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Reproductive ecology of *Aquilaria* spp. in Indonesia

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Abstract

Aquilaria spp. (Thymelaeaceae) are the principal source of Gaharu, a valuable resin, yet information about their reproductive ecology is almost entirely lacking. Individuals of six species (*A. beccariana*, *A. crasna*, *A. filaria*, *A. hirta*, *A. malaccensis* and *A. microcarpa*) in cultivation in Indonesia were investigated to assess reproductive phenology, pollination, seed production and germination. Seed production and seedling dispersion were also assessed in natural populations of *A. beccariana*, *A. malaccensis* and *A. microcarpa* in Kalimantan. Most of the selected trees flowered during the dry season, fruits requiring between 36 and 72 days to develop, depending on the species. Twenty different species of insect were recorded visiting flowering trees. The probability of flowers developing into fruit varied between species from 0.04 to 0.43, although flowers from which pollinators were excluded never produced fruit. Seed production of *A. malaccensis* and *A. microcarpa* peaked at a dbh of approximately 40 and 50 cm, respectively, individual trees producing up to 19,000 seeds in a single season. Germination under nursery conditions was initiated 7–15 days after sowing; seeds of *A. crasna* had the highest probability of germination success (92%) whereas those of *A. filaria* had the lowest (53%). In natural forest, most seedlings (>65%) occurred within 5 m of an adult tree, suggesting limited dispersal. These results indicate that *Aquilaria* spp. have high reproductive potential, but suggest that seed dispersal might be limited in natural forests. The implications of these results for the management of *Aquilaria* spp. are discussed.

Keywords: Reproductive phenology; Pollination; Ecology; Gaharu

1. Introduction

For centuries, trees of *Aquilaria* spp. have been harvested from the wild for the purpose of collecting Gaharu, a highly commercial resinous wood used as incense (Ng et al., 1997; Yamada, 1995; Chakrabarty et al., 1994; Sidiyasa, 1986). The genus, which belongs to the Thymelaeaceae, consists of 15 species, which occur in tropical forest in Asia (CIFOR, 1996; Burkill, 1966; Ding Hou, 1960). Six species of *Aquilaria* occur in Indonesia (Ding Hou, 1960) principally in lowland and upland Sumatra, Kalimantan, Maluku and Irian Jaya (Soehartono and Newton, 2000a). The species occur at relatively low density, and as a result of this and the effect of harvesting of Gaharu, the species has been the focus of increasing conservation concern (Chakrabarty et al., 1994).

Information on the taxonomy and morphology of *Aquilaria* spp. is available (CIFOR, 1996; Burkill, 1966; Ding Hou, 1960). However, information on reproductive ecology and factors influencing reproductive

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success of these species is entirely lacking. This information is highly important for managing species such as *Aquilaria* spp., which are currently harvested entirely from natural forests. For the harvesting of *Aquilaria* spp. to be sustainable, extraction of trees in the wild should not reduce populations beyond their capability to regenerate. In the absence of information about reproductive potential, the level of harvest appropriate for sustainable use of the species cannot readily be defined.

Although many important investigations of the reproductive ecology of tropical trees have been undertaken (Richards, 1996; Whitmore, 1990), most species remain uninvestigated. The research which has been undertaken to date suggests that most tropical tree species are hermaphroditic, and are obligately outcrossing as a result of a variety of incompatibility mechanisms (Bawa et al., 1990, Richards, 1996). However, a minority of tree species exhibit dioecy or monoecy. In general, the majority of tropical trees have recalcitrant seeds which do not exhibit dormancy, although some exceptions exist, particularly among shade-intolerant taxa (Whitmore, 1990; Richards, 1996). No information is available concerning the species that were the subject of this study.

The objective of this investigation was to evaluate the probability of reproduction occurring in *Aquilaria* spp. and to analyze the factors influencing seed production and germination. This was achieved by assessing each of the stages involved in seed production, i.e. flowering, pollination, seed production, germination and dispersal, in trees established both in cultivation and in natural forest. The species investigated were *A. beccariana*, *A. filaria*, *A. hirta*, *A. malaccensis* and *A. microcarpa*, all of which are native of Indonesia (Ding Hou, 1960). In addition, *A. crasna* (from Vietnam) was included for comparative purposes. Individuals of the other Indonesian species, *A. cumingiana*, were not available for study.

2. Study areas

Studies of phenology and seed production were undertaken at (i) Kebun Raya Botanic Garden, Bogor, Java (6° 36′S and 106° 47′E) which has living accessions of *A. beccariana* ($n = 2$), *A. hirta* ($n = 1$), *A. malaccensis* ($n = 1$) and *A. microcarpa* ($n = 2$); and (ii) a plantation site located 2 km to the north of Bogor city (6° 36′S and 106° 49′E) with 67 trees of six different species, namely: *A. beccariana* ($n = 4$), *A. crasna* ($n = 9$), *A. filaria* ($n = 7$), *A. hirta* ($n = 5$), *A. malaccensis* ($n = 29$) and *A. microcarpa* ($n = 13$), established in an intimate mixture at a spacing of 2–3 m. The studies in Bogor were carried out between August 1996 and November 1997; rainfall in this area is generally between 3000 and 4000 mm and the area lies at 200–250 m a.s.l.

