

Growth performance and lignin content of *Acacia mangium* Willd. and *Acacia auriculiformis* A. Cunn. ex Benth. under normal and stressed conditions

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Abstract

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Acacia mangium Willdenow and *Acacia auriculiformis* A. Cunningham ex Bentham are fast-growing species with wide environmental adaptability. Fast-growing species which thrive in otherwise non-arable problematic soil and which hold the added advantage of improving the condition of the soil, can be used to increase production area, and, thus, are highly desired. We investigated the growth performance and lignin content under normal and stressed conditions for these *Acacia mangium* Willd. and *Acacia auriculiformis* A. Cunn. ex Benth. Normal growing conditions was represented by fertile soil, high water-holding capacity due to low soil drainage, high organic matter, low soil temperature, overall consistent rainfall and relatively milder temperatures, whilst stressed conditions were achieved with a sandy soil with low fertility, low water-holding capacity due to high drainage and low organic matter, and high soil temperature accompanied by inconsistent monthly temperature and rainfall. Growth performance under normal conditions was significantly better compared to the stressed conditions. *A. mangium* performed better than *A. auriculiformis* under the normal conditions. However *A. auriculiformis* performed better under stressed conditions due to better adaptability. The lignin content under normal conditions fluctuated from one DBH class to another. As for the stress conditions, *A. mangium* exhibited incremental increases in lignin content with increasing biomass. In contrast, lignin content in *A. auriculiformis* decreased with increasing biomass. The differences in performance may be attributable to both the micro- and macro-environments and adaptive differences between the two species. For growth under normal conditions, *A. mangium* appears to be the superior choice, whereas for problematic soils, *A. auriculiformis* can be recommended. However, for the selection of superior plants with a combination of desired growth rates and lower lignin content the breeding of interspecific hybrids would be a desirable approach.

Keywords: climate change; marginal lands; tree breeding; pulp production; pulp quality

Acacia Miller is a widespread genus that occurs naturally on all continents except Europe and Antarctica (MASLIN et al. 1998). It is com-

prised of three subgenera: *Acacia* and *Aculeiferum* which are pantropical, occurring from Central and South America, through Africa to Southeast Asia,

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and *Phyllodineae* which occurs primarily in Australia (ROSS 1981). Over 1,200 species have been described, 955 of which are confined to Australia (MASLIN et al. 1998).

Commercial plantations have been developed for the tropical species *Acacia mangium* Willdenow, *Acacia auriculiformis* A. Cunningham ex Benth, *Acacia crassiparpa* A. Cunningham ex Benth, and the temperate species *Acacia melanoxylon* R. Brown, *Acacia saligna* (Labillardière) H.L. Wendland, and *Acacia mearnsii* De Wildeman (DORAN, TURNBULL 1997), from the subgenus *Phyllodineae*. *Acacia arabica* (Lamarck) Willdenow and *Acacia senegal* (Linnaeus) Willdenow, from subgenus *Acacia*, have also been established in plantations (CABI 2000). Acacias are legumes (subfamily *Mimosoidae*) that form symbiotic relationships with nitrogen-fixing bacteria of the genera *Rhizobium* and *Bradyrhizobium* (DOYLE 1994) that enable them to grow in problematic soils. They also play an important role in soil improvement and are widely grown for soil rehabilitation, amenity planting and fuel wood. The seeds of many species are used as a rich source of vegetable protein (MASLIN et al. 1998). An ever-increasing demand for paper combined with a declining fibre supply from the forests of the world is forcing the pulp and paper industry to find viable fibre sources to supplement forest-based resources. Today, a large amount of paper is produced from various annual plants (non-wood fibres) in developing countries where forest resources are limited. However, wood pulp is still needed for efficient pulp processing (JAHAN et al. 2008). Natural forestland is decreasing rapidly because of competition with other land uses and deforestation. Thus, it is becoming difficult to continuously supply pulpwood from natural forests to support the increasing size of the paper industry. Plantations of fast-growing species must thus be established to compensate for the declining supply from natural forests. Similarly, growing forest species that thrive on poor lands generally not suitable for the growth of other crops can increase the area used for the production of pulpwood species. Both *A. mangium* and *A. auriculiformis* are adaptable to widely differing soils on degraded lands with poor soil conditions (SHARMA et al. 2011). Fast-growing tree plantations can produce 1.5–2 times more wood per hectare per year and reach maturity 2–3 times faster than long rotation softwood plantations with straight bole (COSALTER, PYE-SMITH 2003). High pulpwood yield in acacias is, however, hampered by high levels of lignin. Separating high quantities of wood lignin leads to utilisation of large quantities of chemicals and en-

ergy resulting in high production costs and a poor environmental image for the industry (BIERMANN 1996). Similarly, lignin causes discolouration and reduces paper brightness (CHIANG et al. 1988). Lignin is an essential component of wood whose concentration ranges from 10–30%. Understanding lignin biosynthesis and content will thus help in selecting planting materials with low lignin content. This study is therefore focused on comparing the growth of *A. mangium* and *A. auriculiformis* under two contrasting growth conditions, i.e., normal and stressed conditions. A second aim was to understand the effect of the growth conditions on lignin content in *A. mangium* and *A. auriculiformis*.

MATERIAL AND METHODS

Two sites were selected for field trials, namely Stesen Penyelidikan Luar Bidor and plot W, Universiti Kebangsaan Malaysia, Bangi. These sites were chosen to represent comparatively stressed (Bidor) and normal (Bangi) conditions and to evaluate the growth response and lignin content within and between the species of *A. mangium* and *A. auriculiformis*. The sample size utilised in this study ranged from 35–50 trees for both *A. mangium* and *A. auriculiformis*. Trees were 10 years old with seeds originating from similar provenances and plant spacing was 2 × 2 m.

