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LADAWAN ATIPANUMPAI

ACACIA MANGIUM: STUDIES ON THE
GENETIC VARIATION IN ECOLOGICAL AND
PHYSIOLOGICAL CHARACTERISTICS OF A
FAST-GROWING PLANTATION TREE SPECIES

ACACIA MANGIUM: TUTKIMUKSIA
NOPEAKASVUISEN VILJELYPUULAJIN
EKOLOGISTEN JA FYSIOLOGISTEN TUNNUSTEN
GENEETTISESTÄ VAIHTELUSTA

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ACACIA MANGIUM: STUDIES ON THE GENETIC VARIATION IN ECOLOGICAL AND PHYSIOLOGICAL CHARACTERISTICS OF A FAST-GROWING PLANTATION TREE SPECIES

Tiivistelmä: *Acacia mangium*: tutkimuksia nopeakasvuisen viljelypuulajin ekologisten ja fysiologisten tunnusten geneettisestä vaihtelusta

Ladawan Atipanumpai

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in Auditorium XII of the University Main Building, Fabianinkatu 33, on 24 November 1989, at 12 o'clock noon

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Genetic variation in the physiological characteristics and biomass accumulation was studied in both field and laboratory conditions. Variation in the growth characteristics, foliar nutrient concentration, phyllode anatomy and stomatal frequency was analyzed in 16 different origins under field conditions in Central Thailand. Family variation and heritability of growth and flowering frequency were calculated using 20 open-pollinated families at the age of 28 months. The effect of environmental factors on diameter growth in different provenances is also discussed. Under laboratory conditions, such physiological characteristics as transpiration rate, leaf conductance and leaf water potential were measured at varying soil moisture conditions. The responses of photosynthesis, photorespiration and dark respiration as well as the CO₂ compensation point to temperature and irradiance were also investigated. All physiological characteristics indicated differences among provenances. An attempt was made to relate the results obtained in the laboratory to the growth performance in the field. Recommendations on provenance selection for the planting of *A. mangium* in Thailand are also given.

Keywords: *Acacia mangium*, carbon dioxide compensation point, dark respiration, dendrometry, foliar analysis, half-sib families, heritability, leaf conductance, photosynthesis, photorespiration, provenance, stomata, transpiration, water stress.

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*Acacia mangium*in fysiologisten tunnusten ja kasvun geneettistä vaihtelua tutkittiin kenttä- ja laboratoriokokeissa. Kasvun sekä lehtien ravinnepitoisuuden, fyllodien anatomian ja ilmarakotiheden vaihtelua selvitettiin käyttäen materiaalina 16 eri siemenalkuperää kenttäkokeissa Keski-Thaimaassa. Kasvun ja kukintarunsauden vaihtelua ja periytyvyyttä tutkittiin 20 vapaa-pölytysjälkeläistön avulla puiden ollessa 28 kk:n ikäisiä. Lisäksi analysoitiin ympäristötekijöiden vaikutusta paksuuskasvun dynamiikkaan. Laboratoriomittauksin selvitettiin haihduntanopeuden, lehtikonduktanssin ja lehden vesipotentiaalin riippuvuutta kasvalustan vesipitoisuudesta; samoin tutkittiin lämpötilan ja valonvoimakkuuden vaikutus yhteyttämiseen, valohengitykseen ja pimeähengitykseen sekä CO₂-kompensaatiopisteeseen. Laboratoriokokeiden aineistona oli kuusi myös kenttäkokeissa mukana ollutta siemenalkuperää. Tutkimuksessa pyrittiin lopuksi löytämään fysiologisten tunnusten ja todellisissa kenttäoloissa saavutettavan kasvun välisiä riippuvuuksia. Tulokseksi saatiin, että kasvua ei voida kovin hyvin ennustaa fysiologisten tunnusten avulla mutta että ekofysiologiset mittaukset silti tarjoavat käyttökelpoisen keinon ympäristöönnsä hyvin sopeutuneiden ja esimerkiksi kuivuutta paremmin kestävien viljelyalkuperien tunnistamiseksi. Tutkimuksessa annetaan suositukset Thaimaan oloihin tällä hetkellä sopivimmiksi todetuista *A. mangium*in alkuperistä.

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PREFACE

The present study consists a number of experiments carried out at the Lad Krating Plantation of the Thai Plywood Company, at Kasetsart University, as well as at the Department of Silviculture and Forestry Field Station of the University of Helsinki between 1984 and 1988. I am deeply in debt to Professor Dr. Olavi Luukkanen, my main supervisor in Finland, and my supervisor at Kasetsart University, Associate Professor Dr. Suree Bhumibhamon. Their guidance, constant encouragement, and constructive criticism throughout are highly appreciated. Professor Luukkanen has also read the manuscript thoroughly and made valuable suggestions and comments for its improvement.

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Helsinki, August 1989

Ladawan Atipanumpai



Figure 1. *Acacia mangium* seedling seed orchard, 28 months old (top). Twig showing phyllodes and pods of *A. mangium* (bottom).

1. ACACIA MANGIUM AS A TROPICAL PLANTATION SPECIES

1.1. Introduction

During the past several decades there has been considerable activity in the exploration of the forest resources in the tropics. However, over-exploitation of the forest resources has simultaneously occurred in most developing countries resulting in a continuous decrease of the forest area. About 11 million ha of tropical forest is now estimated to disappear annually and, apart from environmental degradation, a serious shortage of wood is now a well documented fact in many countries (FAO 1985).

To overcome the problems associated with forest depletion and to maintain a sufficient supply of wood to serve as raw material and fuel, the establishment of man-made forests has been intensified in the tropical world using a wide variety of both indigenous and exotic tree species. The choice of tree species in any planting programme requires proper and intensive selection. However, it is already widely agreed that fast-growing trees presently offer one of the fastest and most promising remedies for the alarming situation when both environmental and economic considerations are taken into account (WCED 1988).

Of the fast-growing trees selected for planting, *Eucalyptus* sp., *Gmelina arborea*, and leguminous tree crops such as *Albizia falcataria* and *Leucaena leucocephala*, have been routinely used. Among the less common species, *Acacia mangium* appears to be one of the most promising for tree planting programmes in the humid tropics, where it has recently been introduced in many countries. The success of *A. mangium* is primarily due to its rapid growth rate, robustness and wide range of uses (Mangium... 1983). When planted as an exotic, it has often shown an unexpectedly good performance, and has now been widely planted throughout tropical Asia, the Pacific Islands, West Africa, and the Americas. Being a relatively new plantation species, it has not yet, however, been thoroughly studied, and little information

and experience on it has so far been gathered. There are many aspects which need to be studied and developed before the true potential of this species can be assessed (Turnbull 1986).

1.2. Species, distribution and ecology

A. mangium Willd. is a leguminous tree species in the subfamily Mimosoideae. The genus *Acacia* includes about 1,200 species of trees and shrubs which occur in Australia, Asia, Africa, and the Americas (The Genus... 1982). *A. mangium* is a tropical lowland species of moderate size and is locally known as brown salwood, black wattle and hickory wattle (Hall et al. 1980). The species has long been misidentified as *A. holosericea* Cunn. ex G. Don which it superficially resembles (Pedley 1977).

According to Pedley (1964), the natural distribution of *A. mangium* concentrates in the southern hemisphere and stretches from Aru Island in the Moluccas and Irian Jaya (the easternmost part of Indonesia), to the River Oriomo in the Western Division of Papua New Guinea and down to the north-eastern part of Australia between Ingham and the River Diantree. The latitudinal limits are about 0° 50' S to 19° S (Fig. 2).

A. mangium is typical lowland species, principally occurring from just above mean sea-level to about 480 m elevation. However, it has been reported to occur on the Atherton Tablelands at about 800 m (Hall et al. 1980). The distribution of the species is mainly along the boundary of the warm and hot (humid or wet) tropical climatic zones. The mean maximum temperature within the natural range is 31–34°C and the mean minimum temperature is 12–16°C. *A. mangium* favours high rainfall sites; the total annual rainfall varying from 1,000 mm to more than 4,500 mm with a relatively dry period of 4 months. It has been suggested by Nicholson (1981) that the disjunction in the species distribution is directly associated with the rainfall pattern.

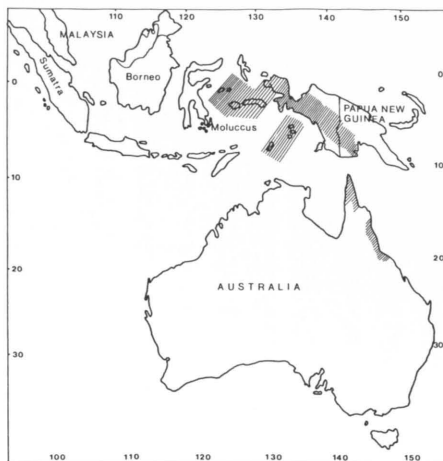


Figure 2. Natural distribution of *A. mangium* (Mangium... 1983).

A. mangium is commonly found along the fringes of the mangrove forests where it is sometimes associated with *Rhizophora* sp. and *Melaleuca* sp. More often it is found along forest margins associated with many species such as *Dillenia alata*, *Acacia cincinata*, *A. aulacocarpa* and *Eucalyptus tessellaris*. Generally, *A. mangium* occurs in small groups; only occasionally does it dominate large areas (Hall et al. 1980).

Under natural conditions, *A. mangium* grows satisfactorily on eroded, rocky to gravelly, thin mineral soils, but sometimes on acidic and clay soils, and also on deeply weathered or alluvial soils (Mangium... 1983, Turnbull et al. 1983).

The tree generally grows to a height of 25–30 m, with a straight bole which may be over half of the total height. Stem diameters up to 90 cm have been measured. However, on a relatively poor sites, the tree more resembles a large shrub with an average height between 7 and 10 m (Hall et al. 1980). The stem has longitudinal furrows and the bark is thick, rough and hard with a colour varying from dark brown to fawn (Hall et al. 1980). Utilization is rather restricted in Australia, but is locally used for construction, boat-building and domestic fuel in Indonesia (Turnbull et al. 1983).

When newly germinated, *A. mangium* has compound leaves made up of minute leaflets;

the leaves are alternate and bipinnate, as in other species of the subfamily Mimosoideae. After a few weeks, the minute leaflets are replaced by a flattening of the petiole and the main axes of each leaflet are transformed into a "phyllode" which is simple and parallel-veined. The phyllodes are exceptionally large, approximately 25 x 10 cm, glabrous or slightly scurfy.

The inflorescences of *A. mangium* occur in rather loose spikes upto 10 cm long composed of tiny white or cream-coloured flowers. The pods are linear, becoming twisted and coiled when ripe. Seed maturity is indicated by the development of a blackish-brown colouration of the pods about 6–7 months after flowering. The small shiny and black to brown seeds are arranged longitudinally with a ribbon-like orange tissue, known as the funicle, surrounding the seed and attaching each seed to the pod.

A. mangium is closely related to *A. auriculiformis* Cunn. ex Benth. with which hybridization readily occurs. The hybrids tend to grow even faster than either parent but retain the considerably poor form of *A. auriculiformis* (Bowen 1981b).

1.3. Biology of flowering and seed production

The phenology of flowering and seed production of *A. mangium* varies with location and age. Generally speaking, flowering of *A. mangium* is profuse and continuous throughout the year, and the species is self-compatible (Bowen 1981a). The species starts to produce seeds within 18 months (Yanthasath 1986), but it takes a longer time at higher latitudes (Pan and Yang 1986). In Australia, the tree is expected to flower some time in May (Hall et al. 1980), while in Kemasul the flowers are found around March (Yap and Wong 1983). Fruiting is quite prolific. At Piru in Indonesia, Suratmo et al. (see Turnbull et al. 1983) observed that the seed is already shed in August and September, and the optimum time for seed collection is between June and July. A similar observation was reported by Yap and Wong (1983). Seed collection on the west coast in Sabah commences during the middle of February, while on the east coast collection does not commence until the middle of June (Bowen and Eusebio 1984a). However, seed collection continues until October in Papua New

Guinea and northern Queensland (Doran and Skelton 1982).

Information on methods of seed harvesting, cleaning and storage are described in detail by Bowen and Eusebio (1984a, b). Branch lopping seems to be the most preferred method for *A. mangium* seed harvesting. Collection is occasionally carried out by climbing the tree and cutting off branches. Pods are better collected using a hook when the majority of them in the crown are dark brown to black in colour and just starting to split. Collection of the fallen seeds on the ground is not recommended because seeds are small and not easily spotted and subsequently increase the cost of seed collection.

The collected intact pods are dried in the sun for 2–3 days to induce dehiscence of the pericarps. Giving a heat treatment at 40–45°C for 24 hours in an oven is also possible (Bowen 1981b). Oven drying does not affect seed viability as indicated by the fact that seeds can withstand temperatures up to 70°C for 24 hours without a significant decrease in viability. Seeds are extracted by placing the dehisced pods in a rotating drum (e.g. cement mixer), or by heavy beating with a piece of wood. Finally, the seeds are winnowed to remove chaffs. Each kilogram of ripe pods yields about 90 grams of seeds (Mangium... 1983, Yap and Wong 1983). The number of seeds per kilogram varies from 70,000 to 120,000 seeds (Bowen and Eusebio 1982).

1.4. Plantation preference

1.4.1. Adaptability

A. mangium has a wide adaptability and it tolerates a wide range of soils and habitats. When planted as an exotic the species often shows outstanding growth. Sim (1986) indicated the potential of *A. mangium* as a plantation species for rehabilitating difficult sites and revegetating newly cleared land. *A. mangium* is well-known for its competition with weed species such as *Imperata cylindrica* grass and *Eupatorium*. The adaptability of *A. mangium* to different topographies was demonstrated in detail by Thomas and Kent (1986).

A noteworthy feature of *A. mangium* is its ability to grow on acidic soils. Hu et al. (1983) indicated the optimum soil pH range for the species is from pH 4 to pH 6. This is

important since acidic soils are widespread throughout the tropics; this characteristic also distinguishes *A. mangium* from other trees such as *Leucaena leucocephala* which requires a pH level above 5.5 (Leucaena... 1977). In contrast, *A. mangium* is a less salt tolerant species (Thomson 1986) and it is therefore not recommended to be grown in saline areas.

A. mangium is sensitive to exposure to prolonged low temperatures and frost; the minimum temperature in its native range never falls lower than 10°C. Pan and Yang (1986) reported the mortality of 5-year-old trees after prolonged exposure to low temperature of 4.9–5.6°C, with cold rain. Wind resistance is also poor. According to observations in Guangdong Province, China, 11% of stems were found to be leaning and 3% broken as a result of wind damage (cf. Pan and Yang 1986).

An unexpected ability of *A. mangium* to tolerate extended drought has been reported (Midgley and Vinekanandan 1986), but no details were given. More studies concerning drought tolerance should be made.

A. mangium was first introduced to Sabah, Malaysia, from Australia in 1966, as a fire-break species (Tham 1976). Up to now, many trial plots of *A. mangium* have been established throughout the humid tropics region, i.e. Malaysia (Doran and Skelton 1982, Yap 1986, Racž and Ibrahim 1986), Indonesia (Na'iem et al. 1985, Suseno and Na'iem 1985, Voss et al. 1987), Thailand (Boonkird 1980, Boontawee and Kuwalairat 1986, Pinyopusarerk and Puriyakorn 1986), the Philippines (Andin 1980, Introducing... 1980, Pettersson and Havmöller 1984), Sri Lanka (Midgley and Vinekanandan 1986), India (Lahiri 1984), Bangladesh (Zashimuddin et al. 1983, Das 1984, Latif et al. 1985), China (Cheng et al. 1983, Wei 1984, Pan 1985), Costa Rica (Glover and Heuvelodop 1985), and Fiji (Zed 1986).

1.4.2. Seed treatment

Because of a hard seed coat which is almost impervious to water, pretreatment of *A. mangium* seeds is necessary to ensure rapid and uniform germination. Apart from the many scarifying methods suggested for *Acacia* seeds, hot water treatment seems to be the most satisfactory method. This is done by

immersing the seed in boiling water for 30 seconds and then soaking them in cool water overnight. The volume ratio of seed to boiling water is very important. The recommended ratio is 1:10 (Bowen and Eusebio 1984b, Sim 1986), although successful germination after soaking of one part of seed to three parts of boiling water for three minutes was also reported by Yap and Wong (1983). Strict observance of the immersion period (30 second) and water temperature (100°C) is essential according to Sim (1986). Bowen (1981a) showed that if seed was pretreated at less than 90°C water temperature, the germination percentage decreased significantly. Storing can be done by drying and placing the seed in a cold store (4–10°C). Pretreated seed can also be stored without significant loss in viability (cf. Sim 1986).

After seed pretreatment, germination starts within three days and is completed in two weeks. Freshly collected seed commonly shows over 90% germination, while the germinability of stored seed has been reported to be 75–80% (Mangium... 1983).

1.4.3. Seedling care

Conventionally, seedlings of *A. mangium* have been raised by sowing the pretreated seeds onto prepared nursery beds and lightly covering them with sand. When the first pair of leaflets emerges, the seedlings are transplanted into polythene bags. Sim (1986) reported a new nursery method by sowing seeds in germination trays (a wet towel method). The germinated seeds are transplanted directly into polythene bags after 6–9 days when the radicle appears. The new method raised the recovery rate from 37% using the conventional seed bed method to 85%, and productivity, in terms of labour, increased. Concerning the substrate used in the nursery, Gavina and Garcia (1987) demonstrated better growth of *A. mangium* seedlings by adding a small amount of ash.

Seedlings are transplanted to the field when they reach 25–30 cm in height (Mangium... 1983, Pan and Yang 1986), while the roots are not long enough as to affect the vigour of the seedlings. Heavy rainfall tends to depress the seedling growth (Jones 1984), and therefore, in regions affected by heavy rain, seedlings should be well protected for the first 6 weeks.

1.4.4. Silviculture

The establishment of a *A. mangium* plantation is easy; the tree can be planted using nursery-raised seedlings, either containerized or bare-rooted. However, bareroot planting is not common and often unsuccessful. Direct seeding has been shown to be the poorest method, while containerized planting has proved to be the best. By using direct seeding, Sulaiman (1986) demonstrated a decrease in the survival of *A. mangium* from 66% to 30% after 3 and 6 months in the field respectively. In comparison, containerized planting showed a survival percentage as high as 90% after 6 months.

A. mangium has a poor coppicing ability if applied in the dry season. In the early rainy season, however, coppicing works well, particularly when the coppice shoots are exposed to sufficient light (Bhumibhamon, personal communication). To develop a second rotation by coppicing may therefore be possible and would be particularly suited to fuelwood production.

The optimum spacing for planting has not yet been determined but, depending mainly on the purpose of the plantation, spacings of 3 x 3 m or 4 x 4 m are considered the best for industrial plantations. The closer the spacing the higher the biomass productivity obtained, but the stem size is relatively small which limits its possible use (Yanthasath et al. 1985).

A. mangium, especially in young plantations, can be easily damaged or killed by fire since it has no fire resistance (Poole 1986). However, the dense canopy of *A. mangium* naturally shades out the ground vegetation, thus reducing the risk of fire (Udarbe and Hepburn 1986). *A. mangium* is therefore often used as a firebreak species.

Like most other acacias, *A. mangium* is often attacked by scale insects and mealy bugs, particularly at the seedling and sapling stages. In Hawaii, it was reported (Mangium... 1983) that *A. mangium* seedlings have been heavily attacked by powdery mildew (*Oidium* sp.). However, serious problems caused by pests and diseases have not yet been reported.

Being a leguminous tree, *A. mangium* usually forms an abundance of nitrogen fixing nodules in the root system together with *Rhizobium* bacteria which copiously provide nitrogenous compounds to the host.

Therefore, nitrogen fertilizer is not necessary in *A. mangium* plantations. Previous investigations have indicated that inoculation *A. mangium* with rhizobia gives healthy seedlings (Umali-Garcia et al. 1988), and thus this practice is recommended for plantation establishment.

A symbiotic relationship with an ectomycorrhizal fungus, *Thelephora ramarioides*, has been identified in Sabah (Gibson 1981). This fungus forms small tree-like dark fruiting bodies, which are found under seedlings both in the nursery and in the plantations. This association is beneficial because of the increased absorption of micro- and macronutrients, enabling the trees to grow better in soil deficient in readily available nutrients.

A. mangium has a poor self-pruning ability. Therefore, the stands should be artificially pruned after the first year of establishment to improve the quality of the timber.

1.4.5. Vegetative propagation

Vegetative propagation of *A. mangium* is still under investigation. Cuttings, grafting, budding and micropropagation (organ and tissue cultures) are reported to be applicable. The species appears to be relatively easily micropropagated, and successful transplants by shoot multiplication have been reported (Crawford and Hartney 1986). Studies on induced callus from seedling tissue have also been initiated (Kosakul and Pothipattana 1986). The results of stem cutting and grafting has not been impressive to date (Sim 1986, Pinyopusarek and Puriyakorn 1986).

1.4.6. Growth and production

A. mangium has shown outstanding growth rates when introduced to new locations. However, large genetic variability in growth is found. On good sites, it is common to find an average increase in diameter of 2–3 cm per year. Untended stands of 9-year-old trees have produced 415 m³ of timber per ha, representing an annual production of 46 m³ per ha (Tham 1976).

On poor sites, including soils with low nutrient contents, shallow or badly disturbed soils, and on hillslopes infested with weeds such as *Imperata* and *Eupatorium*, *A. mangium* has also grown vigorously. Production in such cases is not as high as mentioned above, but annual yields exceeding 20 m³ per ha have often been achieved (Mangium... 1983).

Generally, *A. mangium* shows a rather slow growth rate in the first year compared to other fast growing species, but it grows very rapidly in later years (Yanthasath 1986). Success in growing *A. mangium* has been reported from various areas all over the humid tropics. Some of the data are summarized in Table 1.

Relationships between growth, volume and biomass production of *A. mangium* have been studied by many researchers (e.g. Yanthasath et al. 1985, Brewbaker 1986, Lim 1986). However, the trials are still too young to allow conclusions to be made to meet practical needs.

A. mangium has also proved to be a successful species in agroforestry systems. The species shows a higher biomass production rate when grown in combination with

Table 1. Growth of *A. mangium* at various locations.

Location	Age (yr)	Spacing (m)	HT (m)	DBH (m)	MAI (m ³ /ha)	Reference
Sabah	4	3 × 3	17.3	14.9	—	Mohamad 1986
Sabah	10	2.4 × 2.4	23.0	20.0	44.0	Tham 1979
Sarawak	3.5	3 × 3	15.5	—	—	Lim and Basri 1985
Kalimantan	3.8	3 × 3	15.6	11.6	33.5	Djazuli et al. 1985
Sumatra	1.8	1 × 1	6.6	5.0	46.2	Sudjadi et al. 1985
Wanagama	2.5	4 × 4	5.1	2.0	—	Na'iem et al. 1985
Thailand	2	2 × 2	5.2	5.2	—	Boontawe and Kuwalairat 1986
Taiwan	4	—	8.8	9.4	23.4	Cheng et al. 1983
W. Bengal	1	5 × 5	3.0	2.7	—	Lahiri 1987
Papua New Guinea	2.5	—	8.4	—	—	Skelton and Neville 1986

Table 2. Some physical and chemical properties of 9-year-old *A. mangium* wood (Peh *et al.* 1982).

Physical property	Value	Chemical property	Value (%)
Specific gravity ¹⁾	0.4–0.6		
Basic density (kg/m ³)	483	Holocellulose	69.4
Mean fibre length (mm)	0.94	Alpha-cellulose	44.0
Mean fibre width (micron)	25.0	Lignin	19.7
Mean fibre lumen (micron)	18.8	Alcohol-benzene solubles	5.6
Mean cell-wall thickness (micron)	3.1	1 % alkali solubles	14.8
Coefficient of suppleness (%)	75.3	Hot water solubles	9.8
Rankels ratio	0.32	Pentosans	16.0
Calorific value (kJ/kg) ¹⁾	2 × 10 ³	Ash	0.68

¹⁾ Mangium and other...(1983)

agricultural crops than when grown alone. *A. mangium* and maize seem to constitute a recommendable agroforestry crop combination in Indonesia (Seibert and Kuncoro 1987).

1.5. Wood properties and utilization

A. mangium sapwood is narrow and straw to creamy-white in colour. The heartwood is medium brown, dense, strong and durable. The grain is straight on the tangential face and slightly interlocked on the radial face. The texture is medium and specific gravity is between 0.4 and 0.6. Brewbaker (1986) demonstrated that the specific gravity of 2-year-old *A. mangium* (0.53) compared favourably with that of *A. auriculiformis* (0.51) and *A. mearnsii* (0.47). Bhumibhamon (personal communication), however, found a lower specific gravity in *A. mangium* (0.4) than in *A. auriculiformis* (0.5–0.6) at two years of age. The basic density of a 9-year-old tree was reported to be 420 kg/m³ by Logan and Balodis (1982) while Yanthasath *et al.* (1985) report a basic density value of 616–685 kg/m³ for 15-monthold *A. mangium*. Some physical and chemical properties of *A. mangium* are summarized in Table 2.

A. mangium timber can be sawn easily if the stem is straight, and polished well. It is probably suitable for light-duty construction such as framing and weather-boarding. The wood also makes attractive furniture, cabinets, door frames and sliced veneer. The mixture of 30 percent *A. mangium* and 70 percent *Albizia falcataria* produces excellent particle board with a dark colour. Investigations have indicated that the timber can be treated by the full-cell pressure impregnation method with a satisfactory loading and penetration of the preservative (Mangium... 1983).

The fibre length of *A. mangium* wood is approximately 1.0 to 1.2 mm. According to Logan and Balodis (1982), the wood and wood plus bark chips could be pulped by the sulphate process with moderate amounts of alkali to yield in excess of 50 percent of screened pulp with excellent papermaking properties. The pulps can be readily bleached to acceptable brightness levels for use in fine papers and other bleached grades such as liner boards, bags and wrapping papers.

Concerning the calorific value, Yanthasath (1986) demonstrated a high heating value of 3-year-old *A. mangium* (2.05 × 10³ kJ/kg), compared to *Eucalyptus camaldulensis* (1.93 × 10³ kJ/kg). The species thus clearly makes good fuelwood.

1.6. Genetics and tree improvement

In recent years, there has been general recognition that a breeding programme is important and should be included in any reforestation programme, especially when introducing an exotic species. Tree improvement programmes for *A. mangium* have recently been initiated in many countries with the cooperation of many organizations, e.g. FAO, CSIRO, ACIAR, Winrock International-F/FRED, UNDP, and the coordinate network in the ASEAN region.

Provenance trials have been established in almost all the countries where *A. mangium* has been introduced in order to investigate the provenance variation in various tree characteristics, i.e. growth rate, stem form, resistance, etc., and to find the most promising provenance for future planting programme. Open-pollinated progenies of plus trees has also been studied. It is too early at present to make any conclusions from this research activity.

One of the basic problems in ASEAN countries is that most of the *A. mangium* seed used for planting in many areas is derived from a limited number of parent trees. The genetic pool is thus relatively small, which might cause inbreeding depression in the future. This phenomenon has already been discovered in Sabah and the FIO plantations in Thailand. Observations on progeny trials of *A. mangium* have also indicated a steady decline in vigour because of the narrow genetic base originating from the first introduced half-sib family (Sim 1984). Tree improvement programmes have been rapidly set up in order to broaden the genetic base.

Many selections of plus trees have been

carried out in both natural stands and in mature plantations. Most of the earlier selections were based primarily on the phenotypic appearance, for instance fast growth, stem straightness, and pest and insect resistance. Pettersson and Havmöller (1984) reported that 234 half-sib families from 12 provenances have been selected and used to establish a seedling seed orchard in the Philippines.

Since *A. mangium* is a relatively new plantation species, information about its genetics and tree improvement is very limited. More intensive breeding work should be undertaken.

2. THE APPROACH AND AIM OF THE PRESENT STUDY

2.1. General background

Forest resources in Thailand have been depleted from 58 % in 1959 down to 30 % in 1986 (Wacharakitti et al. 1979, Najnet 1984). Concern about deforestation has been discussed in detail by many researchers, and differences in the changing trend in the forest area between regions and provinces found (Royal Forest Department 1989). There are many complicated factors involved in the depletion of forest resources, such as population pressure and increasing need for land; illegal encroachment, shifting cultivation, the establishment of new agricultural settlements, etc.

The National Forest Policy for Thailand (NESDB 1986) states that it is necessary to maintain a forest cover of about 40 % of the total land area, of which 15 % is designed to be conserved forest and the rest, 25 %, productive forest land. The present situation, as affected by the flood disaster in southern Thailand in 1988, has forced the cabinet to close all concession areas. A large part of exploited forest will be converted to conserved forest, and tree planting is actively promoted. In the mean time, the forest industry in Thailand has to rely on the wood imported from neighboring countries as well as from Africa.

The long-term goal is to use three different ways to increase the growing stock of the productive forest in Thailand: (1) to prevent further degradation of the existing forests, (2) to improve the forest management practices, especially the natural regeneration of the indigenous forest, and (3) to establish new man-made plantations using the best possible species and seed sources.

A. mangium has proved to grow successfully on less fertile soils which are not suitable for the better known species. This is important for tropical countries where there is a need to rehabilitate land degraded by shifting cultivation. Considering the wide ranges of its wood utilization, *A. mangium* seems to exhibit a great potential as a plantation species.

To date, not enough reliable information

is available concerning *A. mangium*. Most of the previous studies have concentrated on growth, nursery techniques, and silvicultural management. The necessity of well-defined tree improvement strategies has been realized, and many investigations have already been started. However, virtually no information about the physiological and ecological characteristics of this species in relation to its silvicultural use are available so far. Additional studies must thus obviously be completed before the full potential of the species is understood.

2.2. The aims of the present study

The specific objectives of the present study on *A. mangium* are categorized as follows:

- (1) To study the extent and pattern of the genetic variation in growth and morphological characteristics;
- (2) To study the seasonal course of diameter growth and the environmental factors affecting it;
- (3) To determine whether genetic variation affects foliar nutrient contents;
- (4) To study the occurrence and pattern of the genetic variation in water relations of the species under different water balance conditions;
- (5) To study the occurrence and pattern of the genetic variation in gas exchange characteristics; and finally,
- (6) To summarize this new knowledge in relation to the potential use of *A. mangium* as a plantation species, so as to achieve improved silvicultural practices, particularly for forest management purposes in Thailand.

2.3. The structure of the present study

The study report consists of a series of field and laboratory experiments, in which the seed materials are the same. In Chapter 3, the aim is to identify the most promising provenances of *A. mangium* established at the Lad Krating Plantation, Central Thailand. In particular, the juvenile-mature relationships of different characteristics of *A. mangium* are discussed. This information could eventually serve as basic information for a further tree improvement programme. The genetic vari-

ability and inheritance patterns of selected characteristics were also studied, so as to gain more basic information about the genetic constitution of the species.

The growth rhythm of trees is an important factor in determining growth capacity and adaptability. Chapter 4 describes the seasonal course of diameter growth of different provenances of *A. mangium* and discusses the ways in which growth is affected by environmental factors on weekly basis.

Chapter 5 characterizes the genetic variability in foliar nutrient content due to differences in geographic origin and explores the relationships between the mineral levels of foliage or soil and tree growth.

Chapter 6 discusses the phyllode anatomy and particularly the differences in stomatal frequency among *A. mangium* provenances. The relationships between stomatal characteristics and early field performance of the trees were also studied.

Chapter 7 explores the variation in leaf transpiration, leaf conductance, and leaf water potential under laboratory conditions

so as to provide information for an analysis of the eco-physiological mechanisms underlying the genetic adaptation of this species to drought and ultimately to facilitate the further selection of seed sources for planting programmes in Thailand.

In Chapter 8 the following parameters associated with CO₂ exchange under laboratory conditions were studied: total and net photosynthetic rates, photorespiration, dark respiration and the CO₂ compensation point. The measurements were conducted to find possible differences in these parameters among provenances and especially to study the responses to light and temperature. Relationships between various CO₂ exchange characteristics were also analyzed and discussed. In addition, a preliminary attempt was made to relate the observed variation in CO₂ exchange to the growth performances of the same *A. mangium* provenances in the field.

Conclusions from the various field and laboratory experiments including silvicultural recommendations for the use of *A. mangium* in Thailand are made in Chapter 9.

3. PROVENANCE AND FAMILY VARIATION IN GROWTH AND SOME MORPHOLOGICAL CHARACTERISTICS OF *A. MANGIUM* GROWN IN THAILAND

3.1. Introduction

Most forest tree plantations in the tropics nowadays consist of exotic species (Evans 1982, Zobel et al. 1987). However, it has become clear that the success of an exotic plantation depends not only on the choice of the species but also on the seed source (provenance) of the species being planted (Lacaze 1978). Steenberg (1983) stated that plantations in developing countries often fail because of the lack of research on provenances or because of the lack of tree improvement programmes in general.

A number of studies are available on provenance variation in the growth performance of trees. Of the species thoroughly studied, the following could be mentioned: *Pinus sylvestris* (Wright and Bull 1963), *P. oocarpa* (Robbins and Hughes 1983), *P. caribaea* (Das and Stephan 1982, Robbins and Hughes 1983), *P. contorta* (Lines 1976), *P. kesiya* (Das and Stephan 1984, Granhof 1984), *Pseudotsuga menziesii* (Sorenson 1983), *Sequoiadendron giganteum* (Melchior and Herrmann 1987), *Tectona grandis* (Keiding et al. 1986), *Gmelina arborea* (Lauridsen et al. 1987), and *Eucalyptus camaldulensis* (Grunwald and Karschon 1983, Otegbeye 1985). Some of these investigations have been carried out long enough to provide quantitative evidence on the value of provenance selection. For instance, studies by Wright et al. (1970) on Douglas fir (*Pseudotsuga menziesii*) in Argentina showed that planting based on simple provenance tests could probably increase productivity by more than 50%. Zobel and Talbert (1984) stated that provenance differences are particularly distinct when a species is grown outside its natural range of distribution.

Recently, there has been a proliferation of *A. mangium* provenance trials, and the importance of seed source has been demonstrated in this species. Successive international *A. mangium* provenance trials have

been reported in many regions and countries, including Sabah in East Malaysia (Tham 1979), Indonesia (Na'iem et al. 1985), China (Pan and Yang 1986), the Philippines (Pettersson and Havmøller 1984), and Thailand (Yanthasart et al. 1985). Seed collections throughout the natural range for provenance studies have been done under the auspices of FAO and CSIRO. During 1981 and 1982, seeds of 234 half-sib families were collected (Pettersson and Havmøller 1984). Studies on family variation of this species are however, relatively few.

3.2. Material and methods

3.2.1. General

A. mangium provenance trials and a seedling seed orchard were established at Lad-Krating Plantation, in Chachoengsao Province located in Central Thailand (13°42' N, 101°06' E, cf. Fig. 3). The planting area is relatively flat and at an altitude of 80 m above mean sea level. The mean annual temperature of the study site is 28°C, and the daily mean temperature varies between 18 and 39°C. The average rainfall is approximately 1220 mm per year. A dry period occurs from November to mid March and there is a marked peak in rainfall in September.

