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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

THE SOCIETY OF FORESTRY IN FINLAND
THE FINNISH FOREST RESEARCH INSTITUTE
ACACIA MANGIUM: STUDIES ON THE GENETIC VARIATION IN ECOCOLOGICAL AND PHYSIOLOGICAL CHARACTERISTICS OF A FAST-GROWING PLANTATION TREE SPECIES

Tiivistelmä: Acacia mangium: tutkimuksia noopekasvuisen viljelypuulajin ekologisen ja fysiologisen tunnusten geneettisestä vaihtelusta

Ladawan Atipanumpai

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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 Tha
land. 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 differ
ent provenances is also discussed. Under laboratory conditions, such physiological characteristics as transpi
ration 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, transpira
tion, water stress.

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PREFACE

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Helsinki, August 1989

Ladawan Atipanumpai
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 falcatoria* 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 northeastern part of Australia between Ingham and the River Daintree. 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.
The leaves are alternate and bipinnate, as in other species of the subfamily Mimosoideae. After a few weeks, the new leaves are replaced by a flattening of the petiole and the main axes of each leaflet are transformed into a "phylloide" 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 up to 10 cm long composed of tiny white or cream-coloured flowers. The flowers are soon deciduous, 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 poorer form of A. auriculiformis (Bowen 1981b).

1.3. Biology of flowering and seed production

The phenology of flowering and seed production of A. mangium is closely related to 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 east coast varieties as early as November (Srinivasan & Srinivasan 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 Kerala 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 varieties were not commencing 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 pericarp, 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. Usually the seeds are winnowed to remove chaffs. Each kilogram of ripe pods yields about 90 grams of seeds (Mangium...). 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. Srinivasan (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 other 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 Vinekandan 1986), but no details were given. More studies concerning drought tolerance should be made.


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 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 cool 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 seeds commonly show over 90% germination, while the germinability of stored seed has been reported to be 75–80% (Mangium... 1983).

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, bare-root 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 tree naturally sheds 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 powder mildew (Odium 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 of *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 ramariae*, 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 macro-nutrients, 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 micro-propagation (organ and tissue cultures) are reported to be applicable. The species appears to be relatively easily micro-propagated, and successful transplants by shoot multiplication have been reported (Corduar and Hartney 1989). Studies on induced callus from seedling tissue have also been initiated (Kosakul and Pothipattana 1986). The results of stem cutting and grafting have not been impressive to date (Sim 1986, Pinyopasarer 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 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
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. Brawbaker (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. macrantha* (0.47). Bhumiibhoom (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 Yantahasath 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.

### 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.
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, Najet 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 varietability 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 adaption 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.


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 (Naem et al. 1985), China (Pan and Yang 1986), the Philippines (Pettersson and Havmoller 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 Havmoller 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 seeding 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 Clayton-skeletal, Kaolinite, Aeric Kanhaputat series (Worrick 1988). A compost mixture was applied at planting, and a complete mineral fertilizer (15:15:15) has been given regularly in early 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 mungbeans, and soybeans 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 (H), length of clear bole (CB), diameter at ground level (DBH), 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):

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

where

- $y_{ij}$ = plot mean in block $j$ for provenance $i$
- $\mu$ = general mean
- $s_i$ = provenance effect
- $b_j$ = block effect
- $e_{ij}$ = random error of the plot mean.

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

<table>
<thead>
<tr>
<th>Register</th>
<th>Location</th>
<th>Latitude (°)</th>
<th>Longitude (°)</th>
<th>Altitude (m)</th>
<th>No. of parent trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>12992</td>
<td>Rex Range NR Mosson, Queensland, Australia</td>
<td>16°30'</td>
<td>145°32'</td>
<td>30</td>
<td>10</td>
</tr>
<tr>
<td>13229</td>
<td>Claren River, Queensland, Australia</td>
<td>12°44'</td>
<td>143°13'</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>13232</td>
<td>Cowley Beach Road, Queensland, Australia</td>
<td>17°41'</td>
<td>146°15'</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>13233</td>
<td>Walsh's Pyramid, Queensland, Australia</td>
<td>17°06'</td>
<td>145°48'</td>
<td>20</td>
<td>10</td>
</tr>
<tr>
<td>13234</td>
<td>Trinity Inlet, Queensland, Australia</td>
<td>17°02'</td>
<td>145°48'</td>
<td>20</td>
<td>10</td>
</tr>
<tr>
<td>13235</td>
<td>Mourilyan Bay, Queensland, Australia</td>
<td>17°35'</td>
<td>146°05'</td>
<td>20</td>
<td>5</td>
</tr>
<tr>
<td>13236</td>
<td>Kurrimine, Queensland, Australia</td>
<td>17°46'</td>
<td>146°05'</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>13237</td>
<td>El Arish, Queensland, Australia</td>
<td>17°50'</td>
<td>146°01'</td>
<td>20</td>
<td>10</td>
</tr>
<tr>
<td>13238</td>
<td>Tully Mission Beach Rd., Queensland, Australia</td>
<td>17°56'</td>
<td>146°02'</td>
<td>70</td>
<td>10</td>
</tr>
<tr>
<td>13239</td>
<td>Syndicate Rd., Tully, Queensland, Australia</td>
<td>17°55'</td>
<td>145°52'</td>
<td>50</td>
<td>10</td>
</tr>
<tr>
<td>13240</td>
<td>Ellerbeck Rd., Cardwell, Queensland, Australia</td>
<td>18°14'</td>
<td>145°58'</td>
<td>60</td>
<td>5</td>
</tr>
<tr>
<td>13241</td>
<td>Brookes Pole Creek, Queensland, Australia</td>
<td>18°21'</td>
<td>146°03'</td>
<td>50</td>
<td>5</td>
</tr>
<tr>
<td>13242</td>
<td>Abergowrie St., Queensland, Australia</td>
<td>18°26'</td>
<td>146°01'</td>
<td>60</td>
<td>10</td>
</tr>
<tr>
<td>13245</td>
<td>Morehead, Papua New Guinea</td>
<td>8°45'</td>
<td>141°18'</td>
<td>10</td>
<td>18</td>
</tr>
<tr>
<td>13460</td>
<td>Oroomo River, Papua New Guinea</td>
<td>8°50'</td>
<td>143°08'</td>
<td>10</td>
<td>18</td>
</tr>
<tr>
<td>13621</td>
<td>Piru, Ceram, Indonesia</td>
<td>3°04'</td>
<td>128°12'</td>
<td>150</td>
<td>9</td>
</tr>
</tbody>
</table>

Duncan's New Multiple Range Test (DNMRT) was used to evaluate various tree traits among provenances. Correlation coefficients between traits were later on computed.
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 still maintained, without the obvious decline in intensive management practices.

Height (H). The average height growth of *A. mangium* provenances at the ages of 18, 24, and 30 months is shown in Table 5. Results 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 growth increased to 6.26 m and ranged from 5.55 m (No. 13159) 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 Abergrove 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 Abergrove provenance (No. 13242), which once again performed better when compared to the overall average (Fig. 4). Differences in height growth were statistically significant amongst provenances at all ages studied (Table 6). The effect of seed source on height growth was higher at the ages of 18 months (67% and 73% of the observed total variation 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
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 (Dg1).** At the age of 18 months, the average Dg1 was 12.85 cm, varying from 11.32 cm (No. 13239) to 14.56 cm (No. 13459). At 24 months, the overall average Dg1 was 15.46 cm, and the average range 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 Dg1 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 Dg1 and exceeded the overall average at 30 months. Proportionately ranked means of Dg1 at all ages studied are shown in Fig. 4.