Study site I: Bangi, Malaysia (normal plot). This study site is located in Bangi, Selangor, Malaysia at 2°55'N latitude and 101°47'E longitude (Fig. 1), and is characterised by high nutrient content, better water-holding capacity, better drainage and low soil temperature. The parent soil material is mainly quartzite (Table 1). The soils are primarily Serdang series (Ultisols-Typic Paleudults), reddish-brown in colour and sandy clay loam in nature. Texturally, the soil is a mixture of black loam and sandy clay with good drainage. The soil naturally has high levels of C, N, P and exchangeable bases.

Study site II: Bidor, Malaysia (stressed plot). This study site comprises three main types of tin tailings: slime, sand and sandy slime. The soils are excessively drained, having a low nutrient content and water-holding capacity with the temperature of the surface soil reaching about 60 °C. The soil is characterised by low levels of C, N, P and exchangeable bases. Table 1 gives a detailed description of the soil profiles for both planting sites (Table 1). The stressed plot is characterised by low fertility, poor water-holding capacity and high drainage, high soil temperature and low organic materials. Bidor, the site

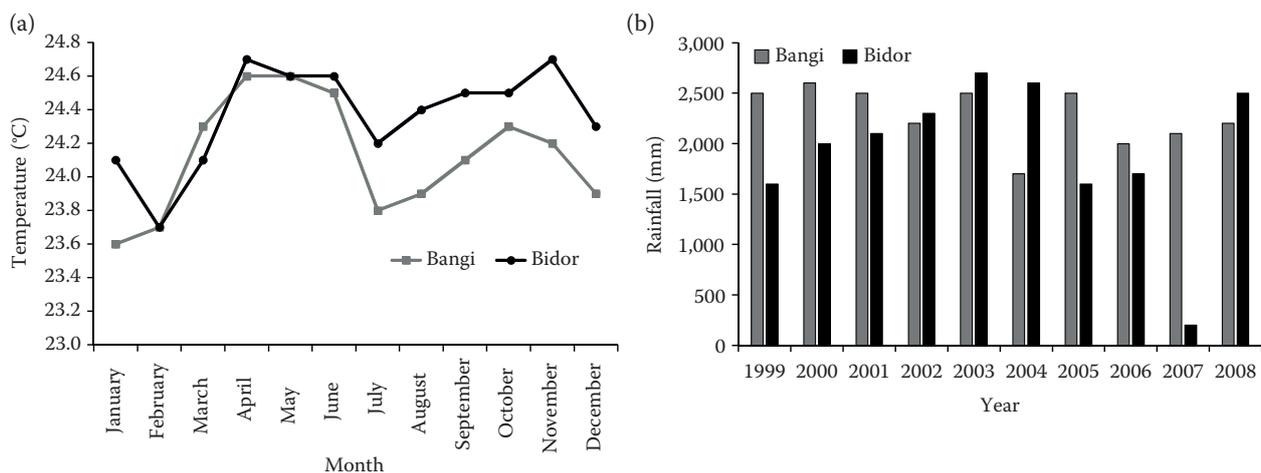


Fig. 1. Average monthly temperature (a), rainfall (b) under normal (Bangi locality) and stressed (Bidor locality) conditions throughout the growth period

of the stressed plot at 4°06'N latitude and 101°16'E longitude (Fig. 1), was a mining town in the 1950s. The tin tailings were later dominated by grasses and also small pioneer species such as *Macaranga* spp. and *Vitex* spp. The soil in the Bidor tailing area is described as entisol with udic moisture regime.

Climate. Data on temperature and rainfall were collected for a period of nine years (1999–2008) from both planting sites to understand the influence of changing climate over time on these sites and the growth of acacias.

Diameter at breast height (DBH). A diameter tape was used and tree diameter was measured at 130 cm a.g.l. For the trees growing on a slope, the circumference at 130 cm from the centre of the slope was measured. When the observed tree began to branch below 130 cm, the smallest circumference below the first branch was measured. In the case of a multi-stemmed (several trunks at ground level) tree, each stem's circumference at 130 cm was measured (HUSCH et al. 1982). DBH for a multi-stemmed tree was calculated using Eq. 1:

$$DBH = \sqrt[3]{a^2 + b^2 + c^2} \quad (1)$$

where:

a, b, c – different DBH values from the stems of the same tree.

Plant height. For trees which were less than 15 m in height total height was measured using a measuring stick, while a hypsometer (Nikon, Japan) was used to measure trees which were more than 15 m in height. The stick was placed at 40 cm from the tree to be measured. Measurements were taken thrice in order to avoid experimental error.

Biomass estimate. Total above-ground biomass for all trees on both sites was calculated from

height and DBH trait data. The relative growth relationship formula for every part and total biomass are as follows (REN, YU 2008), Eqs 2–5:

$$\log W_t = -0.221 + 0.609 \log(D^2 h) r = 0.99 W_b \quad (2)$$

$$\log W_b = -0.243 + 0.458 \log(D^2 h) r = 0.91 W_1 \quad (3)$$

$$\log W_1 = -0.424 + 0.561 \log(D^2 h) r = 0.91 W_T \quad (4)$$

$$\log W_T = -0.154 + 0.568 \log(D^2 h) r = 0.98 \quad (5)$$

where:

- W_t – trunk biomass,
- D – diameter at breast height,
- h – height,
- W_b – branch biomass,
- W_1 – leaf biomass,
- W_T – total biomass.