The soils of the planting area consist of sandy clay loam, containing approximately 49% sand, 26.7% silt, and 24.3% clay, and have been classified according to pedon classification as belonging to the Clayey-skeletal, Kaolinitic, Aeric Kanhapustult series (Winrock 1988). A compost mixture was applied at planting, and a complete mineral fertilizer (15:15:15) has been given regularly early in growing season.

3.2.2. Provenance trials

Seed sources. The seed material consists of thirteen Queensland provenances, two Papua New Guinea provenances, and one Indonesia provenance. Details of the seedlots used in provenance testing are presented in Table 3.

All seedlots were germinated in the nursery at Lad Krating Plantation. The germinated seeds were transplanted into black polythene bags which were placed under 50% shade for two weeks before transferring to full sunlight. During early development, the *A. mangium* seedlings were attacked by defoliators; for this reason

pesticide was applied once a week during the nursery stage. Watering was done regularly twice a day.

Experimental design. *A. mangium* provenance trials were established in October 1983 using a randomized complete block design. The trials comprised of 16 natural seed sources, each with 4 replications. Each plot consisted of 5 x 5 trees planted with a spacing of 8 x 8 m.

Management of trials. Fire control consisted of mechanical weeding carried out with a farm tractor twice a year. Between tree rows, leguminous cover crops such as mungbean, and soybean were planted for soil improvement and to provide additional income. In order to improve the timber quality, artificial pruning was carried out up to two-thirds of the total stem height in May 1985.

Assessment of traits. Periodic assessments of height (Ht), length of clear bole (CB), diameter at ground level (Dgl), diameter at breast height (DBH), and crown diameter (Cw) of each tree were successively made in the provenance trials plots at seedling ages of 18, 24, and 30 months. The survival percentages of each provenance was also recorded.

All analyses of the variables are based on plot means. A two-way analysis of variance was performed according to the general, random effect model (Burley and Wood 1976):

$$y_{ij} = \mu + a_i + b_j + e_{ij}$$

where

y_{ij} = plot mean in block j for provenance i

μ = general mean

a_i = provenance effect

b_j = block effect

e_{ij} = random error of the plot mean.

Duncan's New Multiple Range Test (DNMRT) was used to evaluate various tree traits among provenances. Correlation coefficients between traits were later on computed.

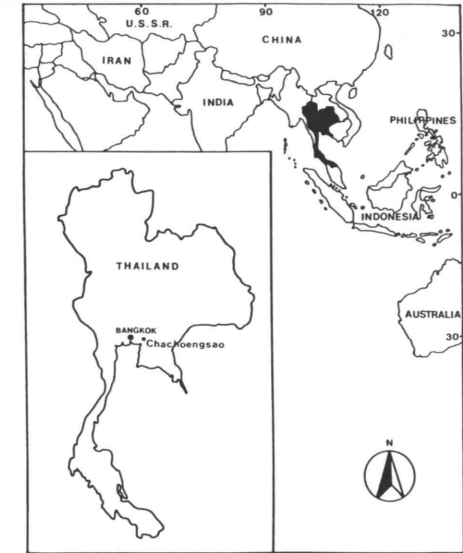


Figure 3. Location of the *A. mangium* provenance trials and seedling seed orchard at Lad Krating Plantation in Chachoengsao, Thailand.

Table 3. Natural seed sources of *A. mangium* in provenance trials.

Register No.	Location	Latitude (S)	Longitude (E)	Altitude (m)	No. of parent trees
12992	Rex Range NR Mosson, Queensland, Australia	16°30'	145°32'	30	10
13229	Claudie River, Queensland, Australia	12°44'	143°13'	60	6
13232	Cowley Beach Road, Queensland, Australia	17°41'	146°15'	5	10
13233	Walsh's Pyramid, Queensland, Australia	17°06'	145°48'	20	10
13234	Trinity Inlet, Queensland, Australia	17°02'	145°48'	20	10
13235	Mourilyan Bay, Queensland, Australia	17°35'	146°05'	20	5
13236	Kurrimine, Queensland, Australia	17°46'	146°05'	10	5
13237	El Arish, Queensland, Australia	17°50'	146°01'	20	10
13238	Tully Mission Beach Rd., Queensland, Australia	17°56'	146°02'	70	10
13239	Syndicate Rd., Tully, Queensland, Australia	17°55'	145°52'	50	10
13240	Ellerbeck Rd., Cardwell, Queensland, Australia	18°14'	145°58'	60	5
13241	Broken Pole Creek, Queensland, Australia	18°21'	146°03'	50	5
13242	Abergowrie Sf., Queensland, Australia	18°26'	146°01'	60	10
13459	W. of Morehead, Papua New Guinea	8°45'	141°18'	30	20
13460	Oriomo River, Papua New Guinea	8°50'	143°08'	10	18
13621	Piru, Ceram, Indonesia	3°04'	128°12'	150	9

3.2.3. Family trials

Families. The seed material consisted of 20 open-pollinated families, fifteen from Australia, four from Papua New Guinea, and one from a plantation in the Philippines. Details of these families are presented in Table 4. The seeds were germinated in 1985, and the seedlings were raised in the nursery in the same way as the seedlings for the provenance trials.

Experimental design. The seedling seed orchard was laid out following a randomized complete block design with 150 replications and one tree per family per replication. A spacing of 3 x 3 m was applied.

Assessment of traits and statistical analysis. Six traits were analyzed for each tree at 28 months of age: height (Ht), diameter at ground level (Dgl), diameter at breast height (DBH), and crown diameter (Cw). Survival percentages were also counted. Flowering (Flw) was assessed using a 5-step score (0 = no flowering; 4 = abundant flowering).

Family means were calculated as the arithmetic mean of all trees per family. A two-way analysis of variance was applied, and random effect model was assumed. Variance components were estimated by equating the mean squares with the corresponding expectation values. Individual (h_f^2) and family (h_f^2) heritabilities were calculated using the following model (Zobel and Talbert 1984):

$$h_f^2 = \frac{4\sigma_f^2}{\sigma_f^2 + \sigma_e^2}$$

$$h_f^2 = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_e^2/n}$$

where

σ_f^2 = variance among families

σ_e^2 = error variance

n = number of individuals per family.

3.3. Results

3.3.1. Provenance trials

3.3.1.1. Provenance growth performance

Survival percentage. The survival percentages of 18-month-old *A. mangium* seedlings were found to be extremely high, varying between 98–100%, as shown in Table 5. The survival largely remained the same during consecutive years. The provenance variation in survival percentages was extremely small. The high survival percentages in the provenance trials were obviously due to the continuous intensive management practices.

Height (Ht). The average height growth of *A. mangium* provenances at the ages of 18, 24, and 30 months is shown in Table 5. Results

Table 4. Origins of *A. mangium* families in the seedling seed orchard at Lad Krating Plantation, Chachoengsao.

Family No.	Origin	Latitude (S)	Longitude (E)	Altitude (m)
3	Oriomo Daru, Papua New Guinea	9°04'	143°12'	8
4-9	Capt. Billy Creek, Queensland, Australia	—	—	—
10-16	Olive River, Queensland, Australia	—	—	—
17	Claudie River, Queensland, Australia	12°44'	143°13'	60
19	The Philippines	—	—	—
20-23	Oriomo River, Papua New Guinea	8°50'	143°08'	10

indicate large variation in height performance at all ages studied. At the age of 18 months, the average height growth of the trees was 5.29 m, ranging from 4.86 m (No. 13232) to 5.97 m (No. 13460). At the age of 24 months, the average height had increased to 6.26 m and ranged from 5.55 m (No. 13233) to 7.24 m (No. 13459). The most promising provenances at the age of 24 months remained in the same sequence as found at 18 months. However, the height of the Abergowrie provenance from Australia (No. 13242) was lower than the average value, while the Piru provenance from Indonesia (No. 13621), for the first time, showed a height growth better than the average.

At the age of 30 months, the average height was 7.56 m, ranging from 6.76 m (No. 13233) to 8.65 m (No. 13460). When compared to the overall average, all previous promising provenances still remained superior in height performances. The only exceptional case was the Abergowrie provenance (No. 13242), which once again performed better when compared to the overall average (Fig. 4).

Differences in height growth were statistically significant among provenances at all ages studied (Table 6). The effect of seed source on height growth was higher at the younger ages (67% and 73% of the observed total variance at the ages of 18 and 24 months respectively, with only 32% at 30 months).

Length of clear bole (CB). Due to the slow natural pruning in *A. mangium*, the clear bole

Table 5. Summary of growth characteristics of *A. mangium* provenances. Mean and standard deviation (in parenthesis) are given.

Register No.	Origin	Survival (%)	Length of clear bole (cm)	Ht (m) at age			Dgl (cm) at age			DBH (cm) at age			Cw (cm) at age	
				18	24	30	18	24	30	18	24	30	24	30
				(months)			(months)			(months)			(months)	
12992	Australia	98 (4)	1.74 (0.05)	5.42 (0.24)	6.43 (0.26)	7.73 (0.22)	13.47 (1.16)	16.17 (1.43)	19.50 (1.35)	7.74 (0.74)	10.72 (0.90)	13.90 (1.01)	4.19 (0.43)	4.55 (0.64)
13229	Australia	100 (0)	1.84 (0.12)	5.81 (0.39)	6.98 (0.37)	8.33 (0.37)	12.77 (1.72)	15.66 (1.33)	19.24 (1.60)	7.79 (0.72)	10.95 (0.68)	13.90 (1.11)	4.61 (0.30)	5.22 (0.28)
13232	Australia	99 (2)	1.74 (0.17)	4.86 (0.17)	5.80 (0.31)	6.97 (0.36)	12.52 (1.34)	15.24 (0.90)	19.15 (0.97)	5.90 (0.46)	9.28 (0.56)	12.42 (0.48)	3.96 (0.15)	4.53 (0.38)
13233	Australia	100 (0)	1.86 (0.19)	4.97 (0.08)	5.55 (0.17)	6.76 (0.24)	13.06 (0.58)	14.78 (0.69)	18.59 (1.17)	6.06 (0.29)	8.78 (0.50)	11.89 (0.65)	3.92 (0.25)	4.43 (0.46)
13234	Australia	100 (0)	1.70 (0.09)	4.98 (0.19)	5.58 (0.19)	7.00 (0.22)	12.27 (0.94)	14.12 (0.72)	18.16 (1.32)	6.77 (0.56)	9.35 (0.77)	12.36 (0.95)	4.12 (0.30)	4.42 (0.44)
13235	Australia	100 (0)	1.82 (0.09)	5.46 (0.25)	6.35 (0.45)	7.59 (0.52)	13.50 (0.76)	16.49 (1.00)	20.07 (0.63)	7.20 (0.52)	10.20 (0.80)	13.17 (0.43)	4.21 (0.11)	4.42 (0.32)
13236	Australia	100 (0)	1.72 (0.04)	4.92 (0.22)	5.84 (0.25)	7.05 (0.31)	12.13 (1.33)	14.51 (1.36)	18.39 (1.61)	5.89 (0.39)	8.91 (0.49)	12.06 (0.81)	3.87 (0.23)	4.44 (0.31)
13237	Australia	100 (0)	1.75 (0.09)	4.91 (0.21)	5.88 (0.48)	7.18 (0.58)	12.69 (1.37)	15.51 (1.85)	19.16 (1.40)	6.11 (0.61)	8.96 (0.71)	12.34 (0.78)	3.96 (0.22)	4.45 (0.49)
13238	Australia	100 (0)	1.81 (0.09)	5.22 (0.18)	5.96 (0.14)	7.31 (0.43)	12.27 (0.49)	15.35 (0.61)	19.22 (0.49)	6.47 (0.41)	9.59 (0.51)	12.87 (0.60)	4.21 (0.16)	4.69 (0.33)
13239	Australia	100 (0)	1.64 (0.12)	5.02 (0.41)	5.98 (0.40)	7.39 (0.58)	11.32 (1.19)	14.25 (0.49)	18.52 (0.99)	6.20 (0.59)	8.85 (0.67)	11.75 (0.76)	4.06 (0.35)	4.32 (0.33)
13240	Australia	100 (0)	1.91 (0.05)	5.56 (0.29)	6.55 (0.40)	7.83 (0.45)	13.38 (1.37)	15.89 (1.70)	19.50 (1.37)	7.36 (0.58)	10.19 (0.89)	13.27 (1.05)	4.29 (0.27)	4.55 (0.48)
13241	Australia	100 (0)	1.79 (0.09)	5.13 (0.28)	6.11 (0.22)	7.30 (0.25)	12.61 (1.18)	15.33 (1.12)	18.69 (0.98)	6.83 (0.36)	9.89 (0.74)	12.94 (0.61)	4.27 (0.21)	4.87 (0.46)
13242	Australia	100 (0)	1.90 (0.18)	5.37 (0.05)	6.22 (0.12)	7.62 (0.23)	13.78 (0.70)	15.91 (0.62)	20.15 (0.75)	7.73 (0.48)	10.71 (0.33)	13.86 (0.27)	4.26 (0.20)	4.90 (0.30)
13459	Papua New Guinea	100 (0)	1.95 (0.15)	5.91 (0.26)	7.24 (0.28)	8.57 (0.53)	14.56 (0.54)	17.06 (0.51)	21.51 (0.41)	8.24 (0.46)	11.63 (0.70)	14.78 (0.40)	4.84 (0.30)	5.02 (0.48)
13460	Papua New Guinea	99 (2)	1.86 (0.08)	5.97 (0.17)	7.22 (0.33)	8.65 (0.34)	13.86 (1.07)	16.82 (0.77)	20.68 (1.22)	8.01 (0.24)	11.28 (0.38)	14.43 (0.40)	4.66 (0.36)	5.18 (0.44)
13621	Indonesia	100 (0)	1.80 (0.10)	5.19 (0.24)	6.11 (0.40)	7.52 (0.45)	11.39 (1.40)	14.22 (1.75)	16.75 (1.44)	6.68 (0.62)	9.73 (0.61)	11.92 (0.78)	4.18 (0.12)	4.22 (0.70)
\bar{x}		99.8	1.80	5.29	6.26	7.56	12.85	15.46	19.20	6.94	9.94	12.99	4.23	4.64
$s_{\bar{x}}$		0.58	0.09	0.37	0.53	0.65	0.89	0.92	1.10	0.80	0.91	0.96	0.27	0.31
CV, %		0.58	5.00	6.99	8.47	8.60	6.93	5.95	5.73	11.53	9.15	7.39	6.38	6.68

Table 6. Summary of analysis of variance on growth characteristics of *A. mangium*.

Source of variation	df	Ht18	Ht24	Ht30	CB	Dgl18	Dgl24	Dgl30	DBH18	DBH24	DBH30	Cw24	Cw30
MEAN SQUARES													
Provenance	15	0.553	1.139	0.975	0.029	3.148	3.366	4.861	2.560	3.334	3.656	0.298	0.373
Block	3	0.038	0.362	0.894	0.077	7.184	4.414	6.699	0.311	1.827	0.580	0.191	2.058
Residual	45	0.061	0.083	0.315	0.009	0.878	1.097	1.004	0.268	0.342	0.524	0.061	0.052
F-TEST													
Provenance		***	***	***	***	***	***	***	***	***	***	***	***
Block		ns	**	*	***	***	*	***	ns	***	ns	*	**
VARIANCE COMPONENTS (%)													
Provenance		66.85	72.53	31.97	27.32	30.87	30.30	41.48	67.92	63.23	59.75	46.06	31.13
Block		0	4.67	6.98	23.50	21.41	11.06	15.32	0.32	7.86	0.27	6.32	48.64
Residual		33.15	22.80	61.05	49.18	47.72	58.63	43.20	31.76	28.91	39.98	47.62	20.23

Significance levels of F-test: * p < 0.05
 ** p < 0.01
 *** p < 0.001
 ns not significant at p < 0.05

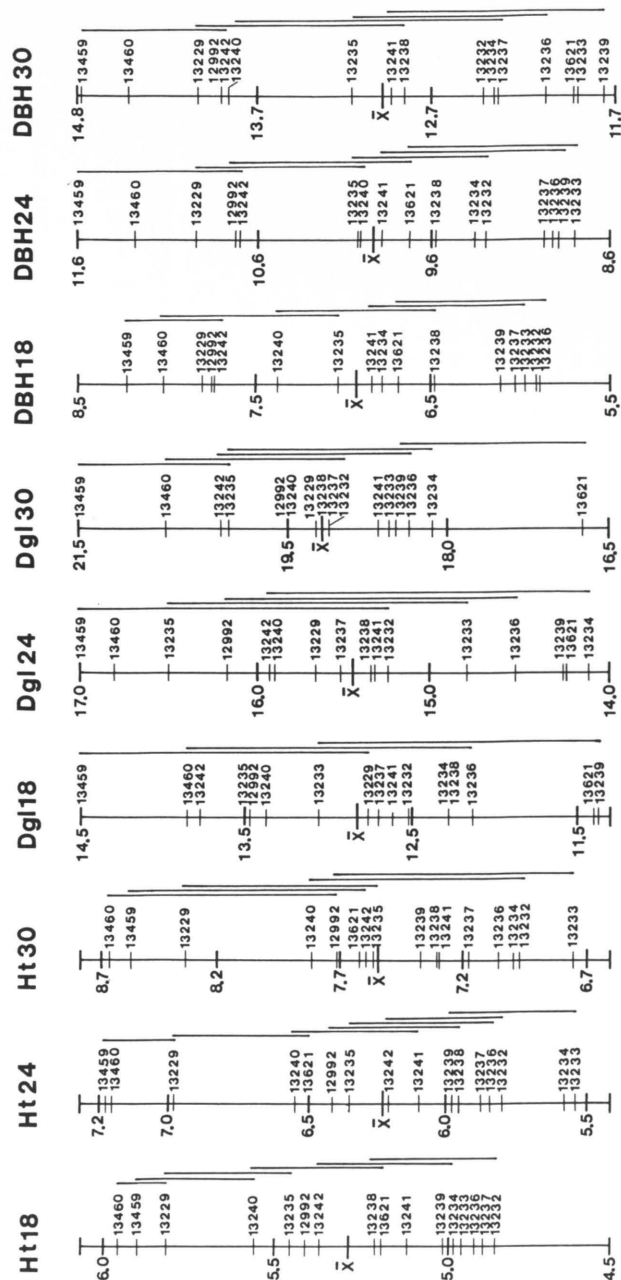


Figure 4. Proportionately ranked means for height (Ht), diameter at ground level (Dgl), and diameter at breast height (DBH), at the age of 18, 24, and 30 months in 16 provenances of *A. mangium*. Vertical lines indicate differences significant ($p < 0.05$) according to Duncan's New Multiple Range Test.

remained relatively short throughout the trial. As shown in Table 5, the average length of the clear bole at the age of 18 months was only 1.8 m, or about 34 % of the total height. It ranged from 1.64 m (No. 13239) to 1.95 m (No. 13459). Statistically significant differences in the length of clear bole were detected among the provenances. However, only 27 % of the observed total variance in clear bole length could be explained by provenance differences.

Diameter at ground level (Dgl). At the age of 18 months, the average Dgl was 12.85 cm, varying from 11.32 cm (No. 13239) to 14.56 cm (No. 13459). At 24 months, the overall average Dgl was 15.46 cm, and the average ranged from 14.12 cm (No. 13234) to 17.06 cm (No. 13459). The provenances exceeding the overall average were the same as those found at 18 months, with the addition of No. 13237 in which the diameter had increased rapidly during the second year.

At 30 months, the overall average Dgl was 19.20 cm, and the value ranged from 16.75 cm (No. 13621) to 21.51 cm (No. 13459). The top eight provenances found at 24 months still showed the largest Dgl and exceeded the overall average at 30 months. Proportionately ranked means of Dgl at all ages studied are shown in Fig. 4.

As a whole, a highly significant variation in Dgl was observed among provenances (Table 6). However, the effects caused by the provenances were relatively less pronounced in Dgl (representing only 30–40 % of the observed total variance) than in height growth.

Diameter at breast height (DBH). Results indicated large variation in DBH at all ages studied (Table 6). At 18 months, the overall average DBH was 6.94 cm, and the average ranged from 5.89 cm (No. 13236) to 8.24 cm (No. 13459). At 24 months, the overall average DBH had increased to 9.94 cm, and the DBH varied from 8.78 cm (No. 13233) to 11.63 cm (No. 13459). At the age of 30 months, the overall average DBH was 12.99 cm, and the range extended from 11.75 cm (No. 13239) to 14.78 cm (No. 13459). All provenances ranking highest at 18 and 24 months still exceeded the overall average DBH at the age of 30 months (Fig. 4).

Similarly to Dgl, DBH also indicated statistically highly significant differences among the provenances, and the provenance differ-

ences were somewhat more pronounced (representing 60–65 % of the observed total variance) when measured in terms of DBH as compared to Dgl.

Crown diameter (Cw). As shown in Table 6, the variation in crown diameter between provenances was found to be statistically highly significant at both ages used for these measurements, 24 and 30 months. At 24 months, the overall average crown diameter was 4.23 m, and the value ranged from 3.87 m (No. 13236) to 4.84 m (No. 13459). At 30 months, the overall average crown diameter was 4.64 m, and the range extended from 4.22 m (No. 13621) to 5.22 m (No. 13229). The crown diameter did not indicate similar ranking among the provenances on the two occasions of observation.

3.3.1.2. Clinal trends in growth performance

Significant linear correlations were found between provenance latitude and the mean provenance performance measured only as height (Table 7). The correlation coefficient

Table 7. Correlation coefficients among geographic variation and provenance performance characteristics.

Dependent variable	Lat.	Long.	Alt.
Ht18	0.494	0.178	0.076
	*	ns	ns
Ht24	0.657	0.382	0.197
	**	ns	ns
Ht30	0.602	0.300	0.148
	**	ns	ns
CB	0.317	0.157	0.150
	ns	ns	ns
Dgl18	0.047	0.253	0.401
	ns	ns	ns
Dgl24	0.141	0.165	0.285
	ns	ns	ns
Dgl30	0.039	0.388	0.479
	ns	ns	ns
DBH18	0.397	0.135	0.087
	ns	ns	ns
DBH24	0.458	0.177	0.070
	ns	ns	ns
DBH30	0.265	0.062	0.139
	ns	ns	ns
Cw24	0.549	0.234	0.122
	*	ns	ns
Cw30	0.224	0.116	0.141
	ns	ns	ns

Significance levels of correlation: * $p < 0.05$
 ** $p < 0.01$
 ns not significant at $p < 0.05$

was 0.49, 0.65, and 0.60 at 18, 24, and 30 months respectively. Longitude and altitude did not show any statistically significant correlation with growth performance. However, the results suggested that *A. mangium* trees originating from near the equator had a

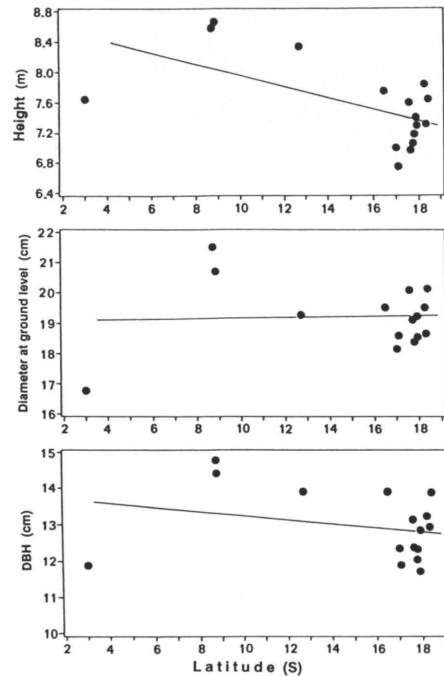


Figure 5. Relationships between growth characteristics of 30-month-old *A. mangium* and the latitude of seed source origin.

better height growth at Lad Krating than those originating from further south, except for the Indonesian origin (Fig. 5).

3.3.1.3. Relationships among various growth characteristics

Correlation coefficients between all growth performance traits studied are shown in Table 8. All possible correlations between the average value of growth characteristics were significant at all ages studied. Heights at different ages were strongly intercorrelated, as were correlations among stem diameters and the crown width at different ages. The results suggested that there might also be strong juvenile-mature relationships in *A. mangium*.

3.3.2. Seedling seed orchard

3.3.2.1. Family growth performance

Survival percentage. The survival of *A. mangium* in a seed orchard at the age of 28 months is shown in Table 9. The average survival percentage was 97.5, and it varied from 94.7 to 100 %. The variation in survival percentage among families was small. Most of the mortality in the present seed orchard occurred after a heavy storm in 1984, when many of the trees were blown down and it was observed that *A. mangium* develops a shallow root system.

Height (Ht). The average height growth of *A. mangium* by families is given in Table 9. The

Table 9. Mean and standard deviation (in parenthesis) of growth and flowering characteristics in 20 *A. mangium* families grown in the seed orchard.

Family No.	Surv. (%)	Height (m)	Dgl (cm)	DBH (cm)	Cw (m)	Flw (score 0-4)
2	94.7	8.58 (1.17)	15.75 (2.26)	12.47 (1.66)	4.65 (0.63)	0.34 (0.63)
3	98.7	8.24 (0.97)	14.81 (1.93)	11.48 (1.71)	4.45 (0.50)	0.39 (0.70)
4	97.3	8.42 (1.26)	14.85 (1.89)	11.52 (1.47)	4.59 (0.52)	0.33 (0.70)
5	94.7	8.65 (0.98)	16.00 (2.08)	12.74 (1.50)	4.74 (0.49)	0.45 (0.72)
6	95.3	8.45 (1.06)	15.74 (2.22)	12.64 (1.63)	4.71 (0.59)	0.40 (0.69)
7	98.7	8.17 (1.33)	14.65 (2.43)	11.36 (2.00)	4.43 (0.57)	0.65 (0.92)
8	98.0	8.65 (1.20)	14.87 (2.10)	11.75 (1.61)	4.56 (0.61)	0.73 (0.90)
9	96.7	8.51 (1.03)	15.01 (1.85)	11.74 (1.45)	4.46 (0.48)	0.46 (0.78)
10	97.3	8.25 (1.17)	14.09 (2.11)	10.93 (1.78)	4.51 (0.47)	0.33 (0.56)
11	100	8.44 (1.06)	14.41 (1.89)	11.59 (2.80)	4.64 (0.48)	0.48 (0.67)
12	98.7	8.35 (1.67)	14.52 (1.98)	11.39 (1.63)	4.42 (0.51)	0.60 (0.81)
13	95.3	8.24 (1.25)	14.14 (2.30)	11.24 (1.90)	4.45 (0.52)	0.42 (0.69)
14	95.3	8.57 (1.11)	14.67 (2.15)	11.39 (1.95)	4.28 (0.55)	0.48 (0.78)
15	100	8.56 (1.14)	14.87 (1.97)	11.67 (1.52)	4.57 (0.52)	0.58 (0.68)
16	98.7	8.48 (1.10)	14.26 (1.93)	11.43 (1.71)	4.34 (0.49)	0.54 (0.80)
17	98.0	8.48 (1.27)	14.12 (2.27)	11.48 (1.97)	4.59 (0.55)	0.44 (0.70)
19	100	8.12 (1.23)	13.99 (2.00)	10.63 (1.75)	4.24 (0.52)	1.75 (1.14)
20	98.0	7.82 (1.26)	12.16 (2.34)	9.32 (1.91)	3.75 (0.66)	1.14 (1.14)
22	98.0	8.06 (1.21)	13.12 (2.07)	10.12 (1.62)	4.00 (0.52)	1.58 (1.19)
23	97.3	8.23 (1.04)	13.82 (2.19)	10.96 (1.74)	4.19 (0.51)	1.78 (1.17)
\bar{x}	97.5	8.36	14.48	11.39	4.43	0.70
$s\bar{x}$	1.68	0.90	2.02	1.74	0.48	0.96
CV, %	1.72	10.82	13.95	15.29	10.84	72.91

Table 8. Matrix correlations of *A. mangium* growth characteristics.

Variables	Ht18	Ht24	Ht30	Dgl18	Dgl24	Dgl30	DBH18	DBH24	DBH30	Cw24	Cw30	CB
Ht18	1.00	0.94**	0.96**	0.68**	0.79**	0.69**	0.92**	0.93**	0.89**	0.94**	0.76**	0.69**
Ht24		1.00	0.98**	0.55*	0.72**	0.57*	0.85**	0.90**	0.81**	0.91**	0.69**	0.60*
Ht30			1.00	0.56*	0.72**	0.62**	0.88**	0.91**	0.84**	0.93**	0.73**	0.57*
Dgl18				1.00	0.90**	0.89**	0.73**	0.75**	0.84**	0.60*	0.61*	0.75**
Dgl24					1.00	0.92**	0.76**	0.82**	0.89**	0.70**	0.66**	0.67**
Dgl30						1.00	0.67**	0.71**	0.84**	0.64**	0.68**	0.59*
DBH18							1.00	0.97**	0.93**	0.61*	0.71**	0.64**
DBH24								1.00	0.96**	0.91**	0.78**	0.67**
DBH30									1.00	0.87**	0.83**	0.66**
Cw24										1.00	0.82**	0.64**
CW30											1.00	0.58*
CB												1.00

Significance levels of correlation: * $p < 0.05$
** $p < 0.01$

overall mean height was 8.36 m, with a range between family means from 7.82 (No. 20) to 8.65 m (No. 5 and 8). The differences among families and within a family were statistically highly significant (Table 10). There was greater environmental variance (differences among blocks) than genetic (family) variance in height growth.

Diameter at ground level (Dgl). The overall mean for Dgl was 14.48 cm, with a range among family means from 12.16 (No. 20) to 16.00 cm (No. 5) and a coefficient of vari-

ation of 14 percent (Table 9). The differences among families as well as within a family were statistically significant. Genetic variances were higher in Dgl than in height growth (Table 10).

Diameter at breast height (DBH). The average growth of all families of *A. mangium* at 28 months of age was 11.39 cm, ranging from 9.32 (No. 20) to 12.74 cm (No. 5). The coefficient of variation was 15.3 %, i.e. slightly higher than that found for Dgl or height growth. The DBH growth was generally con-

Table 10. Analysis of variance, variance components and heritability estimates for growth characteristics in *A. mangium*.

Source of variation	df	Ht	Dgl	DBH	Cw	Flw
MEAN SQUARE						
Block	149	10.62	10.62	6.50	1.34	1.12
Family	19	6.94	111.95	89.88	8.67	32.37
Residual	2831	0.79	3.94	2.92	0.22	0.66
F-TEST						
Block		***	***	***	***	***
Family		***	***	***	***	***
VARIANCE COMPONENT (%)						
Block		37.12	6.61	4.89	17.65	2.23
Family		3.04	14.43	15.76	17.65	24.44
Residual		59.84	78.96	49.35	64.70	73.33
h^2		0.88	0.96	0.97	0.97	0.98
h^2		0.19	0.62	0.66	0.86	0.98

Significance levels of F-test: *** $p < 0.001$

sistent with Dgl growth. The genetic variance of DBH was 15.8 % of the total variance (Table 10).

Crown diameter (Cw). The development of crown diameter was found to vary among the families as well as within a family (Table 10). The average crown diameter of 28-month-old *A. mangium* (grown with a spacing of 3 x 3 m) was 4.43 m, ranging from 3.75 (No. 20) to 4.74 m (No. 5). The genetic variance of crown diameter was 17.6 %, which was a higher value than that for height or diameter growth.

3.3.2.2. Flowering frequency

Generally, *A. mangium* produces flowers at an early age. In the present study, flowering was observed in all families already at 28 months of age. The average results on flowering in *A. mangium* by score (0-4) by families are given in Table 9. Family No. 23 showed the highest (1.78) and Families No. 4 and No. 10 showed the lowest flowering scores (0.33). The percentages of flowering in each class are shown in Table 11. In general, the families from Papua New Guinea (No. 20-23) were particularly prolific flower producers. However, the results also indicated that the majority of the trees (56 %) still remained at the juvenile stage. The variation in flowering was relatively high, the coefficient of variation being 72.9 %. Statistically significant differences were found in this

Table 11. Distribution of flowering frequency score classes (%) in each family in the seed orchard; 0 = no flowering; 4 = abundant flowering.

Family No.	Score class				
	0	1	2	3	4
2	73.76	20.57	4.26	1.42	—
3	70.75	22.45	4.08	2.72	—
4	75.17	20.00	2.76	0.69	1.38
5	65.25	26.95	4.96	2.84	—
6	69.50	23.40	4.96	2.13	—
7	57.53	26.71	10.27	4.11	1.37
8	49.32	34.93	9.59	5.48	0.68
9	67.59	23.45	5.52	2.76	0.69
10	71.23	25.34	2.74	0.68	—
11	60.40	33.56	4.03	2.01	—
12	56.85	29.45	10.27	3.42	—
13	66.91	25.90	5.04	2.16	—
14	64.34	26.57	6.99	0.70	1.40
15	52.70	36.49	10.81	—	—
16	61.22	26.53	9.52	2.04	0.68
17	64.08	30.99	1.41	3.52	—
19	16.67	24.67	31.33	22.00	5.33
20	40.41	21.23	23.29	13.70	1.37
22	20.41	33.33	20.41	19.73	6.12
23	13.70	32.19	23.97	22.60	7.53
\bar{x}	55.89	27.24	9.81	5.74	1.33
$s_{\bar{x}}$	18.83	4.94	8.34	7.37	2.25

characteristic both among families and within a family (Table 10).

3.3.2.3. Correlation among traits

Correlation coefficients between different growth traits are shown in Table 12. Statistically significant correlations were found in this

Table 12. Matrix of phenotypic correlations of *A. mangium* families.

Characteristic	Ht	Dgl	DBH	Cw	Flw
Ht	1.00	0.33***	0.36***	0.32***	0.02
Dgl		1.00	0.77***	0.57***	0.04*
DBH			1.00	0.56***	0.01
Cw				1.00	-0.03
Flw					1.00

Significance levels of correlation: * $p < 0.05$
*** $p < 0.001$

tween all traits, with the exception of the flowering score. Height, diameter, and crown width all showed mutual positive correlation. The results were consistent with the results obtained in the provenance study.

3.3.2.4. Heritability estimates

Both individual and family heritabilities are presented in Table 10. The narrow sense heritability values obtained in the present study were considerably high, indicating that these characteristics were strongly inherited and significant gains can be expected from selection. Family heritabilities followed a trend similar to that found in individual heritability estimates but were of much greater magnitude. The individual heritability of height growth was only 0.19, while the family heritability for the same characteristic equaled 0.88. Flowering was the most strongly inherited characteristic with an average heritability value of 0.98.

3.4. Discussion

When new provenances are introduced the question of survival during the rotation period is of crucial importance (Hagman 1973). Generally, the survival percentages of tropical trees under plantation conditions vary considerably, depending on tree adaptation, damages caused by biotic agents or forest fire, site condition, and other environmental factors. In the present study, different provenances of *A. mangium* showed a remarkably high survival percentage (cf. Tables 5 and 9). The results also indicated that all provenances had adapted well to the conditions prevailing at Lad Krating Plantation. The good results could also be attributed to the site preparation and care provided at this

particular site. Na'iem et al. (1985) have earlier reported that the survival percentage in *A. mangium* provenance trials in Indonesia after 17 months was only 66 %, ranging from 45 to 90 %. It is known, however, that the condition of the nursery stock or the handling of seedlings during transport or field planting may affect the survival of seedlings (Pásztor and Coelho 1977).

