SITE CONDITIONS FOR REGENERATION OF *HOPEA ODORATA* IN NATURAL EVERGREEN DIPTEROCARP FOREST IN SOUTHERN VIETNAM

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DONG TL, BEADLE CL, DOYLE R & WORLEDGE D. Site conditions for regeneration of *Hopea odorata* in natural evergreen dipterocarp forest in southern Vietnam. Matching species to suitable sites is important in reforestation. This study investigated the site conditions that support regeneration of *Hopea odorata,* a valuable timber species, in a secondary evergreen natural forest. Stand structure, light intensity at seedling level and soil condition were examined in three representative 50 × 50 m plots. The upper canopy was dominated by four dipterocarps: *H. odorata, Shorea roxburghii, Anisoptera costata* and *Dipterocarpus alatus.* The prevailing stand structure supported vigorous germination but not development of seedlings of all four species. Low light levels near the forest floor were the major constraint on seedling development of *H. odorata.* There was no regeneration when the mean per cent transmitted incident daily photosynthetic active radiation (PAR) was 2.2%; seedling germination but not development was supported when PAR was 6.6%; regeneration and development occurred when PAR was 11.4%. The soils were slightly acidic with low clay and high sand contents and low nutrient concentration, but this was apparently not a constraint on growth given adequate light conditions. The results suggest that the re-establishment of *H. odorata* on degraded sites using nurse crops should be possible provided that high levels of shading are avoided.

Keywords: Gap regeneration, photosynthetically active radiation, site requirement

INTRODUCTION

Valuable tropical timber species have a history of overharvesting (Lamb 2011). One of these species is *Hopea odorata*, a late successional tropical dipterocarp which is naturally distributed in many South-East and South Asian countries (Prosea Foundation 1993). Its timber is valued because of its durability and resistance to insects, and use for weight-bearing construction. *Hopea odorata* is currently assessed as vulnerable in the IUCN Red List of threatened species (IUCN 2012). In Vietnam, it is listed as a priority species in need of immediate conservation (Hong 2012).

Under natural conditions, usually in riparian and moist forest, *H. odorata* grows with other dipterocarps which eventually occupy the upper storey and become dominant. Natural regeneration occurs where there is shade, suggesting that seedlings are shade tolerant (Sakai et al. 2009). Young trees become more light demanding (Thao 1995). While shade is considered important for germination and initial establishment within the understorey (Kettle 2009), it is associated with low rates of growth, rates increasing when light intensities are increased (Appanah 1998). Continuous shade can compromise survival (Kamaluddin & Grace 1993).

There have been many attempts using enrichment planting or planting with nurse crops to re-establish *H. odorata* for either timber or conservation (Weinland 1998). In Vietnam, it has been a major species in reforestation programmes, but many of these have failed because of the use of inappropriate planting sites and silvicultural treatments (Tam 2007). Nutrient deficiency and soil compaction led to poor seedling establishment on degraded rainforest soils in Sabah (Nussbaum et al. 1995). In lowland tropical dipterocarp forest, inadequate incident light and the low availability of soil nutrients and moisture are the major constraints affecting seedling recruitment (Kettle 2009).

To successfully re-introduce *H. odorata* into degraded environments, it is important to understand the site requirements for its regeneration and growth in its natural habitat. This knowledge can then be used as a basis for selecting silvicultural treatments which lead to certainty of establishment in plantations. The present study examined stand structure, light and soil conditions associated with the regeneration of *H. odorata* in a remnant but healthy natural forest in southern Vietnam.

MATERIALS AND METHODS

Study sites

The study was conducted in the Dong Giang Conservation Forest, Binh Thuan province. The site is in a hilly area at 11° 12' N and 107° 55' W at an altitude of approximately 390 m. The climate has distinct wet and dry seasons; mean annual rainfall of 1650 mm is concentrated between May and October. The mean annual temperature is 26.9 °C. Mean air humidity is 81.7% (Binh Thuan Statistical Office 2011). The forest was selectively logged until 1994 and then managed for water conservation only with no disturbance. The dominant trees are the late successional evergreen dipterocarps *H. odorata, Shorea roxburghii, Anisoptera costata* and *Dipterocarpus alatus.*

Sampling and sample analyses

Field sampling was carried out in June and July 2011. Three representative 2500-m^2 (50 m × 50 m) plots were established in the lower (Plot 1), middle (Plot 2) and upper (Plot 3) parts of the site. The difference in altitude and the distance between each plot were 15 m and approximately 500 m respectively.