Klason lignin determination. Wood discs were collected by means of a destructive sampling method and chopped into small cubes of 1 × 0.5 cm. The samples were air-dried at room temperature

Table 1. Properties of soils under normal (Serdang series) and stressed (sand tailings) conditions (ANG et al. 1994; geography department, Bangi)

	Normal	Stressed
Wet pH	4.1–4.6	4.2–5.1
Organic carbon (%)	1.21–1.4	0.042–0.062
N (%)	0.07–0.08	0.012
Available P (ppm)	7.02–7.10	0.48–0.76
Exchangeable cations (meq ⁺ ·100 g ⁻¹ soil)		
K ⁺	0.24–0.36	0.012–0.03
Mg ²⁺	0.58–0.70	0.007–0.059
Ca ²⁺	0.27–0.41	1.62–1.92

for two days and passed through a Thomas Willey mill, with a 10-mesh screen. The lignin content of wood tissues was determined using procedures described in TAPPI T 222-om-88 (SCHÖNING, JOHANSSON 1965).

Klason lignin of the investigated tissues was determined from the extracted free wood. About 1g of wood meal was placed in a 100-ml beaker followed by the addition of 15 ml of 72% H₂SO₄. The mixture was subjected to occasional stirring for 2 h at room temperature. The solution was then transferred into a 1 l Erlenmeyer flask (Fisher Scientific, USA), topped up with deionized water to 575 ml and refluxed for 4 h. The solution was filtered using crucible No. 4 and the acid-insoluble lignin was determined gravimetrically.

Statistical analysis. All growth measurements were recorded in triplicate, and the average value for each tree was derived. The data were subjected to statistical analysis (one-way ANOVA) using the Minitab statistical software (Version 17, 2010). In the case of a significant difference between the treatments, Tukey's post hoc test was used to determine the differences for individual sites. Pearson correlation analysis was conducted to understand the relationships between different traits under both conditions.

RESULTS

Climatic data was collected for a period of nine years from both planting sites. Both planting sites on average received the same amount of rainfall and temperatures were similar; however, their monthly distributions were significantly different (Fig. 1). For example, the stressed plot experienced longer periods of high temperatures and low rain compared to normal conditions (Fig. 1). At the normal plot in Bangi, average monthly temperature (Fig. 1) ranged

from 23.6–24.8 °C and mean relative humidity was 95%. The temperature exhibited a bimodal distribution with peaks in March to June and September to November. The period from March to June was drier compared to the one from September to November. On the other hand, Bidor had an average monthly temperature ranging from 23.8–24.8 °C (Fig. 1), and a mean relative humidity of 94%. Similarly, a bimodal distribution was obtained at the same peak intervals (Fig. 2b). The Bangi and Bidor plots experienced average wind speeds of 0.86 and 0.89 m·s⁻¹, respectively. The mean total annual rainfall during the growth period ranged from 1,779.8–2,630.1 mm for Bangi and 1,609.8–2,749.3 mm for Bidor (Fig. 1).

Effect of site on plant height, diameter growth, trunk biomass and lignin content

The effect of the two planting sites on the DBH, height and biomass of *A. mangium* and *A. auriculiformis* is shown in Table 2. All three traits were found to be significantly different between the two sites ($P > 0.01$), and the two species showed distinct growth patterns and responses to growing conditions. Interspecific comparison based on DBH demonstrated significantly different results between the two sites (Fig. 2a). Generally, both species had higher DBH under normal conditions (Fig. 2b) compared to stressed conditions (Fig. 3a). DBH had a unimodal distribution and was normally distributed in both species; however, values were widely skewed in *A. mangium* compared to *A. auriculiformis*. *A. mangium* had higher mean and more variable DBH compared to *A. auriculiformis* under both field conditions. *A. mangium* DBH ranged from 9–53.9 cm while in *A. auriculiformis* DBH ranged from 9–35.9 cm under normal conditions (Fig. 2b). The majority of *A. auriculiformis* trees (17 trees) fell into the 18–26.9 cm DBH class,

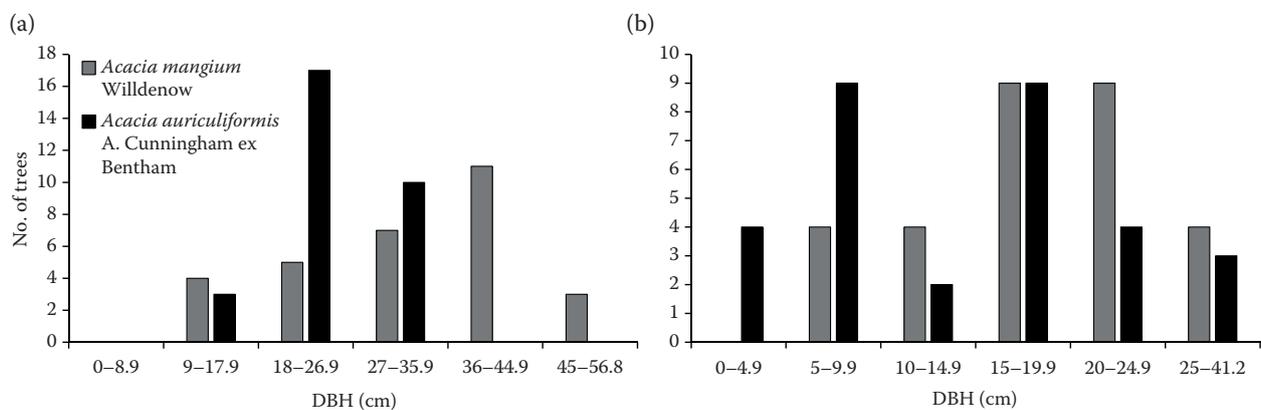


Fig. 2. Tree DBH frequency distribution under normal (a), stressed (b) conditions

Table 2. Analysis of variance showing effect of different growing conditions on DBH, height and biomass of *Acacia* spp.