As a whole, a highly significant variation in Dg1 was observed among provenances (Table 6). However, the effects caused by the provenances were relatively less pronounced in Dg1 (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 range 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 Dg1, DBH also indicated statistically highly significant differences among the provenances, and the provenance differences were somewhat more pronounced (representing 60–65% of the observed total variance) when measured in terms of DBH as compared to Dg1.

**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>
<thead>
<tr>
<th>Dependent variable</th>
<th>Lat.</th>
<th>Long.</th>
<th>Alt.</th>
</tr>
</thead>
<tbody>
<tr>
<td>H18</td>
<td>0.494</td>
<td>0.178</td>
<td>0.076</td>
</tr>
<tr>
<td>H24</td>
<td>0.657</td>
<td>0.382</td>
<td>0.197</td>
</tr>
<tr>
<td>H30</td>
<td>0.602</td>
<td>0.300</td>
<td>0.148</td>
</tr>
<tr>
<td>CB</td>
<td>0.317</td>
<td>0.157</td>
<td>0.150</td>
</tr>
<tr>
<td>Dg18</td>
<td>0.047</td>
<td>0.253</td>
<td>0.401</td>
</tr>
<tr>
<td>Dg24</td>
<td>0.141</td>
<td>0.165</td>
<td>0.285</td>
</tr>
<tr>
<td>Dg30</td>
<td>0.039</td>
<td>0.388</td>
<td>0.479</td>
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<tr>
<td>DBH18</td>
<td>0.397</td>
<td>0.135</td>
<td>0.087</td>
</tr>
<tr>
<td>DBH24</td>
<td>0.458</td>
<td>0.177</td>
<td>0.070</td>
</tr>
<tr>
<td>DBH30</td>
<td>0.265</td>
<td>0.062</td>
<td>0.139</td>
</tr>
<tr>
<td>Cw24</td>
<td>0.549</td>
<td>0.234</td>
<td>0.122</td>
</tr>
<tr>
<td>Cw30</td>
<td>0.224</td>
<td>0.116</td>
<td>0.141</td>
</tr>
</tbody>
</table>

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

---

Figure 4. Proportionally ranked means for height (Ht), diameter at ground level (Dg1), and diameter at breast height (DBH) at the age of 16, 24, and 30 months in 16 provenances of A. grandis. Vertical lines indicate differences significant (p < 0.05) according to Duncan's New Multiple Range Test.
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 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 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 variation 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 8. Matrix correlations of *A. mangium* growth characteristics.

<table>
<thead>
<tr>
<th>Variables</th>
<th>H18</th>
<th>H24</th>
<th>H30</th>
<th>Dgl18</th>
<th>Dgl24</th>
<th>Dgl30</th>
<th>DBH18</th>
<th>DBH24</th>
<th>DBH30</th>
<th>Cw18</th>
<th>Cw24</th>
<th>Cw30</th>
<th>CR</th>
</tr>
</thead>
<tbody>
<tr>
<td>H18</td>
<td>1.00</td>
<td></td>
<td></td>
<td>0.94**</td>
<td>0.96**</td>
<td>0.68**</td>
<td>0.79**</td>
<td>0.69**</td>
<td>0.92**</td>
<td>0.91**</td>
<td>0.69**</td>
<td>0.71**</td>
<td>0.69**</td>
</tr>
<tr>
<td>H24</td>
<td>1.00</td>
<td>0.98**</td>
<td>0.55*</td>
<td>0.72**</td>
<td>0.57*</td>
<td>0.85*</td>
<td>0.90*</td>
<td>0.81*</td>
<td>0.91*</td>
<td>0.69*</td>
<td>0.71*</td>
<td>0.69*</td>
<td>0.70**</td>
</tr>
<tr>
<td>H30</td>
<td>1.00</td>
<td>0.96**</td>
<td>0.56*</td>
<td>0.72**</td>
<td>0.62**</td>
<td>0.88**</td>
<td>0.91*</td>
<td>0.84**</td>
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<td>0.99**</td>
<td>0.71**</td>
<td>0.85**</td>
<td>0.86**</td>
<td>0.64*</td>
<td>0.61*</td>
<td>0.77**</td>
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<td>0.76**</td>
<td>0.66**</td>
<td>0.67**</td>
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</tr>
<tr>
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<td>0.71**</td>
<td>0.84**</td>
<td>0.64**</td>
<td>0.66**</td>
<td>0.59*</td>
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<td>DBH18</td>
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<td>0.97**</td>
<td>0.91**</td>
<td>0.61*</td>
<td>0.71**</td>
<td>0.66**</td>
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<td>0.91**</td>
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<td>0.83**</td>
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<tr>
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</table>

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

<table>
<thead>
<tr>
<th>Family No.</th>
<th>Surv. (%)</th>
<th>Height (m)</th>
<th>Dgl (cm)</th>
<th>DBH (cm)</th>
<th>Cw (cm)</th>
<th>Pw (score 0–4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>94.7</td>
<td>8.58</td>
<td>15.75</td>
<td>12.47</td>
<td>4.65</td>
<td>0.34</td>
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<td>3</td>
<td>98.7</td>
<td>8.24</td>
<td>18.41</td>
<td>11.48</td>
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<td>4</td>
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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 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 between 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 Ladj 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 (Pässztor and Coelho 1977).

It has also been reported that under plantation conditions, the survival percentages of many species, e.g. *Pinus kestya*, *P. merkusii*, *P. elliotti*, commonly decrease with plantation age (Burley 1973, Grantham 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 affecting 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 fertilization 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 Pettit and Havmoller (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 the coefficients previously reported in Indonesia by Na’iem et al. (1985), the height growth of 24-month-old
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 results are applied to a site.

Callaham and Hazel (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 occur usually among trees within each provenance. Thus the selection of provenance followed by selection of individual trees 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 1-year-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 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 decreases the height growth if the removal of basal branches amounted to less than 30% (Slabaugh, 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 kestya* (Changtraagoon 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 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 for a young forest 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, climatic 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 cline expression is exhibited differently in different environments (White and Ching 1985).