Stand structure

Each plot was subdivided into 25 sub-plots of 10 m × 10 m. For the adult tree layer, defined as trees with diameter at breast height (dbh) ≥ 10 cm, all trees in each sub-plot were identified at species level. Their dbhs were recorded by tape. The total height of 25 trees in each of Plots 1 and 2 was measured using a Vertex ultrasonic hypsometer. For the sapling layer, trees with dbh < 10 cm and total height ≥ 2 m, three randomly-selected 10 m × 10 m sub-plots (12% of total plot area) in each plot were used to record the species and dbh. For the seedling or regenerating layer, i.e. individuals < 2 m total height, 12 sub-sub-plots measuring 2 m × 2 m each (2% of plot area) were set up systematically at 8-m intervals in each plot in two transects crossing at the plot centre; the two end sub-sub-plots were placed 5 m from the plot border. The total height and abundance of all tree species present were recorded. Adjacent to Plot 1, 10 additional 2 m × 2 m plots placed at 4-m intervals along an old logging track and six additional 2 m × 2 m plots placed at 4-m intervals along the sensor line to the north of the track (the first centred 6 m from the track) were used to examine seedling growth of *H. odorata* and the other dipterocarp species in contrasting incident light conditions.

Light environment

Plot 1, which had the highest abundance of *H. odorata* regeneration around mother trees but little seedling development, was selected for estimates of percentage-transmitted photosynthetically active radiation (PAR). Adjacent was an old logging track which had been abandoned for at least five years, and which supported naturally regenerating and vigorously growing seedlings of *H. odorata*. Outside the plot and on the opposite, north side of the track, mother trees were present but there was no seedling regeneration. To capture the difference in light conditions between these contrasting environments, 16 quantum sensors were installed at 1.5-m height above the ground. The sensors were placed at 6-m intervals, eight along the track, and four each through Plot 1 and where there was no regeneration. The sensors were connected to a data logger and multiplexer between 12 and 25 July 2011. Data as μmol m^{-2} s^{-1} PAR were recorded automatically every 5 min as the average of measurements taken every 30 s. In the same way, total incident PAR was measured using three quantum sensors located in an open area 2 km from the site. For each treatment, relative daily transmitted PAR was calculated. For estimates of gap openness and leaf area index

(LAI), vertically-pointing digital photographs of the canopy were taken at each sensor point using a horizontally-mounted digital camera.

Soils

In each sampling plot, soil was collected between the 0–20 and 20–40 cm depths from 10 randomly-selected 10 m × 10 m sub-plots. In each, a composite mineral soil sample for each layer was aggregated from five randomly-collected soil cores using a 100-mm diameter auger. To estimate bulk density (BD), three cores were randomly collected from each layer in each sub-plot using a 53-mm diameter ring.

Preparation and analysis of the soil samples followed Rayment and Higginson (1992). Bulk density was determined after the cores were dried at 105 °C to constant weight. The soil mineral samples were air-dried and put through a 2-mm sieve. Soil pH_{H_2O} and electrical conductivity (EC) were measured by a handheld Lab Navigator in a 1:5-mixture of soil and distilled water, and soil in a 1:5-mixture of soil pH_{CaCl_2} and 0.01M $CaCl_2$. Total carbon (TC) and total nitrogen (TN) were determined using a CHNS/O Element Analyser and extractable phosphorus (Ext-P) using the Olsen manual colour method and a spectrophotometer at wavelength 882 nm. Exchangeable cations (Ex-K, Ex-Ca, Ex-Mg and Ex-Na) were extracted with 0.01M silver-thiourea $(AgTU)^+$; exchangeable K^+ and Na^+ were determined by flame photometry, and Ca^{2+} and Mg^{2+} by atomic absorption spectroscopy. Particle sizes were determined on sub-samples dispersed by heating in water followed by 16-hour end-over-end shaking in the presence of NaOH and Calgon. Fractions were determined by settling with a Bouyoucos hydrometer. All data are reported as unit per oven-dry weight.

Data analysis

The works of Ho (1999) and MARD (2000) were used for nomenclature and to identify species, genus and family. Importance value index (IVI) of each species was determined as the sum of relative abundance (%), relative dominance (%) and relative frequency (%), where abundance and dominance are tree number and total basal area respectively, of a given species in a plot, and frequency is the number of sub-plots in which the species appeared (Curtis & McIntosh 1950). Species diversity was assessed using Simpson's index (Simpson 1949), Shannon–Wiener's index and species evenness (Shannon 1948).