Sources of variation	DBH		Height		Biomass	
	MS	F-value	MS	F-value	MS	F-value
Site × species	2,669.2	38.8**	1,766.8	58.06**	244,591	55.80**
Residual	68.8		30.4		4,384	

MS – mean square, **highly significant

whereas in the case of *A. mangium*, the majority of trees occupied the 36–44.9 cm DBH class. Under stressed conditions, meanwhile, DBH classes for *A. mangium* and *A. auriculiformis* ranged from 5–29.9 and 0–29.9 cm, respectively. Mean DBH was significantly different under normal conditions (Fig. 2b); however, both species responded similarly to stressed conditions and produced significantly lower DBH. *Acacia* height seemed to be affected by growing conditions; moreover, the results were significantly different both between species under normal conditions and between the two growing conditions, and both species responded similarly under stressed conditions (Table 3). *A. auriculiformis* showed more height variation under normal conditions (Fig. 3b) compared to *A. mangium* with values of 0–44.9 and 9–44.9 m, respectively (Table 3). Similarly, *A. auriculiformis* showed more variation than *A. mangium* under stressed conditions. *A. auriculiformis* trees grew faster under stressed conditions than *A. mangium* (Fig. 4).

The Pearson correlation coefficients for the relationship between height and DBH are presented in Table 4. The height and DBH relationship was stronger under the stressed conditions compared to the normal conditions. *A. auriculiformis* had the highest correlation value of 0.798 under stressed conditions and 0.679 under normal conditions. This was followed by *A. mangium* under stressed (0.589) and normal (0.499) conditions.

The total tree above-ground biomass was higher under normal conditions than in the stressed conditions. The highest mean biomass value for *A. mangium* (273.5 kg) was higher than that for *A. auriculiformis* (149.0 kg). At the selected DBH classes, the biomass estimate of the selected parts of the tree were similar irrespective of the study sites. We observed a trend of increasing trunk biomass allocation with increasing DBH and decreasing branch biomass allocation with increasing DBH. The incremental increase in trunk biomass was accompanied by a decrement in leaf and

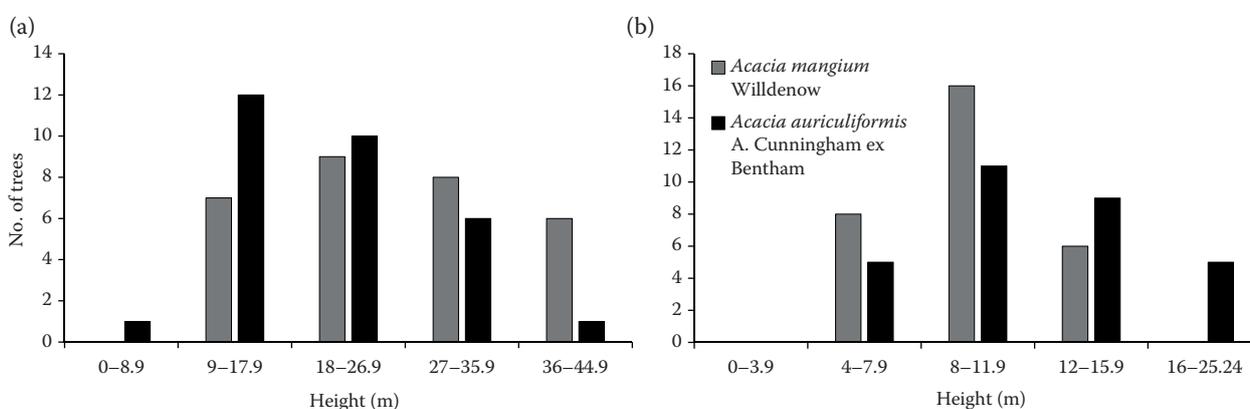


Fig. 3. Tree height frequency distribution under normal (a), stressed (b) conditions

Table 3. Mean height, DBH and biomass under normal (Bangli locality) and stressed (Bidor locality) conditions

Species	Height (m)	DBH (cm)	Biomass (kg)
Bangi			
<i>Acacia mangium</i> Willdenow	24.39 ^a	33.18 ^a	273.50 ^a
<i>Acacia auriculiformis</i> A. Cunningham ex Bentham	19.78 ^b	24.53 ^b	149.00 ^b
Bidor			
<i>A. mangium</i>	9.83 ^c	17.40 ^c	68.63 ^c
<i>A. auriculiformis</i>	11.76 ^c	13.95 ^c	63.00 ^c

means having the same letter within a row are not significantly different at 5% level