Crowns 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 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 (Cotterell 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

*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) Claude River, Australia, No. 13229; (4) Abbergworhe, 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), Harkins (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 (Kikuo 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 accuracy of dendrometer bands have been discussed elsewhere (Hall 1944, Mesavage and Smith 1960, Bormann and Kozlowski 1962, Bower and Blocker 1966, Yocom 1970, Auchmoodie 1976, Cameron and Lea 1980, Cattelino 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 Cattelino et al. (1986). All the dendrometer bands were fitted at breast height (1.3 m) on smooth stem. 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 (Richards 1959) fitted to the cumulative diameter growth, were carried out using SAS programmes (SAS 1985). The Richards function used in the present study was

\[ D = a \left(1 + e^{\left(b-cw\right)}\right)^{-1/m} \]

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 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 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, Provenance 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 14.0 cm (No. 13236).
4.3 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 discernible. 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 differences of maximum 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 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 various 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 (R²) 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) (R² = 0.89), while Provenance No. 13237 was the least affected 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 relationship 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 | RAIN|^2 | RH  | (RH)^2 | RHP | R^2 |
|------------|------|------|------|------|------|------|------|------|--------|--------|------|--------|------|--------|------|------|------|------|
| 12992      | 0.022| 0.032*| 0.004|      |      |      |      | 0.677**| 0.026**| 0.023| 0.017| 0.801***|
| 13229      |      |      |      |      |      |      |      |      |        | 0.019 |      | 0.021**|
| 13232      |      |      |      |      |      |      |      |      |        | 0.007| 0.023| 0.017**|
| 13233      | 0.007| 0.018| 0.006|      |      |      |      | 0.630**| 0.005 |      | 0.005 | 0.665**|
| 13234      |      |      |      |      |      |      |      |      |        | 0.005| 0.003| 0.017| 0.015| 0.851**|
| 13235      |      |      |      |      |      |      |      |      |        | 0.016| 0.032| 0.055| 0.032*| 0.808**|
| 13236      | 0.034*| 0.045*| 0.019|      | 0.019| 0.019|      | 0.571**| 0.037*| 0.032*| 0.014 | 0.737**|
| 13237      |      |      |      |      |      |      |      |      |        | 0.006| 0.006| 0.012 | 0.012| 0.846**|
| 13238      |      |      |      |      |      |      |      |      |        | 0.011| 0.013| 0.017 | 0.012| 0.812**|
| 13239      |      |      |      |      |      |      |      |      |        | 0.016| 0.012| 0.014 | 0.011| 0.765**|
| 13240      |      |      |      |      |      |      |      |      |        | 0.007| 0.008| 0.004 | 0.004| 0.846**|
| 13241      |      |      |      | 0.008| 0.008| 0.008|      | 0.656**| 0.010|      | 0.011| 0.747**|
| 13242      |      |      |      | 0.005| 0.005| 0.005|      | 0.699**| 0.029|      | 0.005| 0.812**|
| 13459      |      |      |      |      |      |      |      | 0.738**| 0.021*| 0.014| 0.008| 0.801***|
| 13460      |      |      |      |      |      |      |      | 0.728**| 0.021*| 0.014| 0.008| 0.801***|
| 13621      | 0.014| 0.017| 0.006| 0.022| 0.020| 0.005| 0.612***| 0.015|      | 0.051| 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)
R = Rainfall of the measured week (mm)
RAIN = Rainfall of the previous week (mm)
RH = Relative humidity of the measured week (%)
RHP = Relative humidity of the previous week (%)
R^2 = Coefficient of multiple determination

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

<table>
<thead>
<tr>
<th>Location</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Alt (m)</th>
<th>Mean Temp. (°C)</th>
<th>Mean monthly rainfall (mm)</th>
<th>Mean annual rainfall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cairns</td>
<td>16°33'S</td>
<td>145°45'E</td>
<td>3</td>
<td>421 422 460 264</td>
<td>110 72 39 42 43 50 98 203</td>
<td>2224</td>
</tr>
<tr>
<td>(13233—13234)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cardwell</td>
<td>18°16'S</td>
<td>146°02'E</td>
<td>3</td>
<td>457 466 471 211</td>
<td>92 50 33 29 36 52 107 193</td>
<td>2143</td>
</tr>
<tr>
<td>(13240—13242)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Morehead</td>
<td>8°43'S</td>
<td>141°38'E</td>
<td>3</td>
<td>332 262 318 157</td>
<td>154 86 54 52 38 80 114 224</td>
<td>1913</td>
</tr>
<tr>
<td>(13459)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Duta</td>
<td>9°04'S</td>
<td>143°12'E</td>
<td>3</td>
<td>280 258 325 321</td>
<td>223 108 93 52 42 55 111 204</td>
<td>2063</td>
</tr>
<tr>
<td>(13460)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lad Krating</td>
<td>13°42'N</td>
<td>101°06'E</td>
<td>3</td>
<td>38 22 51 72 102</td>
<td>97 149 197 242 219 36 0 1225</td>
<td>1225</td>
</tr>
</tbody>
</table>
evergreen trees are not uniform but exhibit some seasonal variation associated with external abiotic factors. 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 (Kozlowski 1971, Kramer and Kozlowski 1979). Trees from different geographic areas vary in growth rates, form, and adaptation to environmental conditions (Callaham 1970). Differences in seasonal growth rhythm among tree races reflect 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. The climatic factors, which are 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 is consistent with 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 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, Simmer 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 above-ground 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, Pietarin 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 for 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.

Kozlowski and Peterson (1962) observed the variation in seasonal growth pattern during successive years, indicating extreme sensitivity of diameter growth to environmental stress. Kramer and Kozlowski (1979) stated that cambial growth was generally affected by environmental stress to a larger extent than shoot production. 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 Kozlowski 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 Guevara 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, Leikolu 1969). Kozlowski 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 on 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 to 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 foliar nutrient absorption 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 example, have been reported (Will 1966, Comerford 1973).

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, foliation below the most part of the canopy and from branches with uniform exposure is considered the best to sample (Lowry and Avarad 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. 1967, and Sower and Sower 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 variation. For example, Gerhold (1966) reported significant differences in foliar nitrogen, calcium, magnesium, and iron contents among provenances of 19-year-old Scots pine. Steinbeck (1966) demonstrated differences among provenances 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 broadleaf 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 between foliated nitrogen, potassium (Chutpong et al. 1976), and magnesium (Thaitusa 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. elliottii* (Humphreys and Pitchett 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 Thaitusa (1981). The inconsistency in the results implies that correlations between soil analysis and foliar analysis are dependent upon habitat (cf. Paarlalhhti et al. 1971); and, in certain cases, elements in soil may not be available or they may 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 has an influence also from foliar potassium. Similar results have also been reported for red pine (Hoyle and Mader 1964), loblolly pine (MacCarthy and Davey 1967). Lacey et al. (1966) successfully demonstrated a high correlation between foliar phosphorus concentration and the growth of *Eucalyptus grandis* seedlings. On the other hand, Fuchigami (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 subplots from the corresponding location of 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 using 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 Osen 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 nutrients levels. The same model as the analysis for the variation in growth performance 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 Ranges Test was applied. Simple correlation coefficients 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 54 soil samples were 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

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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 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* phylloids 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 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 provenances 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. 13342 (Australia) had high concentrations of nitrogen (2.74%), phosphorus (0.98%), zinc (25 ppm), and copper (14 ppm), but a small concentration of calcium (0.5%) and iron (163 ppm). In contrast, Provenance No. 13460 (Papua New Guinea) had low levels of nitrogen (1.9%), 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 magnesium (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 presented 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).
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 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 between 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.

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### 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.