The digital photographs were used to calculate canopy openness by CAN-EYE V6.3.3 software after correcting for barrel distortion using Photoshop CS3 (Adobe). All canopy objects including leaves, stems and branches were defined as closed area and sky as gap area; leaf area index was determined from the same photographs using a simplified technique based on Fuentes et al. (2008) and ImageJ 1.47u software (Schindelin et al. 2012).

Several common equations for estimating top height from dbh in natural forests (van-Laar & Akça 2007) were fitted to the sub-sample of measured tree heights and the best-fitting used for calculation of the total height of all trees ≥ 10 cm dbh in the three plots. For these trees, basal area (m^2 ha^{-1}) was calculated as the sum of the cross-sectional area over bark at breast height of all individuals per hectare; standing volume (m^3 ha^{-1}) was the sum of standing volumes of all individuals per hectare, with volume for each tree calculated as the product of its basal area, top height and stem form factor (*f*, FIPI 1995).

RESULTS

Floristic richness and dominance

Forty species from 30 families were represented in the 'adult' tree layer. The Dipterocarpaceae were dominant (4 spp., Table 1). Other families with more than one species were Myrtaceae (3 spp.), Lythraceae (2 spp.), Ebenaceae (2 spp.), Combretaceae (2 spp.), Fabaceae (2 spp.) and Euphorbiaceae (2 spp.). Not all families or species were represented in each plot. In the sapling layer, there were 28 species belonging to 22 families, and in the seedling layer 13 species belonging to nine families. Dipterocarpaceae were also dominant in sapling (4 spp.) and seedling (3 spp.) layers. Many non-dipterocarp species represented in the tree layer were not found in the sapling and seedling layers. Some species were represented in the seedling or sapling layers of a plot but not in its tree layer.

Species richness in the tree layer was in inverse proportion to the abundance of the dipterocarp trees. In Plots 1 and 2 where their abundance was high (89 and 94 trees), there were 18 and 14 non-dipterocarp species respectively; in Plot 3, where 45 dipterocarp trees were present, there were 31 non-dipterocarps (Table 1). The Simpson's

Table 1 Dominant families, numbers of trees and numbers of species in each 2500 m^2 plot

Family	Total three plots (30 families)				Plot 1 (26 families)				Plot 2 (24 families)				Plot 3 (36 families)			
	No. of trees	Number of species			No. of trees	Number of species			No. of trees	Number of species			No. of trees	Number of species		
		Tr	Sa	Se		Tr	Sa	Se		Tr	Sa	Se		Tr	Sa	Se
Dipterocarpaceae	228	4	4	3	94	4	4	3	89	3	1	3	45	3	1	2
Myrtaceae	41	3	2	1	1	1	2	1	22	1	2	1	18	3	2	1
Lythraceae	32	2	2	2	6	2	1	1	8	2	1		18	2	2	2
Dilleniaceae	24	1	1		2	1	1		14	1	1		8	1	1	
Verbenaceae	22	1	1		2	1	1		8	1			12	1	1	
Lecythidaceae	20	1			5	1			11	1						
Ebenaceae	19	2	2		5	2	2		9	1	1		5	2	1	
Ixonanthaceae	15	1							3	1			12	1		
Combretaceae	9	2	1		3	2	1						4	2		
Chrysobalanaceae	6	1	1	1					1	1	1	1	5	1	1	
Other species	90	22	14	6	26	8	8	3	15	5	5	5	55	18	5	1
Total	506	40	28	13	144	22	20	8	180	17	12	10	182	34	14	6

Tr = tree layer, Sa = sapling layer, Se = seedling layer

diversity indices ranged from 0.78–0.95, the Shannon–Wiener diversity indices 2.04–3.12 and species evenness 0.72–0.89; each was highest in Plot 3 and lowest in Plot 2 (Table 2).

Dipterocarps in the tree layer expressed their importance in the stand by high IVI (Figure 1). In Plot 1, *H. odorata*, *A. costata* and *S. roxburghii* had IVI of 64.5, 62.0 and 51.5 respectively; *D. alatus* had 8.7. In Plot 2, *S. roxburghii* had IVI of 114.4 followed by *D. alatus* (13.5) and *H. odorata* (11.8). In Plot 3, *D. alatus* had IVI of 43.9 followed by *H. odorata* (25.2) and *S. roxburghii* (18.0).