It has also been reported that under plantation conditions, the survival percentages of many species, e.g. *Pinus kesiya*, *P. merkusii*, *P. elliotii*, commonly decrease with plantation age (Burley 1973, Granhof 1984, Das and Stephan 1984). Generally, when trees grow older they are faced with more environmental factors and various biotic injuries. However, the survival percentages of *A. mangium* in the present study did not yet show any decreasing trend after planting for 30 months. This was obviously due to the degree of management of the experimental trials, but probably the observation time was too short to give conclusive information. It is obvious that surveys on survival percentages and damages caused by biotic injuries should be done on yearly basis over several years.

Generally, the genetic background is one of the main factors influencing the growth and development of tropical trees (Whitmore 1975). Characters used to identify the inherent adaptive variation related to the ecological variability within species depend on the utilization point of view (van Wyk 1978, Keiding et al. 1984). In the present study, the height performance, length of clear bole, diameter growth and crown diameter as well as flowering, were the selected characters.

As reported by Pettersson and Havmöller (1984), no statistically significant differences among provenances were found in the height growth of *A. mangium* at the age of 6 months, but differences within provenances were evident. In the present study, the height performance differed remarkably among provenances and families (cf. Tables 6 and 10).

In the present study, the height at 18 months was much greater than indicated in the same seed origins in Leizhou, China (1.88-2.61 m) by Pan and Yang (1986). However, the ranking of height performances by seed origins between the two sites was very similar. As compared to the results previously reported in Indonesia by Na'iem et al. (1985), the height growth of 24-month-

old *A. mangium* was smaller in the present study. This could be caused by the so-called GEI effect. The interaction between provenance and the environment has been earlier discussed and summarized by Zobel and Talbert (1984). Awareness about this phenomenon is obviously important when the effects are applied to a new site.

Callaham and Hasel (1961) suggested that the early development of height growth in *Pinus ponderosa*, for instance, could not be used as a criterion in the selection of suitable provenance for a general planting programme. Nevertheless, a similarity in growth and development during the study period of 18–30 months was observed in most provenances in the present study (cf. Table 8). The large variability in growth development within *A. mangium* provenances probably indicates a high insensitivity in tree selection in the registered stands. Each seedlot of a selected provenances presumably had considerably varying gene pools.

Zobel et al. (1987) stated that great individual differences usually occur among trees within each provenance. Thus the selection of provenance followed by selection of individual trees within a provenance will give the best gains. This fact was also supported by the study on family variations in the present study. The average height growth of 28-month-old *A. mangium* in the seed orchard was better than that of 30-month-old trees in the provenance trials. Moreover, the best family in the seed orchard did not come from the best provenance in the provenance trials. However, as Zobel and Talbert (1984) have emphasized, the height growth is to a lesser degree under genetic control as compared to other traits and strongly influenced by environmental factors.

In the present study, *A. mangium* had a poor self-pruning ability. At the age of 18 months, the average length of clear bole was only 1.8 m. The planting spacing seemed to have a small influence on the crown development and the length of clear bole. Results showed that some variability on the length of clear bole was found among provenances. Directional selection on this tree characteristic is needed particularly within promising stands.

Removal of live branches may be needed at an early age so as to limit the scar size. As explained by Kramer and Kozlowski (1979), a reduction of the live crown decreases both

the leaf area and the amount of respiring tissues. The removal of basal branches of *A. mangium* probably would not decrease the height growth if the removal of basal branches amounted to less than 30 % (Slabough, 1957). In comparison, Reeb (1984) found that an early pruning of widely spaced Douglas fir will show the highest return on investment.

The large variation in Dgl and DBH in the present study indicated the need of mass selection for diameter growth in promising provenances. Variability in diameter growth was proportionally larger when *A. mangium* trees grew older. Such a trend in diameter development has previously been reported in *Pinus kesiya* (Changtragoon 1984).

The diameter differences observed in the present study were obviously mainly due to variation in the genetic adaptability of *A. mangium* provenances to Lad Krating plantation conditions. However, as knowledge about juvenile-mature relationships in *A. mangium* is still limited, it might be too early to evaluate provenances at this early age, even though the ranking by Dgl or DBH would already provide information for further immediate selection. Kageyama (1984) found that the selection of eucalypts at the age of 2 (for 6–7 years rotations) gave good estimations of genetic gain. On the other hand, Darrow (1986) reported a considerable change in ranking of *Eucalyptus saligna* seedlots between 4 and 8 years. Similar results were reported for *Pinus oocarpa* by Chagala and Gibson (1984). Zobel et al. (1987), however, believed that it is possible to make predictions of mature provenance performance at a young age when the trees are grown as exotic species. An evaluation based on several characteristics will obviously give better information for practical recommendations, particularly for importing seed of promising provenances, than an evaluation based on one trait alone.

In the present study, the provenance trials comprised of 16 seed sources collected throughout the natural range of *A. mangium*. As expected, clinal variation in height development was observed (cf. Fig. 5). The continuity of variation has earlier been emphasized, particularly by Langlet (1958). However, for deeper theoretical studies on clines, provenance trials established in other areas would also be needed, since the clinal expression is exhibited differently in different

environments (White and Ching 1985).

Crown shapes of most provenances and families in the present study were slightly different. Significant variation in crown diameter was also observed. The different spacings used in the provenance trials and the seed orchard did not much effect the crown development. Thus, in a general planting programme, the spacing can probably be reduced without any harmful effects as a consequence. However, more information on the crown development of *A. mangium* is needed.

A. mangium is generally a precocious species. In a seed orchard for genetically improved seed, frequent and abundant flowering is essential. The variation in flowering generally depends on both environmental and genetical factors. In China, Pan and Yang (1986) reported that *A. mangium* planted at northern latitudes started flowering at 3–4 years of age, while in southern latitudes flowering started 20 months after establishment.

During the present study, the trees in the seed orchard started flowering but there was distinct genetic differences (cf. Table 10). Similar results have been reported in many species (Mergen 1961, Heimburger and Fowler 1969). When grown on the same site, *A. mangium* families from more northern latitudes flower earlier than the more southern families.

The narrow sense heritability of all traits studied was extremely high. The results indicated the necessity of selection; significant gains can be expected from progeny test selection for any of the traits studied. Family heritabilities showed greater values than individual heritabilities since they are based on averages from many progenies. This reflects the greater reliability of progeny performance as a guide for the breeding value as compared to individual performance (Cotterill and Zed 1980). Heritability values were also found to decrease with age (Kageyama 1984).

Family heritabilities have been calculated for many species. For instance, Brigden and Williams (1984) reported the heritabilities for height, diameter, and volume of 5.5-year-old

Table 13. Priority list of *A. mangium* by based on the scoring system.

Provenance No.	Characteristic evaluated					Total score
	Ht	CB	Dgl	DBH	Cw	
12992	6	—	6	7	3	22
13229	8	5	4	8	10	35
13232	—	—	1	1	2	4
13233	—	6	—	—	—	6
13234	—	—	—	—	—	—
13235	3	4	7	4	—	18
13236	—	—	—	—	—	—
13237	—	—	2	—	1	3
13238	1	3	3	2	5	14
13239	2	—	—	—	—	2
13240	7	9	5	5	4	30
13241	—	1	—	3	6	10
13242	4	8	8	6	7	33
13459	9	10	10	10	8	47
13460	10	7	9	9	9	44
13621	5	2	—	—	—	7

Pinus caribaea as 0.86, 0.89, and 0.86 respectively. Harahap and Soerianegara (1977) calculated the heritabilities for height, clear bole, diameter, and stem form in 25-year-old teak to be 0.67, 0.69, 0.87, and 0.94 respectively. The heritabilities for height, diameter, and volume for *P. radiata* at the age of 17 months were 0.81, 0.62, and 0.72 respectively (Cotterill and Zed 1980). Nevertheless, the heritabilities obtained in the present study were higher for all traits compared to these earlier reports.

For practical purposes, in evaluating the best provenances at the age of 30 months a score was given for five characteristics and then summed to give a provenance score. The best ten provenances were given rank scores from 10 (best) to 1 (tenth best), and the remaining six provenances were given a score of 0. The summed provenance scores are given in Table 13. Accordingly, the five best *A. mangium* provenances to be grown at Lad Krating Plantation or in nearby areas are as follows; (1) W. of Morehead, Papua New Guinea, No. 13459; (2) Oriomo River, Papua New Guinea, No. 13460; (3) Claudie River, Australia, No. 13229; (4) Abergowrie, Australia, No. 13242; and (5) Ellerbeck Rd. Cardwell, Australia, No. 13240.

4. SEASONAL DIAMETER GROWTH OF *A. MANGIUM* PROVENANCES

4.1. Introduction

Studies on the seasonal variation in the growth development of trees have long since been carried out in the temperate zone. The first efforts to measure the annual diameter growth of trees were published in the 1750's, and the course of diameter growth during one growing season was already recorded in the 1830's (see Leikola 1969). The seasonal growth rhythm varies greatly among species and individual trees, being determined by environmental conditions (Kramer and Kozlowski 1979). A large number of researchers have studied the seasonal diameter growth and the effect of various environmental factors on the radial growth of trees, e.g. Fritts (1960), Harkin (1962), Kozlowski and Peterson (1962), Bassett (1966), Leikola (1969), Jintana et al. (1983), and Palmer and Ogden (1983). So far, such studies have only been carried to a limited extent in the tropics. Furthermore, available studies in the tropics have been mainly restricted to deciduous species, and only to a lesser extent have studies been concerned with intermittently growing evergreens (Kikuro et al. 1958, Alvim 1964).

Several methods have been developed to determine precisely the diameter growth of trees. The use of a dendrometer band is one of the most practical methods, providing an easy and convenient way for measuring changes in the diameter of trees and supplying valuable information on growth responses of trees.

Since the introduction of dendrometer bands by Liming (1957), they have become a popular tool in many aspects of forest research where accurate measurement of diameter is desired. For instance, Lea et al. (1979) used dendrometer band to compare the response of Northern hardwoods to fertilization. Leikola (1969) used dendrometer band to study the influence of environmental factors on the diameter growth of forest trees in Finland. Details of the principle, construction, installation and ac-

curacy of dendrometer bands have been discussed elsewhere (Hall 1944, Mesavage and Smith 1960, Bormann and Kozlowski 1962, Bower and Blocker 1966, Yocom 1970, Auchmoody 1976, Cameron and Lea 1980, Cattellino et al. 1986).

4.2. Material and methods

The present study was conducted in an *A. mangium* provenance trial, consisting of 30-month-old *A. mangium* trees from 16 different provenances. The details of the seed origins and the study area have already been described earlier in the previous chapter (3.2.1, Table 3).

Eight healthy trees of each provenance (all together 128 trees), of average size and with a straight, clear bole were selected as sample trees. Changes in diameter of the selected trees were measured by dendrometer bands of the type described by Hall (1944), modified by Liming (1957), and recently described in detail by Cattellino et al. (1986). All the dendrometer bands were fitted at breast height (1.30 m) on smoothen stems. Changes in stem diameter were measured weekly for the period January–December 1985. The first year slackness were not taken into account in the present study. In order to minimize the effects of diurnal shrinkage mentioned by Byram and Doolittle (1950), all readings were made at 08:00–09:00 h. To illustrate some apparent effects of local environmental factors on the weekly diameter growth of *A. mangium*, climatic factors including weekly average maximum and minimum air temperature, relative air humidity, and weekly precipitation were calculated from daily recordings.

The results were presented as absolute values. Statistical and regression analyses, as well as a computation of the Richards function (Hunt 1982) fitted to the cumulative diameter growth, were carried out using SAS programmes (SAS 1985). The Richards function used in the present study was

$$D = a(1 + \exp(b-cw))^{-1/m}$$

where
D = cumulative diameter growth at week w;
a, b, c, and m are constants over w.

4.3. Results

4.3.1. Seasonal course of diameter growth

The diameter growth of *A. mangium* in the present study varied greatly among provenances, and times of measurement (Table

Table 14. Temporal and between-provenance variation in the diameter growth of *A. mangium*.

Source of variation	df	MS	F
Time	49	0.1914	126.36***
Provenance	15	0.1473	9.72***
Time × Provenance	735	0.0020	1.31**
Residual	4255	0.0015	

Significance levels of F-test: *** p < 0.001

14). The degree of the variation among provenances and within any provenance depended on the season. *A. mangium* is an evergreen tree species which has generally been believed to show continuous growth without any seasonal rhythm. In the present study, however, *A. mangium* did show a seasonal rhythm in diameter growth. During January and February, *A. mangium* of most provenances grew less than 0.01 cm per week (5% of the maximum growth rate), which are considered as no growth (Fig. 6). The results imply that there must be growth cessation within this period. The duration of diameter growth cessation varied among provenances from a

few weeks to a few months. For instance, Provenances No. 13236, 13238 and 13242 (all from Australia) showed diameter cessation for only 1–2 weeks, while Provenance No. 13621 (from Indonesia) showed complete cessation in diameter growth for about three months (January–March).

A marked increase in growth occurred in April in all provenances. The peak of diameter growth of all provenances, except Provenance No. 13238, occurred in June, and varied from 0.14 cm (No. 13234) to 0.22 cm (No. 13235) per week. Provenance No. 13238 showed no peak in diameter growth, but rather remained constant throughout the growing season (Fig. 6). No statistical differences in the variation of the maximum diameter growth and diameter growth during the wet season (April–November) were found. However, statistically significant differences among provenances were found during the dry season (December–March) and they accounted for the significant differences in annual diameter growth among provenances (p < 0.01). The annual diameter growth of *A. mangium* ranged from 3.68 (No. 13234) to

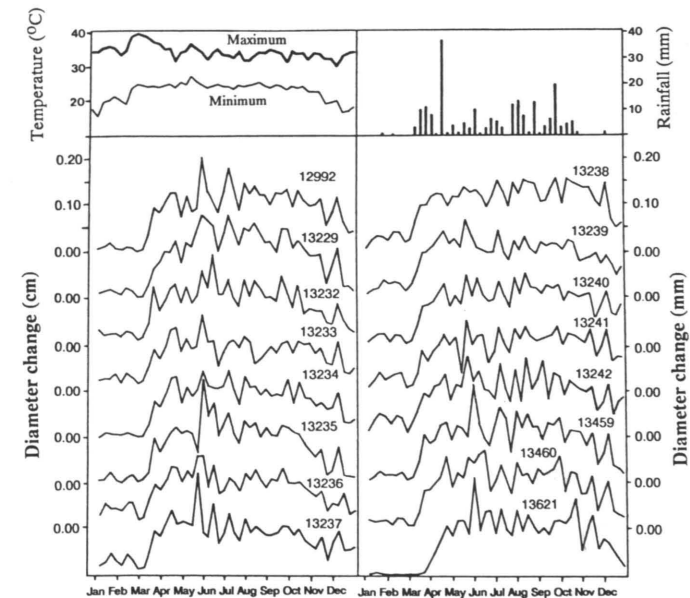


Figure 6. Average seasonal changes in weekly diameter growth of 16 provenances of *A. mangium*. Maximum and minimum temperature, and amount of rainfall are also shown.

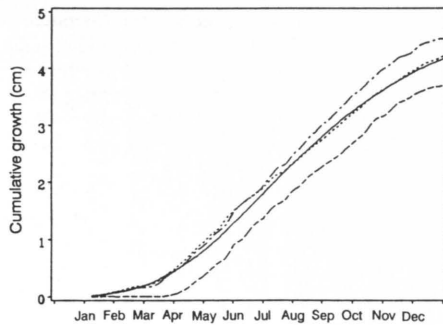


Figure 7. Diameter growth of three representative provenances (..... 13239, - - - - - 13459, - - - - - 13621), and the Richards function (—) fitted to the overall mean diameter of *A. mangium*.

4.93 cm (No. 13238). Diameter growth of most of the trees dropped remarkably in December. Fig. 6 shows the weekly average diameter growth of each *A. mangium* provenance during the 1-year measurement period. Maximum and minimum weekly temperature, and rainfall are also given.

The seasonal growth pattern of *A. mangium* was generally consistent for all provenances, showing a typical sigmoidal growth curve. Diameter growth begins at a slow rate, then accelerates in April to late November, and then slows down again in the dry season. Several growth curves including the logistic, Gompertz, polynomial and the Richards function were fitted to the present data. However, the Richards function was found to be the one best fitting the data. The objective of fitting growth curves in the present study was to summarize the differences in diameter growth process among the *A. mangium* provenances.

When the growth curve comparison technique described by Kappenman (1981) was applied, it was found that the cumulative diameter growth curves of *A. mangium* differed significantly among provenances. Fig. 7 shows the seasonal growth pattern constructed from the weekly averages of all trees using the Richards function, and the growth patterns of three representative provenances (Australia, Papua New Guinea, and Indonesia). The curves of the remaining provenances are not presented as they were all rather similar and little difference is discern-

ible. The results show that the Richards function well described the cumulative diameter growth of *A. mangium*, and resulted in very small sum of square residuals. The earliness of the start of diameter growth affected the final diameter growth more than rate of diameter growth. The slope of the curve showing almost no difference among provenances. This is also supported by the results obtained from the analysis of variance.

4.3.2. Dependence of the weekly diameter growth on environmental factors

Correlation coefficients were calculated for weekly diameter increment and the various climatic factors; including average maximum and minimum air temperature, difference of average maximum and minimum temperature, rainfall, and average relative air humidity of both the same and preceding week of measurement. The results are summarized in Table 15. Growth was highly correlated ($p < 0.01$) with all the climatic factors studied. In general, weekly diameter growth was positively correlated with minimum temperature, rainfall, and air relative humidity, and negatively correlated with maximum temperature as well as different between maximum and minimum temperature. The most consistent correlation in all provenances was the remarkably high negative correlation between differences of maximum and minimum temperature and the diameter growth. The correlation coefficients of minimum temperature of the previous week were higher than of the measured week in all cases. Rainfall and air relative humidity showed rather low correlations with diameter growth compared to temperature. The amount of rainfall had the highest correlation in the case of Provenance No. 13460 (Papua New Guinea, $p < 0.01$). Relations between some environmental factors and weekly diameter growth of selected *A. mangium* provenances are plotted in Fig. 8.

Before further conclusions can be made about the relationships of diameter growth and climatic factors, the mutual relationships among the various factors must be taken into account. Therefore, the correlation matrix of climatic factors used in the present study was calculated and is presented in Table 16. Statistical correlations exist among the vari-

Table 15. Correlation coefficients for weekly diameter growth of *A. mangium* and various environmental factors of the week of measurement (week), and the preceding week (week-1) of measurement ($df = 414$).

Provenance No.	Max. Temp.(°C)		Min. Temp.(°C)		Diff. Max.-Min.(°C)		Rainfall (mm)		RH (%)	
	Week	Week-1	Week	Week-1	Week	Week-1	Week	Week-1	Week	Week-1
12992	-0.465	-0.276	0.440	0.529	-0.711	-0.657	0.405	0.287	0.364	0.297
13229	-0.470	-0.307	0.499	0.574	-0.760	-0.713	0.375	0.294	0.420	0.393
13232	-0.302	-0.177	0.431	0.495	-0.596	-0.561	0.356	0.262	0.285	0.293
13233	-0.381	-0.175	0.468	0.535	-0.681	-0.601	0.385	0.252	0.372	0.265
13234	-0.442	-0.220	0.445	0.539	-0.700	-0.630	0.417	0.228	0.372	0.342
13235	-0.326	-0.205	0.493	0.527	-0.663	-0.607	0.352	0.307	0.374	0.338
13236	-0.275	-0.198	0.455	0.485	-0.588	-0.564	0.328	0.297	0.247	0.279
13237	-0.263	-0.162	0.362	0.406	-0.497	-0.467	0.273	0.281	0.238	0.255
13238	-0.401	-0.249	0.395	0.476	-0.620	-0.587	0.323	0.252	0.229	0.243
13239	-0.343	-0.188	0.467	0.566	-0.645	-0.616	0.364	0.299	0.254	0.307
13240	-0.482	-0.302	0.438	0.529	-0.711	-0.665	0.411	0.248	0.280	0.289
13241	-0.507	-0.350	0.330	0.449	-0.637	-0.600	0.342	0.261	0.217	0.254
13242	-0.362	-0.207	0.366	0.444	-0.567	-0.526	0.346	0.214	0.194	0.293
13459	-0.381	-0.175	0.468	0.535	-0.681	-0.601	0.385	0.252	0.372	0.265
13460	-0.428	-0.233	0.468	0.550	-0.705	-0.644	0.476	0.289	0.363	0.292
13621	-0.426	-0.378	0.424	0.482	-0.665	-0.677	0.220	0.230	0.356	0.320

Table 16. Matrix correlation of climatic factors at Lad Krating Provenance Trial.

	MAX	MIN	DIFF	RAIN	RH
Maximum temperature, °C (MAX)	1.000	0.336*	0.280*	-0.293*	-0.082
Minimum temperature, °C (MIN)		1.000	-0.810***	0.323*	0.483***
Temperature max.-min., °C (DIFF)			1.000	-0.511***	-0.543***
Rainfall, mm (RAIN)				1.000	0.360**
Air relative humidity, % (RH)					1.000

Significance levels of correlation: * $p < 0.05$
 ** $p < 0.01$
 *** $p < 0.001$

ous climatic factors, except maximum temperature and air relative humidity.

Multiple regression analysis was used to examine the effect of combinations of climatic variables on the diameter growth of each *A. mangium* provenance. The squares of each climatic factors, as well as the factors of the previous week were used in the regression analysis. The partial correlation coefficients as well as the degree of determination (R^2) for each model are presented in Table 17. Different climatic factors effect the diameter growth of *A. mangium* differently among provenances. Climatic factors had the most influence on the diameter growth of Provenance No. 13229 (Australia) ($R^2 = 0.89$), while Provenance No. 13237 was the least effected by the climatic factors. In general, the results of multiple regression analysis confirm the importance of the difference in weekly maximum and minimum temperature in determining diameter growth. When the best subsets of the climatic factors were applied in the regression equation, as much

as 49 to 88 percent of the variation in the diameter growth of *A. mangium* could be explained.

4.4. Discussion

In the present study, the analysis on the seasonal diameter growth of *A. mangium* was carried out at a provenance trial, located in Central Thailand. The seasonal distributions of climatic factors at the study area (northern hemisphere) and the native habitat (southern hemisphere) of *A. mangium* are different, as presented in Table 18. The seasonal growth rhythm of *A. mangium* demonstrated in the present study may therefore differ from that in its natural habitat.

Unlike the temperate climate, the tropical climate is often regarded as non-seasonal, with trees growing almost continuously without a noticeable seasonal rhythm (Longman and Jenik 1974, Richards 1981). However, Alvim (1964) believed that growth rates of

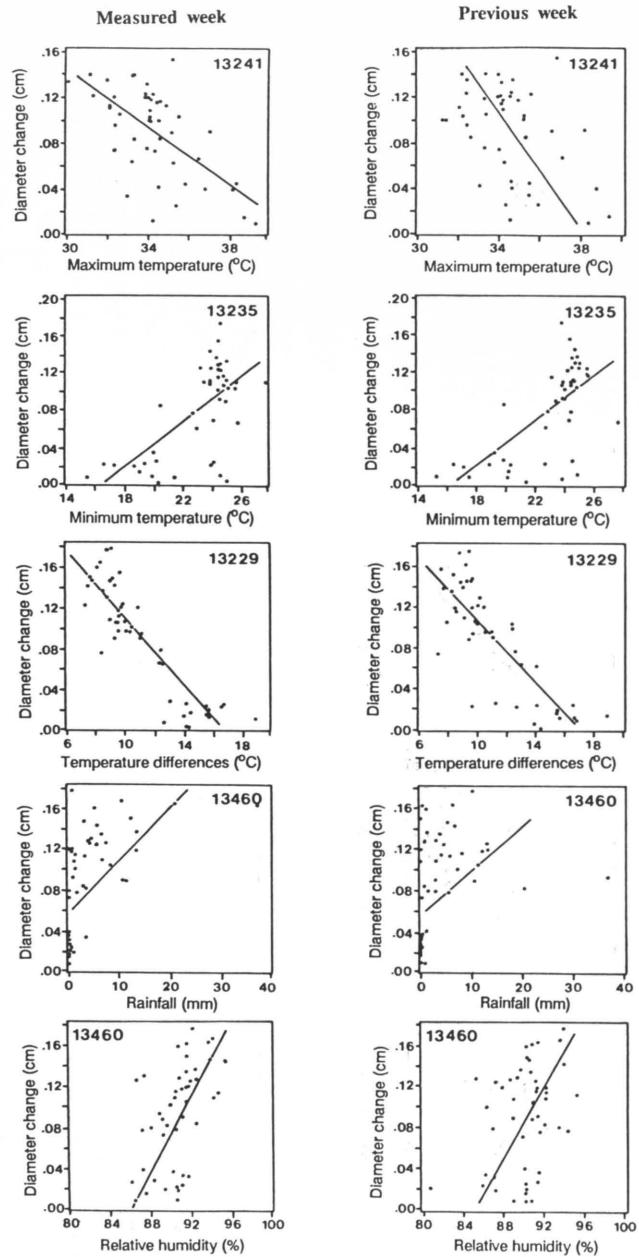


Figure 8. The relationships of weekly diameter growth of *A. mangium* provenances on some climatic factors of the measured week and preceding week. The number indicates the provenance (see Table 3).

Table 17. Partial correlation coefficients for diameter growth of 16 *A. mangium* provenances.

Provenance	MAX	(MAX) ²	MAXP	MIN	(MIN) ²	MINP	DIFF	(DIFF) ²	DIFFP	RAIN	(RAIN) ²	RAINP	RH	(RH) ²	RHP	R ²
12992	0.022	0.032*	0.004			0.002	0.677**	0.023*	0.007	0.005	0.018*	0.004	0.026*	0.023	0.017	0.801***
13229							0.782***	0.604***	0.008	0.005	0.005	0.007	0.032**	0.014	0.019	0.887***
13232							0.630***	0.748***	0.015	0.005	0.003	0.007	0.017	0.011	0.011	0.669***
13233	0.007	0.018	0.024*	0.018	0.005	0.005	0.689***	0.004	0.008	0.005	0.003	0.016	0.032*	0.032*	0.032*	0.686***
13234				0.008	0.019	0.019	0.571**	0.689***	0.037*	0.032*	0.032*	0.016	0.032*	0.032*	0.032*	0.808***
13235							0.465**	0.732***	0.014	0.011	0.013	0.007	0.006	0.006	0.006	0.737***
13236	0.034*	0.045*					0.732***	0.008	0.014	0.011	0.013	0.007	0.006	0.006	0.012	0.491***
13237							0.665***	0.029	0.033*	0.016	0.016	0.012	0.004	0.004	0.011	0.846***
13238	0.047	0.005	0.005	0.008	0.005	0.005	0.669***	0.029	0.033*	0.016	0.016	0.012	0.004	0.004	0.011	0.812***
13239							0.594***	0.010	0.010	0.008	0.017	0.008	0.004	0.004	0.011	0.785***
13240	0.026*	0.039**					0.594***	0.010	0.011	0.015	0.011	0.009	0.015	0.034	0.011	0.742***
13241	0.013	0.096***					0.544***	0.009	0.004	0.015	0.011	0.009	0.015	0.034	0.011	0.742***
13242	0.031	0.014					0.738***	0.021*	0.004	0.014	0.006	0.015	0.027*	0.026*	0.031**	0.686***
13459							0.728***	0.021*	0.004	0.014	0.006	0.015	0.027*	0.026*	0.031**	0.826***
13460	0.014	0.017					0.020	0.005	0.004	0.014	0.006	0.015	0.010	0.010	0.004	0.801***
13621	0.014	0.017					0.020	0.005	0.004	0.014	0.006	0.015	0.010	0.010	0.009	0.782***

Significance levels: * p < 0.05
 ** p < 0.01
 *** p < 0.001

where MAX = Maximum temperature of the measured week (°C)
 MAXP = Maximum temperature of the previous week (°C)
 MIN = Minimum temperature of the measured week (°C)
 MINP = Minimum temperature of the previous week (°C)
 DIFF = MAX-MIN of the measured week (°C)
 DIFFP = MAX-MIN of the previous week (°C)

RAIN = Rainfall of the measured week (mm)
 RAINP = Rainfall of the previous week (mm)
 RH = Air relative humidity of the measured week (%)
 RHP = Air relative humidity of the previous week (%)
 R² = Coefficient of multiple determination

Table 18. Comparison of climatic data at the Lad Krating Provenance Trial and some sites where *A. mangium* is natural.

Location	Latitude	Longitude	Alt (m)	Mean monthly rainfall (mm)												Mean annual rainfall		
				Max.	Min.	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct		Nov	Dec
Cairns (13233-13234)	16°53'S	145°45'E	3	32	13	421	422	460	264	110	72	39	42	43	50	98	203	2224
Cardwell (13240-13242)	18°16'S	146°02'E	6	32	17	457	466	417	211	92	50	33	29	36	52	107	193	2143
Moreshead (13459)	8°43'S	141°38'E	31	—	—	332	262	318	157	154	86	54	52	38	80	114	224	1913
Daru (13460)	9°04'S	143°12'E	8	32	22	280	258	325	321	223	108	93	52	42	55	111	204	2063
Lad Krating	13°42'N	101°06'E	80	38	18	38	22	51	72	102	97	149	197	242	219	36	0	1225

evergreen trees are not uniform but exhibit some seasonal variation associated with external factors. Several ecologists have observed that growth of tropical trees actually does occur in cycles (Alvim 1964, Hopkins 1970). This is also supported by the results from the present study, which showed clear periodic growth in diameter of *A. mangium* (cf. Fig. 6).

Individual trees vary in growth characteristics, as tree growth development is generally determined by hereditary and environmental factors (Kozłowski 1971, Kramer and Kozłowski 1979). Trees from different geographic areas vary in growth rates, form, and adaptation to environmental conditions (Callahan 1970). Differences in seasonal growth rhythm among tree races reflects variation in physiological processes, which may be related to variations in the adaptation of a specific variety to different levels of environmental stress. In the present study, *A. mangium* from different geographic sources exhibited significantly different seasonal diameter growth rhythms (cf. Table 14), resulting in differences in the annual growth of the trees. Variation in diameter growth among provenances was found mostly during the dry season (December–March), rather than during the wet season. These results indicate variation in physiological processes among provenances in response to environmental stress. When the climatic factors were not limiting, the trees grew similarly in all provenances. However, the results of the variations in annual diameter growth among provenances of *A. mangium* in the present study are not consistent with results of the periodical variation in diameter development reported in the previous chapter. This is probably due to the error in sampling in the present study, as the results presented are the mean of only eight sample trees in each provenance. The results in the previous chapter were obtained from all trees (100 trees per provenance). Further, the trees may perform differently as they grow older, since the present study was carried out after the last measurement of the previous study. Therefore, the juvenile-mature relationship is an important characteristic to be first determined (Burley et al. 1976).

There is considerable evidence in the literature that newly installed dendrometer bands tend to underestimate growth during the first season because of slack that can not

be completely eliminated from the band during installation (Auchmoody 1976, Jintana et al. 1983, Palmer and Ogden 1983, Fuller et al. 1988). However, in the present study, the first year slackness has not been taken into account, as the results are in accord with the second year after fitting the bands (but the results are not presented here). This is probably due to the special care that was given during the installation, and *A. mangium* grows relatively fast. Auchmoody (1976) found that the degree to which dendrometers underestimated true first-year diameter varied directly with the growth rate and tree size.

The basic pattern of the cumulative curve of radial growth of trees throughout a season is similar in form to the cumulative curve for shoot growth over the life of a plant (Fritts 1976). The curve is basically a modified sigmoid curve. This pattern seemed to hold also for the seasonal cumulative diameter growth of *A. mangium* in the present study (cf. Fig. 7). Models of tree growth have long been developed and different types of fitted curve have been widely employed to analyze growth (Pienaar and Turnbull 1973, Venus and Causton 1979, Hunt 1982, Pietarinen et al. 1982). The pattern of seasonal diameter growth in the present study was satisfactorily described by fitting the Richards function to the cumulative diameter increment. Causton et al. (1978) have shown that this function is a reasonable model of a growth system in nature. However, the fitted curves showed consistent patterns of over-estimation at the beginning and under-estimation at the end of the period for almost all provenances. Special attention must therefore be taken when applying the growth pattern as an empirical growth function.

Kozłowski and Peterson (1962) observed the variation in seasonal growth pattern during successive years, indicating extreme sensitivity of diameter growth to environmental stress. Kramer and Kozłowski (1979) stated that cambial growth was generally affected by environmental stress to a larger extent than shoot elongation. Hence, fluctuations in the diameter growth rate during the year can be explained by variations in limiting factors of the environment (Fritts 1976), and it is reasonable to assume that the duration of diameter growth is determined by environmental factors.

It was not possible to monitor several relevant environmental factors such as solar

radiation, wind velocity, and soil moisture content in the present study. However, the relationships between diameter growth and some climatic factors were determined. As shown in Table 15, the weekly minimum temperature was one of the climatic factors measured that exerted a strong effect on diameter growth. Maximum temperature had a much smaller effect in comparison. These results are in accord with Kozłowski et al. (1962). Through a series of multiple regression analyses of radial growth, Fritts (1960) concluded that the growth of beech (*Fagus grandifolia*) was closely correlated with maximum temperature but not minimum temperature. When the maximum and minimum temperature difference was used in the present analysis, a strikingly high correlation was achieved. The correlation coefficients were larger than for weekly minimum or maximum temperatures alone in all cases. Hedge (1987) reported the findings by Guevaarra that one of the factors causing seasonal variation in the growth of *Leucaena* was the temperature differences between day and night.

Richards (1981) stated that the main external factor controlling the periodic growth rhythms of tropical vegetation was seasonal drought, rather than temperature, as in temperate climates. This does not appear to be the case in the present study, as the seasonal precipitation was not especially correlated with diameter growth. The low correlation between rainfall and diameter growth was probably due to the fact that rainfall affects diurnal diameter growth rather than weekly diameter growth; soil moisture content would probably play a more important role than the rainfall.

Although diameter growth is related to

prevailing environmental conditions, there is a time lag effect which should be taken into account. Several investigators have shown the importance of a lag in growth response to environmental factors (e.g. Fritts 1960, Leikola 1969). Kozłowski et al. (1962) identified the possibility of a 1-day lag effect of temperature on growth of oak (*Quercus ellipsoidalis*) but the absence of a 2-day lag effect. In the present study, the diameter increment of *A. mangium* was dependent more on the minimum temperature of the preceding week rather than of the measured week for all provenances (cf. Table 15). None of the other climatic factors showed such a lag.

When the effects of several climatic factors were analyzed through a series of multiple regression, higher partial correlation coefficients were obtained (cf. Table 17). The differences in multiple regression models for each provenance can be assessed and related to the ecological requirements of each geographic race. Fritts (1960) suggested that multiple regression should be used as a tool for clarification of the relationships involved in the growth-environmental complex. In using multiple regression, attention must be paid on the correlation among various environmental factors, which may have a direct influence on growth. Such a correlation may cause the factors in question to appear more related to growth than it actually is.

A problem in studying environmental effects on growth is that the relative importance of an environmental factor can change yearly. Therefore, although some significant differences in seasonal diameter growth were found in the present study, it must be remembered that the results are based upon a single season.