<table>
<thead>
<tr>
<th>Nutrient elements</th>
<th>Source of variation</th>
<th>Among provenances (df 15, 54)</th>
<th>Within provenances (df 5, 54)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen, %</td>
<td>1.63**</td>
<td>0.88**</td>
<td></td>
</tr>
<tr>
<td>Phosphorus, %</td>
<td>0.91**</td>
<td>0.41**</td>
<td></td>
</tr>
<tr>
<td>Potassium, %</td>
<td>1.98**</td>
<td>4.09**</td>
<td></td>
</tr>
<tr>
<td>Calcium, %</td>
<td>3.16**</td>
<td>16.60**</td>
<td></td>
</tr>
<tr>
<td>Magnesium, %</td>
<td>3.74**</td>
<td>1.70**</td>
<td></td>
</tr>
<tr>
<td>Iron, ppm</td>
<td>1.65**</td>
<td>3.30**</td>
<td></td>
</tr>
<tr>
<td>Copper, ppm</td>
<td>1.52**</td>
<td>5.15**</td>
<td></td>
</tr>
<tr>
<td>Manganese, ppm</td>
<td>2.50**</td>
<td>12.50**</td>
<td></td>
</tr>
<tr>
<td>Zinc, ppm</td>
<td>0.69**</td>
<td>1.04**</td>
<td></td>
</tr>
<tr>
<td>Sodium, ppm</td>
<td>1.32**</td>
<td>1.50**</td>
<td></td>
</tr>
</tbody>
</table>

Significance levels of the F-value: ** p < 0.01; * p < 0.05; ns significant at p < 0.05

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### 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.

<table>
<thead>
<tr>
<th>Proven. No.</th>
<th>% dry weight</th>
<th>ppm in dry weight</th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>Ca</th>
<th>Mg</th>
</tr>
</thead>
<tbody>
<tr>
<td>13294</td>
<td>2.53**</td>
<td>0.99%</td>
<td>1.282</td>
<td>0.504</td>
<td>0.124</td>
<td>0.071</td>
<td>0.064</td>
</tr>
<tr>
<td>13295</td>
<td>2.59**</td>
<td>0.89%</td>
<td>1.105</td>
<td>0.559</td>
<td>0.132</td>
<td>0.066</td>
<td>0.056</td>
</tr>
<tr>
<td>13296</td>
<td>2.83**</td>
<td>0.92%</td>
<td>1.376</td>
<td>0.453</td>
<td>0.130</td>
<td>0.067</td>
<td>0.069</td>
</tr>
<tr>
<td>13297</td>
<td>2.34**</td>
<td>0.92%</td>
<td>1.144</td>
<td>0.500</td>
<td>0.106</td>
<td>0.050</td>
<td>0.050</td>
</tr>
<tr>
<td>13298</td>
<td>2.45**</td>
<td>0.88%</td>
<td>1.157</td>
<td>0.504</td>
<td>0.114</td>
<td>0.055</td>
<td>0.055</td>
</tr>
<tr>
<td>13299</td>
<td>2.45**</td>
<td>0.76%</td>
<td>1.010</td>
<td>0.663</td>
<td>0.136</td>
<td>0.080</td>
<td>0.080</td>
</tr>
<tr>
<td>13300</td>
<td>2.05**</td>
<td>0.83%</td>
<td>1.079</td>
<td>0.694</td>
<td>0.160</td>
<td>0.069</td>
<td>0.069</td>
</tr>
<tr>
<td>13301</td>
<td>2.45**</td>
<td>0.86%</td>
<td>1.153</td>
<td>0.598</td>
<td>0.149</td>
<td>0.053</td>
<td>0.053</td>
</tr>
<tr>
<td>13302</td>
<td>2.40**</td>
<td>0.88%</td>
<td>1.287</td>
<td>0.566</td>
<td>0.134</td>
<td>0.054</td>
<td>0.054</td>
</tr>
<tr>
<td>13303</td>
<td>2.59**</td>
<td>0.92%</td>
<td>1.344</td>
<td>0.405</td>
<td>0.139</td>
<td>0.066</td>
<td>0.066</td>
</tr>
<tr>
<td>13304</td>
<td>2.42**</td>
<td>0.83%</td>
<td>1.157</td>
<td>0.510</td>
<td>0.137</td>
<td>0.056</td>
<td>0.056</td>
</tr>
<tr>
<td>13305</td>
<td>2.42**</td>
<td>0.88%</td>
<td>1.208</td>
<td>0.535</td>
<td>0.116</td>
<td>0.052</td>
<td>0.052</td>
</tr>
<tr>
<td>13306</td>
<td>2.42**</td>
<td>0.88%</td>
<td>1.289</td>
<td>0.505</td>
<td>0.141</td>
<td>0.055</td>
<td>0.055</td>
</tr>
<tr>
<td>13307</td>
<td>2.34**</td>
<td>0.83%</td>
<td>1.110</td>
<td>0.619</td>
<td>0.146</td>
<td>0.072</td>
<td>0.072</td>
</tr>
<tr>
<td>13308</td>
<td>1.95**</td>
<td>0.696%</td>
<td>0.969</td>
<td>0.581</td>
<td>0.128</td>
<td>0.068</td>
<td>0.068</td>
</tr>
<tr>
<td>13309</td>
<td>2.49**</td>
<td>0.88%</td>
<td>1.281</td>
<td>0.489</td>
<td>0.117</td>
<td>0.055</td>
<td></td>
</tr>
</tbody>
</table>

---

Figure 10. Proportionately ranked means for foliar nutrient concentrations in 16 provenances of 30-month-old *A. mangium*, including overall means (G).
Table 24. Correlation coefficients (r) matrix of foliar nutrient concentrations of 30-month-old *A. mangium* at Lad Krating Provenance Trial, Chachoengsao.