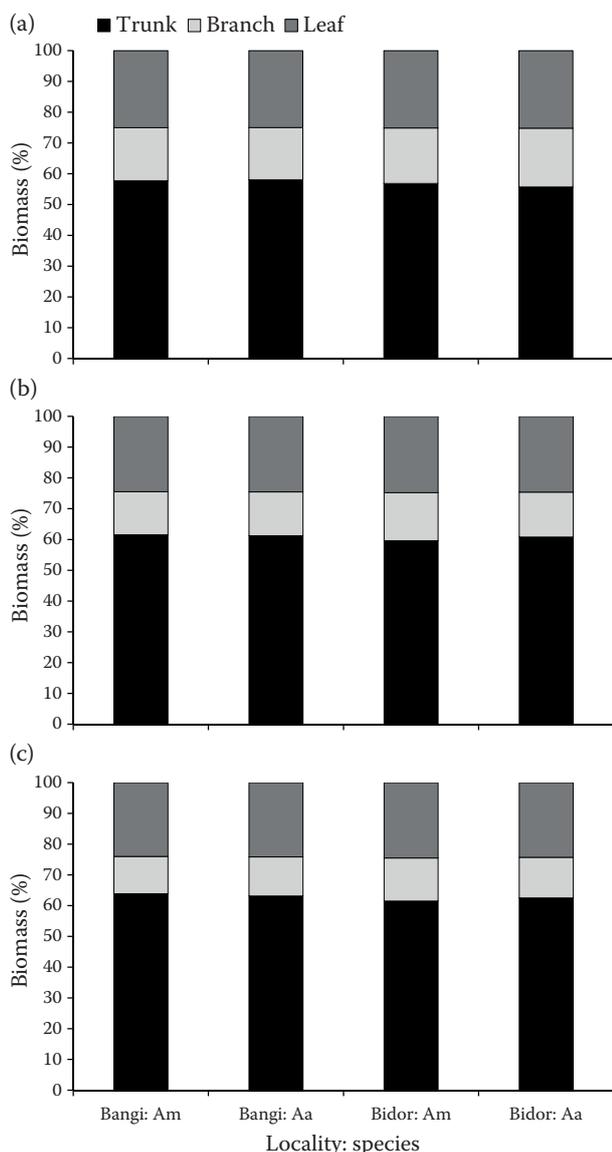


Fig. 4. Above-ground biomass allocation under normal (Bangi locality) and stressed (Bidor locality) conditions at DBH values of 10 cm (a), 20 cm (b), 30 cm (c)
 Am – *Acacia mangium* Willdenow, Aa – *Acacia auriculiformis* A. Cunningham ex Bentham

branch biomass. At DBH = 10 and 20 cm, the leaf biomass estimate remained constant (25%), but a 1% decrement was estimated at DBH = 30 cm. Thus, the canopy of the plantation had reached its limit at DBH = 10–20 cm. This limit would have

been determined by the availability of water, nutrients and sunlight at the site. The 1% decrement in the leaf biomass estimate was paralleled by an increment in the trunk biomass estimate.

Klason lignin content under normal conditions ranged from 18–46 and 22–42% for *A. mangium* and *A. auriculiformis*, respectively (Table 5). *A. mangium* exhibited a gradual increment in lignin content from the minimum to maximum DBH class. The maximum class harboured 46.59% of lignin representing a 12% increase relative to the mean class. Under normal conditions, *A. auriculiformis* exhibited an increase of 46% from the minimum to mean class and a 14% decrease in the maximum class. The minimum class harboured 22.54% Klason lignin with a standard error value of 0.26. The mean class had 42.09% Klason lignin with the lowest standard error value of 0.14, followed by the maximum class with 36.76% of Klason lignin and a standard error of 0.40 (Table 5). Under stressed condition, the Klason lignin content ranged from 26–30% for both *A. mangium* and *A. auriculiformis*. *A. mangium* showed a gradual increment in Klason lignin content from the minimum (26.83%) to mean (28.35%) class followed by maximum (29.29%) class with standard error values of 0.09, 0.30 and 0.29, respectively (Table 5). The percentage of increment was 5 and 3% from minimum to mean and mean to maximum, respectively. As for *A. auriculiformis*, the minimum class harboured 28.89% of Klason lignin, which fell by 9 to 26.46% of Klason lignin in the mean class. A slight increment of 3% was observed in the maximum class with 27.40% Klason lignin. The standard error value for the min, mean and the maximum classes were 0.10, 0.14 and 0.18, respectively (Table 5). The lignin content under the stressed conditions in all the DBH classes had standard error values which were less than 0.30 (Table 5). This indicates consistency in the lignin content obtained from the replicates of each sample. It is clear that the lignin content values increased with increasing biomass for *A. mangium*. However, *A. auriculiformis* exhibited a slight decrement followed by a slight increment with increasing biomass. The varying amounts of

Table 4. Relationship between DBH and height under stressed and normal conditions

Condition	Species	Pearson's coefficient
Normal	<i>Acacia mangium</i> Willdenow	0.499
	<i>Acacia auriculiformis</i> A. Cunningham ex Bentham	0.679*
Stressed	<i>A. mangium</i>	0.589
	<i>A. auriculiformis</i>	0.798*

*P-value < 0.05

Table 5. Klason lignin content based on DBH classes under normal (Bangi locality) and stressed (Bidor locality) conditions

Species	DBH classes (cm)		
	10	20	30
	Klason lignin \pm SE (%)		
Bangi			
<i>Acacia mangium</i> Willdenow	18.17 \pm 0.45	41.19 \pm 0.78	46.59 \pm 0.34
<i>Acacia auriculiformis</i> A. Cunningham ex Bentham	22.54 \pm 0.26	42.09 \pm 0.14	36.76 \pm 0.40
Bidor			
<i>A. mangium</i>	26.83 \pm 0.09	28.35 \pm 0.30	29.29 \pm 0.29
<i>A. auriculiformis</i>	28.89 \pm 0.10	26.46 \pm 0.14	27.40 \pm 0.18

SE – standard error

lignin present in the wood tissue provided a hard mass of wall material well-suited to resist stresses. The fluctuation in lignin content in *A. auriculiformis* from one DBH class to another is most probably due to the response of the tree to variable levels of environmental stress. No relationship between the lignin content and biomass was found under stressed conditions. Generally, the lignin content under the normal conditions was higher than under the stress conditions. The rates of increment and also decrement from one class to another were sharper under normal conditions as compared to the stress conditions.