5. VARIATION IN THE FOLIAR NUTRIENT STATUS OF *A. MANGIUM* PROVENANCES GROWN IN THAILAND

5.1. Introduction

Foliar analysis has been widely used as a means of assessing plant nutritional requirements or status, and soil nutrient availability. The technique is particularly suited to even-aged stands such as in plantation forestry (Qureshi and Srivastava 1966, Humphreys et al. 1972). Numerous experiments have been carried out into various aspects of foliar nutrient analysis during the last twenty years (e.g. Miller 1966, Groves 1967, Humphreys et al. 1972, Ellis 1975, Burdon 1976, Raupach and Clarke 1978, Evans 1980, Bunderson et al. 1985).

There are several sources of variation influencing the levels of nutrients in foliage; including genetic background, age of foliage, position of leaf in tree crown, seasonal fluctuation, and year-to-year variation (Wells and Metz 1963, Groves 1967, Humphreys et al. 1972, Leaf 1973, Ellis 1975, Knight 1978, Mead 1984). Standardization of sampling procedures has therefore been a major difficulty in relating actual sample foliar nutrient levels to the overall nutrient status of trees. Several investigations have been concentrated on sampling techniques and methods of chemical analysis in order to make results more reliable (Zinke 1968, Everard 1973, Leaf 1973, Bell and Ward 1984). White (1954) stated that it is not always easy to obtain reliable samples that represent the tree nutrient status of any trees, especially those of the large crown canopy. However, the critical levels of elements in pine needles planted on infertile sites, for examples, have been reported (Will 1966, Comerford 1981).

The current foliage is generally accepted as the most useful for diagnostic purpose (Leaf 1973), since current foliage usually has higher nutrient levels and often lower between-tree variability (Mead and Will 1976). Generally, foliage from the uppermost part of the canopy and from branches with uniform exposition is considered the best to sample (Lowry and Avard 1968, Everard 1973). In

the case of tropical fast-growing species, sampling from the upper crown is also suggested, since it is difficult to determine leaf age and the upper crown is known to be the most active part of light demanding tree species. However, a single sampling position is unlikely to be suitable for all elements studied (Lamb 1976). It is also considered better to sample more trees rather than more branches within a tree (Tamm 1964, Scott et al. 1975).

Genetic variation in the nutrient requirements and accumulation in trees has received less attention compared to tree age and growth, for example. However, variation in foliar nutrient concentrations associated with seed sources of forest trees has been described by several investigators (Mergen and Worrall 1965, Steinbeck 1966, Woessner et al. 1975, Kleinschmit and Sauer 1976, Knight 1978, Goddard and Hollis 1984). The genetic variation in nutrient uptake by trees has mainly been limited to coniferous species with wide, natural geographic or edaphic ranges. For example, Gerhold (1959) reported significant differences in foliar nitrogen, calcium, magnesium, and iron contents among provenances of 19-year-old Scots pine. Steinbeck (1966) demonstrated differences among seed sources in their ability to extract magnesium from soil at low magnesium concentrations. Data on tree-to-tree variation in foliar nutrient concentrations of Jack pine (Mergen and Worrall 1965), Norway spruce (Giertych and Fober 1967), radiata pine (Forrest and Ovington 1971, Knight 1978), loblolly pine (Woessner et al. 1975), as well as broadleaved evergreen tree such as *Eucalyptus cladocalyx* (Groves 1967) are available.

Numerous studies have successfully demonstrated relationships between the chemical composition of foliage and corresponding contents of elements in the soil. Positive correlations have been reported for nitrogen, potassium (Chutpong et al. 1976), and magnesium (Thaiutsa 1981) in the case of *Pinus kesiya*; for magnesium in the case of *P.*

sylvestris (Steinbeck 1966); for magnesium and zinc in the case of *P. radiata* (Knight 1978); and for phosphorus in the case of *P. elliotii* (Humphreys and Pritchett 1972). On the other hand, Cech et al. (1974) found no correlation between nutrient concentrations in *P. nigra* needles and soil contents. Similar results are reported by Metz et al. (1966); Moschler et al. (1970); and Thaiutsa (1981). The inconsistency in the results implies that correlations between soil analysis and foliar analysis are dependent upon habitat (cf. Paarlahti et al. 1971); and, in certain cases, elements in soil may not be available or they may be occur in excess of normal requirements.

Tree growth in relation to foliar nutrient concentrations has attracted considerable attention. Height growth seems to have been the most common growth parameter used in this context. Knight (1978) concluded that height growth of radiata pine can be predicted from foliar manganese and zinc, while Raupach and Clarke (1972) found that foliar potassium also had an influence also from foliar potassium. Similar results have also been reported for red pine (Hoyle and Mader 1964) and loblolly pine (MacCarthy and Davey 1976). Lacey et al. (1966) successfully demonstrated a high correlation between foliar phosphorus concentration and the growth of *Eucalyptus grandis* seedlings. On the other hand, Lee (1968) failed to relate any growth or morphological characteristic with nutrient levels in *Pinus nigra* needles.

5.2. Material and methods

5.2.1. Field sampling

The material used in the present investigation consists of 16 provenances of *A. mangium* planted at Lad Krating Plantation, in Central Thailand. The details of the seed sources used and the study area have been previously described in Chapter 3 (3.2.1, Table 3).

Four trees from each provenance (one from each replicate plot) were randomly selected. About twenty fully grown leaves of each selected tree were collected from the southern aspect of the uppermost crown in May 1986. The total height, diameter at breast height and crown diameter of the sample trees were also measured.

Soil samples from 10–20 cm depth were taken from three pits dug two meters apart around each tree. The three subsamples were combined on an equal by volume basis.

All samples were then analyzed at the Forest Soil Laboratory of Kasetsart University in Bangkok.

5.2.2. Foliar analysis

All foliage samples were oven-dried at 70°C for a minimum of 24 hours, and were then finely ground in a Wiley mill to pass a 20-mesh screen.

Total contents of nitrogen were determined using the micro-Kjeldahl procedure. The total contents of phosphorus was determined by the vanadate-molybdate-yellow method. After dry washing, potassium, calcium, magnesium, zinc, manganese, iron, copper, and sodium contents were determined by standard atomic absorption spectrophotometric methods as described by Chapman and Pratt (1961). Concentrations of all elements are expressed on an oven dry weight basis.

5.2.3. Soil analysis

All soil samples were air-dried and the analyses were carried out on the < 2 mm fraction. The following methods were used in chemical analyses: soil pH was read from a 1:1 soil to distilled water suspension with a standard pH meter (Peech 1965); total soil nitrogen was determined by the micro-Kjeldahl method (Bremner 1965); available phosphorus by Bray II (Watanabe and Olsen 1965); exchangeable potassium, calcium, magnesium, sodium, iron, copper, manganese, and zinc from a neutral ammonium acetate extraction by atomic absorption spectrophotometry (Chapman 1965a); and cation exchange capacity (CEC) by the ammonium saturation method (Chapman 1965b).

5.2.4. Data analysis

A two-way analysis of variance was performed to determine the differences in soil and foliar nutrient levels. The same model as the analysis for the variation in growth performances in Chapter 3 (3.2.2) was used. Both between and within provenances sources of variation were calculated, and, in order to determine significant differences between provenances, the Duncan's New Multiple Range Test was applied.

Simple correlation coefficients (r) between concentrations of each element for soil and foliage were calculated as well as the correlation between foliar nutrient levels and the corresponding soil nutrient levels. Growth performance as a function of the nutrient concentrations of soil and foliage was also determined.

5.3. Results

5.3.1. Soil nutrients

The results of the chemical analysis of the 64 composite soil samples are presented in Table 19. Although there is variation in the soil chemical properties, there were no significant differences in nutrient levels within the plot. Soil homogeneity is also suggested by the insignificant variation among plots for all elements concerned. Soil potassium, manganese and zinc showed the most variation, with coefficient of variation of approximately

30 percent. pH, sodium and CEC showed the least variation (CV < 10 %).

The simple correlation coefficient matrix for the soil properties is given in Table 20. High coefficients ($p < 0.01$) are observed for pH and calcium ($r = 0.85$); phosphorus and potassium ($r = 0.78$); and calcium and magnesium ($r = 0.77$). Negative correlations were also found between soil nutrient contents. Iron especially was negatively correlated with other elements except nitrogen and sodium, but was positively correlated ($p < 0.01$) with copper ($r = 0.50$) and zinc ($r = 0.67$).

5.3.2. Foliar nutrient composition

Average foliar nutrient concentrations of all provenances of *A. mangium* are shown in Table 21. They are generally consistent with values for most woody plants species previously reported. The order of magnitude in the concentration of nutrient elements in *A. mangium* phyllodes were as follows: N > K > Ca > Mg > P >> Mn > Fe > Zn > Cu > Na. Coefficients of variation ranged from 6.4 to 23.3, being relatively low for nitrogen, phosphorus and sodium (< 10 %), intermediate for potassium, calcium, magnesium, zinc and manganese (10–20 %), and high for iron and copper (> 20 %). Micro-nutrients showed considerably more variation compared to the macro-nutrients, except sodium.

Foliar nutrient concentrations for each provenance are given in Table 22. Statistically significant differences occur for potassium ($P < 0.05$), calcium ($p < 0.01$) and magnesium ($P < 0.01$). Results of a two-way

Table 19. Soil chemical properties for the 64 plots of *A. mangium* Provenance Trial, Lad Krating Plantation.

Soil properties	Mean	Standard deviation	Coefficient of variation (%)	F-value* (df 15,45)
pH	5.304	0.251	4.7	0.57 ^{ns}
Total nitrogen, %	0.067	0.007	10.2	0.96 ^{ns}
Phosphorus, ppm	6.010	1.144	19.0	0.64 ^{ns}
Potassium, ppm	53.750	16.665	31.0	0.66 ^{ns}
Calcium, ppm	364.000	62.070	17.1	0.74 ^{ns}
Magnesium, ppm	54.390	8.787	16.2	0.99 ^{ns}
Iron, ppm	60.218	7.450	12.4	0.47 ^{ns}
Copper, ppm	1.240	0.147	11.9	0.41 ^{ns}
Manganese, ppm	27.720	8.620	31.1	1.19 ^{ns}
Zinc, ppm	0.779	0.231	29.7	0.93 ^{ns}
Sodium, ppm	61.170	2.777	4.5	1.26 ^{ns}
CEC, meq/100g	3.810	0.353	9.3	1.15 ^{ns}

* ns — not significant at $p < 0.05$

analysis of variance, summarized in Table 23, reveals a higher variation within provenances than among provenances for phosphorus, potassium, copper ($P < 0.01$) and iron ($P < 0.05$). No significant differences both within and among provenances were found for nitrogen, sodium, manganese, and zinc.

The ranges of variation of foliar nutrient contents of provenance means and individual trees are presented as frequency distributions in Fig. 9. The distributions of all nutrient elements were similar and followed the normal distribution.

It appears that there is no particular rank of foliar nutrient concentrations among provenances (Fig. 10). For example, Provenance No. 13242 (Australia) had high concentrations of nitrogen (2.74 %), phosphorus (0.098 %), zinc (25 ppm), and copper (14 ppm), but a small concentration of calcium (0.50 %) and iron (163 ppm). In contrast, Provenance

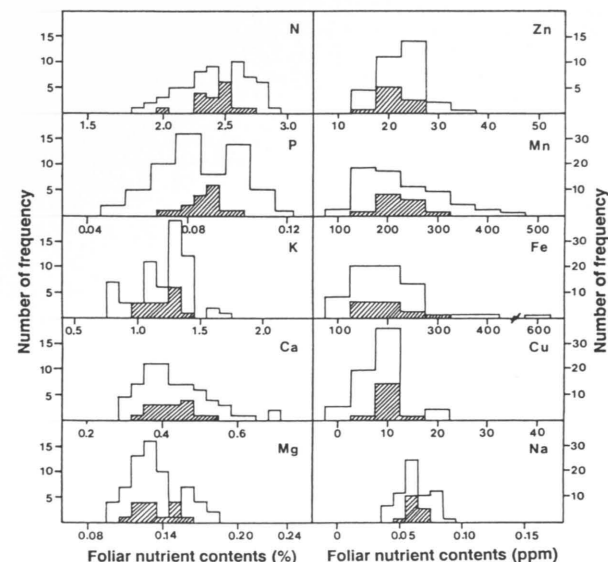


Figure 9. Frequency distribution of foliar nutrient contents of 30-month-old *A. mangium*, provenance means (shaded) and individual trees (unshaded).

No. 13460 (Papua New Guinea) had low levels of nitrogen (1.99 %), phosphorus (0.07 %), potassium (0.97 %), and iron (159 ppm), but rather high levels of calcium (0.58 %) and copper (11 ppm).

The matrix of correlation coefficients among the different elements in the foliage of *A. mangium* is presented in Table 24. High and significant correlations ($P < 0.01$) were found between foliar nitrogen and phosphorus ($r = 0.65$), nitrogen and potassium ($r = 0.50$); phosphorus and potassium ($r = 0.68$); calcium and magnesium ($r = 0.49$); and zinc and manganese ($r = 0.37$). High negative correlations ($p < 0.01$) between foliar potassium and calcium ($r = -0.67$), potassium and manganese ($r = -0.39$), phosphorus and calcium ($r = -0.36$); and iron and copper ($r = -0.34$) were found. Relationships between pairs of some foliar nutrient elements are illustrated in Fig. 11.

5.3.3. Relationships between foliar and soil nutrient contents

Correlation coefficients between the content of nutrients in the foliage and soil are pre-

Table 21. Foliar nutrient concentrations of 30-month-old *A. mangium* at Lad Krating Provenance Trial, Chachoengsao.

Foliar nutrient	Mean	Standard deviation	Coefficient of variation (%)
Nitrogen, %	2.426	0.155	6.4
Phosphorus, %	0.086	0.007	8.1
Potassium, %	1.190	0.122	10.3
Calcium, %	0.541	0.077	14.2
Magnesium, %	0.132	0.015	11.4
Iron, ppm	195.410	41.344	21.2
Copper, ppm	10.040	2.337	23.3
Manganese, ppm	221.290	34.977	15.8
Zinc, ppm	21.680	2.269	10.5
Sodium, ppm	0.062	0.006	9.7

sented in Table 25. Some of the relationships are depicted in Fig. 12. Significant correlations ($p < 0.05$) between corresponding soil and foliage nutrients were only found for phosphorus ($r = 0.30$), potassium ($r = 0.28$) and sodium ($r = 0.27$). Sodium was the only element showing a negative correlation between the level in the soil and in the leaves, i.e. the more sodium in the soil, the less sodium accumulated in the leaves. Foliar manganese concentrations, in particular, appear to be influenced by soil chemistry (Table 25, Fig. 12).

Table 20. Correlation coefficient (r) matrix of soil properties determined at Lad Krating Provenance Trial, Chachoengsao.

Variable	pH	N	P	K	Ca	Mg	Fe	Cu	Mn	Zn	Na	CEC
pH	1.00	0.23	0.50**	0.37**	0.85**	0.59**	-0.39**	-0.05	0.30*	-0.15	-0.02	0.50**
N		1.00	0.28*	0.25*	0.35**	0.42**	-0.02	0.07	0.17	0.03	-0.13	0.24
P			1.00	0.78**	0.68**	0.55**	-0.37**	-0.17	-0.09	0.01	0.22	0.35**
K				1.00	0.58**	0.60**	-0.40**	-0.20	-0.10	-0.07	0.24	0.35**
Ca					1.00	0.77**	-0.51**	-0.14	0.28*	-0.17	0.09	0.66**
Mg						1.00	-0.40**	-0.07	0.25*	-0.16	0.02	0.61**
Fe							1.00	0.50**	-0.34**	0.67**	-0.21	-0.39**
Cu								1.00	0.04	0.55**	-0.36**	-0.10
Mn									1.00	-0.33**	-0.31**	0.22
Zn										1.00	-0.09	-0.18
Na											1.00	0.07
CEC												1.00

Significance levels of correlation: * $p < 0.05$
** $p < 0.01$

Table 22. Mean foliar nutrient concentrations of 30-month-old *A. mangium* by provenances at Lad Krating Provenance Trial, Chachoengsao. Values in column followed by the same letter are not significantly different at the 0.05 level of significance using Duncan's New Multiple Range Test.

Prov. No.	% in dry weight					ppm in dry weight				
	N	P	K	Ca	Mg	Zn	Mn	Fe	Cu	Na
12992	2.533 ^a	0.091 ^a	1.282 ^{bc}	0.594 ^{cdef}	0.124 ^{abcd}	20.31 ^a	225.00 ^a	181.25 ^a	3.13 ^a	0.064 ^a
13229	2.315 ^a	0.080 ^a	1.016 ^{ab}	0.556 ^{abdef}	0.132 ^{abcde}	25.00 ^a	212.50 ^a	314.06 ^a	7.81 ^a	0.056 ^a
13232	2.284 ^a	0.092 ^a	1.376 ^c	0.438 ^{ab}	0.130 ^{abcde}	18.75 ^a	170.31 ^a	168.75 ^a	9.25 ^a	0.069 ^a
13233	2.341 ^a	0.092 ^a	1.141 ^{abc}	0.500 ^{abcd}	0.106 ^a	21.88 ^a	190.63 ^a	185.94 ^a	10.94 ^a	0.063 ^a
13234	2.459 ^a	0.091 ^a	1.281 ^{bc}	0.456 ^{abc}	0.111 ^{ab}	21.88 ^a	259.38 ^a	190.63 ^a	9.38 ^a	0.055 ^a
13235	2.450 ^a	0.076 ^a	1.000 ^{ab}	0.663 ^{ef}	0.153 ^{ef}	18.75 ^a	242.19 ^a	248.44 ^a	10.81 ^a	0.063 ^a
13236	2.503 ^a	0.085 ^a	1.078 ^{abc}	0.694 ^f	0.160 ^f	25.00 ^a	267.19 ^a	243.75 ^a	12.50 ^a	0.071 ^a
13237	2.424 ^a	0.080 ^a	1.157 ^{abc}	0.588 ^{bdef}	0.149 ^{def}	20.31 ^a	240.63 ^a	170.31 ^a	9.38 ^a	0.069 ^a
13238	2.407 ^a	0.085 ^a	1.282 ^{bc}	0.563 ^{abdef}	0.124 ^{abcd}	21.88 ^a	190.63 ^a	204.69 ^a	9.38 ^a	0.062 ^a
13239	2.556 ^a	0.093 ^a	1.344 ^c	0.463 ^{abc}	0.130 ^{abcde}	23.44 ^a	192.19 ^a	192.19 ^a	9.38 ^a	0.071 ^a
13240	2.538 ^a	0.084 ^a	1.282 ^{bc}	0.425 ^a	0.122 ^{abc}	17.19 ^a	215.63 ^a	217.19 ^a	9.38 ^a	0.060 ^a
13241	2.429 ^a	0.088 ^a	1.203 ^{abc}	0.531 ^{abcde}	0.136 ^{bdef}	21.88 ^a	218.75 ^a	150.00 ^a	12.44 ^a	0.058 ^a
13242	2.743 ^a	0.098 ^a	1.235 ^{abc}	0.500 ^{abcd}	0.149 ^{def}	25.00 ^a	246.88 ^a	162.50 ^a	14.06 ^a	0.068 ^a
13459	2.345 ^a	0.083 ^a	1.110 ^{abc}	0.619 ^{def}	0.146 ^{cdef}	21.88 ^a	175.00 ^a	165.63 ^a	10.94 ^a	0.055 ^a
13460	1.995 ^a	0.069 ^a	0.969 ^a	0.581 ^{bdef}	0.128 ^{abcde}	20.31 ^a	193.75 ^a	159.38 ^a	10.94 ^a	0.053 ^a
13621	2.490 ^a	0.089 ^a	1.281 ^{bc}	0.481 ^{abcd}	0.117 ^{ab}	23.44 ^a	300.00 ^a	171.88 ^a	10.94 ^a	0.057 ^a

5.3.4. Tree growth as a function of foliar nutrient contents

Average growth characteristics of the 30-month-old *A. mangium* sample trees for each provenance are presented in Table 26. Significant differences among provenances were found for height ($P < 0.01$), and diameter at breast height (DBH, $P < 0.05$), but not for crown diameter. More detailed results concerning the variation in growth characteristics of *A. mangium* among the provenances in the study have been presented earlier in Chapter 3—the results presented in Table 26 refer only to the 64 sample trees in the present study. Provenance No. 13459 (Papua New Guinea) had the best height and DBH growth, while Provenance No. 13233 (Australia) was the poorest for both characteristics.

The simple correlation coefficients between tree growth characteristics and the concentration of each nutrient element are given in Table 27. The correlations are, for the most part, low and inconsistent. Only three out of the ten foliar nutrients measured were significantly correlated with tree growth. Phosphorus was the only macro-element to be positively correlated ($p < 0.05$) with crown diameter ($r = 0.25$). A significant negative correlation ($p < 0.05$) was found between foliar manganese and height growth ($r = -0.28$), and iron was negatively correlated with diameter growth ($r = -0.27$) and crown diameter ($r = -0.30$). The relationship be-

Table 23. F-value from a two-way analysis of variance of nutrient concentrations in the foliage of 30-month-old *A. mangium* from 16 provenances.

Nutrient elements	Source of variation	
	Among provenances (df 15,45)	Within provenances (df 3,45)
Nitrogen, %	1.63 ^{ns}	0.88 ^{ns}
Phosphorus, %	0.91 ^{ns}	4.10 ^{**}
Potassium, %	1.98 ^{ns}	4.89 ^{**}
Calcium, %	3.16 ^{**}	16.60 ^{**}
Magnesium, %	3.74 ^{**}	1.70 ^{ns}
Iron, ppm	1.65 ^{ns}	3.30 [*]
Copper, ppm	1.52 ^{ns}	5.15 ^{**}
Manganese, ppm	0.91 ^{ns}	1.16 ^{ns}
Zinc, ppm	0.69 ^{ns}	1.04 ^{ns}
Sodium, ppm	1.32 ^{ns}	1.50 ^{ns}

Significance levels of the F-value: * $p < 0.01$, ** $p < 0.05$, ns not significant at $p < 0.05$

tween selected growth characteristics and nutrient contents are depicted in Fig. 13.

5.3.5. Tree growth as a function of soil nutrient contents

As with the contents of nutrients in the foliage, the correlations between tree growth characteristics and the concentrations of nutrient elements in soil were computed. The coefficients (r) are presented in Table 28. The results show that soil CEC is the only soil property significantly related ($p < 0.01$) to growth namely height growth ($r = 0.33$). This relationship is depicted in Fig. 14.

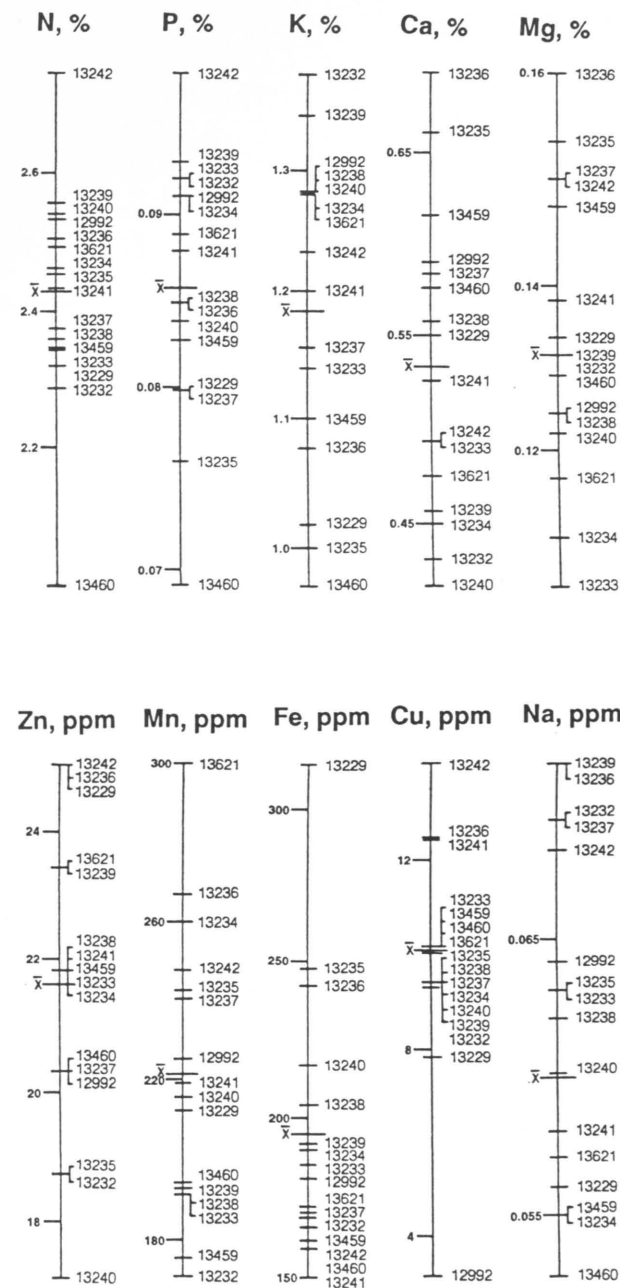


Figure 10. Proportionately ranked means for foliar nutrient concentrations in 16 provenances of 30-month-old *A. mangium*, including overall means (\bar{x}).

Table 24. Correlation coefficients (r) matrix of foliar nutrient concentrations of 30-month-old *A. mangium* at Lad Krating Provenance Trial, Chachoengsao.

Variable	N	P	K	Ca	Mg	Zn	Mn	Fe	Cu	Na
N	1.00	0.65**	0.50**	-0.23	0.04	0.05	0.10	-0.03	0.12	0.15
P		1.00	-0.68**	-0.36**	-0.12	0.10	-0.16	-0.13	0.01	0.04
K			1.00	-0.67**	-0.33*	-0.07	-0.39**	-0.09	-0.14	-0.09
Ca				1.00	0.49**	0.08	0.31*	0.02	0.23	0.05
Mg					1.00	0.10	0.15	-0.04	0.20	0.31*
Zn						1.00	0.37**	0.09	0.10	-0.01
Mn							1.00	0.08	0.16	0.13
Fe								1.00	-0.34**	-0.09
Cu									1.00	-0.07
Na										1.00

Significance levels of correlation: * p < 0.05
** p < 0.01

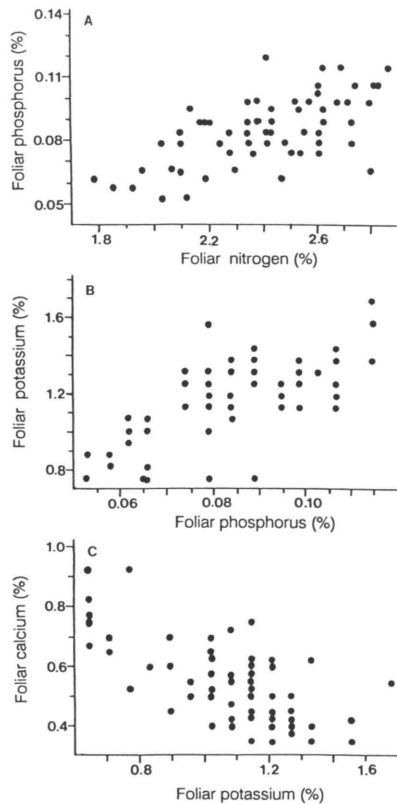


Figure 11. Relationships between foliar nutrient concentrations of 30-month-old *A. mangium*: A) nitrogen and phosphorus ($r = 0.65$); B) phosphorus and potassium ($r = 0.68$); C) potassium and calcium ($r = -0.67$).

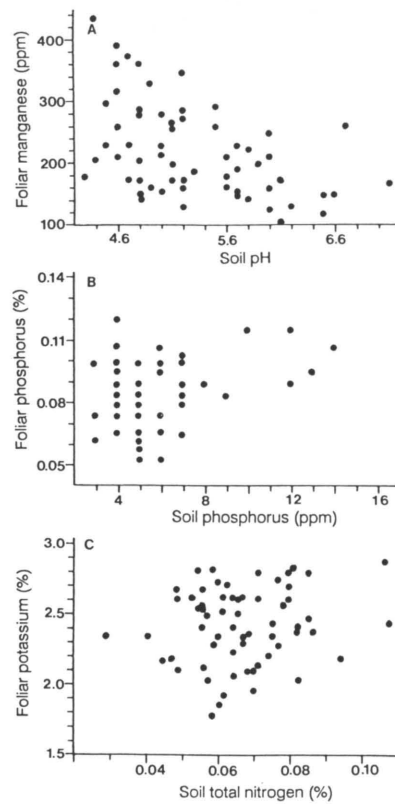


Figure 12. Relationships between foliar and soil nutrient concentrations of 30-month-old *A. mangium*, at Lad Krating Provenance Trial: A) foliar manganese and soil pH ($r = -0.49$); B) foliar phosphorus and soil phosphorus ($r = 0.30$); C) foliar potassium and soil nitrogen ($r = 0.36$).

Table 25. Correlation coefficient (r) between foliage composition of *A. mangium* and soil chemical properties at the Provenance Trials, Chachoengsao.

Soil	Foliage									
	N, %	P, %	K, %	Ca, %	Mg, %	Zn, ppm	Mn, ppm	Fe, ppm	Cu, ppm	Na, ppm
pH	0.10	0.23	0.24*	-0.01	0.05	-0.07	-0.49**	-0.12	0.20	-0.07
N, %	0.15	0.22	0.36**	-0.21	-0.17	0.06	-0.16	-0.29*	-0.02	-0.05
P, ppm	0.14	0.30*	0.24*	-0.00	-0.13	-0.23	-0.25*	0.13	0.00	-0.22
K, ppm	0.01	0.21	0.28*	-0.07	-0.12	-0.26*	-0.35**	0.19	-0.06	-0.24*
Ca, ppm	0.07	0.22	0.15	0.09	0.04	-0.19	-0.45**	-0.06	0.16	-0.04
Mg, ppm	0.10	0.14	0.12	0.05	0.04	-0.19	-0.26*	0.04	0.19	-0.05
Zn, ppm	0.02	-0.08	-0.00	-0.03	-0.06	-0.04	0.20	-0.17	0.04	-0.23
Mn, ppm	0.02	0.11	0.05	-0.04	0.11	0.09	-0.16	-0.21	0.10	0.30*
Fe, ppm	0.02	-0.09	-0.07	-0.05	0.07	0.07	0.18	-0.16	-0.07	-0.01
Cu, ppm	0.07	-0.15	0.02	-0.02	-0.06	-0.21	0.10	-0.17	-0.05	0.02
Na, ppm	-0.13	0.00	-0.06	0.09	-0.08	-0.23	-0.06	0.09	0.07	-0.27*
CEC, meq	0.12	0.18	0.02	0.13	0.07	-0.15	-0.39**	-0.04	0.15	0.08

Significance levels of correlation: * p < 0.05
** p < 0.01

Table 26. Growth parameters of 30-month-old *A. mangium* by provenances at Lad Krating Provenance Trial, Chachoengsao. Values in column followed by the same letter are not significantly different at the 0.05 level of significance using Duncan's New Multiple Range Test.

Provenance No.	Height (m)	DBH (cm)	Crown diameter (m)
12992	8.00 ^{abc}	13.82 ^{ab}	4.94 ^a
13229	8.87 ^{bc}	14.75 ^{ab}	5.70 ^a
13232	7.22 ^a	13.05 ^{ab}	4.76 ^a
13233	6.92 ^a	11.50 ^a	4.39 ^a
13234	7.10 ^a	12.12 ^{ab}	4.90 ^a
13235	7.82 ^{abc}	12.87 ^{ab}	4.30 ^a
13236	7.00 ^a	12.50 ^{ab}	4.55 ^a
13237	7.92 ^{abc}	12.80 ^{ab}	4.51 ^a
13238	7.40 ^{ab}	13.37 ^{ab}	4.60 ^a
13239	7.78 ^{abc}	13.37 ^{ab}	5.05 ^a
13240	7.92 ^{abc}	13.22 ^{ab}	4.96 ^a
13241	8.05 ^{abc}	13.75 ^{ab}	4.59 ^a
13242	8.25 ^{abc}	13.37 ^{ab}	5.12 ^a
13459	9.07 ^c	15.50 ^b	5.05 ^a
13460	8.35 ^{abc}	13.50 ^{ab}	5.06 ^a
13621	7.75 ^{abc}	12.90 ^{ab}	4.86 ^a
Mean	7.84	13.27	4.83
SD	0.62	0.95	0.35
F-value	3.56**	1.94*	0.96 ^{ns}

Significance levels of the F-value: * p < 0.05
** p < 0.01
ns not significant at p < 0.05

Table 27. Correlation coefficients (r) between *A. mangium* growth and foliar nutrient concentrations at Lad Krating Provenance Trial, Chachoengsao.

Nutrient element	Height (m)	DBH (cm)	Crown diameter (m)
Nitrogen, %	-0.00	0.05	0.07
Phosphorus, %	-0.01	0.11	0.26*
Potassium, %	-0.06	0.00	0.05
Calcium, %	0.02	0.03	-0.11
Magnesium, %	0.20	0.18	0.10
Iron, ppm	-0.03	-0.27*	-0.30*
Copper, ppm	-0.00	-0.04	0.10
Manganese, ppm	-0.28*	-0.15	-0.05
Zinc, ppm	-0.11	-0.05	0.18
Sodium, ppm	-0.10	0.06	-0.03

Significance levels of correlation: * p < 0.05

of a species due to genetic variations should be considered. Tree-to-tree variation in response to nutrient levels has been found for several traits by several investigators. Goddard and Hollis (1984) noted that there is a potential for utilizing such variation in practical breeding programmes, if genetic differences in response to nutrient levels are sufficient to affect yield.

The average foliage concentrations of the ten nutrients determined in the present study (cf. Table 21) corresponded well with values given in other studies. More specifically, while nitrogen concentrations of *A. mangium* foliage were higher (1.99–2.74% dry weight) than those reported for pine needles (< 2.0% dry weight) (Prichett and Llewellyn 1966, Le Tacon 1974, Knight 1978, Thaitutsa 1981), they were generally similar to those reported for other tropical broadleaves species. For

5.4. Discussion

Foliage nutrient contents have frequently been shown to exhibit genetic variation (Burley and Wood 1976). The main importance of foliage analysis is in the evaluation of soil nutrient deficiencies. However, in evaluating the effect of soil nutrient deficiency, the possibility of differences in nutrient demand

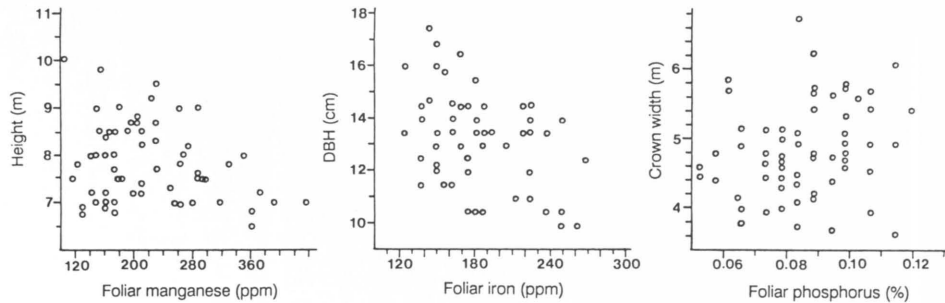


Figure 13. Relationships between foliar nutrient contents and growth of 30-month-old *A. mangium*, at Lad Krating Provenance Trial, Chachoengsao.