Natural regeneration

Dipterocarp species were the most abundant in the seedling layer. Abundance was high in the < 20-cm height class but declined sharply with seedling development (Figure 2). Total abundance in height class < 20 cm ranged from 8125 ha^{-1} (Plot 3) to 115,625 ha^{-1} (Plot 1) and for *H. odorata* from 1042 ha^{-1} (Plot 3) to 83,333 ha^{-1} (Plot 1). For seedling height classes from 50–99 to 150–199 cm, total abundance decreased from 1667–2500 ha^{-1} to 417–1250 ha^{-1} and *H. odorata* was absent. For seedlings < 20 cm, there was an order of magnitude difference between abundance in Plot 1 (115,625 ha^{-1}) and the other plots (≤ 12,292 ha^{-1}). However, for seedlings ≥ 50 cm, abundance in Plot 1 was the lowest.

On the abandoned logging track, the total abundance of seedlings was 15,250 ha^{-1} comprising 14,000 ha^{-1} dipterocarps and 1250 ha^{-1} non-dipterocarps. *Hopea odorata* was the most abundant with 3000 seedlings ha^{-1}, in height class < 20 cm, 7500 in 20–49 cm and 1000 in 50–99 cm. In the closed forest to the north of the track, there were 3500 seedlings ha^{-1}, all of them non-dipterocarps. Seedlings in the 50–99 cm height class were only found along the track.

In the sapling layer, *H. odorata* (67 saplings ha^{-1}) and *A. costata* (133 saplings ha^{-1}) were present only in Plot 1. *Shorea roxburghii* was present in all plots and *D. alatus* (67 saplings ha^{-1}) in Plot 3 only.

Stand structure

The best fitting relationship for predicting tree height was the exponential equation of Freese (1964) described by van-Laar & Akça (2007) where height = $e^{[0.695 + 0.784 \ln (dbh) - 0.009 dbh]}$ ($r^2 = 0.71$).

Stand density, basal area and standing volume varied between 576 and 728 trees ha^{-1}, 27.5 and 32.9 m^2 ha^{-1}, and 292 and 385 m^3 ha^{-1} respectively (Table 3). Although Plot 1 had the lowest stand density, the total number of dipterocarps and their basal area and volume were the highest of the three plots; *H. odorata* also had the highest stand density (104 trees ha^{-1}), basal area (11 m^2 ha^{-1}) and volume (145 m^3 ha^{-1}), equal

Table 2 Diversity indices

Plot	Simpson's index (1 – D)	Shannon–Wiener's index	
		H'	Evenness (H'/H_{max})
1	0.86	2.36	0.76
2	0.78	2.04	0.72
3	0.95	3.12	0.89

Simpson's index (1 – D) is a measure of the probability that two randomly-selected individuals in the community belong to different categories; Shannon–Wiener's index (H') is a measure of the rarity or commonness of a species in a community; evenness (H'/H_{max}) is a measure of the similarity of abundance of different species; H_{max} is the maximum value of H'

