

## FACTORS INFLUENCING THE SURVIVAL AND GROWTH OF *AQUILARIA MALACCENSIS* SEEDLINGS IN INDONESIA

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**SOEHARTONO, T., NEWTON, A. C. & MARDIASTUTI, A. 2002. Factors influencing the survival and growth of *Aquilaria malaccensis* seedlings in Indonesia.** *Aquilaria malaccensis* (Thymelaeaceae) is the principal source of gaharu, one of the most valuable tropical forest products in international trade. Despite its economic importance, the autecology of this species is virtually unknown. Seedling growth and survival of *A. malaccensis* was monitored over a 15-month period in natural forest in West Kalimantan. Mean height growth rate was  $21.2 \pm 2.3$  cm year<sup>-1</sup>, and was positively related to light availability ( $r^2 = 0.79$ ,  $p < 0.001$ ), but unrelated to distance to the nearest mature tree or seedling density. By the end of the observation period, fewer than 20% of seedlings surveyed initially were still alive, trampling and cutting being one of the main causes of mortality. A nursery experiment examined the influence of soil (two treatments), light availability (four treatments) and seedling density (four treatments) on growth. Although a decrease in irradiance was associated with significantly ( $p < 0.01$ ,  $t$ -test) lower values for height and stem diameter, seedlings were able to survive under the low light treatment. Lower height growth rates and leaf increment were observed with higher seedling densities on the more fertile soil; no such effects of density were observed on the relatively infertile soil. The implications of these results for the sustainable management of *A. malaccensis* are discussed.

Key words: Gaharu - agar wood - non timber forest product - autecology - regeneration

**SOEHARTONO, T., NEWTON, A. C. & MARDIASTUTI, A. 2002. Faktor yang mempengaruhi kemandirian dan pertumbuhan anak benih *Aquilaria malaccensis* di Indonesia.** *Aquilaria malaccensis* (Thymelaeaceae) ialah sumber utama gaharu, salah satu hasil hutan tropika yang paling bernilai dalam perdagangan antarabangsa.

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Walaupun ia penting dari segi ekonomi, autekologi spesies ini hampir tidak diketahui. Pertumbuhan anak benih dan kemandirian *A. malaccensis* dipantau selama 15 bulan di hutan asli di Kalimantan Barat. Min kadar pertumbuhan ketinggian ialah  $21.2 \pm 2.3$  cm tahun<sup>-1</sup>, dan berkaitan secara positif dengan ketersediaan cahaya ( $r^2 = 0.79$ ,  $p < 0.001$ ), tetapi tiada kaitan dengan jarak ke pokok matang yang terdekat atau kepadatan anak benih. Pada akhir tempoh cerapan, kurang daripada 20% anak benih yang dikaji pada awalnya masih hidup; pijakan dan tebang merupakan antara sebab utama kematian. Ujian di tapak semaian mengkaji pengaruh tanah (dua rawatan), ketersediaan cahaya (empat rawatan) dan kepadatan anak benih (empat rawatan) terhadap pertumbuhan. Walaupun pengurangan cahaya adalah berkaitan dengan ketinggian dan diameter batang yang lebih rendah ( $p < 0.01$ , ujian-*t*), anak benih berupaya hidup di bawah rawatan cahaya rendah. Kadar pertumbuhan ketinggian yang lebih rendah dan pertambahan daun dicerap dengan kepadatan anak benih yang lebih tinggi di tanah yang lebih subur; kesan yang sama tidak dicerap di tanah yang secara relatifnya tidak subur. Implikasi keputusan ini terhadap pengurusan berkekalân *A. malaccensis* dibincangkan.

## Introduction

Tropical trees in the genus *Aquilaria* (Thymelaeaceae) are of exceptional economic importance, being the source of gaharu (agarwood, eaglewood or karas), one of the most valuable forest products in international trade. Gaharu is a fragrant wood used for incense, perfume, traditional medicines and other ornamental products (Chakrabarty *et al.* 1994). The genus *Aquilaria* is distributed throughout southern Asia from India to China, and much of Indonesia (Ding Hou 1960, Whitmore 1972). In recent years, Indonesia has become one of the principal sources of gaharu, with annual revenues of up to US\$6 million (Anonymous 1996) derived from international trade. Significant volumes are also being exported from India (Chakrabarty *et al.* 1994). Approximately 2000 tonnes year<sup>-1</sup> of gaharu are traded in Singapore (Yamada 1995).