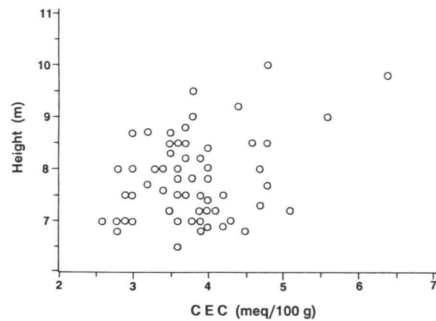


Figure 14. Relationships between soil CEC and height growth ($r = 0.33$) of 30-month-old *A. mangium*, at Lad Krating Provenance Trial, Chachoengsao.

Table 28. Correlation coefficients (r) between *A. mangium* growth parameters and soil nutrient concentrations at Lad Krating Provenance Trial, Chachoengsao.

Nutrient element	Height (m)	DBH (cm)	Crown diameter (m)
pH	0.18	0.14	0.14
Nitrogen, %	0.04	0.13	0.09
Phosphorus, ppm	0.04	0.14	0.04
Potassium, ppm	0.15	0.17	0.07
Calcium, ppm	0.21	0.21	0.15
Magnesium, ppm	0.17	0.04	0.07
Iron, ppm	-0.08	0.00	0.04
Copper, ppm	-0.10	-0.14	-0.17
Manganese, ppm	0.05	0.08	0.19
Zinc, ppm	-0.01	0.05	0.11
Sodium, ppm	0.07	-0.09	-0.08
CEC, meq/100g	0.33**	0.21	0.20

Significance levels of correlation: ** $p < 0.01$

instance, Evans (1979) reported nitrogen concentrations in *Gmelina arborea* ranging from 1.39–2.10% dry weight for different crown positions, while Lamb (1977) reported a range of 0.64–2.04% dry weight in *Eucalyptus deglupta* with an optimum N/P ratio of 10.4. The quotients of N/P, N/K or K/P have been successfully used for diagnostic purposes (Leyton 1958). The optimum N/P, N/K, and K/P ratios for *Pinus nigra* needles ranges are 8.6–9.1, 2.2–2.5 and 3.4–4.0, respectively (Lee 1968). Comparable values from the present study are 28.2, 2.04, and 13.8 for N/P, N/K, and K/P. The distinctly high ratio of N/P and K/P might partly be due to a deficiency of phosphorus. The optimum phosphorus concentration in pine needles specified by Ingestad (1962) is 0.15–0.4% dry weight. The average phosphorus content of *A. mangium* phylloides in the pre-

sent study was 0.086% dry weight (ranging from 0.069 to 0.098%), which compares to a value of 0.31% dry weight reported earlier by Yantasath et al. (1984). The phosphorus content of *A. mangium* foliage in the present study is therefore remarkably low.

Micro-nutrient concentrations generally show considerable variation both among and within species, making comparisons more difficult. However, micro-nutrient concentrations found in the present study (cf. Table 21) corresponded well with those reported for *Eucalyptus camaldulensis* by Bhimaya and Kaul (1966).

Due to the geographic separation of natural populations of *A. mangium*, each provenance may be expected to have adapted to different edaphic conditions whereby each provenance absorbs and utilizes various nutrients differently. The results obtained in

the present study indicate differences among provenances in their ability to accumulate potassium, calcium, and magnesium; but not nitrogen, phosphorus, and micro-nutrients (cf. Table 23). Since soil nutrient conditions in the provenance trial site are considered to be homogeneous (cf. Table 19), the variation in foliar nutrient content among provenances can not reasonably be attributed to site variation. The observed differences in the foliage nutrient composition among the provenances are therefore considered to be due to genetic differences in their ability to absorb and utilize soil nutrients.

Variations in foliar nutrient levels were greater among individual trees than among provenances (cf. Table 23, Fig. 9), indicating that the seeds used in the present study were from different gene pools. As stated by Kleinschmit and Sauer (1976), the nutrient contents of the trees can be considered to be under strong genetic control. If trees with the highest foliage nutrient concentration grow the fastest, mass selection of trees in the promising provenance should be followed up.

Non-significant differences in foliar nitrogen, phosphorus and micro-nutrients among provenances observed in the current investigation have also been found for European black pine (*Pinus nigra*) provenances (Lee 1968) and for tropical pine, *Pinus kesiya*, provenances (Thaiutsa 1981). There have been surprisingly few studies which have examined the genetic variation in foliar nutrient contents of tropical broadleaves species.

The lack of differences among provenances in nitrogen, phosphorus, and micro-nutrient concentrations in *A. mangium* leaves may actually be due to imprecision in determining the foliar nutrient concentrations as concentration are low.

Although no consistent rank among the provenances of *A. mangium* was found for all foliar nutrient contents (cf. Fig. 10), Provenances No. 13236 and No. 13242 (both from Australia) were often ranked first or second, while Provenance No. 13460 (Papua New Guinea) often had the lowest rank for most nutrients. If the generally higher nutrient contents in the foliage for the two provenances (No. 13236 and 13242) are mostly due to superior nutrient uptake potential, these provenances are preferable from the nutritional point of view. On the other hand,

the two mentioned provenances can be considered to be the most nutritionally demanding provenances.

It is unfortunate that information about the soil chemical properties of the site before the provenance trial was established is not available, since tree planting can induce nutrient changes in the soil. Nevertheless, soil nutrient concentrations were remarkably low, particularly for soil phosphorus, despite the regular application of fertilizers every growing season. Available soil phosphorus is mostly controlled by aluminum and iron under low pH conditions (Khanna and Ulrich 1984). Soil pH at the site was low, 4.9–5.8. Perhaps phosphorus fertilization for *A. mangium* should therefore be considered. However, it is difficult to draw general conclusions about soil fertility requirements suitable for *A. mangium* from the present results and there is limited information in the literature.

The lack of correlations between the corresponding nutrients in the soil and in the leaves found in the present study (cf. Table 25) implies that foliage analysis of *A. mangium* can not be used to predict soil fertility. However, soil analysis in the present study was limited to only one soil layer (10–20 cm). Perhaps the analysis of other soil depths would give better results. Nevertheless, a high concentration of roots is generally developed in the topmost 10–20 cm layer (Kramer and Kozlowski 1979).

The ambiguity observed in the relationships between soil and plant nutrients in the current study has also been found by many other investigators. For instance, non-significant correlations between soil and loblolly pine needle contents of phosphorus and calcium were reported by Moschler et al. (1970). Cech et al. (1974) were unable to find any clear correlations between the amounts of 14 elements in soil and those in the needles of Austrian pine. A possible reason pointed out in that study was the immature state of the seedlings, and a similar explanation may be given for the present study since the trees were only 30-month-old.

Several investigators have, however, successfully found close correlations between soil and foliar nutrient concentrations, when trees were grown under nutrient stress conditions. In the present study a slight deficiency in phosphorus, potassium, and sodium might be suspected, but deficiency

symptoms were not observed. The addition of fertilizers presumably kept the foliar nutrient levels within the limits necessary for the health of the trees.

Different growth parameters appear to relate differently to tree nutrition. For example, Hoyle and Mader (1964) found that height growth of red pine correlated strongly with calcium levels, while basal area growth was associated with potassium. In the present study, height growth of *A. mangium* was found to be negatively correlated with foliar manganese; DBH growth was negatively correlated with iron; and crown diameter was positively correlated with phosphorus but negatively correlated with iron (cf. Table 27 and Fig. 13). The relationship of foliar manganese and growth corresponded to the findings of Ingestad and Jakobson (1962). Supporting the results of the current study, Paarlahti et al. (1971) and Veijalainen (1977) reported a negative correlation between the height growth of Scots pine and the content of various micro-nutrients in the needles, except in the poorly growing (unfertilized) stands. Poor relationships between growth performance and foliar nutrient concentrations in nine clones of radiata pine were demonstrated also by Knight (1978).

Similarly, poor correlation coefficients between *A. mangium* growth and soil nutrients were obtained in this study (cf. Table 28). Generally, *A. mangium* is known to be suited to acidic soil. Hu et al. (1983) reported that *A. mangium* grew better in acidic than in neutral or alkaline soils. The optimum soil pH range is from 4 to 6. Possibly because the soil pH obtained in the present study fell within the optimal range for *A. mangium* and the variation in soil pH was relatively

narrow, no correlations between soil pH and growth were detected.

MacCarthy and Davey (1976) reported a significant correlation between height of loblolly pine and available phosphorus in the soil and recommended liming and phosphate fertilization in order to increase height growth. Although there was no significant correlation between tree growth and soil phosphorus in the present study, liming and phosphate fertilization should perhaps be considered, as soil phosphorus is considered deficient in the study area due to low pH conditions.

The data collected in the present study related to young trees at only one site and it is therefore difficult to make generalizations. However, the relative differences among the provenances are potentially important and provide some basic information about the genetic background of *A. mangium*. Despite the selection of healthy trees in the present study, there is little reason to believe that the sample trees have given an unrepresentative picture of the genetic variability regarding foliar nutrient concentrations and nutritional characteristics.

Because of the restricted sampling in the present study, which took no account of possible provenance variation in within-crown distribution of nutrients, and because of the lack of biomass data, the foliar analysis data gave no clear indication of efficiency of nutrient utilization by *A. mangium*. Thus, the question as to whether a provenance with consistently low foliar nutrient concentrations has an inherently lower requirement than other provenances, or has a different distribution pattern within the crown remains unanswered.

6. PHYLLODE ANATOMY AND STOMATAL FREQUENCY

6.1. Introduction

Variation in the physiological processes of trees is determined by both environmental conditions and plant characteristics. Among the major plant factors which play an essential role in physiological processes are leaf area, root-shoot ratio, stomatal size, stomatal frequency, control of stomatal aperture, and leaf anatomy (Kramer 1969). A knowledge of leaf structure is, therefore, a prerequisite to understanding the physiological functioning of trees (cf. Pyykkö 1966).

The stomata normally serve as the principle pathways through which gaseous exchange takes place between the intercellular spaces of the leaf and the surrounding atmosphere. A number of experiments have been carried out in an endeavour to discover the structure, ontogeny, and distribution of stomata (Korn 1972, Johnson and Riding 1981), as well as the role of stomata in regulating plant water status (Holmgren et al. 1965, Siwecki and Kozłowski 1973, Davies et al. 1974) and net photosynthesis (Luukkanen and Kozłowski 1972, Pieters and Zima 1975, Luukkanen 1978).

Basic aspects of stomatal behavior have been reviewed earlier e.g. Meidner and Mansfield (1968), Salisbury and Ross (1978), Esau (1979), and Jarvis and Mansfield (1981). In general, a stoma consists of a pore surrounded by two guard cells which, in most dicotyledons, are kidney-shaped; having localized ledges or projections of thick cell wall or cuticle. The pattern of stomata on leaf surfaces and the structure of stomatal complex appears to be species-specific. The area of stomatal pores usually occupy less than 1% of the total leaf surface (Kramer and Kozłowski 1979), but may exceed 3% when fully open (Kramer 1969). The number and size of stomatal pores varies considerably according to the species of plants, and somewhat even on any one plant.

Besides genetic characters, environmental conditions have been shown to influence the structure, size and frequency of stomata. Plants grown under optimal moisture con-

ditions show lower stomatal frequency than plants grown under stress conditions. A result was reported by Dobrenz et al. (1969) for blue panicgrass: drought tolerant clones had fewer stomata per unit area than drought susceptible clones. Shading has also been shown to reduce stomatal frequency in a number of plants (Brown and Rosenberg 1970). Temperature appears to have relatively little influence on stomatal frequency but it does produce abnormalities in stomatal morphology (Miskin and Rasmusson 1970). However, Wood (1934) suggested that variations in stomatal frequency were connected more closely with genetic and family characters than with environmental conditions.

Stomatal frequency has been reported to be heritable in sorghum and barley (Miskin et al. 1972). As for forest trees, Snyder et al. (1977) demonstrated a fairly high narrow-sense heritability ($h^2 = 0.56$) for stomatal frequency in *Pinus palustris* and Davies et al. (1973) found great variation in the size and frequency of stomata within the genera *Crataegus*, *Fraxinus* and *Quercus*. Significant variation in stomatal size and frequency within a species has been reported for a number of species, for instance, barley (Miskin and Rasmusson 1970), wheat (Teare et al. 1971), and apple (Slack 1974). For forest trees, the within-species variation has been reported in *Populus* (Siwecki and Kozłowski 1973, Pallardy and Kozłowski 1979a), *Juglans nigra* (Carpenter 1974), and *Pinus palustris* (Snyder et al. 1977).

In a single tree, the number of stomata per unit area varies on different leaves. The stomatal frequency is reported to decrease from the top to the bottom of the crown (Doley 1981). The number of stomata per unit area varies considerably also with location on the same leaf. Salisbury (1927) showed that stomatal densities were highest near leaf tips and lowest near the petioles, and increased from the midrib to the leaf margin. The variation in stomatal density is considered to be due to differences in the rate of growth of stomatal mother cells (Reed and Hirano 1931). In contrast, Slavik (1974) re-

ported that dicotyledons, in general, have fewer stomata in the apical part of the leaf blade and that these stomata were usually larger than those in the basal part. The middle part of the leaf blade is thus usually suggested for the study of stomatal size and frequency (Coward 1935).

Despite a number of investigations into the leaf structure and role of stomata in forest trees, adequate studies in tropical trees are still lacking. Cintron (1970) observed a wide range of both stomatal frequency and size in forest trees of Puerto Rico and found that stomata in species of a high altitude mossy forest were generally more numerous and larger than those in a lower montane forest. The larger stomatal pore dimensions were associated with the low water vapor pressure gradients between leaf and air. Pyykkö (1979) described the leaf morphology and anatomy of 22 woody species from the humid tropical forests of Venezuela and concluded that the anatomical similarity of foliage of woody plants of humid tropical forests seemed to be the result of adaptation to the environment. The leaf anatomy and stomatal characteristics of some mangrove species in Thailand has been described by Traiperm (1977) and Riwluang (1986). However, the intra-species variation of leaf structure and stomatal characteristics of tropical hardwood species has so far received much less attention.

6.2. Material and methods

6.2.1. Phyllode anatomy

Mature phyllodes of 30-month-old *A. mangium* trees from each of the 16 provenances grown at the Lad Krating Provenance Trial, Chachoengsao, Central Thailand, were collected randomly from the exposed, middle crown section of the southern side of each sample tree (the same sample trees as in Chapter 5). The details of provenance sources and the study area have been described in Chapter 3 (3.2.1, Table 3). Sections of $5 \times 5 \text{ mm}^2$ were cut from the middle part of the phyllodes, perpendicular to the midrib, and fixed in formalin-acetic acid-ethanol (FAA). The material was then taken back to Seed Laboratory, Department of Silviculture, Kasetsart University.

For observation under light microscope, the FAA-fixed material was washed and dehydrated with a tertiary-butyl alcohol (TBA) series and embedded in paraplast. Serial cross sections by rotary microtome (10 microns thick) were placed on glass slides, stained with safranin-fast green and mounted in Canada balsam (Johansen 1940).

For viewing under a scanning electron microscope (SEM), fresh sections of $5 \times 5 \text{ mm}^2$ were excised from

the mid-portions of the phyllodes and fixed in 3% glutaraldehyde in 0.1 M phosphate buffer. The specimens were mounted on stubs, and coated with carbon and gold. Photographs were taken under scanning electron microscope.

6.2.2. Stomatal size and frequency

Impressions of the phyllode surfaces were taken with Duco cement (containing butyl acetate and acetone), placed on a glass slide and examined at $\times 40$ magnification under a microscope. Stomatal frequency was determined by tallying the number of stomata of five microscope fields, and the number of stomata per mm^2 were calculated. Stomatal size was determined by measuring the length of guard cell of ten stomata in each microscope field with filar micrometer.

Within-leaf variation. Twenty fully expanded phyllodes of one open-pollinated *A. mangium* tree were randomly collected throughout the crown. The phyllodes were then divided into three parts from the tip to the base. Impressions of adaxial and abaxial phyllode surfaces were taken from three positions; apex, middle and base. Stomatal size and frequency were observed as described above. An analysis of variance of stomatal size and frequency was then computed.

Provenance variations. Five mature phyllodes from each sample tree (the same sample trees as in Chapter 4) were collected from the exposed, middle crown section in the southern part of the crown. Stomatal frequencies were determined from the abaxial phyllode surfaces at the middle point of the phyllode.

A two-way analysis of variance and Duncan's New Multiple Range Test were used in evaluating the variations of stomatal frequency and to facilitate a comparison among provenances.

Correlation analyses between abaxial stomatal frequency and growth characteristics data reported in Chapter 3 were performed using both provenance means and individual trees.

6.3. Results

6.3.1. Description of phyllode anatomy

The flattened leaf-like petiole of the *A. mangium* phyllode was sclerophyllic and glabrous. The epidermis was heavily cutinized on both surfaces, and cells were square or rectangular in transection (Fig. 15a, b). The phyllode structure presented an isolateral. The mesophyll consisted of two-layers palisade tissue, densely arranged and filled with abundant chloroplasts. The spongy parenchyma was slightly round and loosely arranged in the middle of the blade. The spongy cells are supposed to play an essential role in water storage. The close arrangement of mesophyll cells only allowed for a limited intercellular space, except in the substomatal chamber beneath the guard cells (Fig. 15b).

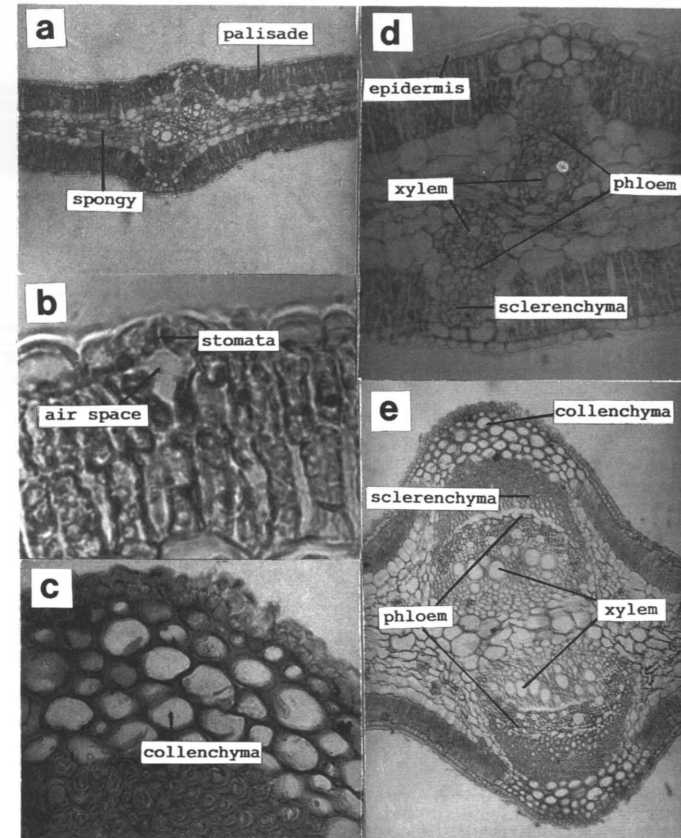


Figure 15. Transections of *A. mangium* phyllode, Provenance No. 13621 (Indonesia) -Overview of phyllode transection, $\times 30$ (a). Stomata and sub-stomatal chamber of abaxial surface, $\times 100$ (b). Collenchyma in midrib, $\times 100$ (c). Small vascular bundles in lateral vein, $\times 50$ (d). Main vascular bundles in the midrib, $\times 30$ (e).

The *A. mangium* phyllode was found to be amphistomatous, with numerous stomata on both surfaces of the phyllode. The stomata were of the paracytic type. Under SEM, the stomata appeared to be level with the epidermis or a little elevated above it. Small secondary reticulate veins lie over the stomatal complexes (Fig. 16a-c). The stomata were observed to be regularly distributed over the whole blade, but only a few stomata occurred along the parallel veins of the phyllode. No contiguous or abnormal stomata were observed in the present study.

The vascular tissues followed the simple parallel vein. Vascular bundles existed in

pairs, one on each side of the phyllode, oriented with xylem towards the center of the organ. Larger bundles were often observed opposite a smaller bundle and alternating at fairly regular intervals on either side of the phyllode. Sclerenchyma was observed always at the phloem end (Fig. 15d).

The large vascular bundles presented in pairs in the midrib region, were generally collateral and consisted of epidermis tissue. The major vascular bundles were surrounded by parenchymatous tissue with few chloroplasts. Beneath the epidermis a multilayer of collenchyma cells developed, which were of the angular or annular collenchyma type

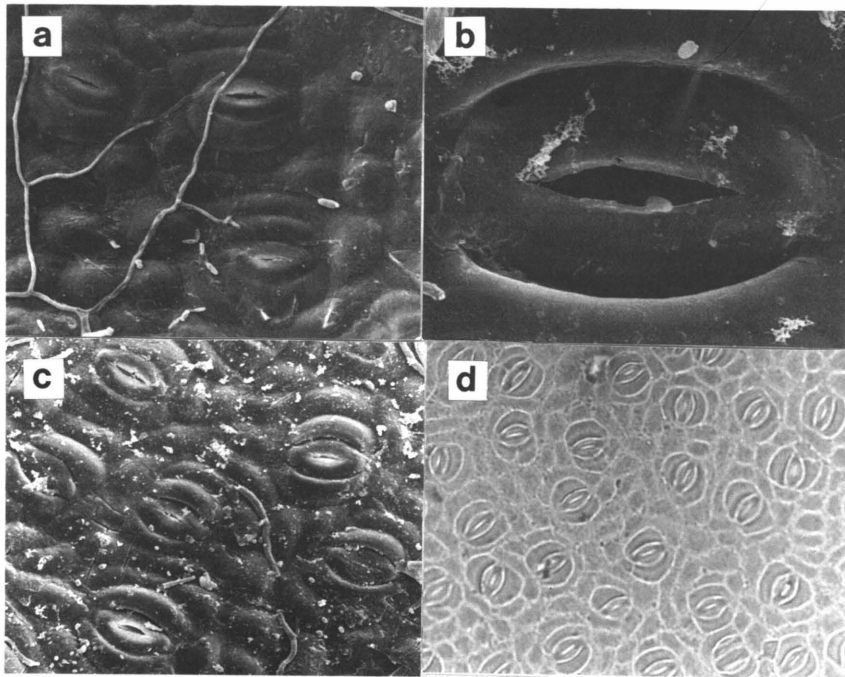


Figure 16. Scanning electron micrographs of *A. mangium* phyllode surfaces showing stomata of Provenance No. 13459 (Papua New Guinea), x660 (a); Provenance No. 13236 (Australia), x4000 (b); Provenance No. 13621 (Piru, Indonesia), x660 (c). Microphotograph of Duco cement impressions of the abaxial phyllode surface of *A. mangium* with stomata reprints, x100 (d).

(Fig. 15c). Abundant sclerenchyma tissue developed in association with the vascular bundles (Fig. 15e).

No anatomical differences in the phyllode and stomata were discernible among provenances of *A. mangium*, at least from the photographs taken in the current study.

6.3.2. Stomatal size and frequency within phyllode

The size and frequency of stomata were quite variable on both surfaces of the phyllode. The average density of stomata varied from 265 to 450 stomata/mm², with an average of 385 and 373 stomata/mm² on the adaxial and abaxial surfaces, respectively. The length of the guard cells varied from 23 to 32 μm, with an average of 26.9 and 26.8 μm on the adaxial and abaxial surfaces, respectively.

Stomatal frequency increased progressively

from the tip to the base consistently on both surfaces of the phyllode. The length of guard cell varied considerably but no systematic differences among locations on the phyllode were found. The mean and standard deviations of stomatal size and frequency over a single phyllode of *A. mangium* are presented in Table 29. Smaller deviations among subsamples taken at the middle of the phyllode were observed. No significant differences were found between the phyllode surfaces, nor among positions on the phyllode. The stomatal frequency and length of guard cell were not related.

6.3.3. Variation of stomatal frequency among provenances

Mean stomatal frequencies of the abaxial epidermis for all provenances of *A. mangium* are given in Table 30. The results indicate

Table 29. Mean and standard deviation of stomatal size and frequency on the adaxial and abaxial epidermal surfaces at three different positions on the phyllode of *A. mangium*.

Position	Stomatal frequency/mm ²		Stomatal length (μm)	
	Adaxial	Abaxial	Adaxial	Abaxial
Apex	324.90±49.84	332.53±51.44	26.79±0.32	26.73±0.31
Middle	372.05±33.40	380.92±34.80	26.67±0.30	26.75±0.32
Base	458.03±46.49	404.62±42.32	27.17±0.17	26.83±0.33
Average	384.99±67.50	372.69±36.74	26.88±0.26	26.77±0.53

Table 30. Average abaxial stomatal frequency of *A. mangium* phyllodes from 16 provenances. Values in column followed by the same letter are not significantly different at the 0.05 level of significance using Duncan's New Multiple Range Test.

Provenance No.	Stomatal frequency	Standard deviation
12992	378.77 ^b	21.68
13229	375.90 ^b	22.17
13232	393.98 ^d	30.74
13233	397.44 ^d	39.69
13234	420.94 ^c	34.93
13235	375.00 ^b	22.66
13236	401.35 ^d	38.59
13237	375.00 ^b	32.96
13238	389.91 ^{cd}	28.85
13239	392.77 ^{cd}	28.00
13240	375.60 ^b	31.52
13241	383.74 ^c	32.85
13242	390.51 ^{cd}	18.52
13459	353.46 ^a	11.73
13460	383.28 ^{bc}	36.43
13621	401.05 ^d	20.64
Average	386.79	14.84

Table 31. Correlation coefficients between stomatal frequency and some growth characteristics of 30-month-old *A. mangium*.

Growth characteristic	Stomatal frequency	
	Individual trees (126 df)	Provenance means (14 df)
Height	-0.325**	-0.780**
DBH	-0.108 ^{ns}	-0.742**
Crown width	-0.176 ^{ns}	-0.146 ^{ns}

Significance levels of correlation: ** p < 0.01
ns not significant at p < 0.05

large variation in the numbers of stomata among provenances. Stomatal frequency varies from 353 to 421 stomata/mm², with an average of 387 stomata/mm². The provenance with the highest stomatal frequency was Provenance No. 13234 (Australia), while the provenance with the lowest stomatal

frequency was Provenance No. 13459 (Papua New Guinea). Significant differences in stomatal frequency among provenances (P < 0.01) as well as among trees within provenances (P < 0.05) were detected. Tests of mean differences by Duncan's New Multiple Range Test identified five different groups in the number of stomata of *A. mangium* phyllode. However, these groups were not related to the latitude of the seed sources. On the other hand, no clinal variations in stomatal density were observed.

6.3.4. Stomatal frequency as related to tree growth

Relationships among the observed stomatal frequency and tree growth characteristics (i.e. height, DBH, and crown diameter) as determined in Chapter 3 are reported in Table 31. Negative correlations were obtained in all cases. The correlation coefficients for the provenance mean data gave higher values than for all trees together in cases of height and DBH. High significant correlations (p < 0.01) were found between abaxial stomatal frequency and height growth (r = -0.78), as well as diameter at breast height (r = -0.74), when provenance means are considered. When all the trees are treated together, only height growth was found to correlate (p < 0.01) with the stomatal frequency (r = -0.32). There was no statistical significant correlation between stomatal frequency and crown diameter either by using provenance means or all the tree data.

6.4. Discussion

The study of laterally flattened phyllodes of some certain species of *Acacia* by Boke

(1940) revealed fundamental differences in development, including the dominance of the adaxial meristem in producing the flattened organ. Boke concluded that the phyllode of *Acacia* sp. was homologous to the petiole and rachis of a pinnately compound leaf. This is in contrast to phyllodes of *Oxalis* sp., in which the petiole of a palmately compound leaf loses its leaflets in development (cf. Metcalfe and Chalk 1979).

It has been noted that the foliar organs with reduced laminae or without laminae occur particularly in desert plants, and acacia phyllodes are generally considered to be a xeromorphic feature (Metcalfe 1983). In contrast, *A. mangium* is naturally a humid tropical species which requires highly rainfall. Bentham (1875) has suggested, however, that there is no relationship between environment and the appearance of the phyllode structure, since native stands of phyllodineous and non-phyllodineous species occur together in the same regions.

A. mangium phyllode is a simple structure. The phyllode is glabrous, without hairs or trichomes. The non-hairiness of plants is a common characteristic of species growing in shady and wet habitats (cf. Pyykkö 1966). *A. mangium* represents a minority of the angiosperms that are completely devoid of trichomes. Boke (1940) reported some curious epidermal structures at the bases of trichomes, which consisted of deeply stained cells, in some species of *Acacia*. However, such structures were not observed in *A. mangium* in the present study.

Although phyllodes are normally associated with xeromorphy, the stomata of *A. mangium* are of the paracytic type, which is a typical mesomorphic characteristic (cf. Fig. 16a-c), and reported by Metcalfe and Chalk (1979) as being the common type in species of the Mimosaceae family.

The stomatal size and frequency observed for *A. mangium* in the present study (cf. Table 29) are within the ranges given for other species. According to the Wilkinson stomatal size classification, *A. mangium* can be classified as intermediate in size ($15 < \bar{x} < 38 \mu\text{m}$). In general, stomatal size and frequency are inversely correlated (Miskin and Rasmusson 1970, Davies and Kozlowski 1974). Species with fewer stomata per unit of leaf surface tend to have larger stomata. However, in the present study, no correlation between stomatal size and frequency was

found. This might be partly due to the large variation in recorded stomatal frequency, but a similar result was previously demonstrated by Teare et al. (1971) in wheat.

Many investigators have reported significant differences between adaxial and abaxial stomatal density of amphistomatous leaves. For instance, Miskin and Rasmusson (1970) demonstrated more numerous stomata on the abaxial surface of the leaves of barley. Teare et al. (1971) reported a higher number of stomata on the adaxial surface of the leaves of wheat. In the present study, the average stomatal frequency was slightly higher on the adaxial surface, but the difference was not statistically significant.

Theoretically, stomatal frequency varies appreciably on the same leaf, with the greatest density at the tip and the lowest towards the base (Salisbury 1927). In contrast, the number of stomata observed in the current study increased from the tip towards the base of the phyllode (cf. Table 29). A similar result has been reported for wheat by Teare et al. (1971). Reed and Hirano (1931) demonstrated the average density of stomata was least at the base, greatest at the middle and intermediate at the tip in citrus leaves.

Investigations about the effect of stomatal size and frequency on physiological processes, as well as on the productivity of plants, might be more meaningful if the extent of intra-species variation in frequency and size of stomata were known. If certain stomatal traits are beneficial, they should be selected for in any tree improvement programme. Genetic variability in stomatal size and frequency has been discussed by a number of investigators (e.g. Miskin and Rasmusson 1970, Teare et al. 1971, Miskin et al. 1972, Siwecki and Kozlowski 1973, Carpenter 1974, Snyder et al. 1977, Pallardy and Kozlowski 1979a). However, variations between different seed sources have received much less attention. Although stomatal size and frequency are often correlated, many investigators have considered stomatal size to be too variable to be of diagnostic value. Dunn et al. (1965), for example, studied the imprints of stomata of miscellaneous dicotyledons and concluded that stomatal size was an unreliable character. However, many authors have noted that stomatal size is more reliable if the full size range is determined (cf. Wilkinson 1979).

Since the stomatal frequency of *A. man-*

gium showed larger variation than stomatal size, only the number of stomata is used as a diagnostic character among different provenances in the present study. The data obtained revealed a statistically significantly difference in the stomatal frequency both among and within the provenances of *A. mangium* (cf. Tables 30). Therefore, if measurements of photosynthesis and leaf resistances among seed origins are to be made, many trees from the same sources would have to be sampled in order to average out the variation in stomatal density.

Since stomatal activity is one of the factors controlling both photosynthetic and transpiration rates, the differences in stomatal frequency observed among *A. mangium* provenances could affect physiological processes, and thus might be a characteristic worthy of studying in tree growth or productivity improvement programmes. The relationships

between stomatal characters and growth and productivity have periodically been attempted with varying success. In the present study, height and diameter growth of *A. mangium* were found to be strongly negatively correlated with stomatal frequency (cf. Table 31). Heichel (1971) also reported a negative correlation between the yield of two maize varieties and stomatal frequency. Nevertheless, a positive correlation has been demonstrated in poplar clones by Ceulemans et al. (1978), while Teare et al. (1971) and Pallardy and Kozlowski (1979a) found no correlation between stomatal frequency and yield of *Populus*.

Further investigations should be aimed at examining the role of stomatal behaviour in controlling the physiological processes of trees under different environmental conditions, with regard to tree growth and the magnitude of genetic differences.

7. PROVENANCE VARIATION IN TRANSPIRATION AND STOMATAL CONDUCTANCE UNDER WATER STRESS

7.1. Introduction

Transpiration can be regarded as the dominant process in the water relations of plants, since the energy gradient caused by the transpiration of water provides the energy for the movement of water through plants (Kramer and Kozłowski 1979, Kramer 1983). The transpiration rate is controlled by stomatal activity and the physical factors that control evaporation. The physiological process and the factors affecting transpiration in trees have been discussed in detail by several investigators (Kozłowski 1968, 1982; Lange et al. 1976, Kramer and Kozłowski 1979, Turner and Kramer 1980, Jarvis and Mansfield 1981, Lange et al. 1982, Kramer 1983, Larcher 1983).

One of the most important external factors affecting the transpiration rate is the availability of soil water (Hsiao 1973). Numerous investigations concerning the water relations of plants under conditions of soil water stress have been carried out (Lopushinsky and Klock 1974, Unterscheutz et al. 1974, Davies and Kozłowski 1975, Luukkanen et al. 1975, Kelliher et al. 1980, Örlander and Due 1986, Abrams 1988). When plant water stress develops, the transpiration rate is at first mainly controlled by the stomatal resistance (Hsiao 1973). Hansen (1971) also noted that stomata are highly responsible for controlling transpiration during water stress. The increased resistance to transpiration is mainly caused by a reduction in stomatal aperture. Siwecki and Kozłowski (1973) in their studies on poplar clones, found that genetically controlled variations in transpiration were more related to differences in the rate of stomatal closure than to stomatal morphology. The reduction in stomatal aperture of leaves is, however, affected both by the internal plant water balance, and by external factors (Meidner and Mansfield 1968, Kramer 1983). Since the water loss from plants is primarily controlled by stomatal resistance, measurements of stomatal resistance also offer a

means for monitoring the genetic adaptation to drought.

The improvement of porometers during the past decade has facilitated the study of transpiration and stomatal responses to environmental conditions. Porometers measure the approximate rate of diffusion of water vapor from leaves which can be converted into leaf resistance or its reciprocal, conductance. Measurement by porometers gives the value of total leaf resistance, but if cuticular transpiration is very small it is a reasonable approximation of the stomatal resistance. The principles of porometer measurements have been discussed in detail by Slavík (1974). Nonetheless, concrete relationships between stomatal resistance, transpiration rates and plant water status are not well defined, especially under stress conditions (Turner et al. 1985, Örlander and Due 1986).