In addition, studies of seed production and dispersal were undertaken in West and East Kalimantan between October 1996 and April 1998. The observations made in West Kalimantan were carried out at Desa Sebadu-Buluh Kecamatan Mandor (0° 23′N and 108° 45′E), a ±60 ha area of lowland (50–80 m a.s.l.) secondary mixed forest and rubber plantation. The nearest climate station at Mandor, 15 km to the south, recorded a mean annual rainfall between 2600 and 3000 mm. The first field site in East Kalimantan (1° 20′N and 118° 15′E) was situated at the Mentoko Research Station in the Kutai National Park in a ±200 ha area of lowland (±50 m a.s.l.) primary forest, dominated by mixed dipterocarps. Prior to the study, the area was lightly burnt by forest fire in 1983 and 1988. The National Park offices in Sengata, East Kalimantan indicated that annual rainfall in this area ranges between 2800 and 3400 mm. The second area in East Kalimantan (Malinau) is an upland primary forest at 400–1400 m a.s.l. of approximately 2000 ha in extent dominated by mixed dipterocarps (2° 45′N and 116° E). Annual rainfall ranges between 2700 and 3500 mm. This area is known as one of the major sources of Gaharu in the North East of Kalimantan.

3. Methods

3.1. Species identification

Specimens of leaves, fruits and seeds collected from the plantation at Bogor and the study areas in West and East Kalimantan were collected and identified by reference to herbarium specimens and standard texts in Herbarium Bogoriensis, Bogor of the Institute for Indonesian Sciences. The specimens collected were deposited in the herbarium for reference.

3.2. Flowering and fruiting

A single flowering tree of each of *A. beccariana* (dbh = 10 cm), *A. crasna* (dbh = 17.2 cm), *A. filaria* (dbh = 12.3 cm), *A. hirta* (dbh = 6.0 cm), *A. malaccensis* (dbh = 28.5 cm) and *A. microcarpa* (dbh = 15.2 cm) were selected for observation in the plantation site at Bogor. Buds, flowers and fruits from each selected tree were tagged for observation ($n = 30$ in each case) and assessed daily to determine the period of flowering and fruiting of each species and the longevity of each reproductive stage. The number of flowers per inflorescence and the number of inflorescence per floral axis was also counted.

3.3. Pollination

In order to examine whether *Aquilaria* spp. are autogamous, clusters of young flower buds of *A. crasna*, *A. filaria*, *A. malaccensis* and *A. microcarpa* ($n = 15$ in each case) were covered by 15 cm × 15 cm bags of narrow mesh white cotton cloth for 2 weeks. The selected flowers were examined after the cloth was opened to assess whether any fruit development was taking place.

A study of pollinator visit was undertaken in the plantation area during the month of September 1997 when most of the trees of *A. hirta*, *A. malaccensis* and *A. microcarpa* were flowering. The insects which visited flowers of the observed trees were assessed at an interval of every 2 h between 6 am and 10 pm for 20 consecutive days. The visiting insects were trapped with sweep nets, labeled and according to the time and place they were trapped, then subsequently identified by staff at the Zoology Museum of the Indonesian Institute for Sciences at Bogor.

3.4. Seed production

A total of 56 individual trees of six species were selected for observations of seed production in four different study sites (Table 1). As described by CIFOR (1996) and Ding Hou (1960), upon ripening, the fruit of *Aquilaria* spp. splits loculicidally in half from the apex, and the seeds are suspended on thin threads for about an hour before the threads break and the seed is dispersed. Because of the difficulties in trapping the seeds, seed production was inferred from the capsules which were trapped in nets. The nets were constructed of narrow mesh black nylon. In the plantation and Botanic Garden, the nets were of the same area as the tree canopy projected to ground level, and set up 1 m above the ground. The traps were visited every day for 3 months, for capsule collection and cleaning. For trees in the field sites in Kalimantan, five 1 m × 1 m nets of black nylon were positioned under the canopy of each selected tree. These traps were visited every 2 weeks for 3 months, for capsule collection and cleaning. The total seed production of each tree in Kalimantan was estimated by calculating the ratio of trap area to the canopy area using the formula: $r/t \times n$, where r is the canopy area projection, t the trap area and n the number of capsules trapped. The dbh, height and canopy areas of the observed trees were also measured.

3.5. Seed germination

Seed germination of *A. beccariana*, *A. crasna*, *A. filaria*, *A. hirta*, *A. malaccensis* and *A. microcarpa* was observed in the nursery of the plantation area, Bogor, between March and November 1997. One hundred seeds of each species taken from trees in the *Aquilaria* plantation were sown in five plastic

Table 1
The number of individuals of *Aquilaria* spp. selected for observations of seed production in different locations[a]

Species	n[b]	Location
A. beccariana	4	Plantation (3) and Botanical Garden (1)
A. crasna	3	Plantation
A. filaria	3	Plantation
A. hirta	2	Plantation
A. malaccensis	17	West Kalimantan (11), plantation (5) and Botanic Garden (1)
A. microcarpa	26	West Kalimantan (4), East Kalimantan (14), plantation (6) and Botanic Garden (2)

[a] For details of each location, see text.
[b] Number of selected trees of *Aquilaria* spp. is denoted by n.

boxes (40 cm × 30 cm × 15 cm tall) containing river sand which had previously been sterilized with boiling water. The boxes were placed out of doors in full sunlight. Air temperature and humidity of the nursery area were recorded three times each day (07.00, 12.00 and 15.30 h) with a hygrometer. The number of germinating seeds of each species (as indicated by the presence of a shoot >2 mm in length) was recorded every day for 2 months.

3.6. Size and mass of fruit and seed

Fruits of *A. beccariana*, *A. crasna*, *A. filaria*, *A. malaccensis* and *A. microcarpa* were collected from the plantation area and Botanical Garden, Bogor. The fruit size was measured using calipers to the nearest 0.01 cm. Seed mass was measured using a digital balance (hf-200GD; AND Ltd., Tokyo) to the nearest 0.001 g.

