8
	Total	rpq-1	19
sub-plot factors	nutrients	(a-1)	1
	species	(b-1)	1
	nutrient x species	(a-1)(b-1)	1
	nutrient x light	(a-1)(p-1)	1
	species x light	(b-1)(p-1)	1
	nutrient x species x light	(a-1)(b-1)(p-1)	1
	error	(ab-1)p(rq-1)	1
	Total	rpqab-1	79

where:
r = number of growth rooms
p = number of main plot treatments (high and low light)
q = number of blocks per growth room (5)
a = number of sub-plot treatments - high and low nutrients
b = number of sub-plot treatments - two species

SAS code for the full model:

```
proc glm data=sorted;
        class cabinet light block species nutrient;
        model arc_myco = cabinet light light*cabinet block(cabinet)
                light*block(cabinet) species nutrient species*nutrient
                light*nutrient light*species light*species*nutrient;
        test h=cabinet light cabinet*light e=light*block(cabinet);
        contrast ’nut in Sl hlight’ nutrient 1 -1 species*nutrient 1 -1 0 0
                light*nutrient 1 -1 0 0
                light*species*nutrient 1 -1 0 0 0 0 0 0;
        contrast ’nut in Sv hlight’ nutrient 1 -1 species*nutrient 0 0 1 -1
                light*nutrient 1 -1 0 0
                light*species*nutrient 0 0 1 -1 0 0 0 0;
        contrast ’nut in Sl llight’ nutrient 1 -1 species*nutrient 1 -1 0 0
                light*nutrient 0 0 1 -1
                light*species*nutrient 0 0 0 0 1 -1 0 0;
        contrast ’nut in Sv llight’ nutrient 1 -1 species*nutrient 0 0 1 -1
                light*nutrient 0 0 1 -1
                light*species*nutrient 0 0 0 0 0 0 1 -1;
run;
```

Plants were sub-sampled for nutrient, chlorophyll and photosynthetic measurements, and the results analysed using a simple 3 way ANOVA design (split plots and blocking ignored):

```
proc glm data=sorted;
class light species nutrient;
        model Icomp = species|light|nutrient;
        contrast ’nut in Sl hlight’ nutrient 1 -1 species*nutrient 1 -1 0 0
                   light*nutrient 1 -1 0 0
                   light*species*nutrient 1 -1 0 0 0 0 0 0;
        contrast ’nut in Sv hlight’ nutrient 1 -1 species*nutrient 0 0 1 -1
                   light*nutrient 1 -1 0 0
                   light*species*nutrient 0 0 1 -1 0 0 0 0;
        contrast ’nut in Sl llight’ nutrient 1 -1 species*nutrient 1 -1 0 0
                   light*nutrient 0 0 1 -1
                   light*species*nutrient 0 0 0 0 1 -1 0 0;
        contrast ’nut in Sv llight’ nutrient 1 -1 species*nutrient 0 0 1 -1
                   light*nutrient 0 0 1 -1
                   light*species*nutrient 0 0 0 0 0 0 1 -1;
        run;
```

Analysis results

For explanation of variables and units refer to their tabulated values in Chapter 5

initial height

Source of variation	f	p
LIGHT	0.41	0.5419
SPECIES	11.77	0.0012
NUTRIENT	0.28	0.6002
SPECIES*NUTRIENT	0.33	0.5668
LIGHT*NUTRIENT	0.29	0.5906
LIGHT*SPECIES	0.00	0.9513
LIGHT*SPECIE*NUTRIEN	1.65	0.2047
nutrients in *S. leprosula* high light	2.14	0.1489
nutrients in *S. parvifolia* high light	0.16	0.6938
nutrients in *S. leprosula* low light	0.13	0.7197
nutrients in *S. parvifolia* low light	0.12	0.7301