During the past two decades, water potential has been widely accepted as the fundamental measure of plant water status (cf. Hsiao 1973). A number of techniques have been developed to study the water potential in plants. Various methods of measuring water relations in plants are discussed in detail by Slavík (1974). Of the techniques, the pressure chamber method, popularized by Scholander et al. (1965) for measuring tissue water potentials, is considered to be a reliable method for characterizing plant water status (Barrs 1968). Studies on plant water potential measured using the pressure chamber techniques have been reported by a number of investigators (Beadle et al. 1979, Pallardy and Kozłowski 1979b, Cleary and Zaerr 1980, and Örlander and Due 1986). The equipment is simple and convenient, especially for the field measurement. A pressure chamber developed in Finland has been successfully used earlier in field studies on tropical trees (Kaarakka et al. 1983).

The relationship between stomatal conductance and xylem water potential has been

characterized for many species, e.g. *Beta vulgaris* (Hansen 1971), *Picea sitchensis* (Beadle et al. 1979), *Populus* sp. (Pallardy and Kozłowski 1979b). The sensitivity of stomata to decreased leaf water potential varies among species and is influenced by the age and growth conditions of the plant (Davies 1977). In both field and laboratory grown plants, it has been shown that the stomata do not respond to decreasing leaf water potentials until a threshold value is reached, but beyond that value, the closing of the stomata occurs rapidly (Ludlow 1980).

Water relations in plants, as indicated by transpiration rate, leaf conductance or water potential, are known to differ among genotypes (Hellkvist 1970, Siwecki and Kozłowski 1973, Abrams 1988). Plants belonging to the same species but originating from different habitats can exhibit very different water potentials (Davies et al. 1981). A study by Ferrell and Woodard (1966) revealed considerable genetic variability in drought resistance in Douglas-fir over its natural range. In their study on this species, Zavitkovski and Ferrell (1970) reported that the transpiration rate decreased more rapidly in populations adapted to dry sites as compared to those originating from a moist environment, when studied simultaneously during decreasing soil moisture.

The most critical period in respect to drought for newly planted tree seedlings occurs in the year of establishment. The ability of seedlings to avoid severe desiccation during periods of increasing soil moisture stress is critical for seedlings survival (Kauppi 1984). It is therefore especially important to understand the water relations of species used in plantation forestry. Identification of intraspecific differences in drought tolerance would permit more effective matching of genotypes with environments and thereby increase the productivity of plantation forestry.

7.2. Material and methods

7.2.1. Plant material

A. mangium seedlings were raised at the University Forestry Field Station in Hyttälä, Finland (latitude 61°51'N, longitude 24°20'E) starting in September 1984. Six provenances (No. 13229, No. 13236, No. 13240, No. 13459, No. 13460 and No. 13621) representing the range of *A. mangium* were selected for the present study. The location and altitude of the provenances used have been

described in Chapter 3 (Table 3). The seeds were germinated following hot water pretreatment, and the seedlings transplanted into plastic pots, each containing 300 g (dry weight) of fertilized commercial garden peat (FINNPEAT ST-400 B6), and grown in a glass house. The ambient temperature was 25 to 30°C during the day and around 15°C at night. Relative humidity varied between 70 and 90%. HQI lamps were used to maintain the photoperiod at 13 h. The seedlings were watered regularly and supplied weekly with nutrients in the form of 0.1% Superex 5 nutrient solution.

7.2.2. Experimental procedure

In July 1985, eight healthy seedlings of average size were selected from among each provenance batch. The pots were saturated by watering from below and then drained to remove the free, gravitational water. Each pot was then enclosed in a polythene bag which was tied around the stem base of the seedling to prevent direct loss of water from the soil surface. The potted seedlings were weighed immediately, and the initial weight was recorded. Four of the eight sample seedlings of each provenance were maintained at near field capacity (about 700% of peat dry weight) by watering daily using a hypodermic syringe, whereas the remaining four sample seedlings were subjected to slow drying. In the pots which were allowed to dry, the substrate was maintained at four successively drier levels of soil moisture content, including >400%, 300–400%, 200–300% and less than 200% moisture, calculated from peat dry weight (dw) (Fig. 17). The stressed seedlings were kept at each level for a few days and water was given just to maintain the soil moisture content at the specific level. The amount of water available to plants (substrate water potential) was

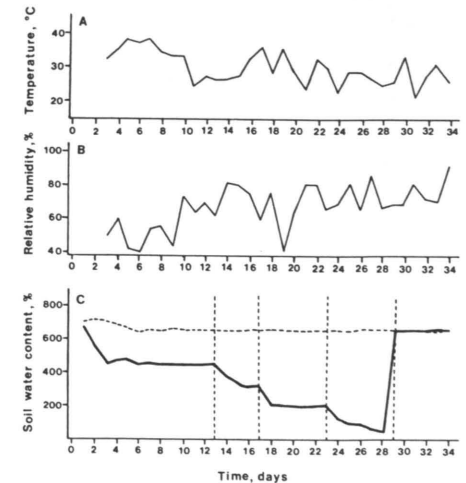


Figure 17. Air temperature (A), air relative humidity (B) at 14:00 h; and soil water content of peat in control (-----) and stressed (——) pots (C), during the experiment. Vertical dashed lines show the time at which each soil water level was applied.

estimated using a pressure membrane apparatus. These measurements indicated that the water content (calculated from peat dry weight) at the field capacity (-0.015 MPa) was 741 %, and at permanent wilting point (-1.5 MPa) was 69 %. These values are similar to those reported for garden peat by Puustjärvi (see Vaapauro 1985).

When the transpiration rates of stressed plants declined to near zero, the amount of soil water was again increased to the initial high level (Fig. 17).

7.2.3. Measurement procedure

During the period 6 July to 9 August 1985, transpiration losses were followed by weighing the potted

seedlings twice a day, at 07:00 and 19:00 h (GMT+2 h). Simultaneously, total leaf conductances of the experimental seedlings were determined at 07:00 and 14:00 h with a diffusion porometer (Delta-T MkII) on fully expanded phyllodes. Leaf conductance (g) rather than leaf resistance (r) was used in the subsequent analysis, since it was more linearly related to transpiration rate. Measurements were taken on both adaxial (g_{ad}) and abaxial (g_{ab}) surfaces of the same phyllodes throughout the study period. Air temperature, and air relative humidity were recorded during the measurements (Fig. 17).

At the end of each soil moisture stress treatment, before a new level of stress was imposed, one fully-developed phyllode was randomly selected from each seedling, and the leaf water potential was measured

with a pressure chamber, using the technique developed by Scholander et al. (1965). Owing to the limited number of phyllodes, only one plant from each provenance and each treatment was used on each occasion. At the end of the drought treatment, leaf water potential measurements were made on all seedlings.

7.2.4. Statistical calculation

The mean, standard deviation, and standard error of the mean of each characteristic were calculated for each provenance. The significance of differences in transpiration among provenances subjected to drought was tested by a one-way analysis of variance.

The significance level of differences among provenances means were determined with Duncan's New Multiple Range Test. Relationships between various characteristics were analyzed using regression analysis. All the computation were done using the SAS programme (SAS 1985).

7.3. Results

7.3.1. Transpiration

The transpiration values presented in the present experiment are based on single phyllode surface areas. The daily means of transpiration rates in each provenance, as measured gravimetrically for the 12-h period, during the experiment, are depicted in Fig. 18. The actual values of transpiration fluctuated daily depending on environmental

factors. On warm and sunny days when the air temperature reached 38°C, the transpiration rates of well-watered seedlings ranged from 11 to 19 mg cm⁻² h⁻¹. On cloudy days (at about 21°C), the transpiration rates dropped to only 1.2 to 3.3 mg cm⁻² h⁻¹. During the night (19:00-7:00 h) the transpiration rates were relatively low and constant, approximately 0.2-2.0 mg cm⁻² h⁻¹.

The daily transpiration rates of well-watered seedlings varied significantly ($p < 0.05$) among provenances studied (Table 32). The highest rates (7.2 to 15.2 mg cm⁻² h⁻¹ for a 12-h period) were observed in Provenance No. 13621 (Indonesia) consistently, and the lowest ones (4.7 to 10.5 mg cm⁻² h⁻¹) in No. 13229 (Australia).

The transpiration rate decreased gradually concomitantly with the depletion of soil moisture (Fig. 18, 19). The transpiration rates of stressed and well-watered plants did not, however, differ significantly until the third stage of stress, at which the soil moisture content decreased to 300 %. When, at the beginning of the last stage of stress, the soil moisture content was approximately 200 %, the transpiration rate of stressed seedlings dropped to about 50 % of the well watered ones. The transpiration rate decreased more rapidly when the soil moisture was below 200 %. At the end of the drought period (at ap-

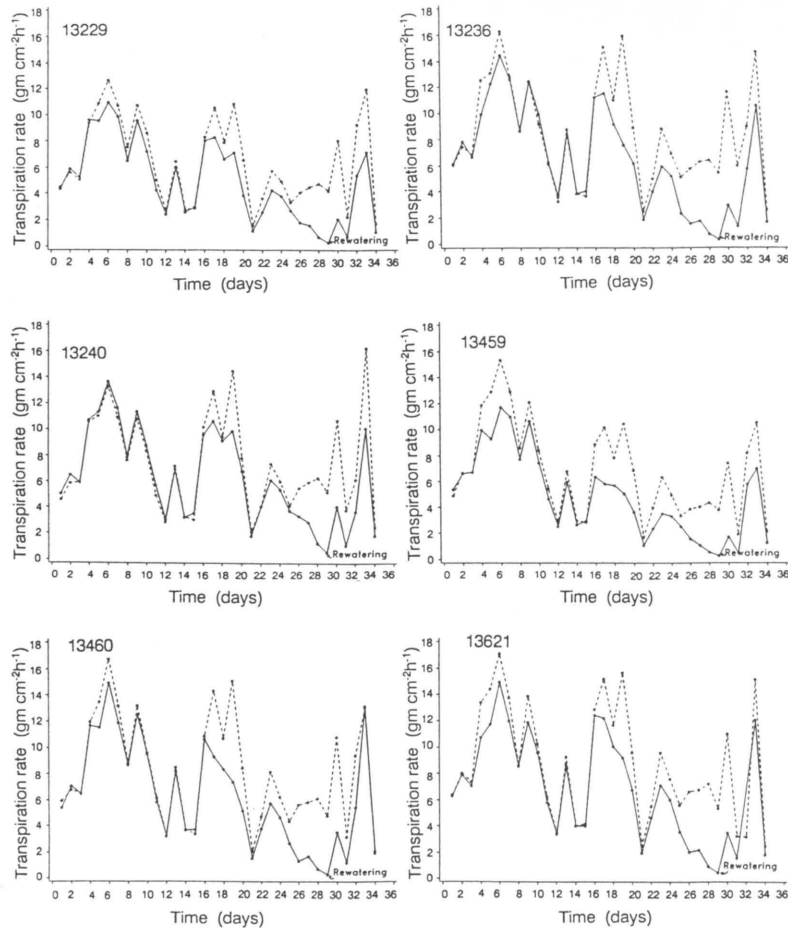


Figure 18. Daily means of transpiration rates (07:00-19:00 h) in control (dash line) and stressed (solid line) seedlings for each of the six provenances.

Table 32. Transpiration rate (mg cm⁻² h⁻¹, calculated from projected single phyllode area) and its standard deviation for each provenance under control and stress conditions. Values in columns followed by the same letter are not significantly different at 0.05 level of significance in Duncan's New Multiple Range Test.

Provenance No.	Days of stress treatment									
	3		13		17		23		28	
	Control	Stress	Control	Stress	Control	Stress	Control	Stress	Control	Stress
13229	5.03 ^a ±1.31	5.23 ^a ±1.50	6.47 ^a ±1.02	6.01 ^a ±1.67	10.53 ^a ±1.86	8.27 ^a ±3.46	5.75 ^a ±1.08	4.22 ^a ±1.27	4.72 ^{ab} ±0.90	0.70 ^{ab} ±0.32
13236	6.82 ^{ab} ±0.73	6.64 ^a ±0.79	8.34 ^{bc} ±0.66	8.69 ^b ±2.03	15.03 ^b ±2.00	11.49 ^a ±5.03	8.80 ^{cd} ±1.02	5.93 ^a ±1.69	6.40 ^{bc} ±0.86	0.73 ^{ab} ±0.21
13240	5.92 ^{ab} ±1.63	5.87 ^a ±1.19	7.21 ^{ab} ±0.59	6.96 ^{ab} ±2.03	12.88 ^{ab} ±0.95	10.63 ^a ±5.11	7.39 ^{abc} ±1.07	6.10 ^a ±3.30	6.28 ^{abc} ±1.08	1.27 ^a ±0.86
13459	6.72 ^{ab} ±1.31	6.73 ^a ±1.08	6.80 ^a ±0.98	5.95 ^a ±0.98	10.17 ^a ±1.60	5.80 ^a ±1.69	6.34 ^{ab} ±0.93	3.50 ^a ±1.09	4.34 ^a ±0.60	0.55 ^a ±0.07
13460	6.43 ^{ab} ±0.87	6.46 ^a ±1.07	8.50 ^{bc} ±0.63	8.21 ^{ab} ±0.81	14.25 ^b ±1.65	9.29 ^a ±2.93	8.15 ^{bcd} ±0.47	5.75 ^a ±1.28	6.11 ^{abc} ±0.95	0.72 ^{ab} ±0.15
13621	7.38 ^b ±0.42	6.61 ^a ±1.05	9.28 ^c ±0.97	8.08 ^{ab} ±1.36	15.18 ^b ±3.45	10.74 ^a ±3.74	9.62 ^d ±2.49	6.62 ^a ±2.73	7.24 ^c ±2.29	1.01 ^{ab} ±0.30
Mean	6.38	6.26	7.77	7.32	13.00	9.37	7.67	5.35	5.85	0.83
CV, %	17.57	18.13	10.68	21.25	15.88	41.06	17.35	38.63	21.24	49.53
F	2.13 ^{ns}	1.09 ^{ns}	7.07*	2.31 ^{ns}	4.60**	1.18 ^{ns}	4.91**	1.39 ^{ns}	3.14*	1.65 ^{ns}

Significance levels of the F-test: * $p < 0.05$
 ** $p < 0.01$
 ns not significant at $p < 0.05$

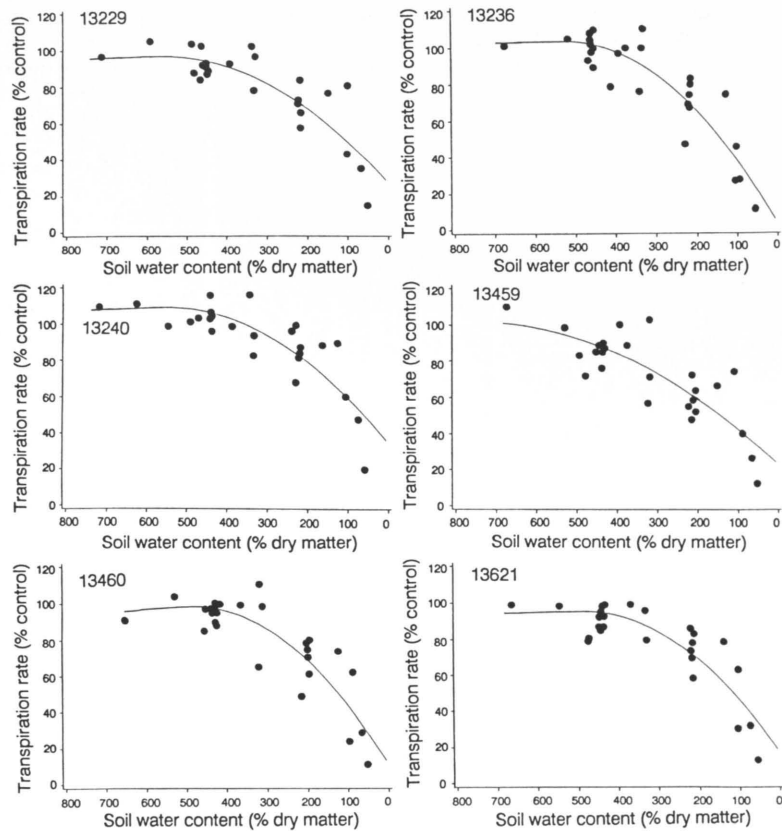


Figure 19. Relative daily transpiration rates as a function of soil water content in seedlings representing six provenances. The curves are hand-fitted. Dots represent individual seedlings.

proximately 60 % soil moisture), the transpiration rates of stressed seedlings were only about 10–20 % of the control values.

Provenance No. 13240 (Australia) showed the highest and No. 13236 (Australia) and 13460 (Papua New Guinea) the lowest relative transpiration rates under stress conditions. Transpiration did not cease completely at the end of the experiment, possibly indicating that the stomata were not completely closed even if the seedlings showed signs of wilting.

When the seedlings were subjected to drought, the responses of the transpiration rate to soil moisture differed among provenances (Fig. 19, Table 32). For instance, in Provenance No. 13459 the transpiration rate

started decreasing as soon as the soil moisture content was lowered from the saturation level, and reached not more than 80 % of the control value at 400 % soil moisture. Stressed seedlings of Provenance No. 13240 (Australia) transpired at a rate 80 % of that of control seedlings, even when the soil moisture was less than 300 %. In the latter provenance, the transpiration rates in stressed and unstressed seedlings did not differ significantly at soil moisture contents above 200 %.

When the stressed seedlings were re-watered after the soil moisture had decreased to approximately 60 % of dry weight (representing the permanent wilting point of the peat used in the present study), the transpi-

ration rates started to increase gradually. Four days after rewatering, Provenance No. 13460 (Papua New Guinea) showed nearly complete recovery of transpiration rate (93 % of control). Provenance No. 13459 (Papua New Guinea) exhibited the poorest recovery (59 % of control), whereas transpiration rate in the remaining provenances recovered to about 70 % of the control in four days.

7.3.2. Leaf conductance

The trend in mean daily leaf conductance (measured at 14:00 h each day) over the

study period was similar to the transpiration rate (Fig. 20). In the morning (07:00 h), leaf conductance was generally higher than in the afternoon (14:00 h) (Table 33). Since the adaxial and abaxial leaf conductances in *A. mangium* did not differ much, the following results only refer to one (abaxial) surface.

In the case of the well-watered seedlings, leaf conductance ranged from 0.05 to 1.0 cm s^{-1} . In the seedlings subjected to drought, leaf conductance declined approximately in the same way as did the transpiration rate (Fig. 21). The effect of soil moisture depletion on leaf conductance was evident when the soil moisture content was below

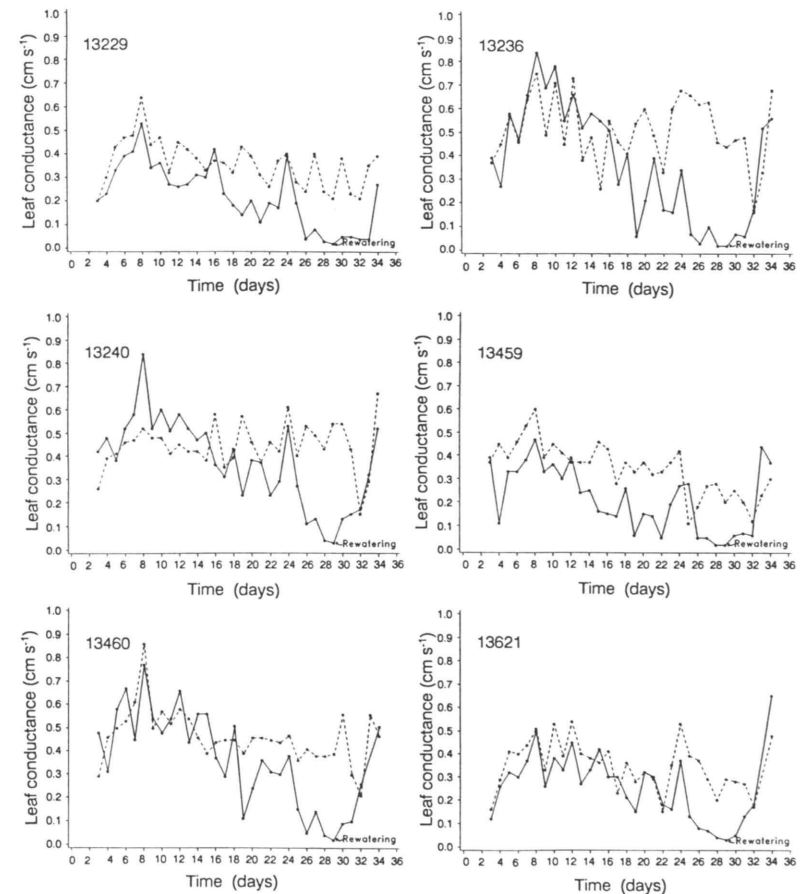


Figure 20. Leaf conductance (at 14:00 h) in control (dash line) and stressed (solid line) seedlings for each of the six provenances.

Table 33. Abaxial leaf conductance (cm s^{-1}) and its standard deviation for each provenance under control and stress conditions. Values in columns followed by the same letter are not significantly different at 0.05 level of significance in Duncan's New Multiple Range test. Morning values were measured at 7:00 and afternoon values at 14:00 h.

Provenance No.	Days of stress treatment																																																																																																																																					
	3			13			17			23			28																																																																																																																									
	Morning Control	Morning Stress	Afternoon Control	Morning Control	Morning Stress	Afternoon Control	Morning Control	Morning Stress	Afternoon Control	Morning Control	Morning Stress	Afternoon Control	Morning Control	Morning Stress	Afternoon Control	Morning Control	Morning Stress	Afternoon Control	Morning Control	Morning Stress	Afternoon Control	Morning Control	Morning Stress	Afternoon Control	Morning Control	Morning Stress	Afternoon Control	Morning Control	Morning Stress	Afternoon Control	Morning Control	Morning Stress	Afternoon Control	Morning Control	Morning Stress	Afternoon Control	Morning Control	Morning Stress	Afternoon Control																																																																																															
13229	0.46 ^{ab} ±0.12	0.30 ^a ±0.19	0.20 ^{ab} ±0.04	0.52 ^{ab} ±0.11	0.41 ^a ±0.25	0.27 ^a ±0.08	0.48 ^{ab} ±0.09	0.36 ^a ±0.10	0.36 ^a ±0.18	0.23 ^a ±0.22	0.37 ^a ±0.05	0.17 ^a ±0.10	0.24 ^{ab} ±0.11	0.03 ^a ±0.01	13236	0.71 ^b ±0.13	0.67 ^b ±0.12	0.37 ^a ±0.20	0.72 ^b ±0.06	0.77 ^b ±0.07	0.52 ^b ±0.25	0.67 ^b ±0.15	0.46 ^a ±0.15	0.28 ^a ±0.25	0.60 ^a ±0.13	0.16 ^a ±0.09	0.46 ^b ±0.17	0.02 ^a ±0.01	13240	0.40 ^a ±0.11	0.47 ^{ab} ±0.15	0.26 ^a ±0.23	0.57 ^{ab} ±0.11	0.57 ^{ab} ±0.06	0.42 ^a ±0.10	0.59 ^{ab} ±0.07	0.57 ^{bc} ±0.11	0.35 ^a ±0.17	0.31 ^a ±0.33	0.42 ^a ±0.11	0.29 ^a ±0.11	0.43 ^{ab} ±0.18	0.04 ^a ±0.02	13459	0.28 ^a ±0.17	0.50 ^{ab} ±0.09	0.37 ^a ±0.24	0.43 ^a ±0.18	0.50 ^a ±0.12	0.37 ^a ±0.10	0.40 ^a ±0.14	0.35 ^a ±0.14	0.28 ^a ±0.35	0.14 ^a ±0.13	0.37 ^a ±0.17	0.19 ^a ±0.10	0.28 ^{ab} ±0.80	0.02 ^a ±0.00	13460	0.44 ^{ab} ±0.28	0.51 ^{ab} ±0.11	0.29 ^a ±0.14	0.60 ^{ab} ±0.12	0.61 ^{ab} ±0.08	0.44 ^{ab} ±0.15	0.55 ^{ab} ±0.13	0.65 ^c ±0.07	0.45 ^a ±0.17	0.29 ^a ±0.30	0.44 ^a ±0.16	0.30 ^a ±0.19	0.38 ^{ab} ±0.16	0.04 ^a ±0.02	13621	0.42 ^{ab} ±0.25	0.36 ^a ±0.20	0.16 ^a ±0.04	0.49 ^{ab} ±0.21	0.48 ^a ±0.28	0.40 ^a ±0.30	0.63 ^{ab} ±0.25	0.40 ^{ab} ±0.20	0.23 ^a ±0.11	0.31 ^a ±0.12	0.35 ^a ±0.25	0.16 ^a ±0.12	0.20 ^a ±0.17	0.03 ^a ±0.01	Mean	0.45	0.47	0.27	0.33	0.56	0.42	0.55	0.50	0.36	0.26	0.43	0.21	0.33	0.03	CV, %	42.02	31.71	78.51	55.17	25.65	30.34	44.15	25.20	25.46	57.23	91.63	36.73	58.08	45.37	43.76	F	2.24 ^{ns}	3.09 ^{ns}	0.61 ^{ns}	2.29 ^{ns}	1.98 ^{ns}	2.23 ^{ns}	1.98 ^{ns}	5.29 ^{**}	0.79 ^{ns}	0.25 ^{ns}	1.41 ^{ns}	1.17 ^{ns}	2.07 ^{ns}	1.22 ^{ns}

Significance levels of the F-test:

* $p < 0.05$
 ** $p < 0.01$
 ns not significant at $p < 0.05$

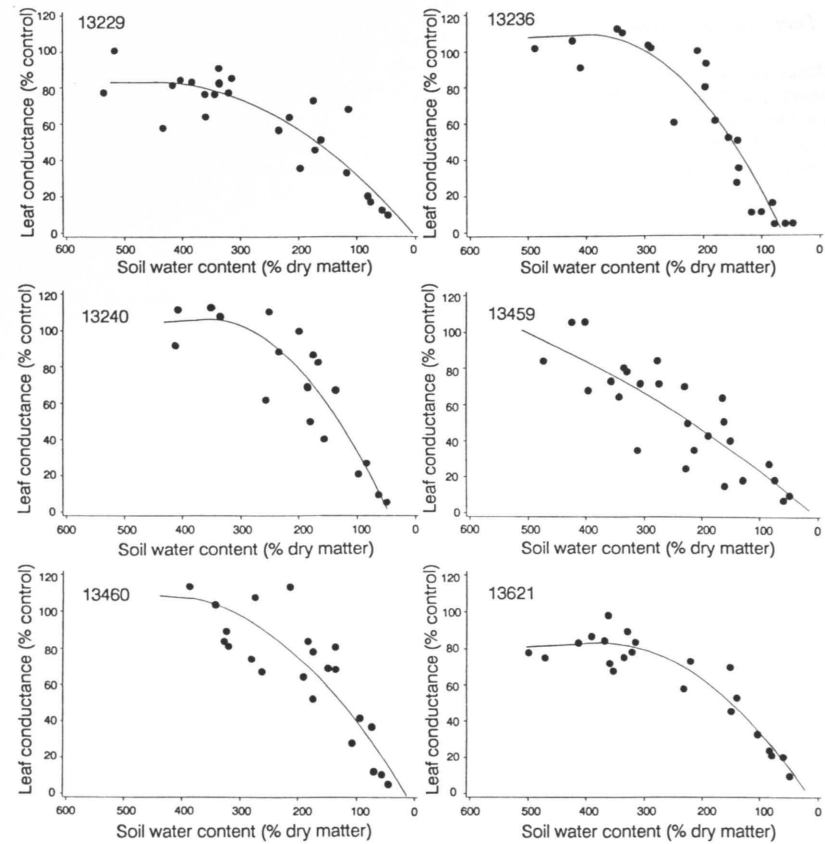


Figure 21. Relative leaf conductance as a function of soil water content in seedlings representing six provenances. The curves are hand-fitted. Dots represent individual seedlings.

300 % ($p < 0.01$). The leaf conductance fell steeply as the soil moisture declined to less than 200 %. At the end of the drying period, conductances varied from 4 to 15 % of the control values.

The rate of leaf conductance decrease varied considerably among provenances. Stomatal closure in Provenances No. 13459 and No. 13460 (both from Papua New Guinea) seemed to occur immediately as the seedling were subjected to soil water deficit. Provenance No. 13229 (Australia) started to close their stomata gradually, while No. 13240 showed very little response to commencing drought. Provenance differences in leaf conductance were not significant except for the afternoon measurements of the 13th ($p <$

0.05) and the morning measurements of the 17th ($p < 0.01$) day. The non-significance among provenances was obviously related to the considerable variation within provenances (Table 33). No consistent ranking of provenances could be made on the basis of leaf conductance at different levels of water stress over the 34-day experiment. Provenance No. 13236 (Australia) and No. 13459 (Papua New Guinea) exhibited the highest and lowest leaf conductances, respectively. After the water stress was discontinued, leaf conductances recovered gradually. Provenance No. 13229 (Australia) showed, the slowest recovery (67 % of control value only, vs. 77 to 136 % in the remaining provenances) during the four-day period after rewatering.

7.3.3. Leaf water potential

The effect of depletion of soil moisture on leaf water potential is depicted in Fig. 22. Due to the nature of *A. mangium* seedlings which only have few phyllodes, changes in water potential could not be observed over the whole range of soil water depletion. At field capacity, leaf water potentials were approximately -0.5 to -1.0 MPa. A comparison of water potentials among the well-watered seedlings did not reveal any statistically significant provenance differences. At 60 % soil water content (permanent wilting point), water potentials differed significantly between stressed and control seedlings ($p < 0.01$) and among provenances ($p < 0.05$). The lowest water potential was associated with Provenance No. 13229 (-2.93 MPa), and the highest with No. 13459 (-2.10 MPa).

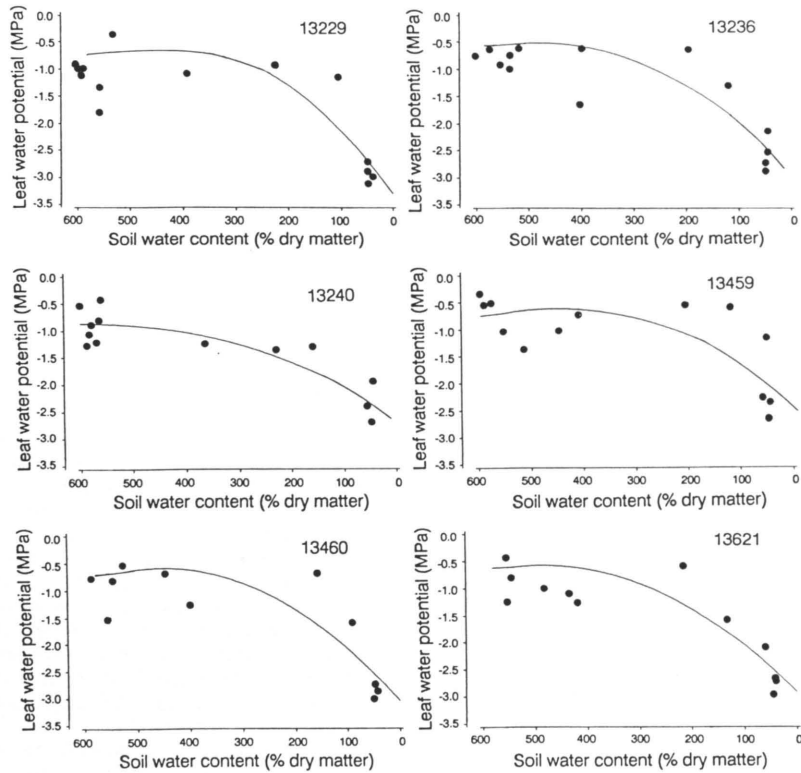


Figure 22. Leaf water potential as a function of soil water content in seedlings representing six provenances. The curves are hand-fitted. Dots represent individual seedlings.

Water potential values were not fully consistent with the observed daily transpiration rates: Provenance No. 13459 (Papua New Guinea) also showed lower transpiration rates earlier than the other provenances during the stress treatment (cf. Fig. 19), but No. 13240 (Australia), which had the highest transpiration rate, also showed a relatively high (-2.35 MPa) leaf water potential.

The relationship between the leaf water potential and the corresponding leaf water content is illustrated in Fig. 23. The leaf water content at the minimum water potential (< -2.0 MPa) ranged from 110 % to 150 %. The highest leaf water content was found in Provenance No. 13459, in which the highest leaf water potential was also observed. The difference in leaf water content (% of dry wt.) between well-watered and stressed seedlings could not be statistically

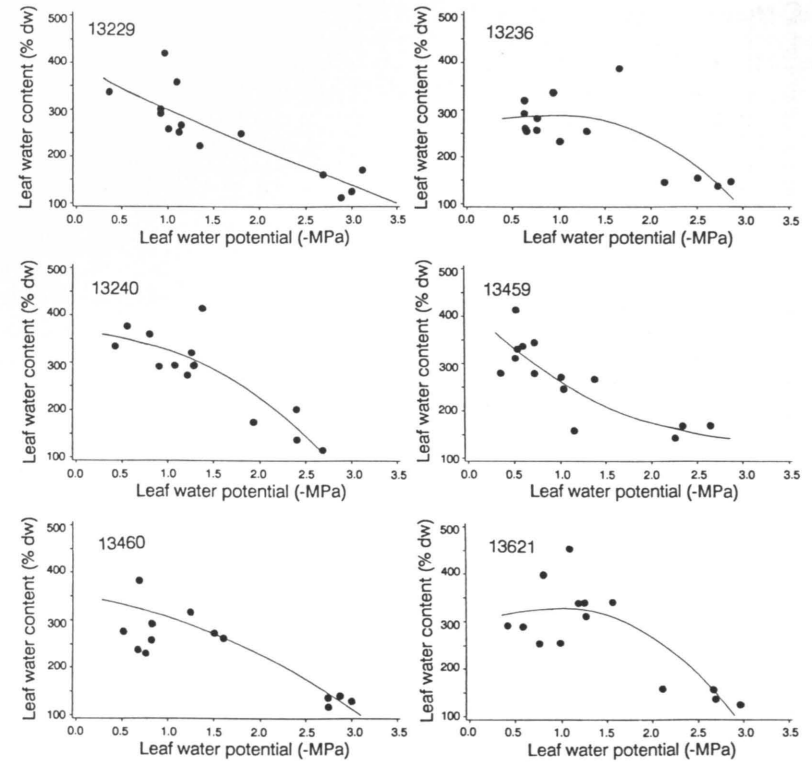


Figure 23. Leaf water content as a function of leaf water potential in seedlings representing six provenances. The curves are hand-fitted. Dots represent individual seedlings.

confirmed.

Leaf conductance as a function of leaf water potential is shown in Fig. 24. In all provenances, the leaf conductance decreased slightly as the water potential decreased from -0.5 to about -1.5 MPa. As the leaf water potential decreased further (< -1.5 MPa), the leaf conductance approached zero, indicating a near complete closure of the stomata.

7.4. Discussion

In earlier studies, the transpiration rate has been found to depend on such environmental factors as air temperature, air humidity and irradiance. An increase in temperature generally increases the transpiration rate and often causes a water deficit in the leaves as a result from stomatal closure (Federer and Gee 1976, Pereira and Kozłowski 1976). Observa-

tions on *A. mangium* made in the present study followed a similar trend and showed, for instance, that in well-watered control seedlings the transpiration rate varied daily and the leaf conductance was generally higher in the morning than in the afternoon. Effects of temperature are confounded by simultaneous changes in saturation deficit and, consequently, the response of leaf conductance to temperature alone is not readily detected (Jarvis 1980). In the present study, effects caused by other factors than water stress were not further clarified, however.