The volume of international trade has led to concern about the impact of gaharu harvesting on the conservation status of *Aquilaria* spp., particularly as gaharu is currently obtained mostly, if not entirely, from natural forests (Chakrabarty *et al.* 1994, Yamada 1995, Peters 1996, Chang 1997, Momberg *et al.* 1997, Ng *et al.* 1997). As an illustration of this increasing concern, *A. malaccensis* (the main source of gaharu) was listed on Appendix II of CITES in 1994 (CITES 1994), in an attempt to regulate trade in gaharu and thereby conserve the species. Recent research has indicated that the gaharu trade may have had a substantial impact on populations of *Aquilaria* spp. in Indonesia, as harvesting generally results in the death of the tree; field observations suggest that more than 90% of *Aquilaria* trees encountered by collectors may be felled for gaharu collection (Soehartono & Newton 2000, 2001). Although *Aquilaria* spp. can be cultivated, production of gaharu in plantations has not yet been successful (Jalaluddin 1977, Ng *et al.* 1997).

In order for *A. malaccensis* to be managed sustainably, information is required on the growth and survival of the species in response to different environmental factors. At present, virtually nothing is known of the autecology of this species, yet such information is fundamental to the development of suitable approaches for

management of the species both in natural forests and plantations. The objectives of this research were therefore to investigate the response of *Aquilaria* seedlings to three environmental factors, namely, light availability, soil type and seedling density, both under nursery and field conditions.

## Materials and methods

### *Study areas*

#### Field observations

Observations of seedling regeneration of *A. malaccensis* in natural forest were undertaken in West Kalimantan at Desa Sebadu-Buluh Kecamatan Mandor ( $0^{\circ} 23' N$  and  $108^{\circ} 45' E$ ), an area of about 60 ha of lowland (50 to 80 m asl) secondary mixed forest and rubber plantation established in an area of flat topography. The nearest climate station at Mandor, 15 km to the south, recorded a mean annual rainfall between 2600 and 3000 mm. The field observations were made between 6 January 1997 and 24 April 1998.

#### Nursery experiment

The nursery experiment was undertaken in the experimental area of IPB (Bogor Agricultural University) at Bogor, Java ( $6^{\circ} 38' S$  and  $106^{\circ} 49' E$ ). Annual rainfall is generally between 3000 and 4000 mm and the area has an altitude of between 200 and 250 m asl. The experiment was undertaken between December 1996 and October 1997.

### *Field observations of natural regeneration*

Following an intensive search, 20 mature trees of *A. malaccensis* were located at the field site in West Kalimantan. Of the 20 selected trees, the presence of young trees within 30 m was recorded for 12 individuals. The number of young trees near ( $< 30$  m) to each mature selected tree varied from 3 to 25. The young trees were classified as seedlings ( $< 0.5$  m height), large seedlings ( $0.5 - < 1.0$  m height), saplings ( $1.0 - 2.0$  m height) or large saplings ( $> 2.0 - 3.0$  m height). All individual seedlings and saplings were tagged ( $n = 215$ ).

The height of selected seedlings and saplings was recorded using a measuring tape to the nearest 0.1 cm, while stem diameter (at the root collar) was measured using calipers to the nearest 0.01 cm. The distance of seedlings and saplings to the nearest mature tree was also measured using a tape to the nearest 0.1 m. Light availability incident just above each seedling and sapling was recorded using a lightmeter (Digital Model: YF-1085; Yu Fung, Taiwan) to the nearest 1 lux. Values were converted to  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ , based on the assumption that daylight reaching the forest floor was diffuse (1 klux (400–700 nm) of diffuse daylight is

equal to  $19 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) (McCree 1981), an assumption consistent with field observations.

The survival and mortality of seedlings and saplings were assessed every four months, terminating in March/April 1998. Composite soil samples taken were composed of three 5 cm (diameter)  $\times$  15 cm (depth) cores. Soils were analysed following the procedures outlined in Moore & Chapman (1986) at the Biological Tropical Institute (BIOTROP), Bogor.

Cumulative growth curves were calculated for young trees, based on measurements made every four months and their mean density was calculated within a 30-m radius of the selected mature trees. Regression analyses were performed to assess the relationship between growth rate of young trees and light availability, distance to the nearest mature tree and seedling density. Survivorship curves of seedlings and saplings were also calculated.

### *Nursery experiment*

A nursery experiment was undertaken to examine the influence of three different factors on seedling growth: soil (two treatments), light availability (four treatments) and seedling density (four treatments). One-month-old seedlings of *A. malaccensis*, which had been raised in sand in plastic pots (60 cm diameter  $\times$  15 cm height), were obtained from a local nursery in Bogor, Java. Seedlings of approximately the same height (25 cm) were selected for the experiment. In January 1997, 64 polythene bags (12 cm diameter  $\times$  17 cm height) were filled near to capacity with one of the selected soils. Seedlings of *A. malaccensis* were transferred into these pots at four different densities: one, two, three or four seedlings per pot. Two types of soil were selected as experimental treatments: latosol and red and yellow podzol. These soils were obtained from near the experimental area of the University IPB in Darmaga, Bogor.