<table>
<thead>
<tr>
<th>Variable</th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>Ca</th>
<th>Mg</th>
<th>Zn</th>
<th>Mn</th>
<th>Fe</th>
<th>Cu</th>
<th>Na</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>1.00</td>
<td>0.65**</td>
<td>0.50**</td>
<td>-0.23</td>
<td>0.04</td>
<td>0.05</td>
<td>0.10</td>
<td>-0.03</td>
<td>0.12</td>
<td>0.15</td>
</tr>
<tr>
<td>P</td>
<td>1.00</td>
<td>-0.68**</td>
<td>-0.36**</td>
<td>-0.12</td>
<td>0.10</td>
<td>-0.16</td>
<td>-0.13</td>
<td>0.01</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td>K</td>
<td>1.00</td>
<td>0.20</td>
<td>-0.67**</td>
<td>-0.31*</td>
<td>-0.07</td>
<td>-0.39**</td>
<td>-0.09</td>
<td>-0.14</td>
<td>-0.09</td>
<td></td>
</tr>
<tr>
<td>Ca</td>
<td>1.00</td>
<td>0.40**</td>
<td>0.08</td>
<td>0.31*</td>
<td>0.02</td>
<td>0.23</td>
<td>0.05</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mg</td>
<td>1.00</td>
<td>0.10</td>
<td>0.15</td>
<td>-0.04</td>
<td>0.20</td>
<td>0.31*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zn</td>
<td>1.00</td>
<td>0.37**</td>
<td>0.09</td>
<td>0.10</td>
<td>-0.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mn</td>
<td>1.00</td>
<td>0.08</td>
<td>0.16</td>
<td>0.13</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fe</td>
<td>1.00</td>
<td>-0.54**</td>
<td>-0.09</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cu</td>
<td>1.00</td>
<td>0.07</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Na</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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 | N, % | P, % | K, % | Ca, % | Mg, % | Zn, ppm | Mn, ppm | Fe, ppm | Cu, ppm | Na, ppm | pH | N, ppm | P, ppm | K, ppm | Ca, ppm | Mg, ppm | Zn, ppm | Mn, ppm | Fe, ppm | Cu, ppm | Na, ppm |
|------|------|------|------|-------|-------|---------|---------|---------|---------|---------|-----|-------|-------|-------|---------|-------|---------|---------|---------|---------|-------|--------|
| N    | 0.10 | 0.23 | 0.24* | -0.01 | 0.05 | 0.07 | -0.49* | -0.12 | 0.20 | -0.75* |
| P    | 0.15 | 0.22 | 0.36** | -0.21 | -0.17 | 0.06 | -0.16 | -0.25* | -0.02 | -0.05 |
| K    | 0.01 | 0.21 | 0.28* | -0.07 | -0.12 | 0.26* | -0.35* | 0.19 | -0.06 | -0.24* |
| Ca   | 0.07 | 0.22 | 0.15 | 0.09 | 0.04 | -0.19 | -0.45** | -0.06 | 0.16 | -0.04 |
| Mg   | 0.10 | 0.14 | 0.12 | 0.05 | 0.04 | -0.19 | -0.26* | 0.04 | 0.19 | -0.05 |
| Zn   | 0.02 | 0.08 | 0.00 | -0.03 | 0.11 | 0.09 | -0.16 | -0.21 | 0.10 | 0.30* |
| Mn   | 0.02 | 0.11 | 0.05 | -0.04 | 0.07 | 0.05 | -0.21 | 0.03 | 0.04 | -0.02 |
| Fe   | 0.07 | 0.15 | 0.02 | -0.02 | 0.06 | -0.21 | 0.10 | 0.17 | -0.05 | -0.02 |
| Cu   | 0.07 | 0.15 | 0.02 | -0.02 | 0.06 | -0.21 | 0.10 | 0.17 | -0.05 | -0.02 |
| Na   | -0.13 | 0.00 | -0.06 | 0.09 | -0.08 | -0.23 | -0.06 | 0.09 | 0.07 | -0.27* |
| pH   | 0.62 | 0.95 | 0.35 | 0.35 |

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.

<table>
<thead>
<tr>
<th>Provenance</th>
<th>Height (m)</th>
<th>DBH (cm)</th>
<th>Crown diameter (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>13292</td>
<td>8.00**</td>
<td>13.82**</td>
<td>4.94**</td>
</tr>
<tr>
<td>13329</td>
<td>8.87**</td>
<td>14.75**</td>
<td>5.70*</td>
</tr>
<tr>
<td>13332</td>
<td>7.22</td>
<td>13.08**</td>
<td>4.76*</td>
</tr>
<tr>
<td>13333</td>
<td>6.92**</td>
<td>11.50*</td>
<td>4.39*</td>
</tr>
<tr>
<td>13334</td>
<td>7.10**</td>
<td>12.12*</td>
<td>4.90*</td>
</tr>
<tr>
<td>13335</td>
<td>7.41**</td>
<td>12.87*</td>
<td>4.30*</td>
</tr>
<tr>
<td>13336</td>
<td>7.00*</td>
<td>12.50*</td>
<td>4.55*</td>
</tr>
<tr>
<td>13337</td>
<td>7.92**</td>
<td>12.80*</td>
<td>4.51*</td>
</tr>
<tr>
<td>13338</td>
<td>7.40*</td>
<td>13.37*</td>
<td>4.60*</td>
</tr>
<tr>
<td>13339</td>
<td>7.78**</td>
<td>13.37*</td>
<td>5.05*</td>
</tr>
<tr>
<td>13340</td>
<td>7.92**</td>
<td>13.22*</td>
<td>4.96*</td>
</tr>
<tr>
<td>13341</td>
<td>8.65**</td>
<td>13.75*</td>
<td>4.59*</td>
</tr>
<tr>
<td>13342</td>
<td>8.25*</td>
<td>13.37*</td>
<td>5.12*</td>
</tr>
<tr>
<td>13450</td>
<td>9.07*</td>
<td>15.50*</td>
<td>5.05*</td>
</tr>
<tr>
<td>13460</td>
<td>8.35**</td>
<td>13.50*</td>
<td>5.06*</td>
</tr>
<tr>
<td>13621</td>
<td>7.75**</td>
<td>12.90*</td>
<td>4.86*</td>
</tr>
<tr>
<td>Mean</td>
<td>7.84</td>
<td>13.27</td>
<td>4.83</td>
</tr>
<tr>
<td>SD</td>
<td>0.62</td>
<td>0.95</td>
<td>0.35</td>
</tr>
<tr>
<td>F-value</td>
<td>3.56**</td>
<td>1.94*</td>
<td>0.96**</td>
</tr>
</tbody>
</table>

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

5.4. Discussion

Foliar nutrient contents have frequently been shown to exhibit genetic variation (Burley and Wood 1976). The main importance of foliar analysis in the evaluation of soil nutrient deficiencies. However, in evaluating the effect of soil nutrient deficiency, the possibility of differences in nutrient demand 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, Thailutta 1981), they were generally similar to those reported for other tropical broadleaves species. For
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* needle 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, respectively (Lee 1968). 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* phylloids in the present 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) correspond 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 cannot 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-nutrient concentrations 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 kestia*, provenances (Thaitusa 1981). There have been surprisingly few studies which have examined the genetic variation in foliar nutrient concentrations in 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 impregnating in determining the foliar nutrient concentrations as concentration are low.

Although no consistent ranking 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 ranks 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 change 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 (Khanja 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 (Kranz 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 content. 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, Paarlathi et al. (1971) and Veijalaenen (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. PHYLOLDE 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. Pykkö 1966).

The stomata normally serve as the principal 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 stomatal complexes (Johnson and Rosen 1981), as well as the role of stomata in regulating plant water status (Holmgren et al. 1965, Siwecki and Kozlowski 1973, Davies et al. 1974) and net photosynthesis (Luukkainen and Kozlowski 1972, Pieters and Zima 1975, Luukkanen 1978).

Basic aspects of stomatal behavior have been reviewed earlier e.g. Meinzer and Mansfield (1965), 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 Kozlowski 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 within the same species.

Besides genetic characters, environmental conditions have been shown to influence the structure, size and frequency of stomata. Plants grown under optimal moisture conditions 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 Rasmussen 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, Prunus 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 Rasmussen 1970), wheat (Teare et al. 1971), and apple (Slack 1974). For forest trees, the variation has been reported in Populus (Siwecki and Kozlowski 1973, Pallardy and Kozlowski 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 margin 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 (Cowan 1935).

Despite a number of investigations into the leaf size of forest trees, adequate studies in tropical trees are still lacking. Cirtimon (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 pores dimensions were associated with the low water vapor pressure gradients between leaf and air. Pyykö (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 Trairum (1977) and Riwuang (1986). However, the inter-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. Phylloide anatomy**

Mature phylloides 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 3). The details of provenance sources and the study area have been described in Chapter 3 (6.2.1, Table 3). Sections of 5 x 5 mm² were cut from the middle part of the phylloides, perpendicular to the midrib, and fixed in formalin-acetic acid-ethanol (FAA). The material was then taken to the 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 microm thick) were placed on glass slides, stained with safranin-fast green and mounted in Canada balsam (Johannsen 1940).