DISCUSSION

A. mangium and *A. auriculiformis* performed better under normal conditions compared to stressed conditions. In a study conducted in Kerala state in India, *A. mangium* was observed to be a species suited to wet zones and hence, localities with long dry spells were not appropriate for establishing *A. mangium* plantations. Heart rot/root rot diseases were among the limiting factors for the cultivation of *A. mangium* in these dry regions (ZAKARIA et al. 1994). Similarly, *A. mangium* is able to grow throughout the year under favourable environmental conditions; however, growth appears to slow down or cease in response to the combination of low rainfall and cool temperatures in January–February. Trees start to grow actively again in April before the start of the rainy season (ATIPANUMPAI 1989). MOYA and PEREZ (2008) explored the effect of soil fertility on wood properties of *Tectona grandis* Linnaeus f. in mature trees and concluded that the chemical soil composition affects many physical properties of wood, which the authors attributed to variations in soil fertility. *A. auriculiformis* seemed less affected than *A. mangium* under stressed conditions. The ability of *A. auriculiformis* to perform better than *A. man-*

gium under stressed conditions compared to normal conditions was also described by KAMIS (1994). The ability of *A. auriculiformis* to perform better than *A. mangium* in a poorer site suggests that the genotype of this species exhibits crossover interactions. Under normal conditions, *A. auriculiformis* failed to perform to the same level (mean) as *A. mangium*. However, no significant difference in the magnitude of the response in relation to the population mean between the two species was obtained under the stressed conditions. On the other hand, the genotype of *A. mangium* does not exhibit crossover interactions as it performs better in good sites and worse in bad sites. Diameter is considered more sensitive to environmental conditions than height, but little is known about the genetic control of diameter growth (COSTA, DUREL 1996). In a study regarding the diameter growth of maritime pine (DANJON 1995), no general pattern was observed with respect to the genetic control of cambial growth. The present study does not indicate the existence of a similar trend in DBH in both stressed and normal conditions, most probably due to environmental factors. Similarly, NIK MUHAMAD and BIMAL (1999) indicated that *A. mangium* grows well up to 30 m in height under normal conditions, but on adverse sites they may not reach even 10 m. Growth performance under normal conditions was significantly better than under the stressed conditions due to the environmental differences between the two contrasting sites. Soil nutrient concentration could have attributed to the slight increases in height and diameter under the normal conditions. Phosphorus has been shown to increase the height of Caribbean pine seedlings (MANIKAM, SRIVASTAVA 1980). Nutrient supply comes mostly from atmospheric decomposition, biological fixation and biomass decomposition (HILTON 1987). *Acacia* spp. are legumes, capable of fixing N from the atmosphere. This has been further supported by AMIR and MILER (1991) in *Koompassia malaccensis* Bentham and also *A. mangium*, respectively,

which demonstrated independent N uptake from Bris soil (Bris is the local name for an association of free-draining soils developed on sandy marine deposits of subdued relief, together with seasonally waterlogged soils formed in the intervening depressions) and in tin tailings. Generally, these two soils are classified as problem soils; however, due to N fixing ability and ability to adapt to poor soil, *Acacia* can be used to transform these lands. In the present study, the soils (Serdang series) at the normal plot had higher levels of exchangeable cations compared to soils at the stressed plot.

Poor growth performance under stress condition has been attributed to sand tailings. Sand tailings consist mainly of fine sand, coarse sand and gravel. They have low fertility due to a lack of organic matter and fine particles such as clay and silt (ANG et al. 1999). Sand tailings situated at more than 1.5 m above the standing water-table level are frequently subjected to periodic drought due to their poor water retention capacity and high temperature (ANG et al. 1994). The low water-holding capacity of these sand tailings can contribute to poor plant growth (RADZIAH, ZULKIFLI 1990). Tin tailings soils are inherently poor in nutrient reserves, which are the basis of tree growth (AMIR, MILLER 1991) under natural forest stands. Survival of trees in the field depends heavily on their ability to regulate their internal water balance under stressful conditions (COPPOCK 1986). Factors that affect water deficit in plants include the supply of water available, as well as water demand and loss. The atmosphere controls the loss of water from plants. High air temperature and low relative humidity would normally affect processes of water loss from plants (GRACE 1983). Leaf water loss to the atmosphere during photosynthesis occurs mainly through stomata with some also escaping through cuticular respiration (GRACE 1983). During a prolonged dry season, when monthly rainfall is below 100 mm, the growth of *Acacia* sp. is slowed and trees are under moisture stress. In Sabah, the growth of *Acacia* spp. was reported to be affected by seasonal conditions (PINYOPUSARERK et al. 1993). Environmental stress tends to limit growth more than process variables such as photosynthesis (KRAMER 1983). In some species, vigorous growth has been correlated with a wide range of morphological and physiological characteristics (SINHA, KHANNA 1975), including net photosynthesis and higher water use efficiency (BLAKE, YEATMAN 1989). *A. mangium* generally has lower relative leaf turgidity as compared to *A. auriculiformis* (KAMIS, De CHAVEZ 1993). This suggests that *A. auriculiformis* has an altered ability to