Three wooden shade frames (each of 2.0  $\times$  1.5 m and 1.5 m tall) were constructed and covered in black nylon netting (Paranet, Taiwan). Three irradiance treatments were produced by using three different grades of netting (18.5  $\text{inch}^{-1}$ ; 13.6  $\text{inch}^{-1}$  and 7.1  $\text{inch}^{-1}$ ), providing 75, 55 and 27.5% light absorption. A control (unshaded) treatment was also included. Four replicates of each of the four different seedling densities, in each of two soil types, were randomly positioned under the four irradiance treatments. The seedlings received natural rainwater supplemented with tap water as required, to field capacity. To assess temperature and humidity, a hygrograph and a maximum/minimum thermometer were placed in each shade frame and assessed every two weeks at 8:00 a. m., 12:00 noon and 4:00 p. m. on the day of recording.

The height, stem diameter and number of leaves of each seedling were recorded every two weeks. Seedling height was measured using a measuring tape to the nearest 0.1 cm and shoot diameter was measured using calipers to the nearest 0.01 cm. Light intensity was recorded using a lightmeter to the nearest 1 lux (values transformed as described earlier). Seedlings were harvested in October

1997 (309 days after establishment). Oven-dried mass of stems and roots were weighed using a digital balance to the nearest 0.1 g after drying at 80 °C for 24 hours.

As the light treatments were not replicated because of space constraints, the experiment was analysed as a randomised block design using ANOVA in which light treatment was equal to block. The assessment of the effect of light on seedling growth was made by comparing the mean values of growth variables (height and stem diameter) from each block, tested using *t*-tests. The interactive effects of seedling density and soil type on seedling growth variables were tested using Duncan's multiple range test, following ANOVA.

## Results

### *Field observations*

Soil characteristics of the field site are given in Table 1. In general the forest soil was slightly lower in terms of pH and CEC, but higher in terms of P availability, than the soils used in the nursery experiment.

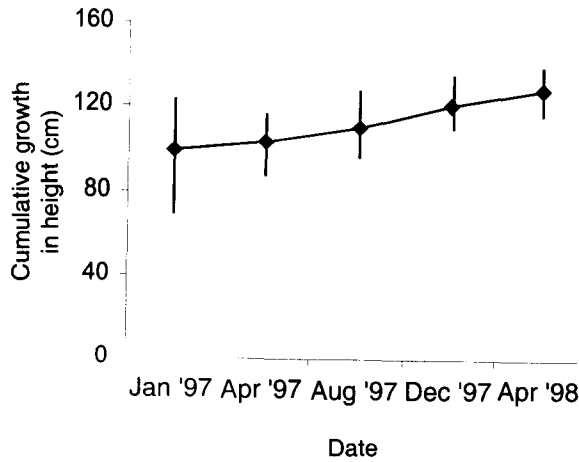
Growth rates of seedlings of *A. malaccensis* in the field were relatively low, compared with the nursery experiment. Seedlings increased by a mean of 32.2% in height and 47.4% in shoot diameter year<sup>-1</sup> (Figure 1); mean growth rate was 21.2 ± 2.3 cm year<sup>-1</sup> for height and 0.17 ± 0.02 cm year<sup>-1</sup> for shoot diameter.

**Table 1** Chemical analysis of soil from the study site in West Kalimantan and of soil used in the nursery experiment (latosol and yellow red podzol)

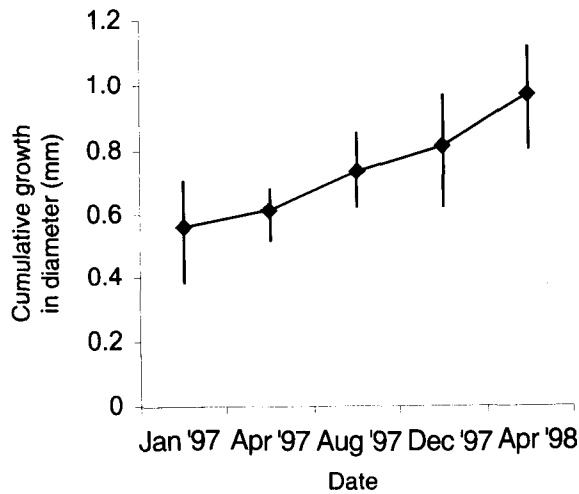
Soil variable	West Kalimantan	Latosol	Yellow red podzol
pH (H <sub>2</sub> O)	4.70	5.11	4.93
pH (KCl)	3.70	4.13	3.85
C-organic	1.02	0.66	0.50
N-total Kjeldahl	0.09	0.06	0.05
P	23.94	11.60	nr
Ca	0.24	1.50	1.15
Mg	0.35	0.33	1.03
K	0.25	0.05	0.13
Na	1.81	nr	nr
CEC	7.32	16.20	9.30
Al	1.45	2.13	2.42
H	0.75	0.56	0.32
Texture (%):			
Sand	21.2	25.9	23.5
Silt	34.7	33.3	27.7
Clay	44.2	40.8	48.9

All variables in ppm except texture in per cent. CEC: cation exchange capacity; nr: not recorded.