3.7. Seedling dispersion

The pattern of seedling dispersion was assessed in East Kalimantan for *A. microcarpa* (March 1997) and *A. beccariana* (April 1998) and in West Kalimantan (April 1997) for *A. malaccensis.* The method followed Setiadi et al. (1997) with a few modifications. Twelve mature trees of each species were selected randomly, and dbh, height and projected canopy areas of each recorded. Four line transects of 30 m length to the North, South, West and East were established from each of the selected trees. Plots of 2 m radius (12.57 m^2 in area) were set up at 5 m intervals along each of the transect lines. The number of *Aquilaria* seedlings (<0.5 m height), large seedlings (0.5–1.0 m height), saplings (>1.0–1.5 m height) and large saplings (>1.5–2.0 m height) within each plot was counted. The pattern of dispersion was examined by χ^2 tests (Steel and Torrie, 1980). Casual observations were also made of seed predators and dispersers in the field sites.

4. Results

4.1. Flowering and fruiting

Although a few flowers of *A. crasna* were found to occur along the trunk (cauliflory), flowers of all six species were borne on terminal branches among the foliage. The flowers were between 5 and 10 mm long and were white to yellow (*A. microcarpa*), green to dirty yellow (*A. malaccensis*), white to yellowish-green (*A. filaria*), white (*A. hirta*), or green to yellowish (*A. beccariana*) in color.

Most of the selected trees in the field site in West Kalimantan flowered and fruited in June and July 1997 but the trees in East Kalimantan flowered during September to October 1997. The flowering and fruiting of *A. beccariana*, *A. malaccensis* and *A. microcarpa* in the Botanical Garden, Bogor occurred between September and December 1997 (Fig. 1). The flowering and fruiting period in the plantation areas occurred from April to December 1997 (early dry season to the middle of the rainy season) for *A. crasna*, *A. malaccensis* and *A. microcarpa. A. filaria* flowered and fruited all year round, whereas *A. hirta* flowered and fruited during the rainy season in January 1998 (Fig. 1). The plantation owner stated that most, if not all, mature trees of *Aquilaria* spp. in the plantation flower every year.

In general it took between 1 and 3 months after the onset of flowering for *Aquilaria* spp. in the plantation to produce seeds (Table 2). In general, flowers of *A. beccariana* were relatively long-lived, and those of *A. filaria* relatively short-lived, compared to the other species (Table 2). The time required for fruit development was longest in *A. malaccensis* and shortest in *A. crasna* (Table 2). The number of flowers per inflorescence also differed among species, as did the number of inflorescences per floral axis (Table 3). *A. malaccensis* displayed the highest probability for its inflorescence to develop into fruit while *A. filaria* displayed the lowest (Table 3).

4.2. Pollination

None of the covered flowers of *A. filaria*, *A. malaccensis* or *A. microcarpa* in the plantation produced fruits, while uncovered flowers did so. Twenty different species of insect were recorded visiting the flowering trees of *A. crasna*, *A. filaria*, *A. malaccensis* and *A. microcarpa* (Table 4). Many of the species demonstrated pronounced diurnal variation in pattern of abundance for example, 10 species were primarily nocturnal, visiting the flowers between 18.00 and 22.00 h (Table 4). One species (*Eupithecia* spp.)

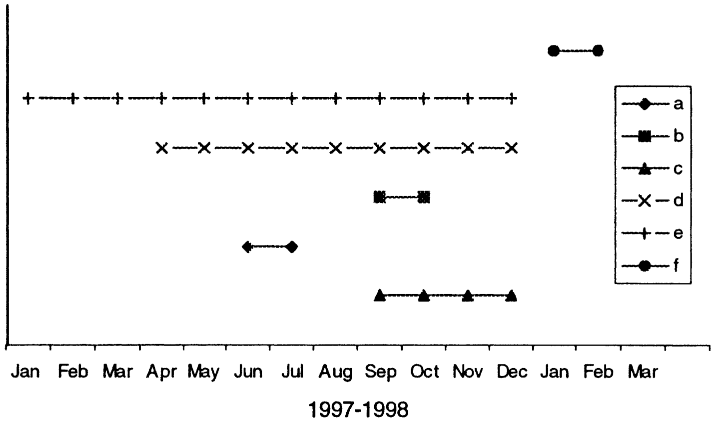

Fig. 1. Flowering phenology of *Aquilaria* spp. in natural forest, plantation and Botanical Garden (a) *A. malaccensis* and *A. microcarpa* in West Kalimantan; (b) *A. microcarpa* in East Kalimantan; (c) *A. malaccensis*, *A. microcarpa* and *A. beccariana* in Botanical Garden; (d) *A. crasna*, *A. malaccensis* and *A. microcarpa* in plantation, Bogor; (e) *A. filaria* in plantation, Bogor; (f) *A. hirta* in plantation, Bogor. For details of locations see text.

Table 2
Longevity of different reproductive structures of *Aquilaria* spp. in a plantation at Bogor, Java[a]

Name of species	Longevity (days)		
	Buds	Flowers	Fruits
A. crasna	8.8 ± 5.3	4.6 ± 1.9	36.0 ± 12.7
A. beccariana	2.1 ± 1.0	10.2 ± 4.8	47.0 ± 4.5
A. filaria	5.6 ± 4.5	2.0 ± 1.2	37.0 ± 8.1
A. hirta	3.7 ± 3.1	7.8 ± 2.4	66.2 ± 7.2
A. malaccensis	4.8 ± 2.2	6.0 ± 2.0	71.6 ± 12.3
A. microcarpa	6.0 ± 5.0	6.1 ± 4.9	39.3 ± 24.7

[a] Values are means ± S.E. ($n = 30$ in each case). The longevity refers to the time between emergence of the structure and its eventual dehiscence or development into another reproductive stage.

although generally nocturnal (Ubaidillah, Museum Zoology Bogor, personal communication) was collected during the daytime.