For viewing under a scanning electron microscope (SEM), fresh sections of 5 X 5 mm² were excised from the mid-portions of the phylloides 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 phylloide surfaces were taken with Duco cement (containing butyl acetate and acetone), placed on a glass slide and examined at X40 magnification under a microscope. Stomatal frequency was determined by tallying the number of stomata of five microscope fields, and the number of stomata per mm² 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 phylloides of one open-pollinated *A. mangium* tree were randomly collected throughout the crown. The phylloides were then divided into three parts from the tip to the base. Impressions of adaxial and abaxial phylloide 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 phylloides 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 phylloide surfaces at the middle point of the phylloide. 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 analysis 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 phylloide anatomy**

The flattened leaf-like petiole of the *A. mangium* phylloide was sclerophyllous and glabrous. The epidermis was heavily cutinized on both surfaces, and cells were square or rectangular in transection (Fig. 15a, b). The phylloide 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 allowed for a limited intercellular air space, except in the substomal chamber beneath the guard cells (Fig. 15b).

The *A. mangium* phylloide was found to be amphotomatus, with numerous stomata on both surfaces of the phylloide. 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 phylloide. 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 phylloide, 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 phylloide. 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 chlorenchyma cells. Beneath the epidermis a multilayer of sclerenchyma cells developed, which were of the angular or annular sclerenchyma type
(Fig. 15c). Abundant sclerenchyma tissue developed in association with the vascular bundles (Fig. 15c).

No anatomical differences in the phyllose 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 phyllose

The size and frequency of stomata were quite variable on both surfaces of the phyllose. 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 phyllose. The length of guard cell varied considerably but no systematic differences among locations on the phyllose were found. The mean and standard deviations of stomatal size and frequency over a single phyllose of *A. mangium* are presented in Table 29. Smaller deviations among subsamples taken at the middle of the phyllose were observed. No significant differences were found between the phyllose surfaces, nor among positions on the phyllose. 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 large variation in the numbers of stomata among provenances. Stomatal frequency varies from 343 to 421 stomata/mm², with an average of 387 stomata/mm². The provenance with the highest 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* phyllose. 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 phylloids 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 phylloide of *Acacia* sp. was homologous to the petiole and rachis of a pinnately compound leaf. This is in contrast to phylloides of *Oxalis* sp., in which the petiole of a palmate compound leaf looses 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 phylloides 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 phylloide structure, since native stands of phyllodineous and non-phyllodineous species occur together in the same regions.

*A. mangium* phylloide is a simple structure. The phylloide is glabrous, without hairs or trichomes. The non-hairiness of plants is a common characteristic of species growing in shady and wet habitats (cf. Pykkö 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 phylloides are normally associated with xeromorphy, the stoma of *A. mangium* are of the paracistic 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 < μ < 38 μm). In general, stomatal size and frequency are inversely correlated (Miskin and Rasmusson 1970, Davies and Kozlowski 1974). Species with few 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 phylloide (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. mun-
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 Kozlowski 1979, Kramer 1983). The transpiration rate is controlled by stomatal activity and the physical factors that control vaporization. The physiological process and the factors affecting transpiration in trees have been discussed in detail by several investigators (Kozlowski 1968, 1982; Lange et al. 1976, Kramer and Kozlowski 1979, Turner and Kramer 1980, Jarvis and Mansfield 1981, Lange et al. 1982, Kramer 1983, Lar- cher 1983).

One of the most important external factors affecting the rate is the water availability of soil water (Hsiao 1973). Numerous investigations concerning the water relations of plants under conditions of soil water stress have been carried out (Lotubinsky and Klock 1974, Unterscheutz et al. 1974, Davies and Kozlowski 1975, Lukakken et al. 1975, Kelliher et al. 1980, Orlander and Due 1986, Abrams 1988). When plant water stress develops, the transpiration rate is at first maintained by 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 Kozlowski (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 leaves are 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 Slavik (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, Orlander 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 Slavik (1974). Of the techniques, the method most popularized by Scholander et al. (1965) for measuring tissue water potentials, is considered to be a reliable method for characterizing plant water status (Barra 1968).

Studies on plant water potential measures using the pressure chamber techniques have been reported by a number of investigators (Beadle et al. 1979, Pallardy and Kozlowski 1979b, Cleary and Zaerri 1980, and Orlander and Due 1986). The equipment is simple and convenient, especially for the field measure- ment. 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 Kozlowski 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 (Hockley 1970, Siwecki and Kozlowski 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 originates 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 an 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 Hyytsälä, 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, No. 13421) 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 B), 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 %. HDI 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 g of plant 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 < 200 % moisture, calculated from pot 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](image_url)
estimated using a pressure membrane apparatus. These measurements indicated that the water content (calculated from peat dry weight) at the field capacity (-0.01 MPa) was 741%, and at permanent wilting point (-1.5 MPa) was 69%. These values are similar to those reported for garden peat by Puustjärv (see Vaanten 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 computations 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 (19:00–07:00 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 70% 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-

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.

<table>
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<tr>
<th>Provenance</th>
<th>No.</th>
<th>Control</th>
<th>Stress</th>
<th>Control</th>
<th>Stress</th>
<th>Control</th>
<th>Stress</th>
<th>Control</th>
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Significance levels of the F-test: *p < 0.05; **p < 0.01; ***p < 0.001; n.s. not significant at p < 0.05.

Atipenerpas, L.

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.

Atra Forskalis Fraxin 206.
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 rewatered 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 transpiration 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
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.

<table>
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<th>Provenance</th>
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<th>Afternoon Control</th>
<th>Afternoon Stress</th>
<th>Days of stress treatment</th>
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</tr>
<tr>
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<td>78.51 55.17</td>
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<td>44.15 39.03 25.20 25.46</td>
</tr>
<tr>
<td>F</td>
<td></td>
<td>2.24b 3.09a</td>
<td>2.12a 2.28b</td>
<td>1.90ab 2.23b</td>
<td>2.01ab 2.95a 0.79ab 2.58a</td>
</tr>
</tbody>
</table>

Significance levels of the F-test: ** p < 0.01  * p < 0.05  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. Data represent individual seedlings.

<table>
<thead>
<tr>
<th>Leaf conductance (% control)</th>
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<tr>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Figure 22. Leaf conductance (% control) for the control and stress treatments and soil moisture contents of 0.1, 0.05, and 0.01 for the six provenances.

Figure 23. Leaf conductance (% control) for the control and stress treatments and soil moisture contents of 0.1, 0.05, and 0.01 for the six provenances.

Figure 24. Leaf conductance (% control) for the control and stress treatments and soil moisture contents of 0.1, 0.05, and 0.01 for the six provenances.

Figure 25. Leaf conductance (% control) for the control and stress treatments and soil moisture contents of 0.1, 0.05, and 0.01 for the six provenances.

Figure 26. Leaf conductance (% control) for the control and stress treatments and soil moisture contents of 0.1, 0.05, and 0.01 for the six provenances.
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 phylloides, 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).