Regression analysis indicated that growth rate (height) was positively related to light availability ( $r^2 = 0.79$ ,  $p < 0.0005$ ) (Figure 2). However, growth rate of stem diameter was not significantly related to light availability. In addition, regression analyses indicated no significant relationship between height growth rate and distance to the nearest mature tree, or density of seedlings ( $r^2 = 0.05$ ).



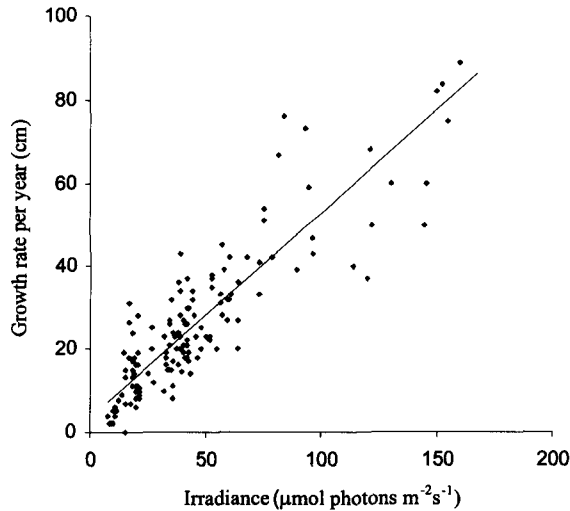
(a)



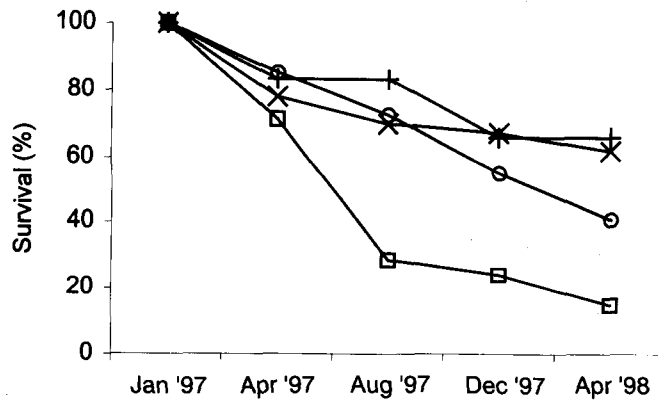
(b)

**Figure 1** (a) Mean height growth and (b) mean stem diameter increment of seedlings of *Aquilaria malaccensis* in West Kalimantan (n=115). Bars represent  $\pm$  SE.

The proportion of young *A. malaccensis* trees surviving declined throughout the period of observation, particularly during the first eight months. These declines tended to be more pronounced in seedlings and small saplings than in larger saplings. By the end of the observation period, fewer than 20% of seedlings surveyed initially were still alive (Figure 3). Trampling and cutting (33.6%) ranked as the major cause of mortality in *A. malaccensis* followed by flooding (32.7%) (Table 2). However, in a number of cases (23.6%), the cause of death was non-attributable (Table 2).



**Figure 2** The relationship between seedling height growth and irradiance measured at mid-day for seedlings of *Aquilaria malaccensis* in West Kalimantan ( $n=115$ ;  $r^2=0.79$ ,  $p < 0.0005$ ).



**Figure 3** Survivorship curves for seedlings and saplings of *Aquilaria malaccensis* in West Kalimantan. Key to symbols:  $\square$  = seedlings (< 0.5 m height) ( $n = 79$ );  $\circ$  = saplings (0.5–1.0 m height) ( $n = 81$ );  $\times$  = saplings (1.0–2.0 m height) ( $n = 48$ );  $+$  = saplings (> 2.0 m height) ( $n = 7$ ).

### Nursery experiment

Irradiance differed significantly between the different shade treatments (Table 3). Means of instantaneous irradiance on sunny days ranged between 29.6  $\mu\text{mol photons m}^{-2}\text{s}^{-1}$  in the 75% shaded area and 347  $\mu\text{mol photons m}^{-2}\text{s}^{-1}$  in the unshaded area (Table 3). The variance associated with these mean values was high, reflecting pronounced day-to-day variation. Mean humidity and temperature did not differ significantly between the shaded and unshaded areas (Tables 3(b) and (c)). However, significantly lower values of humidity were recorded in the late afternoon than in the morning, associated with an increase in temperature.