retain moisture under stressed conditions. Drought adaptation of tree species is related to leaf stomatal frequency and length (ABRAMS 1988) and the total stomata pore area per unit leaf area (TUOMELA 1997). At the leaf level, stomatal characteristics can regulate the transpiration rate under water deficit. *A. auriculiformis* probably has greater leaf stomatal frequency as compared to *A. mangium*. Fast-growing tree species usually develop an extensive root system, particularly in low-fertility soil. *A. auriculiformis* roots grew significantly deeper than *A. mangium* on sand tailings (ANG et al. 1999). These findings concur with the result which indicates that *A. auriculiformis* adapts and thrives on sand tailings by adopting a deeper root system. Larger and deeper root systems result in improved ability to tap moisture at greater depths compared to *A. mangium*. Larger roots produced larger numbers of nodules and exhibited increased N-fixing ability, resulting in an improvement of growth under stressful conditions. Furthermore, it is widely recognised that the turnover and decomposition of fine roots and associated mycorrhizae may contribute substantially more to soil carbon and nutrient pools than above-ground litter-fall inputs (HENDRICK, PREGITZER 1993). Fine root decomposition most probably exceeded forest floor turnover in this study. Decomposed fine roots are incorporated into soil organic matter to supply carbon to soil organisms and to facilitate N-cycling mediated by mycorrhizae. The fine root litter quality and decomposability of *A. auriculiformis* appears to be significantly better than those of *A. mangium*.

Under the normal conditions, the variation in both DBH and height was higher in *A. mangium* as compared to *A. auriculiformis*. In contrast to the normal condition, both the DBH and height variation was higher in *A. auriculiformis* as compared to *A. mangium* under stressed conditions. Tree seedlings in a plantation start to grow using the sunlight, water and nutrient resources available in their immediate vicinity. The different seedlings in the present study grew at different rates despite growing at the same site. Each seedling has its own genetic characteristics which will determine its inherent growth capability (VON WUEHLISCH et al. 1995). Another factor contributing to the variation in individual trees is the availability of water and nutrients from the soil, which may vary from metre to metre across a site (GUO et al. 2004; HUTCHINGS, JOHN 2004). Micro-site variations occur for several reasons, giving rise to differences in individual growth rates. Firstly, the presence of small-scale variation in the topography of the site may influence the movement of water in

soil and consequently its availability to a tree at any particular point. Another factor would be the variation in the soil parent material, which plays vital role in influencing nutrient availability at any given spot. Finally, the vegetation which grows on a site before the plantation is established varies from spot to spot (WEST 2006). These factors bring about variation in the effects of the soil on tree growth. The present study suggests that both height and diameter at breast height are independent from one another in terms of the genotype (G) × environment (E) interaction. These differences reflect the growing conditions, adaptability, seed source and genetic constitution of individual trees. Factors that might have caused differences in growth are seed source, soil properties and climatic factors. Biological processes could have taken place at different rates as the regulating factors such as moisture, temperature and substrate availability vary.

Increases in the total leaf biomass estimates may be due to a greater number of leaves (COYNE, VAN CLEVE 1977) or larger leaves or both (BRIX 1981). Leaf duration depends upon both leaf production and leaf loss. Decomposition of forest litter is the primary means for transforming nutrients into forms available for plant uptake. The decay process is complex, but litter decomposition rates are primarily controlled by microclimate and substrate quality (MEENTMEYER 1978). The decrease in the leaf biomass estimate which overlaps with the increment in the trunk biomass estimate explains the nutrient uptake of the tree from litter decomposition. The leaf biomass estimate is the same for all the samples irrespective of the species and conditions used in this study. The present findings suggest that, under normal conditions, the leaves absorb most of the sunlight falling on the canopy. Thus, shaded leaves near the base of the canopy no longer receive sufficient sunlight for them to carry out photosynthesis. Since they are no longer useful, the leaves are shed and replaced with new leaves near the well-lit top of the canopy (WEST 2006). Under stressful conditions, the availability of nutrients from the soil is relatively low. Trees may recycle nutrients from the more shaded leaves near the base of the canopy to better-lit leaves near the top of the canopy. Those leaves near the top are then better positioned to carry out photosynthesis than the shaded leaves. The nutrient-deficient leaves near the base of the canopy would then be shed.

ZAIHAN et al. (2009) reported the lignin content of both *A. mangium* and *A. auriculiformis* to range from 19–23.5%. It is clear that the lignin content values increase with increasing biomass for *A. man-*