4.3. Seed production and fruit/seed size

All selected trees of *A. malaccensis* in the natural forest produced fruits. In contrast, only four selected trees of *A. microcarpa* in West Kalimantan fruited and 8 of 14 selected trees of *A. microcarpa* in East Kalimantan produced fruits. All selected trees in the plantation and Botanical Garden fruited. No data were collected on flower bud or fruit abortion.

In general, smaller trees of *A. malaccensis* and *A. microcarpa* produced more seed than larger, and

Table 3
Mean number of flowers per inflorescence, mean number of inflorescences per floral axis and the probability of flowers developing into fruits in five *Aquilaria* spp. established in a plantation at Bogor, Java[a,b]

Species	Number of flowers per inflorescence	Number of inflorescences per floral axis	Number of flowers developing into a fruit per inflorescence	Probability of a flower developing into a fruit
A. beccariana	9.0 ± 9.6	15.8 ± 13.7	0.5 ± 1.7	0.06
A. filaria	12.3 ±11.3	7.2 ± 8.6	2.6 ± 4.8	0.21
A. hirta	7.0 ± 1.6	4.4 ± 2.6	0.3 ± 0.6	0.04
A. malaccensis	8.5 ± 3.3	4.3 ± 9.6	3.7 ± 7.6	0.43
A. microcarpa	8.2 ± 6.7	11.0 ± 4.8	1.4 ± 4.2	0.17

[a] For methods, see text.
[b] *A. crasna*: data not available. Values are means ± S.E. ($n = 30$ in each case), except in the case of column 4.

Table 4
Insect species recorded visiting flowers of *A. filaria*, *A. malaccensis* and *A. microcarpa* in a plantation at Bogor, Java during observations over 20 consecutive days (9–28 July 1997)[a]

Name of family, genus and species	Observation time and relative abundance							
	6–8 am	8–10 am	10–12 am	12–2 pm	2–4 pm	4–6 pm	6–8 pm	8–10 pm
Lepidoptera								
Pyralidae								
1. *Spatalistis* spp.	+	−	−	−	−	−	−	−
2. *Pachyzancha pallidadis* Hmps	−	−	−	−	−	−	+++	−
3. *Scoparia* spp.	−	−	−	−	−	−	+++	−
4. *Herpetogramma* spp.	−	−	−	−	−	−	+++	−
5. *Leechia* spp.	−	−	−	−	−	−	+++	−
6. Unidentified spp. 1	−	−	−	−	−	−	+++	−
7. Unidentified spp. 2	−	−	−	−	−	−	+	−
8. Unidentified spp. 3	−	−	−	−	−	−	+	−
Lymantridae								
9. *Euproctis icilia* Stall	−	−	−	−	−	−	−	+++
10. *Euproctis* spp.	−	−	−	−	−	−	−	+++
Geometridae								
11. *Eupithecia* spp.	−	−	+ (?)	−	−	−	−	+++
Syntomidae								
12. *Syntomis huebneri* Boisd	−	−	−	−	−	−	+	−
Coleoptera								
13. *Cicindela icilia* Stall	+	−	−	−	−	−	−	−
Hymenoptera								
Vespidae								
14. *Polistes sagitarius* Sauss	−	−	−	−	++	−	−	−
Eumenidae								
15. *Eumenes atrophicus* F.	+	+++	+	+	++	−	−	−
Specidae								
16. *Ancistrocerus pseudodynerus* D.T	−	+++	−	−	−	−	−	−
Diptera								
Bombicidae								
17. *Hyporalonia chrysolampis* Jm	−	+	−	−	−	−	−	−
Syrphidae								
18. *Eristalis obliqua* Wild	−	−	−	−	+	−	−	−
Homoptera								
Flatidae								
19. *Nephesa coromandelica* Spin	−	−	+++	−	−	−	−	−
Apidae								
20. *Trigona* spp.	−	+++	−	−	−	−	−	−

[a] Minus (−): not recorded. Relative abundance indicated on a scale of (+) (present at low abundance; <10 individuals captured per day), (++) (present at moderate abundance; 10–20 individuals captured per day), (+++) (present at high abundance; >20 individuals captured per day).

presumably older ones. In the natural forest the seed production of *A. malaccensis* declined above a dbh of approximately 40 cm, while the production of seed from trees of *A. microcarpa* declined above a dbh of approximately 50 cm (Fig. 2a). Trees of *A. malaccensis* (dbh 10–30 cm) and *A. microcarpa* (dbh 10–<40 cm) in the plantation or Botanical Garden tended to produce more seed than those produced by the trees of comparable size in natural forest. Trees of *A. microcarpa* of a given size class produced more seed than did those of *A. malaccensis*. The estimated production of seeds of *A. microcarpa* (20–60 cm dbh) ranged between 13,260 and 19,280 seeds per tree, whereas trees of *A. malaccensis* (20–60 cm dbh) produced between 3,900 and 13,270 seeds per tree (Fig. 2b). In the case *A. beccariana, A. crasna* and