**Table 2** Causes of mortality of seedlings and saplings of *Aquilaria malaccensis* in the field site in West Kalimantan (January 1997–April 1998)

Probable cause	West Kalimantan
Browsing	11 (10.0%)
Trampling and cutting	37 (33.6%)
Flooding	36 (32.7%)
Unknown	26 (23.6%)
Total	110

**Table 3** Microclimate recorded in the different shade treatments of the nursery experiment undertaken at Bogor between January and August 1997

(a) Irradiance ( $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ )				
Observation time	Irradiance treatment			
	100%	72.5%	45%	25%
8.00 a. m.	153.07 $\pm$ 100.89	87.93 $\pm$ 52.67	17.98 $\pm$ 10.18	9.68 $\pm$ 5.71
12.00 noon	347.61 $\pm$ 47.43	243.97 $\pm$ 88.42	68.69 $\pm$ 20.91	29.66 $\pm$ 7.19
4.00 p. m.	48.42 $\pm$ 22.72	15.70 $\pm$ 7.98	7.69 $\pm$ 3.80	3.89 $\pm$ 1.96

Values are means  $\pm$  SE; n= 30 days. 100%: full sunlight.

(b) Humidity (%)				
Observation time	Irradiance treatment			
	100%	72.5%	45%	25%
8.00 a. m.	88.86 $\pm$ 6.90	90.71 $\pm$ 6.09	90.96 $\pm$ 4.80	90.97 $\pm$ 3.70
12.00 noon	57.36 $\pm$ 3.45	53.44 $\pm$ 8.45	57.64 $\pm$ 5.41	57.70 $\pm$ 5.30
4.00 p. m.	64.45 $\pm$ 19.27	69.04 $\pm$ 5.54	66.32 $\pm$ 6.70	67.02 $\pm$ 5.70

Values are means  $\pm$  SE; n= 30 days. 100%: full sunlight.

(c) Air temperature ( $^{\circ}\text{C}$ )									
Observation time	Irradiance treatment								
	100%		72.5%		45%		25%		
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	
8.00 a. m.	24.4 $\pm$ 1.6	23.7 $\pm$ 1.5	23.3 $\pm$ 1.5	22.7 $\pm$ 1.4	24.0 $\pm$ 1.3	22.8 $\pm$ 1.9	24.0 $\pm$ 1.0	23.8 $\pm$ 1.0	
12.00 noon	31.2 $\pm$ 1.2	30.5 $\pm$ 0.9	30.4 $\pm$ 0.7	30.2 $\pm$ 0.6	30.4 $\pm$ 0.7	30.3 $\pm$ 1.9	30.9 $\pm$ 0.7	30.4 $\pm$ 0.8	
4.00 p. m.	29.2 $\pm$ 1.3	29.0 $\pm$ 1.3	29.1 $\pm$ 1.0	28.8 $\pm$ 1.0	29.1 $\pm$ 1.0	29.1 $\pm$ 0.9	29.1 $\pm$ 1.0	29.0 $\pm$ 0.9	

Values are means  $\pm$  SE; Min: minimum; Max: maximum; n= 30 days. 100%: full sunlight.