final height

LIGHT	44.77	0.0002
SPECIES	13.08	0.0007
NUTRIENT	0.11	0.7387
SPECIES*NUTRIENT	1.05	0.3098
LIGHT*NUTRIENT	0.09	0.7666
LIGHT*SPECIES	0.00	0.9869
LIGHT*SPECIE*NUTRIEN	0.41	0.5234
nutrients in *S. leprosula* high light	0.27	0.6073
nutrients in *S. parvifolia* high light	1.32	0.2550
nutrients in *S. leprosula* low light	0.03	0.8633
nutrients in *S. parvifolia* low light	0.04	0.8345

final dry mass

LIGHT	270.24	0.0001
SPECIES	5.79	0.0195
NUTRIENT	0.00	0.9483
SPECIES*NUTRIENT	1.09	0.3014
LIGHT*NUTRIENT	0.06	0.8023
LIGHT*SPECIES	1.17	0.2842
LIGHT*SPECIE*NUTRIEN	1.51	0.2247
nutrients in *S. leprosula* high light	0.96	0.3327
nutrients in *S. parvifolia* high light	1.67	0.2011
nutrients in *S. leprosula* low light	0.00	0.9993
nutrients in *S. parvifolia* low light	0.03	0.8535

Relative growth rate (R)

LIGHT	1089.84	0.0001
SPECIES	15.36	0.0003
NUTRIENT	0.01	0.9349
SPECIES*NUTRIENT	1.96	0.1675
LIGHT*NUTRIENT	0.10	0.7557
LIGHT*SPECIES	1.35	0.2509
LIGHT*SPECIE*NUTRIEN	0.03	0.8716
nutrients in *S. leprosula* high light	0.76	0.3867
nutrients in *S. parvifolia* high light	0.45	0.5047
nutrients in *S. leprosula* low light	0.18	0.6726
nutrients in *S. parvifolia* low light	0.68	0.4140

Net assimiliation rate (N)

LIGHT	322.35	0.0001
SPECIES	24.91	0.0001
NUTRIENT	0.09	0.7713
SPECIES*NUTRIENT	4.63	0.0359
LIGHT*NUTRIENT	0.58	0.4492
LIGHT*SPECIES	1.01	0.3189
LIGHT*SPECIE*NUTRIEN	0.91	0.3456
nutrients in *S. leprosula* high light	4.10	0.0479
nutrients in *S. parvifolia* high light	1.07	0.3057
nutrients in *S. leprosula* low light	0.14	0.7139
nutrients in *S. parvifolia* low light	0.71	0.4029

Leaf Area Ratio (LAR)

LIGHT	0.13	0.7237
SPECIES	1.86	0.1784
NUTRIENT	0.39	0.5363
SPECIES*NUTRIENT	1.83	0.1819
LIGHT*NUTRIENT	0.02	0.8975
LIGHT*SPECIES	0.72	0.3990
LIGHT*SPECIE*NUTRIEN	2.56	0.1153
nutrients in *S. leprosula* high light	2.82	0.0992
nutrients in *S. parvifolia* high light	1.54	0.2198
nutrients in *S. leprosula* low light	0.06	0.8005
nutrients in *S. parvifolia* low light	0.25	0.6158

Specific Leaf Area (SLA)

LIGHT	61.04	0.0001
SPECIES	0.14	0.7125
NUTRIENT	1.01	0.3205
SPECIES*NUTRIENT	0.31	0.5772
LIGHT*NUTRIENT	2.35	0.1311
LIGHT*SPECIES	0.52	0.4722
LIGHT*SPECIE*NUTRIEN	0.78	0.3826
nutrients in *S. leprosula* high light	0.21	0.6506
nutrients in *S. parvifolia* high light	0.97	0.3287
nutrients in *S. leprosula* low light	1.23	0.2727
nutrients in *S. parvifolia* low light	2.04	0.1592

leaf loss

LIGHT	0.04	0.8412
SPECIES	14.96	0.0003
NUTRIENT	0.82	0.3683
SPECIES*NUTRIENT	0.46	0.4999
LIGHT*NUTRIENT	0.02	0.8781
LIGHT*SPECIES	0.55	0.4609
LIGHT*SPECIE*NUTRIEN	1.01	0.3203
nutrients in *S. leprosula* high light	1.88	0.1758
nutrients in *S. parvifolia* high light	0.10	0.7574
nutrients in *S. leprosula* low light	0.05	0.8309
nutrients in *S. parvifolia* low light	0.29	0.5925