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 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 Kozlowski 1976). Observations 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 mg cm⁻² 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 mg cm⁻² h⁻¹ in western Australia (Hellmuth 1969). In comparison, Kaul and Negi (1979) reported that *Eucalyptus tereti-
Cercis canadensis; provenances from xeric habitats were least affected by water stress. In contrast, Kelber 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 noted 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 Kozlowski (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 (30.0 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. Hennesey 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 amphiathomas species, a more sensitive response in the adaxial stomata has been reported in many species (Pereira and Kozlowski 1978, 1976, Pattanakiat 1983, Kozlowski et al. 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, as stomatal conductance occurs within very narrow limits of leaf water potential and the stomata close at a leaf water potential of ~0.1 MPa (Vapaavuori 1981, 1980). In Sitka spruce, the critical leaf water potential is ~2.0 MPa, and in Scots pine is ~1.5 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 (Quarishi and Kramer 1970). When A. mangium showed signs of wilting, the leaf 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 ~3.5 MPa. The minimum leaf water potentials obtained in A. mangium in the present study were much higher than those reviewed by Kozlowski (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 Hinckery 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 (Cammas 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, Samuudin and Impens 1979, Lapidó et al. 1984, Natarahana 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, Louworse and Zwerde 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, Korpilhati 1988), and the effect of such external factors as the photoperiod (McGregor et al. 1961, Gordon and Gautherum 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, photosynthesis and a rapid 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, demonstrated 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).

Photosynthesis 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 photosynthesis 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 investigators to suggest that photosynthesis 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. 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 (Vapaavouri 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 photosynthesis rate. It is also used in the determination of photosynthesis 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, Bakov 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 characteristices. 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 Korpilhati (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. 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 temperatures, 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, 1971, 1972, Benner 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. The CO₂ compensation point is therefore (Kramer 1979).

Many investigators have tried to use photosynthetic rates as indices of growth potential of trees. However, a number of investigations 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 ponderosa (Sweet and Waring 1968), and Pinus sylvestris (Gordon and Gautherum 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 are given in Chapter 7 (7.2.1). The provenances used in this Chapter are as follows: Provenance No. 1329 = No. 1, Provenance No. 1326 = No. 2, Provenance No. 1340 = No. 3, Provenance No. 1345 = No. 4, Provenance No. 1340 = No. 5, and Provenance No. 1362 = 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, Korpilhati 1988). A data-logging unit was used to control the measuring system and collect the data. For each gas exchange measurement, a single intact phyllochron was sampled in the water-jacketed plexiglass leaf assimilation chamber, 2,132 dm² in volume. The phyllochron was held in a horizontal position and radiated from above using a 400 W HQI-T lamp. The flow rate of air in the measuring 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. The light intensity at the level of the leaf was monitored with a quantum sensor (Li-Cor LI-1858/1988) placed close to the leaf. 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 μmol m^{-2} 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 minutes was adequate when changing the temperature; and it was also found that there was no significant effect of the time of day on CO₂ exchange. Values of CO₂ compensation point at each temperature mentioned were obtained by recording the equilibrium concentration of CO₂ 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 μmol m^{-2} s^{-1}. Only net photosynthetic rates were recorded for the light response curve.

At all temperatures, the same phylloide of the same seedling was used. The area of the measured phylloides were determined by a photographic method. Rates of gas exchange were expressed as mg CO₂ dm⁻¹ h⁻¹ for a single side of the phylloide. At the end of the experiment, all seedlings were harvested and the dry weights of phylloides, 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 ERAS setup (cf. Hari et al. 1979). Photosynthesis rates were calculated on the basis of the CO₂ compensation point and net photosynthetic rates at the given temperatures according to the extrapolation method described by Forrester et al. (1966) and Luskkanen (1976). Total photosynthesis was derived from the sum of net photosynthesis and calculated photospiration.

Figure 25. (a) Total photosynthesis (Pₚ) and net photosynthesis (Pₚ₋ₚᵢ), and (b) photospiration (Rᵢ) and dark respiration (Rₛ), per gram (dry weight) and phylloide area (single surface) in relation to temperature in A. mangium (all six provenances combined). The curves are hand-fitted.

8.3. Results

8.3.1. Responses of CO₂ exchange characteristics to temperature and irradiance

The average CO₂ exchange characteristics of A. mangium expressed per unit of projected phylloide surface area and phylloide dry weight are summarized in Table 34. Since the phylloides 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 increase up to 30°C. The continued increase in the calculated total photosynthetic rate was caused by an upsurge in the photospiration rate. However, both net and total photosynthesis showed decreasing trends above 30°C (Fig. 25a and Table 34).

Both photospiration and dark respiration increased with temperature, increasing more rapidly at temperatures higher than 30°C (Fig. 25b and Table 34). The calculated photospiration 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 CO₂ exchange balance in A. mangium occurred near 25°C in the present experiment.

The response of net photosynthesis to the external CO₂ concentration, including an extrapolation to zero CO₂ concentration, at different temperatures is illustrated in Fig. 26. The rate of photosynthesis increased linearly with CO₂ concentration, but tended to remain constant (or at lower temperature) slightly decreased when the CO₂ concentration approached 500 ppm. The slope of the response line indicating the relationship between net photosynthesis and CO₂ concentration, which describes the "carboxylation efficiency" as defined by Tregunna et al. (1966), increased with temperature up to 30°C and remained constant thereafter up to 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 μmol m⁻² s⁻¹ of "photosynthetically active radiation", (PAR) and then remained constant with no statistical differences between 600 and 1000 μmol m⁻² s⁻¹. 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 μmol m⁻² s⁻¹ of "photosynthetically active radiation", (PAR) and then remained constant with no statistical differences between 600 and 1000 μmol m⁻² s⁻¹.

8.3.2. Variation in CO₂ exchange characteristics among provenances

The phylloide area and the phylloide weight of A. mangium were highly correlated (r² > 0.9) in the present study, and only the rates expressed...
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 provenences 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 extreme 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 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 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.
Photorespiration and 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 rate of photosynthesis 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 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 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 saturated at around 600 µmol m⁻²s⁻¹ PAR, with no significant increase at the higher photon flux density (1000 µmol m⁻² s⁻¹ PAR). Statistical analyses showed no interaction between provenance and light intensity in CO₂ exchange rates.

### Table 37. Average photosynthesis/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.

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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.

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

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-

Table 38. Matrix correlations between CO₂ exchange parameters of *A. Mangium* seedlings, with six provenances pooled. Symbols represent net photosynthesis (Pn), total photosynthesis (P), photorespiration (Rm), dark respiration (Rd), and CO₂ compensation point (T).