The transpiration rate in well-watered *A. mangium* seedlings ($11-19 \text{ mg cm}^{-2} \text{ h}^{-1}$, taking into account single leaf surface) was relatively low as compared to those observed in *A. craspedocarpa* which reach a maximum of $28 \text{ mg cm}^{-2} \text{ h}^{-1}$ in western Australia (Hellmuth 1969). In comparison, Kaul and Negi (1979) reported that *Eucalyptus tereti-*

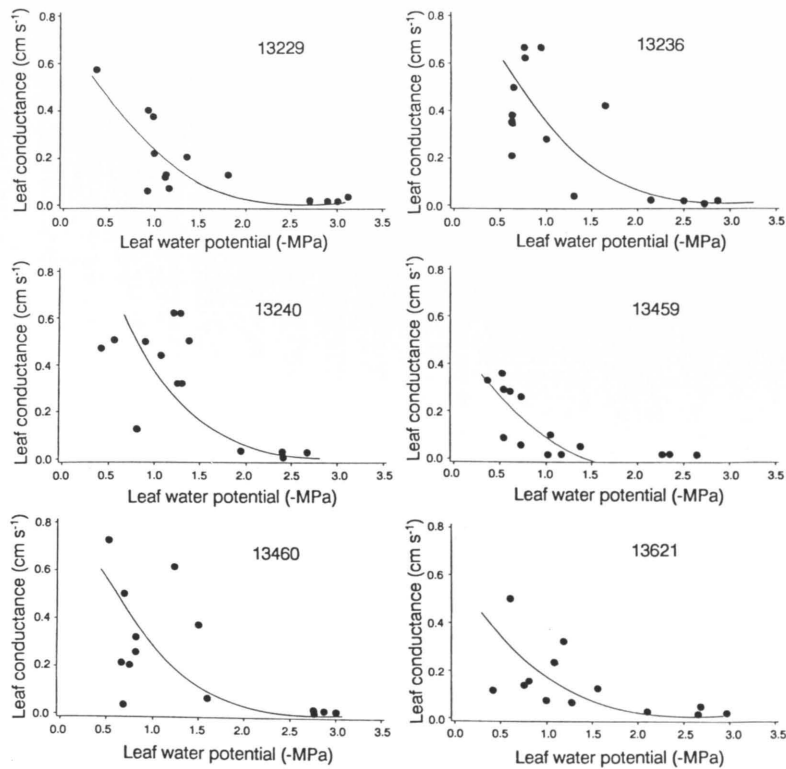


Figure 24. Leaf conductance as a function of leaf water potential in seedlings representing six provenances. The curves are hand-fitted. Dots represent individual seedlings.

cornis exhibits low rates of transpiration (about $2 \text{ mg cm}^{-2} \text{ h}^{-1}$), both during adequate moisture conditions and during water stress. However, in the present experiment, the rates of transpiration refer to 12-h periods and exclude night transpiration.

Under stress conditions, the transpiration rates of *A. mangium* decrease sharply. However, statistically significant decreases, as compared to control seedlings, were found only when the soil moisture was lower than 300 % of peat dry weight. In earlier studies, the transpiration rates of Douglas-fir (Zavitkovski and Ferrell 1970) showed a linear decline over the range from high to low soil moisture. The transpiration rates of *A. mangium* also declined gradually as the soil moisture content decreased. The transpiration rate declined to 50 % of control when the soil moisture content was about 200 % (corresponding to -0.1 MPa). This decrease

in transpiration was found at soil water potentials which were higher than those (-0.3 MPa) causing a 50 % decrease in transpiration in *Pinus cembra* (Havranek and Benecke 1978).

Provenance variation in transpiration rates was statistically confirmed only in control seedlings (cf. Table 32). This is probably due to the fact that the response to water stress varied greatly among individual trees.

A decrease in transpiration rate is likely to be the result of a decreased leaf conductance (Seiler and Johnson 1988). Several researchers have found intra-specific variation in the stomatal behaviour of tree species (Pallardy and Kozłowski 1981). Hennessey et al. (1988) reported differences in leaf conductance among clones of *Alnus glutinosa* grown under different water stress levels. Similarly, Abrams (1988) found variation in leaf conductance among provenances of

Cercis canadensis; provenances from xeric habitats were least affected by water stress. In contrast, Kelliher et al. (1980) found no difference in the stomatal resistance of two clones of eastern cottonwood (*Populus deltoides*) exposed to water stress, and similar results were reported in four families of radiata pine (Dean and Sands 1983).

In the present study, the differences in leaf conductance among provenances could not be statistically confirmed (cf. Table 33). This, again, is probably due to the large within provenance variation. If the experiments had been carried out under more constant environmental conditions, differences may have been easier to detect.

The magnitude of leaf conductance values shown in Table 33 were within the range reported earlier for vascular plants (Körner et al. 1979). Pallardy and Kozłowski (1981) compared the stomatal conductances in eight *Populus* clones under field conditions and found that the maximum and minimum values were 0.76 and 0.05 cm s^{-1} , respectively. Whitehead et al. (1981) reported a very high stomatal conductance in teak and *Gmelina* (about 3.0 cm s^{-1}) in the field; these values were much higher than those reported by Osonubi and Davies (1980) for the same species under greenhouse conditions. Hennessey et al. (1988) reported that the abaxial stomatal conductance of *Alnus glutinosa* subjected to severe drought was 0.06 and 0.08 cm s^{-1} after 20 and 30 days, respectively. In the present study, the abaxial leaf conductance of *A. mangium* at -1.5 MPa soil water potential ranged from 0 to 0.04 cm s^{-1} . In amphistomatous species, a more sensitive response in the adaxial stomata has been reported in many species (Pereira and Kozłowski 1976, Pattanakiat 1983, Kozłowski and Pallardy 1984). Nevertheless, no differences between adaxial and abaxial stomata were observed in *A. mangium*. This result is also in accordance with observations on stomatal frequencies of both leaf surfaces (cf. Chapter 6).

Whitehead (1980) noted that the effect of other environmental variables on stomatal conductance is small in comparison to the effect of leaf water potential. Daily fluctuations in water potential are ecologically not severe enough to reduce the leaf conductance unless a critical limit of water potential is reached. Stomatal conductance in conifers is sensitive to leaf water potential over a wide

range, while in willows the changes in stomatal conductance occur within very narrow limits of leaf water potential and the stomata close at a leaf water potential of -0.9 MPa (Vapaavuori 1985). In Sitka spruce, the critical leaf water potential is -2.0 MPa , and in Scots pine it is -0.8 MPa (Jarvis 1980).

In the present study, the leaf conductance of all *A. mangium* provenances except No. 13240 (Australia) started to decrease when the leaf water potential was lower than -0.5 MPa (cf. Fig. 24). This threshold is lower than the one reported by Lopushinsky and Klock (1974) for North American conifers (-0.2 MPa). The most likely explanation for this difference is that the conifer stomata are more sensitive to decreasing leaf water potentials. In *Eucalyptus*, the leaf water potential decreased with increasing soil water stress, but there were no consistent differences among three different species (Quraishi and Kramer 1970). When *A. mangium* showed signs of wilting, the water potential usually ranged from -2.3 MPa to -2.9 MPa . Federer (1977) reported that the xylem potential of 27 broadleaved species during visible water stress varied from -1.5 to -2.5 MPa . The minimum leaf water potentials obtained in *A. mangium* in the present study were much higher than those reviewed by Kozłowski (1982). This indicates that *A. mangium* is not a drought-tolerant species.

At stomatal closure, or at the end of the stress treatment, the leaf water content of *A. mangium* ranged from 132 % to 159 %. These results are similar to those obtained by Lopushinsky (1969) and Bilan et al. (1977) for conifer seedlings.

Of the provenances studied, Provenance No. 13459 (Papua New Guinea), showed the best ability to conserve moisture by closing their stomata and reducing transpiration under drought conditions. As pointed out by Hinchery et al. (1978), results from laboratory studies may not correctly estimate the sensitivity of the water balance regulation system to drought under field conditions. Many researchers have reported a difference between field and greenhouse grown plants in stomatal sensitivity (Kanemasu and Turner 1969, Jordan and Ritchie 1971). Thus, a programme for evaluating and selecting *A. mangium* provenances according to water stress tolerance should couple short-term screening experiments with long-term field testing.

8. PROVENANCE VARIATION IN PHOTOSYNTHESIS AND RESPIRATION IN RESPONSE TO TEMPERATURE AND LIGHT

8.1. Introduction

Most of the previous work on CO₂ exchange characteristics of woody species has been focused on temperate trees, particularly conifers. Relatively few data are available for tropical species (cf. Luukkanen et al. 1976, Samsuddin and Impens 1979, Ladipo et al. 1984, Natarahan et al. 1985).

The following factors have been shown to be related to the variation in CO₂ exchange in trees: total leaf area (McGregor et al. 1961), leaf age (Helms 1976, Lin and Ehleringer 1982), leaf anatomy (El-Sharkawy and Hesketh 1965, Louwse and Zweerde 1977), the number or size of stomata (Luukkanen and Kozlowski 1972), chlorophyll content (Luukkanen and Kozlowski 1972, Lin and Ehleringer 1982), and ploidy of plants (Bazzaz and Pickett 1980). The seasonal development of CO₂ exchange characteristics (Logan 1971, Pelkonen 1981, Korpilahti 1988), and the effect of such external factors as the photoperiod (McGregor et al. 1961, Gordon and Gatherum 1968) have also been earlier discussed.

The genetic constitution has also been found to determine the gas exchange characteristics of trees. Variation among species, as well as among individuals or populations of the same species have been demonstrated. Luukkanen and Kozlowski (1972) reported large variation in the rates of photosynthesis, photorespiration and dark respiration per unit of leaf area, as well as in CO₂ compensation points among poplar clones. They also discussed the possibility of using the physiological gas exchange characteristics as a basis for selecting superior genotypes. Campbell and Rediske (1966), in their studies on *Pseudotsuga menziesii* progenies, indicated that only a small proportion of the genetic variation in the net photosynthetic rate was additive and that the narrow-sense heritability (h²) for this trait was 0.21. Zelawski et al. (1969), on the other hand, demon-

strated differences in the photosynthetic efficiency among Scots pine provenances, and similar results have been obtained with such species as *Pinus merkusii* (Luukkanen et al. 1976), *Picea abies* (Pelkonen and Luukkanen 1974).

Photosynthetic and respiratory processes in plants are closely related ecologically and physiologically as far as measurement techniques are concerned. Genetically controlled variation in the dark respiration rate has been demonstrated in different tree species. However, variation in dark respiration rates seems to be generally smaller than that in net photosynthetic rates (Gatherum et al. 1967a, b; Luukkanen and Kozlowski 1972, Luukkanen 1978).

Photorespiration is defined as the total CO₂ output from photosynthesizing tissues in light, as compared to that caused by dark respiration. The review by Jackson and Volk (1970) summarized much of the early work on this process. The biochemical pathways associated with photorespiration and their relationships with other processes involved in CO₂ metabolism have also been clarified (cf. Burris and Black 1976). Decker (1970) was one of the first researchers to suggest that photorespiration could be a major factor affecting the within species variation in photosynthetic performance, and that it could thus be used as a criterion for selecting trees for rapid growth. No general confirmation of such a relationship has been obtained however. In contrast, the tight coupling between CO₂ release and fixation through an enzyme (RuBP carboxylase), which mediates both of these processes and which is sensitive mainly to external factors (such as CO₂, O₂, drought), has been emphasized in later studies (Vapaavuori and Valanne 1982, Edwards and Walker 1983).

The CO₂ compensation point is a useful parameter of CO₂ exchange, as well as an indicator for the apparent photorespiration rate. It is also used in the determination of

photorespiration rate by the so-called extrapolation method (cf. Forrester et al. 1966, Luukkanen 1976). A considerable amount of research has been devoted to the CO₂ compensation point, particularly because of the close correlation between the CO₂ compensation point and net photosynthetic rate which occurs in many species (Luukkanen 1978, Bykov et al. 1981). Moreover, the CO₂ compensation point is considered to be a more stable indicator of the physiological state of the plant than the rate parameters of CO₂ exchange. For instance, Luukkanen and Kozlowski (1972) suggested using CO₂ compensation points in the selection of poplar clones for high photosynthetic efficiency.

Physiological processes are influenced by both environmental factors and plant characteristics. A substantial number of investigations have been carried out on the effects of various external factors on photosynthesis and respiration in tree species. A review of the subject can be found in Grace et al. (1981), Linder and Lohammar (1981), Larcher (1983), Hari et al. (1985), and Korpilahti (1988).

The adaptation of photosynthetic performance to light conditions is a common phenomenon. Several investigations have indicated that broad-leaved tree species reach maximum rates of photosynthesis at relatively low light intensities as compared to conifers (cf. Kramer and Kozlowski 1979). The response of photosynthesis to light intensity varies also with type of foliage, stand architecture and the direction of illumination.

Temperature affects photosynthesis directly and also indirectly through its effects on respiration and transpiration. Photosynthesis of woody plants occurs over a wide range of temperature, with the specific range depending on plant age and origin, and season (cf. Kramer and Kozlowski 1979). Temperature optima for photosynthesis are generally higher for tropical than for temperate species. The effect of temperature on the CO₂ exchange has been widely discussed (Larcher 1969, Neilson et al. 1972, Berry and Björkman 1980, Björkman 1981). When all other factors of the environment are favorable for photosynthesis, the rate is usually limited by the low carbon dioxide concentration of the air (cf. Kramer and Kozlowski 1979).

Many investigators have tried to use photosynthetic rates as indices of growth potential of trees. However, a number of in-

vestigations have demonstrated that there is no positive correlation between the rate of net photosynthesis and the yield of plants (cf. Gifford and Evans 1981). Positive correlations between photosynthetic rates and growth have been reported, for instance, in *Pseudotsuga menziesii* seedlings (Campbell and Rediske 1966), *Populus* hybrids (Gatherum et al. 1967a, Fasehun 1978), and *Pinus banksiana* (Logan 1971). By comparison, negative correlations were reported in *Pseudotsuga menziesii* (Krueger and Ferrell 1965), *Pinus contorta* (Sweet and Wareing 1968), and *Pinus sylvestris* (Gordon and Gatherum 1968). However, as emphasized by Ledig (1969), short-term measurements of photosynthetic capacity are not always reliable for estimating growth potential.

8.2. Material and methods

8.2.1. Plant material

The material used in the present study consisted of six provenances of *A. mangium* (the same provenances as in Chapter 7). The conditions under which the experimental seedlings were grown have been described in Chapter 7 (7.2.1). The provenances used in this Chapter are as follows: Provenance No. 13229 = No. 1, Provenance No. 13236 = No. 2, Provenance No. 13240 = No. 3, Provenance No. 13459 = No. 4, Provenance No. 13460 = No. 5, and Provenance No. 13621 = No. 6.

After ten months, four healthy seedlings of average size were selected from each provenance for the CO₂ exchange study. The selected seedlings were arranged in four replications, six randomized provenances in each. The selected seedlings were treated uniformly until measurement started.

8.2.2. Gas exchange measurement

The CO₂ exchange measurement was carried out with an infrared gas analyzer setup (a Hartmann-Braun URAS II). The apparatus resembled that described elsewhere (Hari et al. 1979, Korpilahti 1988). A data-logging unit was used to control the measuring system and collect the data. For each gas exchange measurement, a single intact phyllode was sealed in the water-jacketed plexiglass leaf assimilation chamber, 2.312 dm³ in volume. The phyllode was held in a horizontal position and irradiated from above using a 400 W HQI-T lamp. The flow rate of air in the measurement system was adjusted to 60 l/h. The air inside the assimilation chamber was mixed by a small fan. The air temperature in the chamber was measured using a copper-constantan thermocouple, and the light intensity at the level of the leaf was monitored with a quantum sensor (Li-Cor Li-185B/190SB) placed inside the chamber. Air humidity control was achieved by passing the inlet air through temperature-controlled water.

8.2.3. Experimental procedure

In the temperature-response experiment, the rate of net photosynthesis was measured at 18, 24, 30, and 36°C, all at an irradiance of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The temperature was changed stepwise, with 30-minute intervals to allow the system to come to equilibrium. A separate preliminary experiment proved that 30 minute was adequate when changing the temperature; and it was also found that there was no significant effect of the time of the day on CO_2 exchange. Values of CO_2 compensation point at each temperature mentioned were obtained by recording the equilibrium concentration of CO_2 in the closed system.

As soon as the photosynthetic measurements had been made, the gas exchange chamber was put in absolute darkness, and dark respiration rates at the same temperatures as mentioned above were recorded.

Responses to light were determined only at 24°C for quantum flux densities of 300, 600, and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Only net photosynthetic rates were recorded for the light response curve.

At all temperatures, the same phyllode of the same seedling was used. The area of the measured phyllodes were determined by a photographic method. Rates of gas exchange were expressed as $\text{mg CO}_2 \text{dm}^{-2} \text{h}^{-1}$ for a single side of the phyllode. At the end of the experiment, all seedlings were harvested and the dry weights of phyllodes, stems, and roots were recorded separately after drying them at 70°C for 24 hours. All the measurements were carried out during September-October 1985.

8.2.4. Calculation procedure

The results of net photosynthetic and dark respiration rates were recorded automatically and calculated using a computer attached to the URAS setup (cf. Hari et al. 1979). Photorespiration rates were calculated on the basis of the CO_2 compensation point and net photo-

synthetic rates at the given temperatures according to the extrapolation method described by Forrester et al. (1966) and Luukkanen (1976). Total photosynthesis was derived from the sum of net photosynthesis and calculated photorespiration.

An one-way analyses of variance was computed using the SAS programme (SAS 1985). Differences among provenance means of gas exchange parameters were evaluated for significance with Duncan's New Multiple Range Test. Relationships between the various parameters of CO_2 exchange, seedling dry matter production or field growth performance were also studied using regression analysis.

8.3. Results

8.3.1. Responses of CO_2 exchange characteristics to temperature and irradiance

The average CO_2 exchange characteristics of *A. mangium* expressed per unit of projected phyllode surface area and phyllode dry weight are summarized in Table 34. Since the phyllodes of the experimental seedlings showed no differences in water content, gas exchange rates expressed on a fresh weight basis showed a similar pattern to that on a dry weight basis.

Within the applied temperature range, the photosynthetic rate of *A. mangium* increased with temperature up to 24°C, after which the net photosynthesis started to decrease slightly while the total photosynthesis continued to

Table 34. Summary data on gas exchange characteristics at saturation light intensity of *A. mangium* seedlings maintained at four different temperatures, expressed on phyllode area (single surface) and phyllode dry weight basis. Standard deviations are indicated in parenthesis (all six provenances combined).

Parameter	Temperature (°C)			
	18	24	30	36
Net photosynthesis, $\text{mgCO}_2 \text{dm}^{-2} \text{h}^{-1}$	8.47 (1.03)	9.14 (1.02)	9.02 (1.07)	8.25 (1.34)
Net photosynthesis, $\text{mgCO}_2 \text{g}^{-1} \text{h}^{-1}$	12.69 (2.89)	13.71 (3.26)	13.53 (3.30)	12.38 (3.35)
Total photosynthesis, $\text{mgCO}_2 \text{dm}^{-2} \text{h}^{-1}$	9.49 (1.14)	10.68 (1.24)	11.05 (1.31)	10.95 (1.56)
Total photosynthesis, $\text{mgCO}_2 \text{g}^{-1} \text{h}^{-1}$	14.30 (3.87)	16.14 (4.76)	16.68 (4.78)	16.49 (4.64)
Dark respiration, $\text{mgCO}_2 \text{dm}^{-2} \text{h}^{-1}$	0.48 (0.20)	0.86 (0.32)	1.21 (0.42)	1.76 (0.56)
Dark respiration, $\text{mgCO}_2 \text{g}^{-1} \text{h}^{-1}$	0.73 (0.31)	1.28 (0.38)	1.81 (0.50)	2.64 (0.74)
Photorespiration, $\text{mgCO}_2 \text{dm}^{-2} \text{h}^{-1}$	1.02 (0.94)	1.55 (1.25)	2.04 (1.28)	2.70 (1.25)
Photorespiration, $\text{mgCO}_2 \text{g}^{-1} \text{h}^{-1}$	1.61 (1.18)	2.43 (1.70)	3.15 (1.70)	4.11 (1.59)
CO_2 compensation point, ppm	48.99 (18.80)	57.94 (18.20)	69.56 (18.20)	89.09 (17.80)

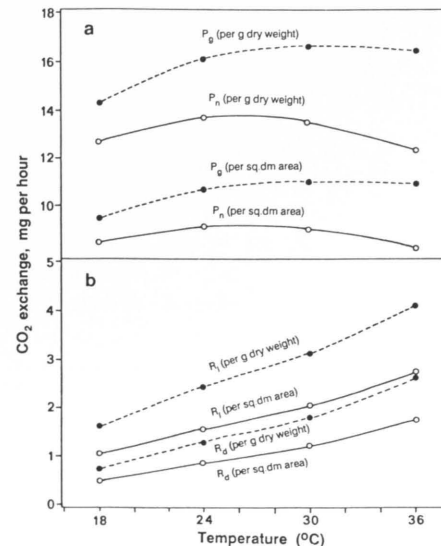


Figure 25. (a) Total photosynthesis (P_g) and net photosynthesis (P_n), and (b) photorespiration (R_d) and dark respiration (R_d), per gram (dry weight) and phyllode area (single surface) in relation to temperature in *A. mangium* (all six provenances combined). The curves are hand-fitted.

increase up to 30°C. The continued increase in the calculated total photosynthetic rate was caused by an upsurge in the photorespiration rate. However, both net and total photosynthesis showed decreasing trends above 30°C (Fig. 25a and Table 34).

Both photorespiration and dark respiration increased with temperature, increasing more rapidly at temperatures higher than 30°C (Fig. 25b, Table 34). The calculated photorespiration rate was generally 1.5–2.2 times greater than the dark respiration rate, but dark respiration increased more rapidly with temperature. An interpolation of the response of net photosynthesis to temperature indicated that the optimum temperature for the CO_2 exchange balance in *A. mangium* occurred near 25°C in the present experiment.

The response of net photosynthesis to the external CO_2 concentration, including an extrapolation to zero CO_2 concentration, at four different temperatures is illustrated in Fig. 26. The rate of photosynthesis increased linearly with CO_2 concentration, but tended to remain constant or (at lower temperature)

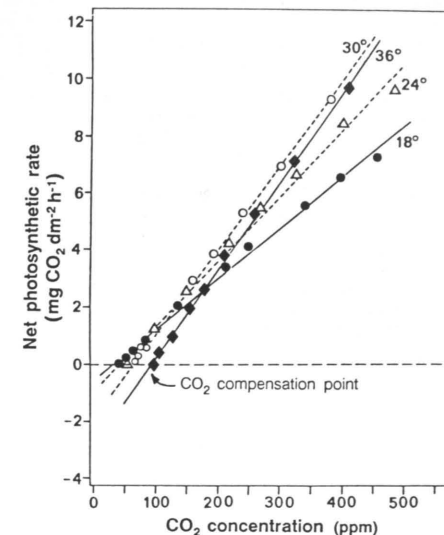


Figure 26. Response of net photosynthesis to the external CO_2 concentration at four different temperatures (six *A. mangium* provenances combined).

slightly decreased when the CO_2 concentration approached 500 ppm. The slope of the response line indicating the relationship between net photosynthesis and CO_2 concentration, which describes the "carboxylation efficiency" as defined by Tregunna et al. (1966), increased with temperature up to 30°C and remained constant thereafter upto 36°C.

The response of net photosynthesis to varying light intensity are summarized in Fig. 27 and Table 35. The net photosynthetic rate increased rapidly with light intensity up to about 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (of "photosynthetically active radiation", PAR) and then remained constant with no statistical differences between 600 and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

8.3.2. Variation in CO_2 exchange characteristics among provenances

The phyllode area and the phyllode weight of *A. mangium* were highly correlated ($r^2 > 0.9$) in the present study, and only the rates ex-

pressed per unit of single surface area are used in the following presentation.

The average CO₂ exchange characteristics in response to temperature under constant light intensity (1000 μmol m⁻² s⁻¹) for each provenance are summarized in Table 36. Variations among provenances were observed in both net and total photosynthesis throughout the temperature range. The variation was confirmed statistically at 18, 24, 36°C (p < 0.05), and 30°C (p < 0.01) for both net and total photosynthesis. The general response was similar in all cases (Fig. 28). No interaction between temperature and provenance was found. The greatest variation in the rate of photosynthesis was caused by the

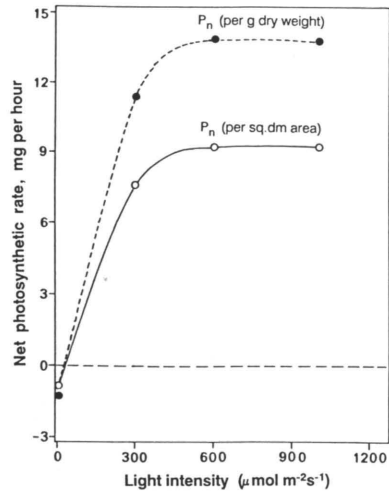


Figure 27. Net photosynthesis (P_n) per gram (dry weight) and unit of phyllode area (single surface) in relation to light intensity in *A. mangium* (data of six provenances combined). The curves are hand-fitted.

Table 35. Net photosynthetic rate in *A. mangium* seedlings at different light intensities, expressed on phyllode area (single surface) and phyllode dry weight basis. Standard deviations are indicated in parenthesis (all six provenances combined).

Parameter	Light intensity (μmol m ⁻² s ⁻¹ PAR)			
	0	300	600	1000
Net photosynthesis, mgCO ₂ dm ⁻² h ⁻¹	0.86 (0.32)	7.56 (1.28)	9.17 (1.29)	9.14 (1.03)
Net photosynthesis, mgCO ₂ g ⁻¹ h ⁻¹	1.28 (0.38)	11.36 (3.17)	13.78 (3.70)	13.71 (3.33)

Table 36. Average net photosynthesis, total photosynthesis, photorespiration, and dark respiration of *A. mangium* in relation to provenances at different temperatures under saturation light intensity. Values in column followed by the same letter are not significantly different at 0.05 level of significance using Duncan's New Multiple Range Test.

Prov. No.	Total photosynthesis mgCO ₂ dm ⁻² h ⁻¹						Net photosynthesis mgCO ₂ dm ⁻² h ⁻¹						Photorespiration mgCO ₂ dm ⁻² h ⁻¹						Dark respiration mgCO ₂ dm ⁻² h ⁻¹					
	18		24		30		36		18		24		30		36		18		24		30		36	
	Temperature (°C)		Temperature (°C)		Temperature (°C)		Temperature (°C)		Temperature (°C)		Temperature (°C)		Temperature (°C)		Temperature (°C)		Temperature (°C)		Temperature (°C)		Temperature (°C)		Temperature (°C)	
1	10.00 ^{ab}	11.09	11.87	11.81	11.09	9.99	9.99	10.09	9.35	1.10 ^a	1.78 ^a	1.10 ^a	1.78 ^a	0.53 ^a	1.00 ^a	1.41 ^a	1.95 ^a	1.00 ^a	1.00 ^a	1.00 ^a	1.41 ^a	1.95 ^a	1.77 ^a	
2	10.26	11.33	11.52	11.42	9.98	9.98	9.78	9.03	0.85 ^a	1.36 ^a	1.74 ^a	1.36 ^a	1.74 ^a	0.48 ^a	0.82 ^a	1.16 ^a	1.62 ^a	0.82 ^a	0.82 ^a	1.16 ^a	1.62 ^a	1.62 ^a	1.62 ^a	
3	9.70 ^{ab}	10.64 ^{ab}	10.91	10.80	9.22	9.22	9.05	8.33	0.87 ^a	1.42 ^a	1.86 ^a	1.42 ^a	1.86 ^a	0.44 ^a	0.50 ^a	0.88 ^a	1.31 ^a	0.50 ^a	0.50 ^a	0.88 ^a	1.31 ^a	1.90 ^a	1.90 ^a	
4	8.24	9.14	9.33	8.88 ^a	7.70 ^a	7.70 ^a	7.45 ^a	6.27 ^a	1.03 ^{ab}	1.44 ^a	1.87 ^a	1.44 ^a	1.87 ^a	0.50 ^a	0.88 ^a	1.31 ^a	1.90 ^a	0.50 ^a	0.88 ^a	1.31 ^a	1.90 ^a	1.90 ^a	1.90 ^a	
5	9.28 ^{ab}	10.61 ^{ab}	11.06	10.98	8.32 ^{ab}	8.32 ^{ab}	8.88	8.18	0.96 ^{ab}	1.55 ^{ab}	2.18 ^{ab}	1.55 ^{ab}	2.18 ^{ab}	0.41 ^a	0.80 ^a	1.10 ^a	1.60 ^a	0.41 ^a	0.80 ^a	1.10 ^a	1.60 ^a	1.60 ^a	1.60 ^a	
6	9.74 ^{ab}	11.49	12.05	12.24	8.27 ^{ab}	8.27 ^{ab}	9.38	8.87	1.47	2.21	2.68	2.21	2.68	0.51 ^a	0.89 ^a	1.22 ^a	1.80 ^a	0.51 ^a	0.89 ^a	1.22 ^a	1.80 ^a	1.80 ^a	1.80 ^a	
X̄	9.49	10.68	11.05	10.95	8.47	8.47	9.14	8.25	1.02	1.55	2.04	1.02	1.55	0.48	0.85	1.21	1.76	0.48	0.85	1.21	1.76	1.76	1.76	
S _x	0.25	0.27	0.29	0.34	0.23	0.23	0.23	0.29	0.10	0.14	0.14	0.10	0.14	0.02	0.04	0.05	0.06	0.02	0.04	0.05	0.05	0.06	0.06	
F	2.25	4.03*	5.81*	4.28*	2.91*	4.44*	5.48**	4.13*	2.42	2.27	2.74	2.42	2.27	0.76	0.35	0.67	0.87	0.76	0.35	0.67	0.67	0.87	0.87	

Significance levels of the F-value: * p < 0.05, ** p < 0.01

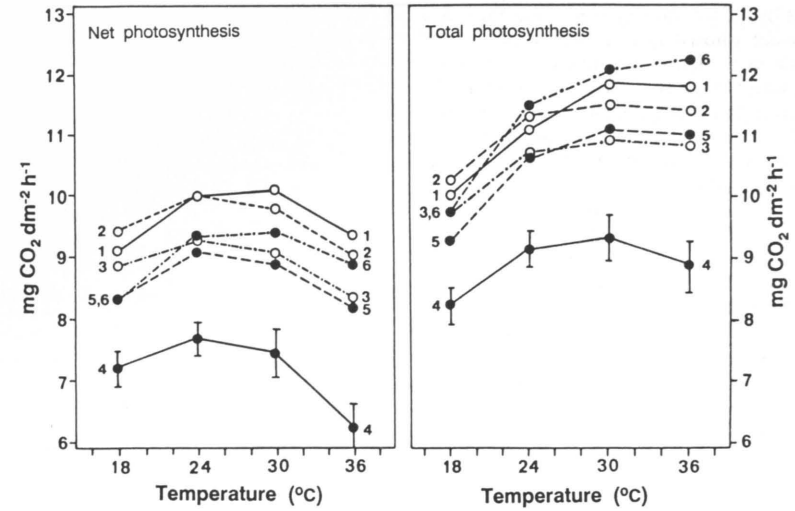


Figure 28. Temperature dependence of the net photosynthesis and total photosynthesis in six provenances of *A. mangium*. Vertical bars indicate the standard error of the mean.

extremely low photosynthetic rate in Provenance No. 4 (Papua New Guinea). The optimal temperature for photosynthesis in all provenances occurred near 24°C, except for No. 1 (Australia) and No. 6 (Indonesia), in which the optimal temperature was close to 30°C.

Compared to the other provenances, the total photosynthesis of Provenance No. 6 (Indonesia) was remarkably high. In this provenance the total photosynthesis rate increased rapidly from 18°C to 24°C and exhibited the highest level observed among all provenances at 24, 30 or 36°C and still showed, in contrast to other provenances, an increasing trend also between highest temperatures (30 and 36°C).

In the present study, the response of the CO₂ compensation point to temperature varied among the provenances, but the differences were not statistically significant. This may be due to the large variation between individual observations. Raising of the temperature, however, caused a distinct increase in the CO₂ compensation point in all cases. Provenance No. 6 (Indonesia) showed the highest CO₂ compensation points throughout the temperature range, while Provenance No. 1 (Australia) showed the lowest ones (Fig. 29). The ranking of prov-

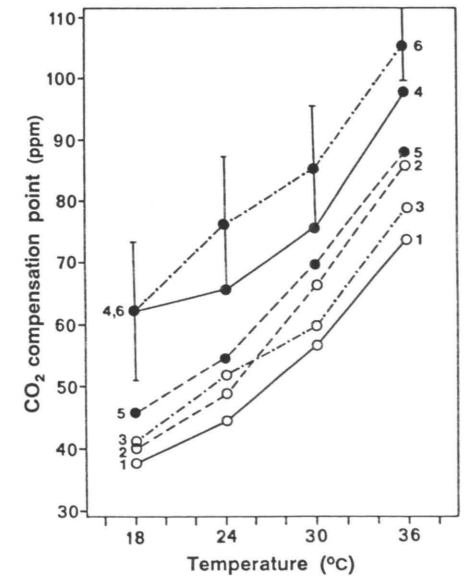


Figure 29. Temperature dependence of CO₂ compensation point in six *A. mangium* provenances. Vertical bars indicate the standard error of the mean.

enances by CO₂ compensation point followed neither net photosynthetic nor total photosynthetic rates clearly. However, No. 1 (Australia) which had the lowest compensation point throughout the temperature range also showed the highest net photosynthetic rates (and the same trend was found in No. 2 at low temperatures).

The calculated photorespiration rates and the measured dark respiration rates (Table 36, Fig. 30) varied among provenances, but no statistical differences, except for the photorespiration rates at 36°C, could be confirmed. This partly resulted from the relatively high variability within provenances, as also was the case with CO₂ compensation points. The variation among provenances in dark respiration was relatively small compared to other gas exchange characteristics. The differences in photorespiration rates among provenances were greater than those in dark respiration rates especially at higher temperatures.

As with the CO₂ compensation point, the photorespiration of Provenance No. 6 (Indonesia) also had the highest values over the entire temperature range; resulting in an increase in the total photosynthetic rate as compared to the net photosynthetic rate. On the other hand, No. 1 (Australia) showed the

highest dark respiration rate, while the lowest dark respiration rate was found in No. 5 (Papua New Guinea), over the entire temperature range. Provenance No. 4 (Papua New Guinea), which showed distinctly low photosynthetic rates, had the second highest rate of dark respiration.

The rates of dark respiration were generally lower than the calculated photorespiration rates, as shown by the photorespiration to dark respiration ratios in Table 37. The highest ratio of photorespiration to dark respiration (2.8–2.0) was found in Provenance No. 6 (Indonesia) throughout the temperature range from 18 to 36°C. However, this difference was not statistically confirmed. The ratio of photorespiration to dark respiration decreased with an increase in temperature in all provenances. The results thus indicate that the dark respiration increases more rapidly than the photorespiration rates as a function of temperature.