Leaf Mass Ratio (LMR)

LIGHT	10.75	0.0112
SPECIES	5.92	0.0183
NUTRIENT	0.49	0.4859
SPECIES*NUTRIENT	2.49	0.1203
LIGHT*NUTRIENT	0.72	0.3996
LIGHT*SPECIES	0.31	0.5808
LIGHT*SPECIE*NUTRIEN	2.22	0.1417
nutrients in *S. leprosula* high light	5.34	0.0247
nutrients in *S. parvifolia* high light	0.58	0.4509
nutrients in *S. leprosula* low light	0.00	0.9760
nutrients in *S. parvifolia* low light	0.01	0.9072

Stem Mass Ratio (SMR)

LIGHT	3.12	0.1153
SPECIES	3.05	0.0866
NUTRIENT	0.00	0.9493
SPECIES*NUTRIENT	1.29	0.2604
LIGHT*NUTRIENT	0.15	0.6971
LIGHT*SPECIES	0.15	0.7007
LIGHT*SPECIE*NUTRIEN	0.78	0.3805
nutrients in *S. leprosula* high light	1.38	0.2453
nutrients in *S. parvifolia* high light	0.72	0.4007
nutrients in *S. leprosula* low light	0.01	0.9199
nutrients in *S. parvifolia* low light	0.13	0.7246

Tap Root Mass Ratio (TRMR)

LIGHT	80.58	0.0001
SPECIES	0.99	0.3249
NUTRIENT	0.09	0.7634
SPECIES*NUTRIENT	0.08	0.7734
LIGHT*NUTRIENT	0.42	0.5210
LIGHT*SPECIES	0.19	0.6628
LIGHT*SPECIE*NUTRIEN	0.01	0.9157
nutrients in *S. leprosula* high light	0.45	0.5044
nutrients in *S. parvifolia* high light	0.08	0.7833
nutrients in *S. leprosula* low light	0.01	0.9363
nutrients in *S. parvifolia* low light	0.07	0.7933

Fine Root Mass Ratio (FRMR)

LIGHT	48.81	0.0001
SPECIES	0.61	0.4397
NUTRIENT	2.23	0.1413
SPECIES*NUTRIENT	1.86	0.1781
LIGHT*NUTRIENT	0.00	0.9506
LIGHT*SPECIES	1.32	0.2560
LIGHT*SPECIE*NUTRIEN	4.62	0.0361
nutrients in *S. leprosula* high light	6.42	0.0142
nutrients in *S. parvifolia* high light	0.96	0.3319
nutrients in *S. leprosula* low light	0.10	0.7479
nutrients in *S. parvifolia* low light	1.23	0.2729

branch frequency

LIGHT	27.62	0.0008
SPECIES	34.21	0.0001
NUTRIENT	0.24	0.6275
SPECIES*NUTRIENT	1.30	0.2594
LIGHT*NUTRIENT	0.01	0.9249
LIGHT*SPECIES	20.10	0.0001
LIGHT*SPECIE*NUTRIEN	0.08	0.7720
nutrients in *S. leprosula* high light	0.05	0.8209
nutrients in *S. parvifolia* high light	0.39	0.5372
nutrients in *S. leprosula* low light	0.18	0.6732
nutrients in *S. parvifolia* low light	1.01	0.3185

total branch length

LIGHT	52.73	0.0001
SPECIES	4.81	0.0326
NUTRIENT	0.35	0.5568
SPECIES*NUTRIENT	0.40	0.5321
LIGHT*NUTRIENT	0.30	0.5843
LIGHT*SPECIES	0.81	0.3707
LIGHT*SPECIE*NUTRIEN	0.46	0.4991
nutrients in *S. leprosula* high light	0.01	0.9336
nutrients in *S. parvifolia* high light	1.50	0.2257
nutrients in *S. leprosula* low light	0.00	0.9632
nutrients in *S. parvifolia* low light	0.00	0.9958