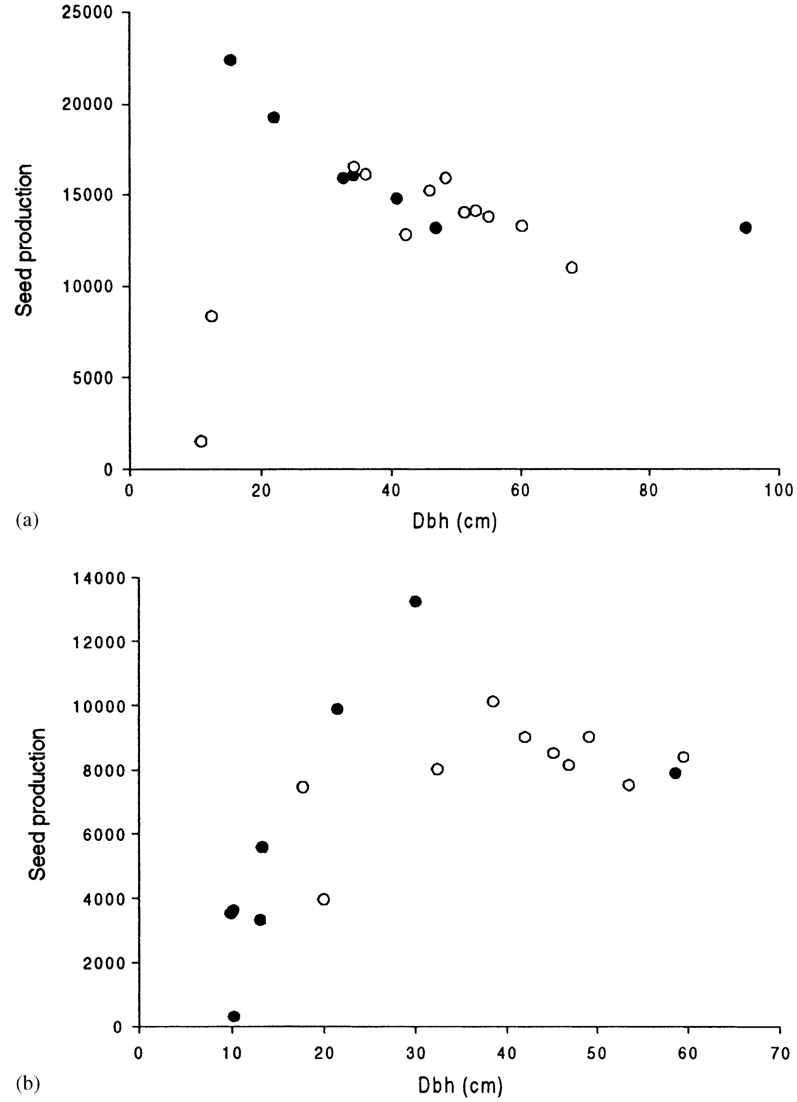

Fig. 2. Scatter diagram indicating the relationship between diameter (dbh) and seed production of (a) *A. microcarpa*; (b) *A. malaccensis* growing in a plantation and Botanical Garden at Bogor, Java (filled circles) and in natural forest in Kalimantan (open circles). For methods see text.

A. filaria, owing to the limited sample size, no relationship between dbh and seed production was apparent (Table 5).

The fruit of *Aquilaria* spp. is firm-fleshed with two locules. Each fruit contains a maximum of two seeds (one per each locule) but often only one. Fruit mass and size was highest in *A. crasna* and lowest in *A. microcarpa* (Table 6).

4.4. Seed germination

The daily mean temperature in the nursery area in June to October 1997 ranged from 23.4 to 30.2°C while the mean daily humidity ranged from 69.5 to 100%. In these conditions seeds of *A. hirta* started to germinate at day 9 after sowing, while seed of *A. malaccensis* did not start germinating until day 15, the

Table 5
Seed production of *A. beccariana*, *A. crasna* and *A. filaria* in a plantation at Bogor, Java

Species	Dbh[a] (cm)	No. of seed collected
A. beccariana	5.78	17
	7.00	21
	7.63	142
A. crasna	17.2	6494
	5.5	307
A. filaria	3.17	1387
	5.04	655
	5.37	1400
	6.04	1449
	7.15	1523

[a] Dbh: diameter at breast height. For methods see text.

other species falling within this range (Fig. 3). The seeds of *A. crasna* had the highest probability of germination success (92%) whereas those of *A. filaria* had the lowest (53%) (Fig. 3).

There was no indication of seed dormancy in any of the six species in the plantation. However, the study located a number of newly germinating seeds of *A. malaccensis* in two locations in the field under canopy gaps near decaying mature trees which had been felled at least 6 months prior to the visit.

4.5. Seedling dispersion and seed dispersal

The size of the three species assessed in the field differed, mean dbh for *A. beccariana*, *A. malaccensis*

Table 6
Size of fruit and fresh mass of fruit and seed of *Aquilaria* spp. collected from a plantation at Bogor, Java[a]

Name of species	Fruit size (cm)		Fruit mass (g)	Seed mass (g)
	Length	Width		
A. crasna	3.75 ± 0.50	2.76 ± 0.53	4.28 ± 0.93	0.17 ± 0.10
A. beccariana	3.39 ± 0.74	0.69 ± 0.29	0.49 ± 0.11	0.03 ± 0.01
A. filaria	1.87 ± 0.30	1.40 ± 0.20	2.19 ± 0.92	0.13 ± 0.06
A. hirta	3.17 ± 0.22	1.12 ± 0.13	NR[b]	NR[b]
A. malaccensis	2.20 ± 1.73	1.30 ± 0.28	3.17 ± 1.36	0.03 ± 0.01
A. microcarpa	1.35 ± 0.32	1.12 ± 0.85	0.75 ± 0.33	0.03 ± 0.01

[a] Values are means ± S.E. ($n = 30$ in each case).
[b] NR: not recorded.