The ratio of net photosynthesis to dark respiration (Table 37) was lowest in No. 4 (Papua New Guinea), while the ratio of net photosynthesis to photorespiration was found to be low both in No. 4 and 6 (Indonesia); these provenances also had the highest CO₂ compensation points. The provenances which showed the highest ratios varied depending

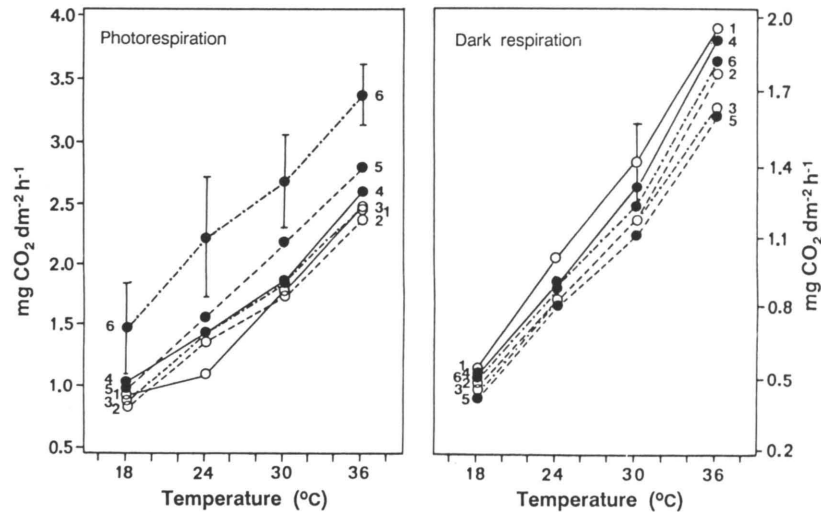


Figure 30. Temperature dependence of the photorespiration rate and dark respiration rate in six *A. mangium* provenances. Vertical bars indicate the standard error of the mean.

Table 37. Average photorespiration/dark respiration, photorespiration/net photosynthesis and dark respiration/net photosynthesis ratios of *A. mangium* at saturation light intensity in relation to provenances at different temperatures. Values in columns followed by the same letter are not significantly different at 0.05 level of significance using Duncan's New Multiple Range Test.

Prov. No.	Photorespiration/dark respiration ratio				Net photosynthesis/photorespiration ratio			Net photosynthesis/dark respiration ratio				
	Temperature (°C)				Temperature (°C)			Temperature (°C)				
	18	24	30	36	18	24	30	36	18	24	30	36
1	1.98 ^a	1.19 ^a	1.34 ^a	1.30 ^a	10.83 ^a	9.12 ^c	5.71 ^b	3.82 ^c	18.41 ^a	10.98 ^a	7.52 ^{ab}	4.88 ^b
2	1.75 ^a	1.67 ^a	1.50 ^{ab}	1.35 ^a	11.78 ^a	7.70 ^{bc}	5.72 ^b	3.82 ^c	19.48 ^a	12.24 ^a	8.45 ^b	5.12 ^b
3	2.11 ^a	1.84 ^{ab}	1.70 ^{ab}	1.57 ^{ab}	11.20 ^a	6.86 ^{abc}	5.17 ^{ab}	3.61 ^{bc}	20.42 ^a	11.58 ^a	8.03 ^{ab}	5.21 ^b
4	2.28 ^a	1.78 ^{ab}	1.57 ^{ab}	1.46 ^{ab}	7.76 ^a	5.69 ^{ab}	4.23 ^{ab}	2.48 ^a	14.84 ^a	9.08 ^a	5.97 ^a	3.38 ^a
5	2.30 ^a	1.96 ^{ab}	1.98 ^{ab}	1.75 ^{ab}	10.99 ^a	6.75 ^{ab}	4.49 ^{ab}	3.14 ^{abc}	21.28 ^a	11.82 ^a	8.17 ^b	5.11 ^b
6	2.82 ^a	2.59 ^b	2.20 ^b	1.97 ^b	7.15 ^a	5.03 ^a	3.82 ^a	2.67 ^{ab}	16.88 ^a	10.74 ^a	7.74 ^{ab}	5.13 ^b
\bar{X}	2.23	1.90	1.75	1.59	9.87	6.65	4.78	3.20	18.56	11.08	7.66	4.80
CV, %	27.97	26.42	23.08	20.61	28.53	19.79	19.07	19.47	20.07	20.28	15.31	18.20
F	1.49	1.71	1.70	1.77	2.04	2.31	2.21	2.78	1.87	1.03	2.29	2.67

on the temperature applied. The ratios always decreased with an increasing temperature.

The response of the net photosynthetic rate to light intensity was also studied separately in different provenances. These results are illustrated by Fig. 31. The net photosynthetic rate in all provenances was satu-

rated at around 600 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PAR, with no significant increase at the higher photon flux density (1000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PAR). Statistical analyses showed no interaction between provenance and light intensity in CO₂ exchange rates.

8.3.3. Relationships between gas exchange parameters

Matrix correlations between the various gas exchange parameters, with data pooled for all provenances, are shown in Table 38. Net photosynthesis was only clearly correlated to total photosynthesis. This result indicates that the loss of respiratory CO₂, either in dark or light, is not directly associated with a net gain of carbon. Total photosynthesis, as determined by the sum of net photosynthesis and estimated photorespiration, was distinctly correlated with net photosynthesis, photo-

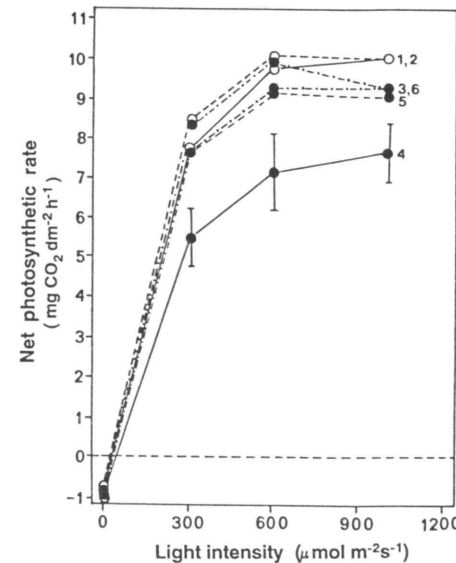


Figure 31. Light dependence of net photosynthesis in six *A. mangium* provenances at 24°C. Vertical bars indicate the standard error of the means.

Table 38. Matrix correlations between CO₂ exchange parameters of *A. Mangium* seedlings, with six provenances pooled. Symbols represent net photosynthesis (P_n), total photosynthesis (P_g), photorespiration (R_i), dark respiration (R_d), and CO₂ compensation point (Γ).

	P _n	P _g	R _i	R _d	Γ
P _n	1.000	0.810**	0.000	-0.109	-0.247*
P _g		1.000	0.590**	0.280**	0.333**
R _i			1.000	-0.109	0.904**
R _d				1.000	0.595**
Γ					1.000

Significance levels of correlation: * p < 0.05
** p < 0.01

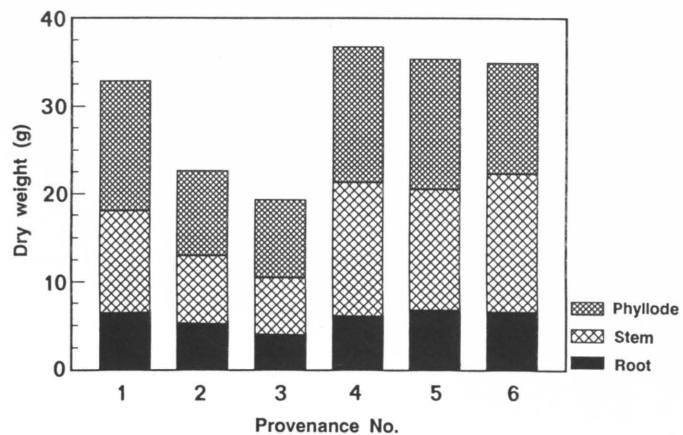


Figure 32. Distribution of dry matter in various parts of 10-month-old *A. mangium* seedlings in relation to provenance.

respiration, dark respiration as well as the CO_2 compensation point ($P < 0.01$). An increase in total photosynthesis, photorespiration or dark respiration was generally associated with an increase in the CO_2 compensation point. In contrast, an increase in the CO_2 compensation point was associated with a decrease in net photosynthesis.

8.3.4. Relationship between gas exchange characteristics and production

At the age of 10 months, the total dry matter production of the experimental seedlings and its distribution among phyllodes, stems and roots differed among provenances (Fig. 32). Statistically significant differences among provenances existed in the dry weights of all parts ($p < 0.01$). Provenance No. 4 (Papua New Guinea) showed the greatest total dry matter production and phyllode dry weight. Provenance No. 6 (Indonesia) had the greatest stem production, while Provenance No. 5 (Papua New Guinea) ranked first in root production.

The correlation between the various CO_2 exchange parameters and seedling dry matter production is presented in Table 39 (only rates at the temperature of 18°C and light intensity of $1000 \mu\text{mol m}^{-2}\text{s}^{-1}$ PAR are shown here). The photosynthetic rate (leaf area basis) showed a highly significant ($p < 0.01$) negative correlation with seedling

Table 39. Correlation coefficients for the relationship between CO_2 -exchange parameters and total seedling dry weight or phyllode dry weight in 10-month-old *A. mangium* seedlings (rates measured at 18°C temperature and $1,000 \mu\text{mol m}^{-2}\text{s}^{-1}$ irradiance only).

CO_2 exchange parameter	Total dry weight	Phyllode dry wt.
Net photosynthesis (area basis)	-0.810**	-0.756**
Net photosynthesis (dry wt. basis)	-0.366	-0.427*
Total photosynthesis (area basis)	-0.739**	-0.708**
Total photosynthesis (dry wt. basis)	-0.265	-0.337
Photorespiration (area basis)	-0.013	-0.057
Photorespiration (dry wt. basis)	0.025	-0.058
Dark respiration (area basis)	-0.005	-0.037
Dark respiration (dry wt. basis)	-0.094	-0.076

Significance levels of correlation: * $p < 0.05$
** $p < 0.01$

dry weight. Provenance No. 4, which showed the lowest photosynthetic rates, had the fastest dry matter production. Noticeably, the photosynthetic rates expressed on phyllode dry weight basis were not correlated with the total dry matter accumulation, but rather with total phyllode dry weight ($p < 0.05$). This might have been due to the fact that the phyllode of *A. mangium* contains much non-photosynthesizing tissue. It is therefore possible that the CO_2 exchange rates expressed per unit area basis are better related to growth than those expressed per leaf dry weight in the case of *A. mangium*.

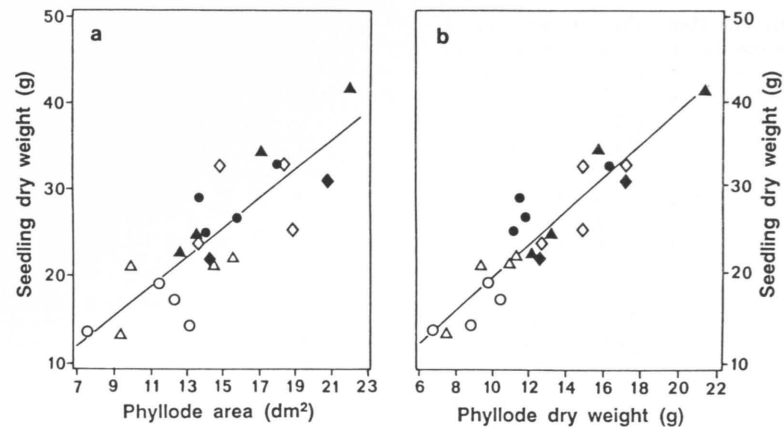


Figure 33. Relationships between phyllode area (a), phyllode dry weight (b), and the seedlings dry matter production of *A. mangium*, under laboratory condition.

Respiration rates did not show any correlation with dry matter accumulation, either when expressed per leaf area or leaf dry weight basis.

Seedling dry matter production was positively correlated ($p < 0.01$) with total phyllode dry weight ($r = 0.93$) and to total phyllode area ($r = 0.83$). These relationships are illustrated in Fig. 33.

Relationships between the net photosynthetic rate (at 18°C) in the present seedling material and the field growth performance of the same *A. mangium* provenances at the age of 30 months (see Chapter 2) are illustrated in Fig. 34. Negative correlations were found between photosynthesis and height as well as photosynthesis and stem diameter, but these were not statistically significant, since only six provenance means were included.

8.4. Discussion

The CO_2 exchange characteristics of tropical tree species have, to date, been studied very little. Some results have been reviewed by Larcher (1969), Bazzaz and Pickett (1980), and Medina and Klinge (1983). The information available suggests that maximum photosynthetic rates of tropical trees are similar to those of temperate trees, but lower than found in many tropical crops (El-Sharkway and Hesketh 1965, Robichaux and Percy 1980).

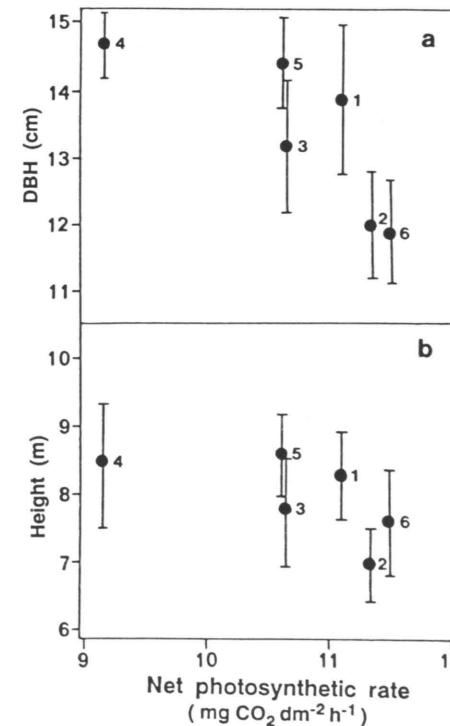


Figure 34. Relationship between the seedling net photosynthetic rate (18°C , light saturation) and tree diameter (a) or height (b) at 30 months of age in six *A. mangium* provenances in the field. The number indicates the provenance.

The present results obtained under laboratory conditions on the net photosynthesis of *A. mangium* were within the range of variation previously reported for tropical rain forest tree species (3–22 mgCO₂dm⁻²h⁻¹; Larcher 1983). The rates expressed per unit dry weight were higher than the rates expressed per unit of phyllode surface area (one side). This is, generally, a characteristic of broadleaved species (Zelawski and Walker 1976). The response curve of the net photosynthetic rate of *A. mangium* to temperature was approximately parabolic in shape (cf. Fig. 25a), resembling the corresponding curves reported for other species (Krueger and Ferrell 1965, Luukkanen and Kozłowski 1972, Neilson et al. 1972, Osonubi and Davies 1980).

The maximum photosynthetic rate of *A. mangium* averaged 9.1 mgCO₂dm⁻²h⁻¹ (single surface) or 13.7 mgCO₂g⁻¹h⁻¹ (dry wt.). This is not a particularly high rate when compared to reported rates for temperate tree species. For instance, Luukkanen and Kozłowski (1972) reported an average rate of 18.6 mgCO₂dm⁻²h⁻¹ in *Populus* clones, and Zelawski et al. (1973) reported the extremely high rate of 35 mgCO₂g⁻¹h⁻¹ in fully exposed 5-week-old *Pinus sylvestris* seedlings. However, the rates obtained in the present study were considerably low compared to the maximum photosynthetic rate of 25.9 mgCO₂dm⁻²h⁻¹ reported for *Leucaena leucocephala*, a tropical fast-growing species (Natarahan et al. 1985). Nevertheless, fast growth associated with a relatively low photosynthetic rate was suggested by Ladipo et al. (1984) to be possible in tropical trees because of a long growing season and to the absence of extreme climatic variations.

The optimum temperature for photosynthesis in *A. mangium* was found to be between 24°C and 30°C. The net photosynthetic rate started to decrease when the temperature was raised above 30°C. The effect of high temperature on CO₂ exchange has been studied by many investigators (e.g. Neilson and Jarvis 1975, Berry and Björkman 1980). The decline in photosynthesis at high temperatures is caused by the inactivation of various enzymes associated with CO₂ exchange (Larcher 1969). Since temperatures in the planting region of *A. mangium* are typically above 30°C, the actual carbon gain may be limited by high temperatures under field conditions.

The respiration rate of *A. mangium* increased almost linearly with temperature (cf. Fig. 25b). The calculated photorespiration rates were about 1.6–2.2 times greater than the measured dark respiration. The differences were smaller at higher temperatures than at low temperatures, since dark respiration increased more rapidly with temperature than photorespiration. The dark respiration rates obtained in the present study were comparable to those reviewed by Larcher (1969) for tropical rain forest tree species.

According to previous investigations, woody species are capable of utilizing substantially higher concentrations of CO₂ than found in the atmosphere (Luukkanen and Kozłowski 1972, Beadle et al. 1981, Doehlert and Walker 1981, Teskey and Shrestha 1985). This is also true for *A. mangium*. The net photosynthetic rate first increased with the CO₂ concentration, but became constant or slightly decreased when the CO₂ concentration went higher than 500 ppm. It is obvious that any changes in atmospheric CO₂ concentrations which might occur in the field could cause large changes in the rates of photosynthesis, especially at high temperatures. Moreover, temperature also affected the slope of the regression between net photosynthetic rate and CO₂ concentration, which equals the carboxylation efficiency as defined by Tregunna et al. (1966) (cf. Fig. 26). The present results showed that carboxylation efficiency in *A. mangium* reached its maximum at about 30°C, and remained at this level even at 36°C. Such a physiological response may have adaptive significance under conditions where high temperatures and a significant decrease in the atmospheric CO₂ concentration during the day are common.

The CO₂ compensation point, at which the respiratory release of CO₂ is in balance with photosynthetic CO₂ fixation, is a parameter commonly used to measure photosynthetic efficiency (Luukkanen 1976). The CO₂ compensation point is influenced by a change in the rate of one or both of its component processes. In the present study, an increase in temperature caused a considerable increase in the compensation point (cf. Table 34). The CO₂ compensation point increased progressively with temperature, which is a common characteristic of C₃ plants (Bykov et al. 1981). The CO₂ compensation points obtained in the present study showed a high

variability among individuals. This differed somewhat from results described in the literature (Luukkanen and Kozłowski 1972, Bykov et al. 1981).

The response curve showing net photosynthesis as a function of light intensity followed a rectangular hyperbola, in common with many other plants (Hesketh and Baker 1967, Robichaux and Pearcy 1980). The CO₂ uptake rates increased sharply as the irradiance increased (cf. Fig. 27 and Table 35). Light saturation of *A. mangium* occurred between 300 to 600 μmol m⁻²s⁻¹, which is much lower than full sunlight under natural conditions. Natarahan et al. (1985) reported that the maximum photosynthetic rate of *Leucaena leucocephala*, a tropical fast-growing tree species, occurred at 565 μmol m⁻²s⁻¹. It is often stated that the light saturation of photosynthesis in woody plants generally occurs at about one-third of full sunlight, and seedlings usually make better use of weak illumination than large trees (Larcher 1983). Therefore, estimations of tree photosynthesis based on measurements of tree seedlings must be done with considerable care.

The effect of geographic variation on gas exchange has been studied in many tree species. These studies have not shown distinct trends, in contrast to the correlation between genotype and growth. However, seed source variability in CO₂ exchange characteristics, particularly in the photosynthetic behaviour, have been reported for many temperate trees, e.g. *Pinus contorta* (Sweet and Wareing 1968), *Pinus banksiana* (Logan 1971), *Pinus monticola* (Townsend et al. 1972), *Picea abies* (Pelkonen and Luukkanen 1974), as well as in such tropical species as *Pinus merkusii* (Luukkanen et al. 1976).

In the present study, differences in the photosynthetic rate among provenances were found, but not in the dark respiration rate (cf. Table 36). The variation in photosynthesis was not consistently related to the latitude of the provenances. In comparison, such relationships have been found, for instance, in Scots pine populations (Gordon and Gatherum 1968). This can be explained by the fact that there is neither extreme climatic variation nor photoperiod variation in the geographic region from which the studied *A. mangium* provenances originated.

Maximum photosynthetic rates observed for all provenances occurred at temperatures

which were lower than the typical day temperatures in environments where *A. mangium* is grown. The maximum net photosynthesis of Provenance No. 1 (Australia) and No. 6 (Indonesia) occurred near 30°C, while the remaining provenances had maximum net photosynthetic rates at near 24°C. The variation in this "optimum" temperature among provenances is difficult to explain.

There were rather distinct differences in the CO₂ compensation point between Australian, Papua New Guinean and Indonesian provenances. The northern (near equator) provenance (Provenance No. 6 from Indonesia) showed the highest value of CO₂ compensation point, as compared to the populations from the south (Nos. 1, 2, and 3 from Australia) (cf. Fig. 29). The equatorial zone from which the present material originated is difficult to compare to geographic regions in which latitudinal trends also in CO₂ compensation points have been observed (cf. Pelkonen and Luukkanen 1974). The large variation found in CO₂ compensation points is, however, similar to that reported for *Pinus monticola* (Townsend et al. 1972).

The importance of photorespiration has generally been underestimated in the past but has been brought to attention in several investigations since the early 1970's (cf. Zelitch 1971). In the present study, a nearly linear temperature response of photorespiration was found in all provenances. The calculated photorespiration rate was higher than the measured dark respiration rate. Provenance No. 6 (Indonesia) showed a particularly high rate of photorespiration which was associated with a high total photosynthetic rate. The results imply that while Provenance No. 6 has a high efficiency in carbon fixation much of the accumulated carbohydrate is lost through respiratory release. In comparison, Provenance No. 4 (Papua New Guinea), which had the lowest photosynthetic rate, showed an intermediate photorespiration rate.

The ratio of photosynthesis to respiration may offer a better criterion for studying geographic variation in CO₂ exchange characteristics than photosynthetic or respiration rates alone. Ogren (1984) suggested that the ratio of net photosynthesis to photorespiration reflects the ratio between carboxylase and oxygenase activities, the enzymes responsible for both CO₂ fixation and photorespiratory CO₂ release. In the present study,

the ratio of net photosynthesis to photorespiration was, as expected, most distinctly affected by temperature (cf. Table 37). It can also be concluded that the geographic origin is reflected in the variation of the net photosynthesis/photorespiration ratio, but the exact mechanism of how this ratio is related to biomass production in *A. mangium* remains unclear.

Zelawski et al. (1973) found a significant difference in the net photosynthesis/dark respiration ratio between lowland Scots pine and highland pines in Poland, while neither photosynthesis nor respiration alone showed clear differences. The net photosynthesis/dark respiration ratios and net photosynthesis/photorespiration ratios obtained in the present study were respectively higher and lower than those reported for temperate trees (cf. Pelkonen and Luukkanen 1974, Luukkanen 1978).

Zelawski (1967) demonstrated that the CO₂ evolution of *Pinus sylvestris* in light was 2.8 times greater than during dark respiration. In the present study, photorespiration exceeded dark respiration by a factor of 2.2 (ranging from 1.75 to 2.8) at 18°C. The differences were smaller at higher temperatures, as dark respiration increased more rapidly than photorespiration. Results from poplar clones indicate that the photorespiration/dark respiration ratio may vary considerably among different genotypes under identical environmental conditions (Luukkanen and Kozłowski 1972). The results obtained in the present study also suggest variation among provenances in this respect, especially at higher temperatures (cf. Table 37).

In the present work, an attempt was made to examine the relationships between gas exchange parameters. Distinct correlations were found, especially between the CO₂ compensation point and rates of photosynthesis or respiration. It has also been suggested that the CO₂ compensation point could be used to predict net photosynthetic efficiency and also utilized as a criterion for the selection of fast-growing genotypes. In the present work, the correlation between CO₂ compensation point and net photosynthesis was negative, which is in agreement with earlier observations on *Populus* sp. (Luukkanen and Kozłowski 1972, Okafo and Hanover 1978).

In silviculture, the aim is not simply to increase the total biomass production in trees but to divert a greater proportion of the

photosynthesis-respiration differential into usable wood. Campbell and Rediske (1966) found high genotypic correlations but low phenotypic correlation between photosynthetic rates and seedling dry weight in Douglas-fir. They suggested that photosynthesis can be used as a criterion in selection for rapid growth. In the present study, Provenance No. 4 (Papua New Guinea) had the lowest photosynthetic rate (expressed per unit of leaf area or weight) of all provenances, at all temperature, but nevertheless achieved the greatest total dry matter production (cf. Fig. 32). This might have been because of its ability to divert more of its photosynthesis-respiration differential into dry matter production and particularly to the production of new photosynthesizing organs. Anatomical differences in phyllodes among the provenances (see Chapter 6) may have been a major cause for apparently reduced photosynthetic efficiency in the more rapidly growing seedlings. In comparison, Fasehun (1978) found that photosynthetic rates per unit leaf area of older leaves of *Populus x euramericana* clones were positively correlated with clone growth. McDonald et al. (1981) found that the stem wood production in eight *Salix* clones was related to maximum photosynthesis. However, single measurements do not allow one to predict the potential productivity of a tree, especially when rate parameters are used (cf. Zelawski 1976).

Many investigations have demonstrated that the total leaf area (and the total photosynthetic production per tree) is sometimes of greater significance in determining differences in growth than the photosynthetic rate per leaf area or weight unit alone (McGregor et al. 1961, Poskuta and Nelson 1986). Previous studies have shown that biomass production may be related more to specific leaf weight (SLW), leaf area or leaf biomass (Okafo and Hanover 1978, Oren et al. 1986). Helms (1976) suggested that to increase productivity of a tree, it is more important to select on the basis of the inherent capacity of the tree to develop a larger total leaf area than photosynthetic efficiency. Nevertheless, there is no general consensus amongst tree crop physiologists on this matter. Since both the area of phyllodes and phyllode dry weight in *A. mangium* were closely associated with total dry matter production (cf. Fig. 33), total phyllode area is probably a convenient

determinant for growth in this species.

Attempts to relate genetic variation in the photosynthetic rate to the performance in the field have been made with varying success. Ladipo et al. (1984) examined relationships between the net photosynthetic rate and height in 4-year-old *Triplochiton scleroxylon* clones. The authors reported that net photosynthesis alone bore no relationship to yield, whereas dark respiration alone was fairly highly correlated with yield. Ceulemans et al. (1980), working with six hybrid poplars, failed to show a relationship that could be declared statistically significant between any gas exchange characteristic and field productivity.

In the present study, an attempt was made to relate the gas exchange characteristics measured under laboratory condition with growth performance in the field. The results clearly imply that photosynthesis per se is

not the primary factor determining biomass production. Provenances which had demonstrably high photosynthetic rates did not appear to be the most productive ones (cf. Fig. 34).

In order to fully understand the relationships between CO₂ exchange processes and biomass production in *A. mangium*, more detailed studies are needed, especially on the causal connections on the one hand between different CO₂ exchange characteristics, and on the other hand between CO₂ exchange and biomass production including the allocation of photosynthesis to different organs. Future studies should also clarify the effect of water stress and nutrient balance on CO₂ exchange or growth. In addition, observations on the CO₂ exchange under field condition should be carried out over entire growing seasons.

9. CONCLUSIONS: PLANTATION SILVICULTURE OF *A. MANGIUM* IN THAILAND IN RELATION TO PHYSIOLOGICAL CHARACTERISTICS AND GENETIC VARIATION

Reforestation is the only long-term measure which can provide sufficient quantities of wood for household and industrial use in the tropics, including Thailand. The expansion in forest plantations is nowadays combined with extensive use of introduced tree species (Evans 1982). Such exotic species have been primarily chosen because of their fast growth compared to indigenous species. This will alleviate the pressure on the remaining natural tropical forests, provide a protective cover to limit erosion and land degradation. The best approach is to match species with site and climatic conditions (Zobel and Talbert 1984). *A. mangium*, a tropical lowland species originating from Australia and Papua New Guinea, has so far proved to be a successful exotic plantation species in many countries, particularly in the Far East. The interest in including *A. mangium* in the Thai planting programme is based on the following facts: (1) the species can grow over a wide range of site conditions with vigorous growth; (2) it is a nitrogen-fixing species; and (3) the wood can be utilized for many industrial purposes, especially for sawn timber and plywood (Wong et al. 1988).

The present study was undertaken to investigate the extent of genetic variation in various characteristics, i.e. growth, foliar nutrients, phyllode anatomy, and numbers of stomata, as well as physiological characteristics such as photosynthesis and transpiration, in *A. mangium*. Basic information needed in the promotion of planting or in domesticating this species in Thailand is provided.

Genetic variation is necessary for the development and success of a tree improvement programme (Namkoong et al. 1988). Differences among the natural populations of *A. mangium* were found in all the characteristics measured in the present study, but large variation also occurred among trees within each provenance. Heritabilities of all growth characteristics studied were relatively high.

The results suggest that all traits of *A. mangium* could be expected to respond to selection based on population or individual performance.

Mortality is a trait of particular importance to the success of tree planting. The survival percentages of *A. mangium* at Lad Krating Plantation were found to be very high, which indicated that the species had adapted well to these new environmental conditions (Chapter 3). In general, it seems that provenances from lower latitudes (southern hemisphere), in particular those from Papua New Guinea, are more suited to conditions in Central Thailand than provenances from higher latitudes. Juvenile-mature relationships among growth characteristics of *A. mangium* found in the present study (Chapter 3) implied that the early performance could be used to predict the relative growth at an advanced age when the rotation is relatively short. This is very useful for an immediate breeding programme.

Rainfall is generally considered as the limiting factor for the growth of *A. mangium*, which is reported to require more than 1,000 mm of precipitation annually (Mangium... 1983). However, the results of the present study showed that the minimum temperature is also one of the climatic factors exerting a strong effect on diameter growth. The difference between maximum and minimum temperatures had a high correlation with diameter development (Chapter 4). This particular environmental factor should thus be taken into consideration when planting sites are selected.

A. mangium does not grow continuously throughout the year. There is a period (December-March) when the species slows down its physiological activity and growth, and this duration differs among provenances (Chapter 4). This particular factor should also be taken into account when considering the timing of carrying out silvicultural treat-

ments, such as fertilization.

A. mangium is generally poor at self-pruning. Wide spacing will lead to the development of thick branches, and thus narrow spacing is preferable. A spacing of 3 × 3 m appears suitable for an industrial plantation, since growth and crown development are not disturbed. Artificial pruning is necessary in an industrial *A. mangium* plantation to improve the wood quality, especially when growing logs for plywood industry. The pruning should be carried out in the dry season during the first and second year to prevent large wounds and damage caused by fungi.

A. mangium is a member of the legume family and thus possess root nodules containing nitrogen-fixing bacteria (Umali-Garcia 1988). The tree normally does not show signs of nitrogen deficiency. However, there is still a need to study the possible intraspecific differences in the ability of *A. mangium* to produce root nodules. Further investigations are also needed to select *Rhizobium* strains which have an improved ability to fix atmospheric nitrogen. *A. mangium* grows well on acidic soils; its optimum soil pH range is from pH 4 to pH 6 (Hu et al. 1983). Consequently, it is often found that the species shows phosphorus deficiency, since the availability of phosphorus in the soil is limited under low pH conditions because of the formation of aluminium and iron phosphates. Phosphorus fertilization is thus recommended in industrial plantations of *A. mangium*.

In the present study, the mineral composition of *A. mangium* foliage (Chapter 5) indicated significant variation among provenances in the ability to accumulate potassium, calcium and magnesium. Height growth was negatively correlated with manganese levels, while DBH was negatively correlated with iron. Crown diameter was negatively related to foliar iron and positively related to the phosphorus level. The results thus supported the hypothesis that nutrient levels in the leaves of *A. mangium* are correlated to the variation in tree growth among populations. Consequently, the selection of provenances suited to specific sites on the basis of nutrient accumulation and utilization characteristics should also be considered.

A. mangium is phyllodineous acacia species with an amphistomatous phyllode. The sto-

mata characteristic on the adaxial and abaxial surfaces were found to be similar. The average stomatal frequency was 380 stomata/mm², and the mean length of the guard cell was 26.8 μm. The stomatal frequency decreased progressively from the base to the tip of phyllode. There was distinct variation in the number of stomata per unit of leaf area among *A. mangium* provenances, and some negative correlations between stomatal frequency and tree growth were found (Chapter 6). The causal physiological mechanisms underlying such variation remain, however, to be clarified in more detailed studies.

Yap (1986) reported that one of the main problems of planting *Acacia* sp. in Peninsular Malaysia is the failure of establishment because of drought. Seedlings that failed to establish themselves were not able to adapt successfully to the site due to genetic or physiological factors. In the present study, the transpiration rate of *A. mangium* varied daily depending on air temperature or soil moisture content; and differences among provenances were also found in this respect (Chapter 7).

When *A. mangium* seedlings were subjected to drought, the transpiration rates of all provenances decreased remarkably. The effect of water deficit on the transpiration rate was quite similar in all provenances. The leaf water potential of *A. mangium* can be as low as -2 MPa without causing injury to the seedlings, and the transpiration rate may still be detectable in such a situation. Provenance No. 13459 (Papua New Guinea) seemed to be most drought-resistant since it showed the best ability to conserve water under stress conditions. Studying transpiration rates gravitationally, as done in the present study, limits the observations to potted seedlings only, and results from such studies may not correspond to the situation in the field. Therefore, in future studies, field experiments on the short-term and long-term variation in water balance are recommended.

In the present study (Chapter 8), the net photosynthesis of the *A. mangium* provenances reached a maximum (7.2 to 10.1 mg CO₂ dm⁻² h⁻¹) at a temperature around 24°C and at a photon flux density near 600 μmol⁻² s⁻¹. The rates are lower than those commonly found for in other tropical plants. Genetic differences among provenances existed in the rates of net and total photosyn-

thesis, and photorespiration. In contrast, the provenance had no effect on dark respiration.

Rates of net photosynthesis were not correlated with dark respiration rates, but they were positively correlated with total photosynthesis and negatively correlated with the CO₂ compensation point. The net photosynthetic rate per unit of phyllode area showed a negative relationship with the dry matter production of the seedlings used in the laboratory studies. For instance, Provenance No. 13459 (Papua New Guinea) had remarkably low net and total photosynthetic rates but a high dry matter production rate. Phyllode area showed a better correlation with seedling dry weight than any CO₂ exchange characteristic, and it was concluded that the area of photosynthesizing organs (and thus the allocation of photosynthesis within the plant) may be better and more causally related to the biomass yield than any

rate parameter. Therefore, in the selection of *A. mangium* for faster growth, total leaf area offers a better criterion than photosynthesis rate. Even if the unit rates of photosynthesis or respiration did not directly offer any firm basis for selecting the best seed sources, the present results obtained on *A. mangium* suggest that gas exchange characteristics are well suited for monitoring the physiological response to such environmental stress factors as drought and offer a basis to select well-adapted provenances accordingly.

It is particularly interesting, from the plantation forestry viewpoint, to note that Papua New Guinea provenances generally appear to be performing better than other provenances in Central Thailand. Further studies should be carried out to exactly determine which physiological characteristics offer the best criteria for the selection and identification of such promising *A. mangium* genotypes.

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