leaf area : stem length ratio

LIGHT	42.01	0.0002
SPECIES	27.88	0.0001
NUTRIENT	0.04	0.8441
SPECIES*NUTRIENT	0.00	0.9603
LIGHT*NUTRIENT	0.03	0.8561
LIGHT*SPECIES	0.38	0.5410
LIGHT*SPECIE*NUTRIEN	0.17	0.6828
nutrients in *S. leprosula* high light	0.00	0.9679
nutrients in *S. parvifolia* high light	0.18	0.6759
nutrients in *S. leprosula* low light	0.04	0.8515
nutrients in *S. parvifolia* low light	0.03	0.8635

internode length / diameter ratio

LIGHT	11.08	0.0104
SPECIES	21.05	0.0001
NUTRIENT	0.84	0.3629
SPECIES*NUTRIENT	0.05	0.8197
LIGHT*NUTRIENT	0.14	0.7111
LIGHT*SPECIES	0.10	0.7515
LIGHT*SPECIE*NUTRIEN	0.46	0.5014
nutrients in *S. leprosula* high light	0.18	0.6753
nutrients in *S. parvifolia* high light	0.75	0.3888
nutrients in *S. leprosula* low light	0.53	0.4712
nutrients in *S. parvifolia* low light	0.03	0.8576

mycorrhizal infection

LIGHT	28.87	0.0007
SPECIES	8.55	0.0056
NUTRIENT	5.26	0.0270
SPECIES*NUTRIENT	2.48	0.1231
LIGHT*NUTRIENT	2.17	0.1488
LIGHT*SPECIES	3.20	0.0809
LIGHT*SPECIE*NUTRIEN	1.55	0.2204
nutrients in *S. leprosula* high light	3.31	0.0763
nutrients in *S. parvifolia* high light	4.22	0.0465
nutrients in *S. leprosula* low light	1.08	0.3058
nutrients in *S. parvifolia* low light	2.83	0.1000

chlorophyll a + b / fresh mass

LIGHT	32.72	0.0001
SPECIES	30.53	0.0001
NUTRIENT	0.36	0.5506
SPECIES*NUTRIENT	5.10	0.0305
LIGHT*NUTRIENT	9.66	0.0038
LIGHT*SPECIES	1.97	0.1696
LIGHT*SPECIE*NUTRIEN	5.76	0.0220
nutrients in *S. leprosula* high light	16.78	0.0002
nutrients in *S. parvifolia* high light	0.23	0.6315
nutrients in *S. leprosula* low light	1.83	0.1847
nutrients in *S. parvifolia* low light	1.34	0.2557

chlorophyll a + b / area

LIGHT	5.00	0.0321
SPECIES	4.67	0.0379
NUTRIENT	0.42	0.5217
SPECIES*NUTRIENT	2.51	0.1224
LIGHT*NUTRIENT	8.06	0.0076
LIGHT*SPECIES	0.62	0.4368
LIGHT*SPECIE*NUTRIEN	4.38	0.0439
nutrients in *S. leprosula* high light	12.29	0.0013
nutrients in *S. parvifolia* high light	0.01	0.9226
nutrients in *S. leprosula* low light	1.90	0.1766
nutrients in *S. parvifolia* low light	0.68	0.4159

chlorophyll a to b ratio

LIGHT	10.05	0.0032
SPECIES	3.50	0.0698
NUTRIENT	0.04	0.8344
SPECIES*NUTRIENT	0.00	0.9631
LIGHT*NUTRIENT	0.22	0.6395
LIGHT*SPECIES	0.14	0.7090
LIGHT*SPECIE*NUTRIEN	2.93	0.0963
nutrients in *S. leprosula* high light	0.98	0.3300
nutrients in *S. parvifolia* high light	0.58	0.4500
nutrients in *S. leprosula* low light	1.44	0.2385
nutrients in *S. parvifolia* low light	0.23	0.6344