gium. However, *A. auriculiformis* exhibited a slight decrement followed by slight increment with increasing biomass. The varying amounts of lignin present in the wood tissue provided a hard mass of wall material well suited to resist stresses. The fluctuation in lignin content in *A. auriculiformis* from one DBH class to another is most probably due to the response of the tree to variable levels of environmental stress, i.e., normal vs. stressed. The increase of free lignin precursors in the xylem sap as well as reduced anionic peroxidase activity could be an indication that drought decreases the biosynthesis of lignin in maize (ALVAREZ et al. 2008). In a previous study, *A. auriculiformis* showed deeper root growth than *A. mangim* and showed better adaptability and better growth under stressed conditions (ANG et al. 1999). Deeper root systems adapted to stressed conditions could help to draw more water and nutrient, and increased surface area would yield more nodulation and thus higher levels of nitrogen fixation. Different regions of the root may respond differently to drought, as the deposition of lignin may be greater in a specific region of the root or at certain times of stress (FAN et al. 2006; YOSHIMURA et al. 2008). It has been shown that the basal part of the roots of maize plants under water stress exhibit a greater reduction in growth than the apical region (FAN et al. 2006). Such a reduction was associated with an increased expression of two genes involved in the biosynthesis of lignin, cinnamoyl-CoA reductase 1 and 2. The reduction was also associated with increased deposition of lignin, which reduced cell wall extensibility and decreased cell wall expansion. Therefore, reduced growth of the basal root might improve the availability of water, minerals and sugars, factors necessary to maintain minimum growth and survival of young cells in the most apical portion, facilitating renewed growth after rehydration (FAN et al. 2006). An increase in the expression of genes related to cell growth and extensibility in the roots of rice (*Oryza sativa* Linnaeus) plants was shown during the initial stages (16 h) of water stress, enabling root growth in these plants (YANG et al. 2004). It was also observed that there was an increased expression of genes involved in lignin biosynthesis during the intermediate and final stages of water stress, such as those coding for phenylalanine ammonia lyase (PAL), p-coumarate 3-hydroxylase, 4-coumarate-CoA ligase, caffeoyl-coenzyme A 3-O-methyltransferase (CCoAOMT), carbamoyl-phosphate synthetase 2 (CAD) and peroxidase. Similar results were obtained with *Citrullus lanatus* (Thunberg) Matsumura & Nakai, which shows an extraordinary resistance to drought (YOSHIMURA et al. 2008). In the early

stages of stress, this plant showed an increase in root growth, which was associated with the induction of the synthesis of proteins involved in morphogenesis as well as the metabolism of carbon and nitrogen. In the final stages of the stress, however, there was a reduction in root growth and induction of lignin biosynthesis, with increasing expression of CCoAOMT and a large number of isoenzymes comprising class III peroxidases. Growth reduction and tolerance to desiccation were associated with more lignin in the roots. Other plant organs such as leaves may show marked physiological changes during drought stress. The growing leaves of maize plants accumulated more catechol-O-methyl transferase, mostly at 10 to 20 cm from the point of leaf insertion; drought resulted in a shift of this region of maximal accumulation toward basal regions (VINCENT et al. 2005). Reduced leaf growth occurred concurrently with an increase in lignin biosynthesis. Overall, there was a large increase in the activities of PAL and ascorbate peroxidase in the early stages of stress (0–14 days), with activity levels decreasing gradually as the period of stress was extended. On the other hand, other enzymes such as guaiacol peroxidase, coniferyl alcohol peroxidase and syringaldazine peroxidase exhibited greater activity during the final stages of stress (14–28 days). Light exposure has been reported to result in increased lignin biosynthesis compared to dark conditions. *A. mangium* has better self-pruning ability compared to *A. auriculiformis*; therefore, the canopy is more exposed to sunlight. Plants in the light showed increased levels of H₂O₂ and lignin, as well as higher levels of diamine oxidase and peroxidase activity (SYROS et al. 2004). Under stress conditions, *Acacia* has been reported to become infected by different insect pests or pathogens which result in the plant producing more lignin (HEARNE 1975).

Under normal conditions, *A. mangium* has a straight stem compared to forked bole in *A. auriculiformis*. Reaction wood (RW) is a type of wood that occurs in leaning stems and branches in order to force them into the normal position. Therefore, in a certain sense, reaction wood may represent a stressful situation. In angiosperms, RW develops above the leaning region, pulling it up: in this context, it is called tension wood – TW (PAUX et al. 2005). The wood reaction involves a marked reprogramming of the genes involved in cell wall formation and therefore significantly affects the properties of the wood (DÉJARDIN et al. 2004). *Eucalyptus nitens* (H. Deane & Maiden) was bent to 45° displayed a TW with high cellulose content, reduced microfibril angle, and less Klason lignin (QIU et al. 2008). A normal plot is characterised by higher levels of N compared

to a stressed plot. Deficiency, as well as abnormally high concentrations of a nutrient can both cause abnormalities in the accumulation of lignin. Increased lignin content was observed at high N levels due to elevated PAL activity (PITRE et al. 2007). A very high level of Ca⁺ was observed in the stressed plot compared to the normal plot. FROMM (2010) described the role of Mg²⁺ and Ca⁺ in poplar trees; at low concentrations, cambial activity as well as the seasonal rate of wood increment, vessel size and lignin content were significantly reduced. It is clear that lignin content values increase with increasing biomass for *A. mangium*. However, *A. auriculiformis* exhibited a slight reduction, followed by a slight increment with increasing biomass. The varying amounts of lignin present in the wood tissue provided a hard mass of wall material well-suited to resist stresses. The fluctuation in lignin content in *A. auriculiformis* from one DBH class to another is most probably due to the response of the tree to varying levels of environmental stress.

CONCLUSIONS

A. mangium and *A. auriculiformis* responded differently to stressful conditions as was evidenced by the significant reduction in growth and lignin contents. The effects on DBH, height, biomass and lignin content in the two species were significantly different within and between the two sites; the significant interaction between species and site with respect to these traits indicates that there is potential for improvement in these traits. *A. mangium* is characterised by superior growth and high lignin content under normal conditions; however, the species lacks the ability to adapt to stressful conditions. Meanwhile, *A. auriculiformis* is hardy and well suited to problematic soils with its low lignin content and disease resistance. However, the species exhibits inferior growth. The large phenotypic variation observed between the two species suggests potential for developing high-yielding interspecific hybrids adapted to stressful conditions.

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