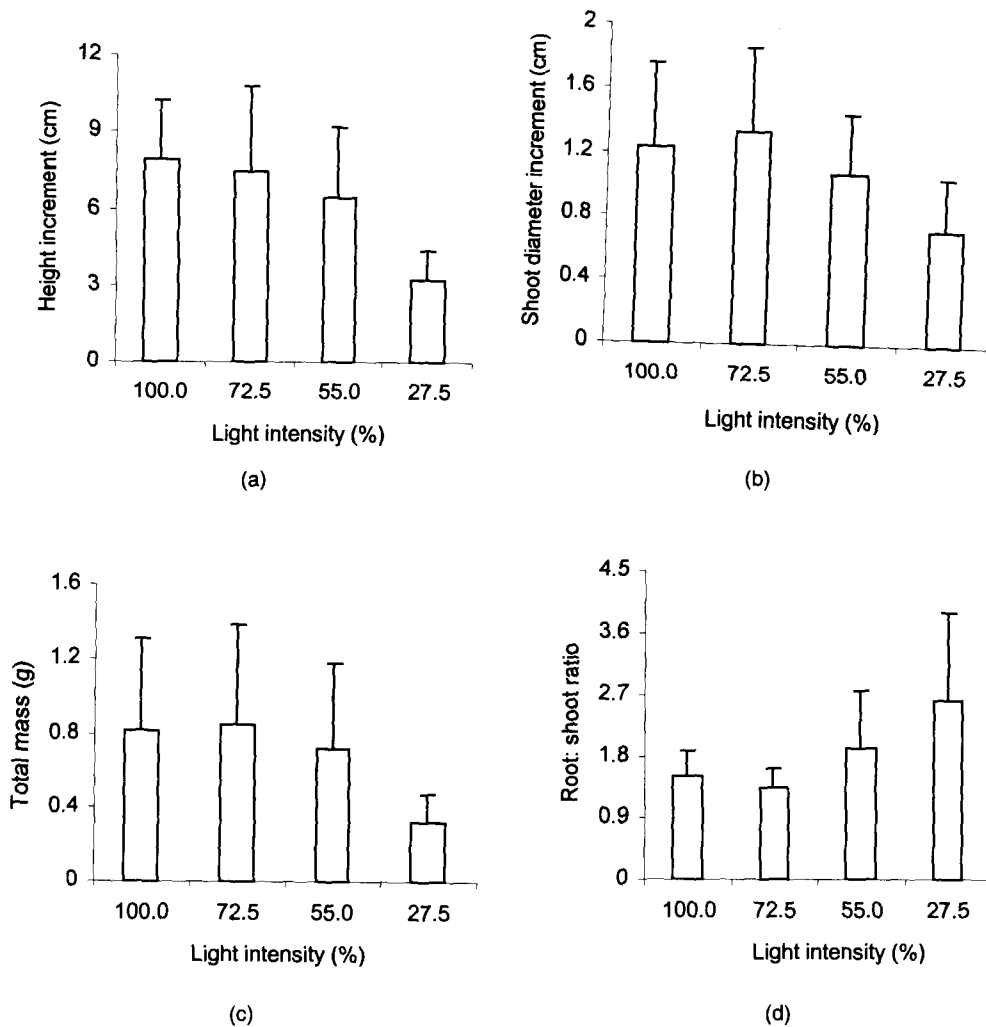


ANOVA indicated that the irradiance treatments (i.e. block) significantly affected all selected growth variables with the exception of leaf increment (Table 4, Figure 4). The decrease in irradiance was associated with lower values for height and stem diameter in the seedlings (Figure 4;  $t$ -test = 4.1,  $p < 0.01$ ,  $df = 29$  for height between 100 and 27.5% irradiance and  $t$ -test = 3.9,  $p < 0.01$ ,  $df = 30$  for stem diameter between 100 and 27.5% irradiance). However, root:shoot ratio increased with the decline in irradiance (Figure 4;  $t$ -test = 2.81,  $p < 0.01$ ,  $df = 29$ ).

**Table 4** Analyses of variance for seedlings of *Aquilania malaccensis* grown in different irradiance, soil type and seedling density treatments in a nursery experiment in Bogor, Java