nitrogen per unit leaf area

LIGHT	17.03	0.0002
SPECIES	3.69	0.0631
NUTRIENT	0.32	0.5735
SPECIES*NUTRIENT	0.36	0.5540
LIGHT*NUTRIENT	3.43	0.0727
LIGHT*SPECIES	0.03	0.8581
LIGHT*SPECIE*NUTRIEN	0.00	0.9458
nutrients in *S. leprosula* high light	0.86	0.3610
nutrients in *S. parvifolia* high light	2.27	0.1407
nutrients in *S. leprosula* low light	0.99	0.3258
nutrients in *S. parvifolia* low light	0.09	0.7641

nitrogen per unit leaf mass

LIGHT	0.49	0.4897
SPECIES	6.64	0.0145
NUTRIENT	0.15	0.7020
SPECIES*NUTRIENT	0.03	0.8656
LIGHT*NUTRIENT	2.69	0.1103
LIGHT*SPECIES	0.05	0.8267
LIGHT*SPECIE*NUTRIEN	0.99	0.3272
nutrients in *S. leprosula* high light	2.44	0.1276
nutrients in *S. parvifolia* high light	0.19	0.6626
nutrients in *S. leprosula* low light	1.13	0.2956
nutrients in *S. parvifolia* low light	0.04	0.8344

phosphorus per unit leaf area

LIGHT	9.85	0.0037
SPECIES	29.17	0.0001
NUTRIENT	16.20	0.0003
SPECIES*NUTRIENT	12.68	0.0012
LIGHT*NUTRIENT	7.00	0.0127
LIGHT*SPECIES	1.89	0.1787
LIGHT*SPECIE*NUTRIEN	0.90	0.3495
nutrients in *S. leprosula* high light	1.24	0.2742
nutrients in *S. parvifolia* high light	36.24	0.0001
nutrients in *S. leprosula* low light	0.40	0.5297
nutrients in *S. parvifolia* low light	3.17	0.0847

phosphorus per unit leaf mass

LIGHT	0.05	0.8189
SPECIES	25.50	0.0001
NUTRIENT	8.74	0.0059
SPECIES*NUTRIENT	5.91	0.0210
LIGHT*NUTRIENT	1.92	0.1753
LIGHT*SPECIES	4.32	0.0460
LIGHT*SPECIE*NUTRIEN	0.00	0.9980
nutrients in *S. leprosula* high light	0.97	0.3325
nutrients in *S. parvifolia* high light	13.31	0.0010
nutrients in *S. leprosula* low light	0.20	0.6610
nutrients in *S. parvifolia* low light	3.18	0.0841

A max per unit leaf area

LIGHT	41.67	0.0001
SPECIES	12.46	0.0028
NUTRIENT	0.45	0.5135
SPECIES*NUTRIENT	0.30	0.5934
LIGHT*NUTRIENT	2.46	0.1367
LIGHT*SPECIES	3.34	0.0863
LIGHT*SPECIE*NUTRIEN	0.47	0.5046
nutrients in *S. leprosula* high light	1.10	0.3099
nutrients in *S. parvifolia* high light	1.41	0.2527
nutrients in *S. leprosula* low light	0.03	0.8715
nutrients in *S. parvifolia* low light	1.13	0.3035

A max per unit leaf mass

LIGHT	6.26	0.0236
SPECIES	8.42	0.0104
NUTRIENT	0.43	0.5233
SPECIES*NUTRIENT	0.56	0.4635
LIGHT*NUTRIENT	0.86	0.3676
LIGHT*SPECIES	0.78	0.3907
LIGHT*SPECIE*NUTRIEN	0.09	0.7716
nutrients in *S. leprosula* high light	1.04	0.3239
nutrients in *S. parvifolia* high light	0.32	0.5819
nutrients in *S. leprosula* low light	0.15	0.7046
nutrients in *S. parvifolia* low light	0.44	0.5184