<table>
<thead>
<tr>
<th>P</th>
<th>P</th>
<th>R</th>
<th>R</th>
<th>T</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.00</td>
<td>0.80*</td>
<td>0.00</td>
<td>-0.10</td>
<td>-0.24**</td>
</tr>
<tr>
<td>1.00</td>
<td>0.50*</td>
<td>0.20</td>
<td>0.30**</td>
<td>0.33**</td>
</tr>
<tr>
<td>1.00</td>
<td>-0.10</td>
<td>0.90**</td>
<td>0.59**</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Significance levels of correlation: * p < 0.05, ** p < 0.01
respiration, dark respiration as well as the CO₂ compensation point (P < 0.01). An increase in total photosynthesis, photosynthesis or dark respiration was generally associated with an increase in the CO₂ compensation point. In contrast, an increase in the CO₂ 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 phyllopy 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 CO₂ 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 μmol m⁻² s⁻¹ PAR are shown here). The photosynthetic rate (leaf area basis) showed a highly significant (p < 0.01) negative correlation with seedling dry weight. Provenance No. 4, which showed the lowest photosynthetic rates, had the fastest dry matter production. Noticeably, the photosynthetic rates expressed on phyllopy dry weight basis were not correlated with the total dry matter accumulation, but rather with total phyllopy dry weight (p < 0.05). This might have been due to the fact that the phyllopy of A. mangium contains much non-photosynthesizing tissue. It is therefore possible that the CO₂ 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.

Table 39. Correlation coefficients for the relationship between CO₂-exchange parameters and total seedling dry weight or phyllopy dry weight in 10-month-old A. mangium seedlings (rates measured at 18°C temperature and 1,000 μmol m⁻² s⁻¹ irradiance only).

<table>
<thead>
<tr>
<th>CO₂ exchange parameter</th>
<th>Total dry weight</th>
<th>Phyllopy dry weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Net photosynthesis (area basis)</td>
<td>-0.810**</td>
<td>-0.756**</td>
</tr>
<tr>
<td>Net photosynthesis (dry wt. basis)</td>
<td>-0.366</td>
<td>-0.427*</td>
</tr>
<tr>
<td>Total photosynthesis (area basis)</td>
<td>-0.739**</td>
<td>-0.708**</td>
</tr>
<tr>
<td>Total photosynthesis (dry wt. basis)</td>
<td>-0.265</td>
<td>-0.337</td>
</tr>
<tr>
<td>Photosynthesis (dry wt. basis)</td>
<td>-0.052</td>
<td>-0.058</td>
</tr>
<tr>
<td>Dark respiration (area basis)</td>
<td>-0.005</td>
<td>-0.017</td>
</tr>
<tr>
<td>Dark respiration (dry wt. basis)</td>
<td>-0.094</td>
<td>-0.076</td>
</tr>
</tbody>
</table>

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

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 phyllopy dry weight (r = 0.93) and to total phyllopy 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 CO₂ 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 Klings (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-Sharkawy and Hesekht 1965, Robichaux and Peary 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 in the range of variation previously reported for tropical rain forest tree species (3.22 mg CO₂ dm⁻² h⁻¹; Larcher 1983). The rates expressed per unit dry weight were higher than the rates expressed per unit photosynthetic surface area per leaf (1.4 mg CO₂ cm⁻² h⁻¹; Larcher and Shaffer 1987). This is, generally, a characteristic of broadleaved species (Zelazowski and Walker 1976). The response curve of the net photosynthetic rate of A. mangium to temperature was approximately parabolic in shape (Fig. 25a), resembling the corresponding curves reported for other species (Krueger and Ferrell 1965, Luukkanen and Kozlowski 1972, Neilson et al. 1972, Osunubi and David 1980). The maximum photosynthetic rate of A. mangium averaged 9.1 mg CO₂ dm⁻² h⁻¹ (single surface) or 13.7 mg CO₂ g⁻¹ h⁻¹ (dry wt.). This is not a particularly high rate when compared to reported rates for temperate tree species. For instance, Luukkanen and Kozlowski (1972) reported an average rate of 18.6 mg CO₂ dm⁻² h⁻¹ in Populus clones, and Zelazowski et al. (1973) reported the extremely high rate of 35 mg CO₂ dm⁻² h⁻¹ in fully exposed 5-week-old Pinus sylvestris seedlings. However, the rates obtained in the present study were considerably lower compared to the maximum photosynthetic rate of 25.9 mg CO₂ dm⁻² h⁻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. (1986) for 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 Jordan 1969). 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 tropics exceed the optimum temperature 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. Larcher and Fig. 25b). The calculated photosynthesis 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 respirations increased more than the thermal compensation temperature than photosynthesis. 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 the atmosphere (Luukkanen and Kozlowski 1972, Beadle et al. 1981, Doehlert and Walker 1981, Teskey and Shaffer 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 concentration which might occur in the field could cause large changes in the rates of photosynthesis, especially at high temperatures. Mostly, 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) increased. The photosynthetic carbon assimilation 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 to the species, considering the high temperatures and a significant decrease in the 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 temperature (Frankland 1973) and by other environmental 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 the temperature, 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 Kozlowski 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, Robson 1985, 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⁻² s⁻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⁻² s⁻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 for the growth 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 (Pepin and Hagen 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 boreal populations (Gordon and Gathamer 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 material 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 photosynthetic rate of Provenance No. 1 (Australia) and No. 6 (Indonesia) occurred near 30°C, while the remaining provenances had maximum net photosynthetic rates 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 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 photosynthesis has generally been underestimated in the past but has been brought to the fore in several investigations since the early 1970s (cf. Zelitch 1971). In the present study, a nearly linear temperature response of photosynthesis was found in all provenances. The calculated photosynthetic rates were higher than the measured dark respiration rate. Provenance No. 6 (Indonesia) showed a particularly high rate of photosynthesis which was associated with a high total photosynthetic rate and high net CO₂ gain; 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 photosynthetic 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 photosynthesis reflects the ratio between carboxylase and oxygenase activities, which are responsible for both CO₂ fixation and photosynthetic carbon release. In the present study,
the ratio of net photosynthesis to photosynthesis 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/photosynthesis 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/photosynthesis 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, photosynthesis 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 photosynthesis. Results from poplar clones indicate that the photosynthesis/dark respiration ratio may vary considerably among different genotypes under identical environmental conditions (Luukkanen and Kozlowski 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 Kozlowski 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 temperatures, 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 photosynthetic 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, Faschun (1978) found that photosynthetic rates per unit leaf area of older leaves of *Populus x euramericaica* 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 phylloide 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 conditions 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 South East Asia. 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 nitrifying species and 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 and others 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 4) indicate 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.

Rootpruning 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 treatments, such as fertilization. A. mangium is generally poor at self-pruning. Wide spacing will lead to the development of thick branches, and thus root spacing is preferable. A spacing of 3 x 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 fungus.

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 intra-specific differences in the ability of A. mangium to produce root nodules. Further investigations are also needed to select Rhizobium strains with 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 because 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 therefore important in industrial plantations of A. mangium.

In the present study, the mineral composition of A. mangium foliage (Chapter 5) indicated significant variation among populations, especially with respect to 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 height growth among provenances. Consequently, the selection of provenances suitable to specific sites on the basis of nutrient accumulation and utilization characteristics should also be considered.

A. mangium is phylloendemic acacia species with an amphistomatous phylloide. The stomata 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 phylloide. 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. Without signs 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 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 all progressively 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 0.2 MPa without any 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 gravimetrically, 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 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·m⁻²·s⁻¹. The rates are lower than those commonly found for other tropical plants. Genetic differences among provenances existed in the rates of net and total photosyn-
thesis, and photospiration. 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 phylloide 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. Phylloide 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.

REFERENCES

Burdon, R.D. 1976. Foliar macronutrient concentra-


Total of 369 references
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