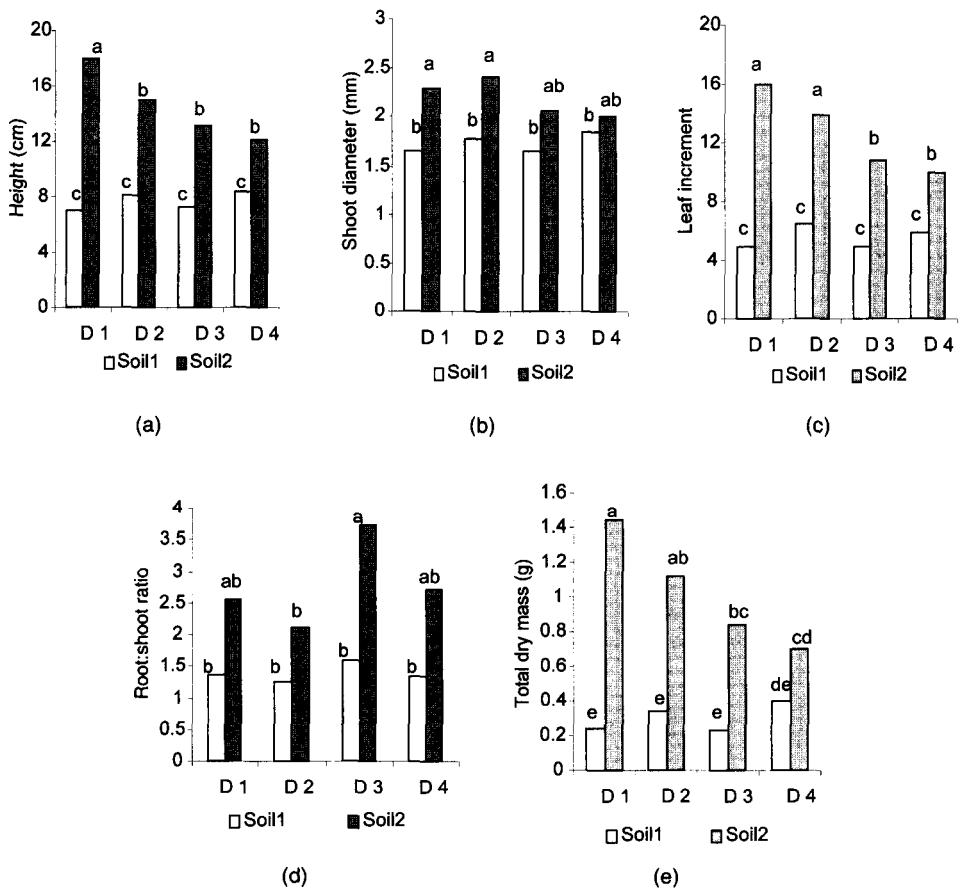
(a) Seedling height					
Source	df	SS	MS	F value	Pr > F
Block	3	511.68	170.56	13.31	0.0001
Soil	1	1461.45	1461.45	114.08	0.0001
Density	3	129.30	43.10	3.36	0.0212
Soil × density	3	215.32	71.77	5.60	0.0013
Error	113	1447.56	12.81		
Total	123				
(b) Stem diameter					
Source	df	SS	MS	F value	Pr > F
Block	3	5.00	1.66	5.32	0.0018
Soil	1	6.64	6.64	21.18	0.0001
Density	3	1.00	0.33	1.07	0.3640
Soil × density	3	1.31	0.43	1.40	0.2459
Error	113	35.44	0.31		
Total	123				
(c) Total dry mass					
Source	df	SS	MS	F value	Pr > F
Block	3	5.29	1.76	9.39	0.0001
Soil	1	15.64	15.64	83.31	0.0001
Density	3	2.11	0.70	3.76	0.0129
Soil × density	3	3.22	1.07	5.72	0.0011
Error	113	21.22	0.18		
Total	123				
(d) Root: shoot ratio					
Source	df	SS	MS	F value	Pr > F
Block	3	28.75	9.58	2.97	0.03
Soil	1	60.27	60.27	18.70	0.0001
Density	3	16.84	5.61	1.74	0.16
Soil × density	3	7.03	2.34	0.73	0.53
Error	113	364.16	3.22		
Total	123				
(e) Leaf number increment					
Source	df	SS	MS	F value	Pr > F
Block	3	85.11	28.37	2.35	0.0759
Soil	1	1540.07	1540.07	127.71	0.0001
Density	3	163.89	54.63	4.53	0.0049
Soil × density	3	219.05	73.01	6.06	0.0007
Error	113	1362.66	12.05		
Total	123				

df = degrees of freedom, SS = sum of squares, MS = mean square



**Figure 4** The influence of light on growth of seedlings of *Aquilaria malaccensis* in the nursery experiment at IPB Darmaga Bogor: (a) height, (b) shoot diameter increment, (c) total dry mass, (d) root:shoot ratio. Values are means  $\pm$  SE in each case.

Growth of seedlings of *A. malaccensis* also differed between soil type and seedling density treatments. Higher values of seedling growth (i.e. height, total dry mass, shoot diameter and leaf increment) were associated with the latosol soil compared with the red and yellow podzol soil (Figure 5). Seedling density also influenced growth rate and plant morphology, with lower values of height, leaf increment and root:shoot ratio recorded with higher seedling densities in the latosol soil. However, there was no effect of seedling density on these variables recorded in the podzol (Figure 5).



**Figure 5** Interaction between density of *Aquilaria malaccensis* seedlings and soil type on seedling growth in the nursery experiment at IPB Darmaga, Bogor: (a) height, (b) shoot diameter, (c) increase in leaf number; (d) root:shoot ratio; (e) total dry mass. Soil 1 (empty bars): yellow red podzol, Soil 2 (filled bars): latosol. Density treatments indicated by number of seedlings per pot: D1, one; D2, two; D3, three; D4, four. Values presented are treatment means (ANOVA); means grouped by the same letter are not significantly different ( $p < 0.05$ ; Duncan's multiple range test).

## Discussion

Numerous studies have defined the responses of different tropical tree species to variation in environmental factors such as light, water and soil nutrients, often with reference to their successional characteristics (Whitmore 1990, Richards 1996, Newbery *et al.* 1998). In particular, the classification of tropical tree species into functional groups based on their light requirement for successful regeneration

has been of value both for understanding patterns of forest dynamics and for developing appropriate silvicultural approaches for those species of economic interest (Hutchinson 1988, Whitmore 1990, Vera *et al.* 1999,). Early-successional, light-demanding species, tend to display higher photosynthetic and growth rates under high light compared with more shade-tolerant species, but display lower survival rates under shade, particularly when young (Whitmore 1990, Richards 1996).