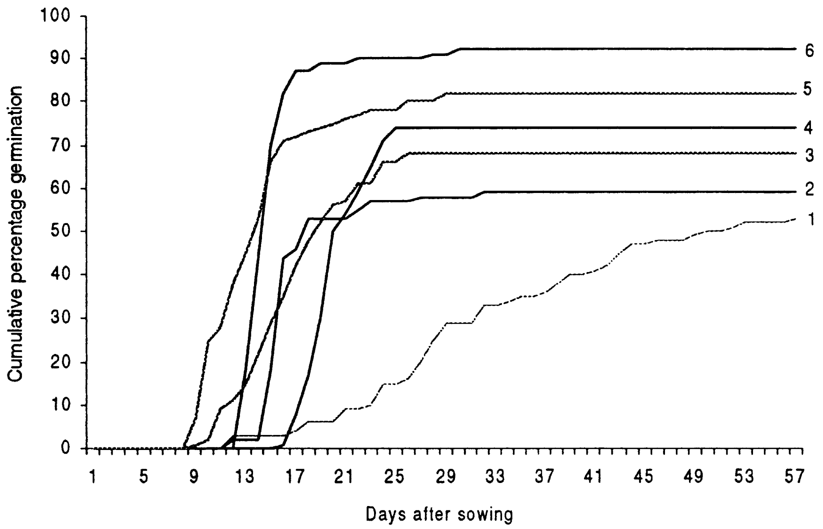

Fig. 3. Cumulative germination percentage of seeds of *Aquilaria* spp. in a nursery at Bogor, Java. 1, *A. filaria*; 2, *A. microcarpa*; 3, *A. hirta*; 4, *A. malaccensis*; 5, *A. beccariana*; 6, *A. crasna*. Number of seeds sown = 100 for each species.

Table 7
Density of seedlings and saplings of *A. beccariana*, *A. malaccensis*, *A. microcarpa* recorded along transects from parent trees (n = 12 parent trees for each species) in three different field sites[a,b]

Distance (m)	Offspring density (m^{-2})			Probability of offspring occurrence under parent tree (%)		
	A. malaccensis	*A. microcarpa*	*A. beccariana*	*A. malaccensis.*	*A. microcarpa*	*A. beccariana.*
5	88.2 ± 8.2	27.3 ± 8.2	1.3 ± 1.1	69.2	70.6	67.5
10	35.0 ± 10.2	6.1 ± 3.7	0.5 ± 0.1	27.5	15.7	27.0
15	3.5 ± 1.7	3.9 ± 1.3	0.1 ± 0.1	2.8	10.2	5.4
20	0.2 ± 0.1	0.7 ± 0.2	0.0 ± 0.0	0.1	2.0	0.0
25	0.0 ± 0.0	0.4 ± 0.1	0.0 ± 0.0	0.0	1.1	0.0
30	0.3 ± 0.1	0.2 ± 0.1	0.0 ± 0.0	0.2	0.4	0.0

[a] For details see text.

[b] Each sample plot was 12.57 m^2 in area; total area of sample plots for each parent tree was 301.44 m^2. Distance: distance from the parent trees; values are mean ± S.E. (n = 12).

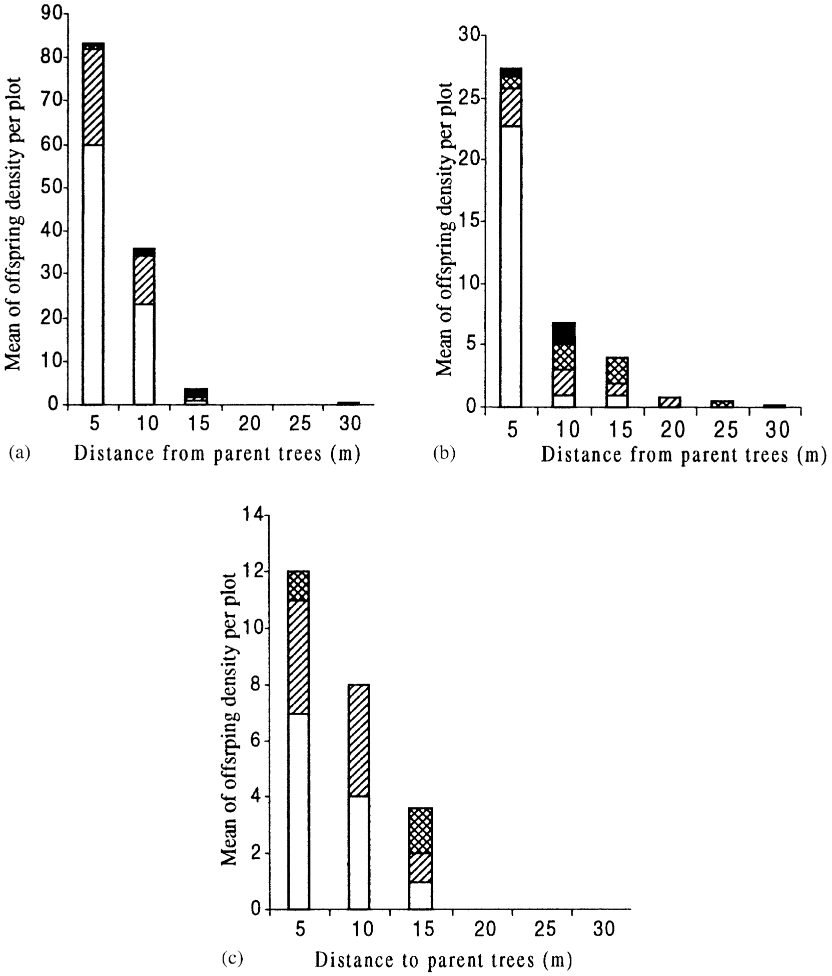

Fig. 4. Mean density of seedlings (0.5 m height; open bars), large seedlings (>0.5–1.0 m; hatched bars), saplings (>1.0–1.5 m height; cross-hatched bars) and large saplings (>1.5–2.0 m height; filled bars) of (a) *A. malaccensis*; (b) *A. microcarpa*; (c) *A. beccariana* along 30 m transects from the parent trees of (a) *A. malaccensis* (n = 12) in West Kalimantan; (b) *A. microcarpa* (n = 12) in East Kalimantan; (c) *A. beccariana* (n = 12) in East Kalimantan. Densities are given per plot (12.57 m^2).