A max per unit leaf nitrogen

LIGHT	2.65	0.1232
SPECIES	3.77	0.0700
NUTRIENT	0.16	0.6972
SPECIES*NUTRIENT	0.37	0.5531
LIGHT*NUTRIENT	0.00	0.9548
LIGHT*SPECIES	2.47	0.1358
LIGHT*SPECIE*NUTRIEN	0.11	0.7496
nutrients in *S. leprosula* high light	0.01	0.9323
nutrients in *S. parvifolia* high light	0.14	0.7181
nutrients in *S. leprosula* low light	0.09	0.7710
nutrients in *S. parvifolia* low light	0.40	0.5347

R_d area

LIGHT	35.87	0.0001
SPECIES	0.79	0.3876
NUTRIENT	2.01	0.1758
SPECIES*NUTRIENT	0.04	0.8362
LIGHT*NUTRIENT	0.08	0.7847
LIGHT*SPECIES	3.26	0.0900
LIGHT*SPECIE*NUTRIEN	0.93	0.3493
nutrients in *S. leprosula* high light	2.06	0.1707
nutrients in *S. parvifolia* high light	0.07	0.7982
nutrients in *S. leprosula* low light	0.04	0.8499
nutrients in *S. parvifolia* low light	0.90	0.3580

apparent quantum efficiency (ϕ)		
LIGHT	12.82	0.0025
SPECIES	2.74	0.1176
NUTRIENT	1.33	0.2656
SPECIES*NUTRIENT	1.18	0.2936
LIGHT*NUTRIENT	3.51	0.0792
LIGHT*SPECIES	0.39	0.5390
LIGHT*SPECIE*NUTRIEN	0.38	0.5445
nutrients in *S. leprosula* high light	0.44	0.5176
nutrients in *S. parvifolia* high light	5.60	0.0309
nutrients in *S. leprosula* low light	0.35	0.5609
nutrients in *S. parvifolia* low light	0.02	0.9003

maximum conductance		
LIGHT	4.82	0.0433
SPECIES	8.39	0.0105
NUTRIENT	1.93	0.1838
SPECIES*NUTRIENT	0.41	0.5312
LIGHT*NUTRIENT	0.05	0.8288
LIGHT*SPECIES	0.12	0.7356
LIGHT*SPECIE*NUTRIEN	1.31	0.2697
nutrients in *S. leprosula* high light	0.91	0.3545
nutrients in *S. parvifolia* high light	0.00	0.9764
nutrients in *S. leprosula* low light	0.28	0.6011
nutrients in *S. parvifolia* low light	0.69	0.4189

Q compensation		
LIGHT	27.90	0.0001
SPECIES	1.52	0.2352
NUTRIENT	1.83	0.1950
SPECIES*NUTRIENT	0.11	0.7493
LIGHT*NUTRIENT	0.00	0.9940
LIGHT*SPECIES	2.46	0.1364
LIGHT*SPECIE*NUTRIEN	0.04	0.8514
nutrients in *S. leprosula* high light	0.37	0.5536
nutrients in *S. parvifolia* high light	0.55	0.4701
nutrients in *S. leprosula* low light	0.18	0.6783
nutrients in *S. parvifolia* low light	0.88	0.3622

Q saturation		
LIGHT	3.38	0.0846
SPECIES	7.39	0.0152
NUTRIENT	0.05	0.8307
SPECIES*NUTRIENT	0.93	0.3486
LIGHT*NUTRIENT	2.71	0.1190
LIGHT*SPECIES	1.33	0.2656
LIGHT*SPECIE*NUTRIEN	0.61	0.4465
nutrients in *S. leprosula* high light	3.26	0.0899
nutrients in *S. parvifolia* high light	0.00	0.9535
nutrients in *S. leprosula* low light	0.39	0.5425
nutrients in *S. parvifolia* low light	0.65	0.4312