Such research has also highlighted the fact that the understorey of tropical forests is generally characterised by low light availability, which presents a significant challenge to the growth and survival of saplings of all tree species, regardless of their ecological grouping (Chazdon *et al.* 1996, Vera *et al.* 1999). For example, in an intensive study of the microclimate of a neotropical forest which had been subjected to some disturbance caused by selective logging, Vera *et al.* (1999) found that irradiances were generally  $< 100 \mu\text{mol m}^{-2}\text{s}^{-1}$ , with occasional peaks recorded of up to  $2000 \mu\text{mol m}^{-2}\text{s}^{-1}$ . Similar results were obtained in the current investigation, where irradiances measured in both field plots were always  $< 200 \mu\text{mol m}^{-2}\text{s}^{-1}$ , and generally  $< 100 \mu\text{mol m}^{-2}\text{s}^{-1}$ .

The positive relationship recorded here between seedling height growth and irradiance indicates the importance of light availability to the early growth of *A. malaccensis*, a finding supported by results from the shadehouse experiment. However, the latter experiment also indicated that seedlings of *A. malaccensis* are able to survive and grow at very low light availabilities; the mean irradiance measured in the 25% shade treatment ( $29.7 \mu\text{mol m}^{-2}\text{s}^{-1}$  at midday) was comparable to that recorded in dense understorey conditions in the field sites. The high seedling mortality recorded in the field cannot, therefore, be attributed simply to a lack of light; the results from the shadehouse experiment suggest that *A. malaccensis* is at least moderately shade tolerant as a young seedling.

In previous studies of the regeneration ecology of tropical trees, a far greater emphasis has been placed on the response of different species to light availability than to soil nutrient availability and the impact of root competition (Coomes & Grubb 2000). However, root interference can, in some situations, have a major impact on seedling growth and survival (Coomes & Grubb 1998). In addition, the response of tree seedlings to light availability is often greatly modified by soil characteristics, such as nitrogen availability (Coomes & Grubb 2000). In the current experiment, the mean growth rate of seedlings in the nursery experiment was three times higher than that recorded in the field, a result not readily attributable to any difference in microclimate between the two situations. Higher growth rates in pot than in field experiments have often been recorded in previous studies (Newton & Pigott 1991), and imply that root competition (particularly with established, mature trees) may have a significant impact on the growth and survival of seedlings. The effect of competition with mature trees may also account for the lack of any effect of seedling density recorded in the field. In the nursery experiment, results suggested that seedlings may be negatively affected by

competition with other seedlings when growth rates are relatively high (as recorded on the relatively fertile soil). However, in this case, the relative influence of competition below- and above-ground is difficult to elucidate; it is conceivable that increased above-ground competition occurred in the high density treatment because of mutual shading among neighbours.

The role of different factors in causing the high seedling mortality observed in the field is difficult to elucidate as the precise cause of death was often difficult to ascertain. However, many seedlings appeared to have been trampled or cut, either by animals or by people visiting the forest. Animals such as deer and wild pig occur widely in Kalimantan and may account for some of the seedling damage observed.

The low light availabilities recorded in the forest understorey, together with the effects of root competition, may also have contributed to the low survivorship observed in the field.

Current estimates suggest that tens of thousands of *Aquilaria* individuals are being harvested annually for gaharu, a rate which does not appear to be sustainable (Soehartono & Newton 2001). If *Aquilaria* spp. are to be conserved, and gaharu supplies maintained, then those populations being exploited should be brought under some form of sustainable forest management. The current results suggest that silvicultural systems, such as the shelterwood or group selection system, which depend upon opening the canopy to encourage existing regeneration, could be successfully applied to *Aquilaria* spp. Such approaches have been successfully applied to light-demanding tropical tree species such as mahogany (Mayhew & Newton 1998). It is possible, given the survivorship recorded here under shade, that the single tree selection system may also be applicable to *Aquilaria* spp. To our knowledge, no attempts have yet been made to introduce such silvicultural systems to stands of *Aquilaria* spp. For their successful development, further information is required on the response of seedlings in the understorey to canopy opening.

In addition to management of natural populations, or as an alternative, *Aquilaria* spp. can be brought into cultivation. The domestication of these species can enable the quality and quantity of gaharu production to be improved, and the pressure on natural populations to be reduced (Leakey & Newton 1994). The current results suggest that seedlings can be readily grown in nursery conditions. A substantial effect of soil type on seedling growth was also recorded here; the higher pH and CEC recorded in the latosol were associated with substantially higher growth rates. An ability to survive and grow rapidly on more fertile soils would suggest that *Aquilaria* could be introduced into agroforestry systems or home gardens, which are widespread in Indonesia. Small plantations of *Aquilaria* spp. have already been successfully established in Indonesia and elsewhere. Although successful techniques for the culture and inoculation of the appropriate fungi required for gaharu production have yet to be developed (Jalaluddin 1977, Ng *et al.* 1997), successful domestication of the species could make a significant contribution to reducing pressures on natural resources of this species.

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