and *A. microcarpa* being 18.5 ± 5.1, 42.2 ± 7.5 and 60.4 ± 14.9 cm, respectively. In each case, offspring density declined rapidly with increasing distance from the mature tree, with the vast majority of seedlings occurring within 5 m of the trunk of the putative parent (Table 7, Fig. 4). Offspring of the selected trees were not distributed evenly along the transects from the selected mature trees ($\chi^2 = 296.24$, $P < 0.05$, d.f. = 5 for *A. malaccensis*; $\chi^2 = 85.29$, $P < 0.05$, d.f. = 5 for *A. microcarpa* and $\chi^2 = 112.27$, $P < 0.05$, d.f. = 5 for *A. beccariana*). Seedling/sapling densities reached a maximum of 88.2 m^{-2} in *A. malaccensis*, but only 1.3 m^{-2} in *A. beccariana* (Table 7).

Few observations were made of seed dispersal or predation by animals or birds, despite repeated visits to the field sites. However, it was discovered that squirrels and rats consumed fresh fruits of *Aquilaria* spp. in the Botanical Garden and plantation.

5. Discussion

An understanding of the reproductive ecology of tree species is fundamental to their effective conservation and management, yet often such information is lacking, even for economically important taxa such as *Aquilaria* spp. To our knowledge, this investigation has provided the first observations of these species either in plantation or field conditions, for most of the variables assessed. Ideally, more detailed information would have been derived from populations in the field, particularly for pollination and reproductive phenology, as the behavior of the trees in cultivation could differ markedly to that in natural situations. However, these data do provide some initial insight into the reproductive characteristics of the species concerned.

According to the position in which flowers occur, Ashton et al. (1977) defined two synusiae: those species where flowers are presented above the canopy and those that flower within the canopy. The latter is the group to which many understorey species belong (Appanah, 1990). As flowers of the six *Aquilaria* spp. observed occurred in foliage (with some evidence of cauliflory in *A. crasna*), it would appear that *Aquilaria* spp. are typical members of the understorey trees, according to Appanah (1990). In natural forests, mature trees of *A. hirta*, *A beccariana* and *A. filaria* often do not reach the top canopy as these species tend not to grow higher than 20 m (Ding Hou, 1960), but mature trees of *A. malaccensis* and *A. microcarpa* can grow up to 40 m in height. Compared to some dipterocarp spp. (Dayanandan et al., 1990), the mean number of flowers per inflorescence of *Aquilaria* spp. appears low.

Flowering of the species assessed in Kalimantan occurred in the dry season. Although many lowland tropical trees reproduce in the dry season (Swaine et al., 1997), it is uncertain whether this pattern is typical for these *Aquilaria* spp., because of the influence of the El Niño Southern Oscillation (ENSO) event in Asia during 1997. Byron and Shepherd (1998) noted that the 1997–1998 ENSO event caused an exceptionally long dry season, occurring from January to October 1997 for West Kalimantan and June 1997 to April 1998 for East Kalimantan. Flowering and fruiting of *A. malaccensis* in the Botanical Garden, Bogor was also concentrated in the dry period, which in 1997 occurred from April to September. For comparison, *A. agallocha* in a plantation in Arunachal Pradesh, India, in 1984 flowered in March and started fruiting in the middle of June (Beniwal, 1989).

Although studies of the pollination ecology of tropical trees have been extensively undertaken in tropical America, knowledge about Southeast Asian species is still very limited (Richards, 1996; Kato, 1996; Bawa et al., 1985, 1990). SE Asian forests are often dominated by members of the Dipterocarpaceae, which are known to be pollinated by thrips (Chan and Appanah, 1980) and honeybees (Dayanandan et al., 1990). In understorey plant communities, long-tongued, traplining solitary bees (Kato et al., 1991) and long-billed sunbirds (Kato et al., 1993) are key pollinators. Appanah (1990) indicated that tree species which present their flower within the canopy or trees which belong to the understorey often have a wide array of unspecialized insect pollinators which are commonly found in the immediate vicinity of the trees. The current data suggest that *Aquilaria* spp. may behave similarly in this respect. However, further observations are required to assess whether the insect visitors observed here actually act as pollinators, as many insects which visit flowers may not actually transfer pollen (Richards, 1996). However, results of the pollinator exclusion experiment clearly indicate that the *Aquilaria* spp. examined here are obligately outcrossing, in common with many other tropical trees (Richards, 1996; Whitmore, 1990).

Long-term studies of fruiting phenology in tropical forest have indicated that fruit production of tropical trees fluctuates widely in time and space (Swaine et al., 1997; Richards, 1996; Terborgh, 1986). Fruit production is also often associated with the availability of pollinators (Ghazoul et al., 1998; Richards, 1996; Bawa et al., 1990). Not all selected trees of *Aquilaria* spp. in Kalimantan produced fruits during the observations in 1997. Variation in fruit production between individuals of similar stem diameter was also observed. Widespread fires occurred throughout Kalimantan during mid-1997 to early 1998, and may have affected the availability of pollinators. For example, Kinnaird and O'Brien (1998) indicated that in lowland South Sumatra, trees located close to forest fire were associated with less flowering and fruiting compared to trees in unaffected forest. Such effects may account for the higher fruiting of *A. malaccensis* recorded here in the plantation and botanical garden than in the natural forest. The low proportion of flowers which developed into fruit may reflect pollinator failure, or the abortion of flowers or young fruit, further research would be required to differentiate between these possibilities.

Mechanisms of seed and fruit dispersal in tropical forest are extremely varied (Suzuki and Ashton, 1996; Richards, 1996). Fruit of most of the *Aquilaria* spp. assessed here were green in color, with the exception of *A. filaria*. On the basis of fruit color and size, rodents are the most likely consumers of fruits of *Aquilaria* spp., based on the classification of Gautier-Hion (1990). *Aquilaria* fruits have a firm fleshy capsule and may therefore, also be attractive to birds or arboreal mammals. Further research is required to evaluate the role of animals and birds as dispersers and predators of *Aquilaria* seed, the pattern of seedling distribution recorded here indicates that few seeds are dispersed more than a few metres from the adult tree. Similarly Setiadi et al. (1997) found that most seedling recruitment of several dipterocarp spp. in Gn. Palung, West Kalimantan, which are dispersed by gravity, occurred within a distance of 15 m from the mature trees.

Although most tropical tree species do not exhibit seed dormancy, it can occur in some species (Richards, 1996). Seeds of *Aquilaria* spp. germinated rapidly under the nursery conditions tested here, in addition the proportion of seed which eventually germinated was relatively high (>50%). Experiments with *A. agallocha* in India indicated similar results, most seed of this species germinated within 3 weeks after sowing (Beniwal, 1989). However, germination rates of *Aquilaria* spp. in natural forests might be different than in the environment tested here. Swaine et al. (1997) pointed out that although shadehouse and laboratory experiments may help in determining the relative importance factors influencing seed germination processes, it is difficult to predict their effect in forest conditions.

Overall, these results suggest that *Aquilaria* trees are generally highly fecund. Although the proportion of flowers developing into a fruit was very low, the number of flowers borne by a mature tree was very high, resulting in the production of thousands of seeds by an individual tree. If the high germination rates recorded here were reproduced under forest conditions, the potential for seedling recruitment would also be high. This conclusion is supported by the relatively high seedling densities recorded in the field. Although many tropical tree species exhibit masting behavior (Richards, 1996; Whitmore, 1990), anecdotal information collected during this investigation suggests that *Aquilaria* spp. are able to reproduce annually. Together, these characteristics confer a high reproductive potential.

These results have a number of implications for management of *Aquilaria* populations. Silvicultural systems dependent on the presence of advanced regeneration would appear to be applicable to *Aquilaria* spp., given the high reproductive potential of the species, if the stands studied here are typical. However, the low seedling densities recorded for *A. beccariana*, together with the low seed set in this species, suggest that regeneration may in some cases be inadequate to ensure stand replacement after silvicultural intervention. Further information is required for all *Aquilaria* spp. on the microsite preferences for seed germination and seedling establishment, and the impacts of canopy opening on these variables.

A key issue relating to the management of populations in natural forest is the provision of seed trees, which is of particular importance for species such as *Aquilaria* spp. which appear not to demonstrate seed dormancy. In fact, the required size and density of seed trees is poorly defined for most tropical trees, although relationships between seed production and dbh have been defined for some other taxa (Chapman et al., 1992). Plumptree (1995) conducted observations of seed trees of commercial timber species at Budongo, Uganda, and revealed that *Entandrophragma* spp. did not produce fruit below 80 cm dbh, while *Khaya* spp. produced fruit at 40 cm dbh. Some tree species (e.g. *Celtis* spp., *Maesopis* spp.) showed a decline in fruit production with increasing size, as recorded here for *Aquilaria*. Similarly Gullison et al. (1996) reported that fecundity of mahogany (*Swietenia macrophylla*) peaks when the trees are about 110 cm dbh.

The present results should be viewed with caution, given the relatively small sample size and the fact that observations were confined to a single season, individual trees might clearly produce different amounts of fruit from 1 year to the next (Newstrom et al., 1994). Despite these limitations, the results suggest that some individuals of a dbh of approximately 40–50 cm should be retained to maintain seed production. This does not generally occur at present in stands harvested for Gaharu, where most of the trees (>90%) may be harvested regardless of size (Soehartono and Newton, 2000b). The limited capacity for seed dispersal recorded here would suggest that a high density of seed trees should be retained to ensure adequate regeneration.

Another option to secure sustainable Gaharu production would be to increase cultivation of *Aquilaria* spp. in plantations. The successful production of viable seed in the plantation-grown trees indicates that plantation crops could be managed as seed orchards facilitating the domestication process (Leakey and Newton, 1994). *Aquilaria* trees in the plantation were between 9 and 10 years of age, indicating that such seed could be produced relatively rapidly. The high seed production and germination rates observed are also conducive to the production of planting stock at a commercial scale. Although a number of small-scale plantations have so far been established in Indonesia, such as the one included in this study, none have so far provided a commercial source of Gaharu. Further research is required on inoculation of the trees with appropriate fungi to stimulate Gaharu production in order for plantations to provide an alternative supply of Gaharu (Ng et al., 1997; Santoso, 1996; Jalaluddin, 1977).

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