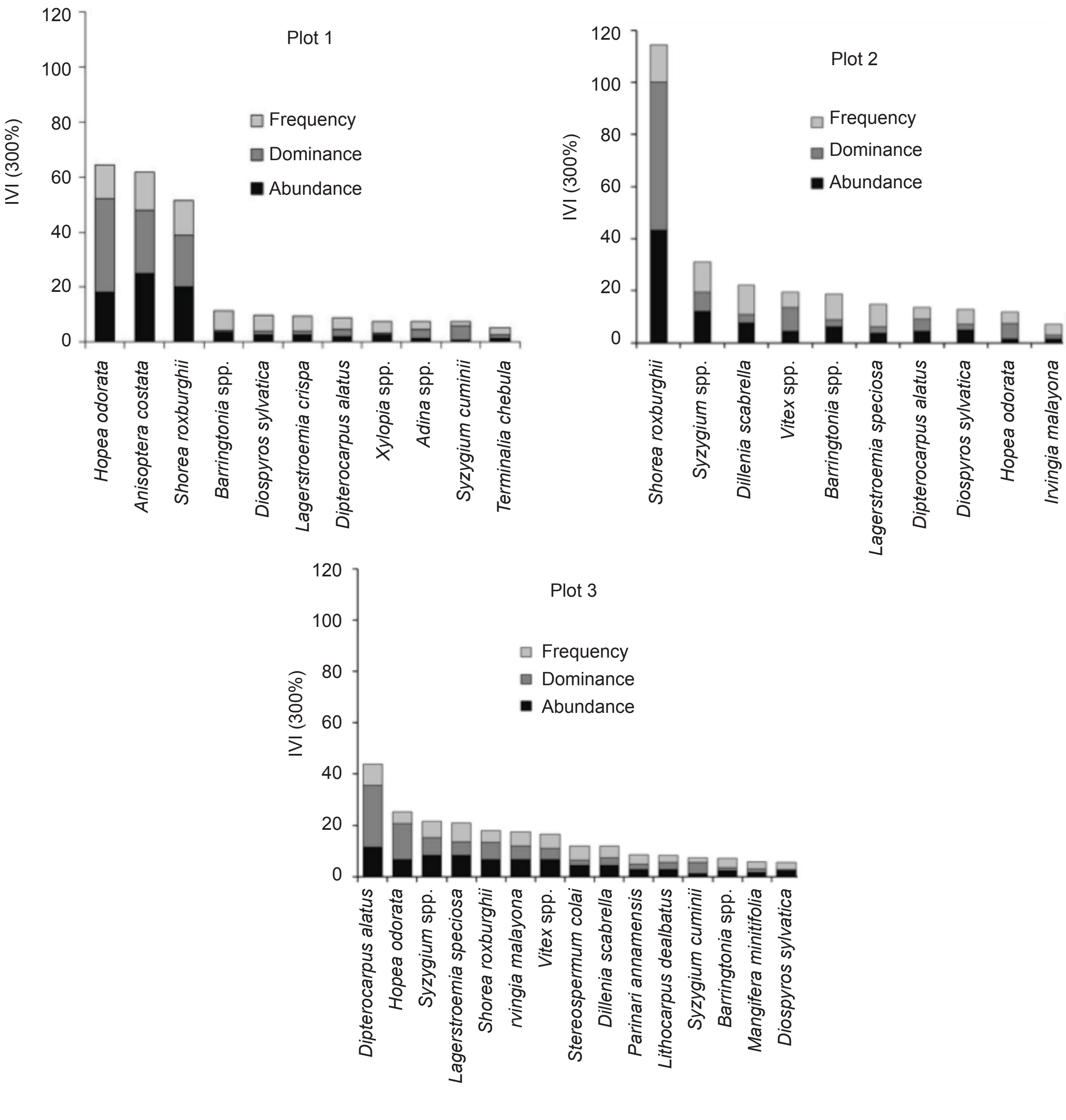

Figure 1 Importance value index (IVI), frequency, dominance and abundance of the most important species (IVI ≥ 5%) in the tree layer; for each plot, relative frequency is percentage of sub-plots where the species is represented; relative dominance is percentage of basal area; relative abundance is percentage of individuals

to 28, 43 and 47% of dipterocarp presence respectively.

The distribution of trees amongst dbh classes in all three plots followed an inverted J-curve shape (Figure 3). Most trees were in the smaller classes with abundance decreasing with increasing dbh. The largest trees had dbh > 60 cm. The greatest number of trees had heights between 13 and 21 m (data not shown).

Light condition

Canopy openness was greatest along the track (20.4%), followed by closed forest in Plot 1 (11.4%) and to the north of the track (6.6%; Table 4). The per cent transmitted PAR for the track, closed forest in Plot 1 and closed forest to the north of the track were 11.4, 6.6 and 2.2% respectively; LAIs were 4.0, 5.9 and 6.6 respectively.

Soil condition

In the 0–20 cm layer, soil pH_{H_2O}, soil pH_{CaCl_2}, EC and TC were respectively 5.67–6.14, 4.60–5.18, 32.4–46.6 µS cm^{-1} and 0.57–0.87%. The levels of soil nutrients were 0.056–0.082% TN, 4.59–5.83 mg Ext-P kg^{-1}, 0.018–0.037 cmol Ex-K kg^{-1},

Table 3 Stand densities, basal areas and standing volumes

Plot	Stand density (trees ha^{-1})			Basal area (m^2 ha^{-1})			Standing volume (m^3 ha^{-1})		
	Stand	Ho	Dipterocarp	Stand	Ho	Dipterocarp	Stand	Ho	Dipterocarp
1	576	104	376	32.4	11.0	25.4	385	145	308
2	720	12	356	32.9	1.93	22.2	363	26.5	255
3	728	48	180	27.5	3.87	12.4	292	48.4	151

Ho = *Hopea odorata*

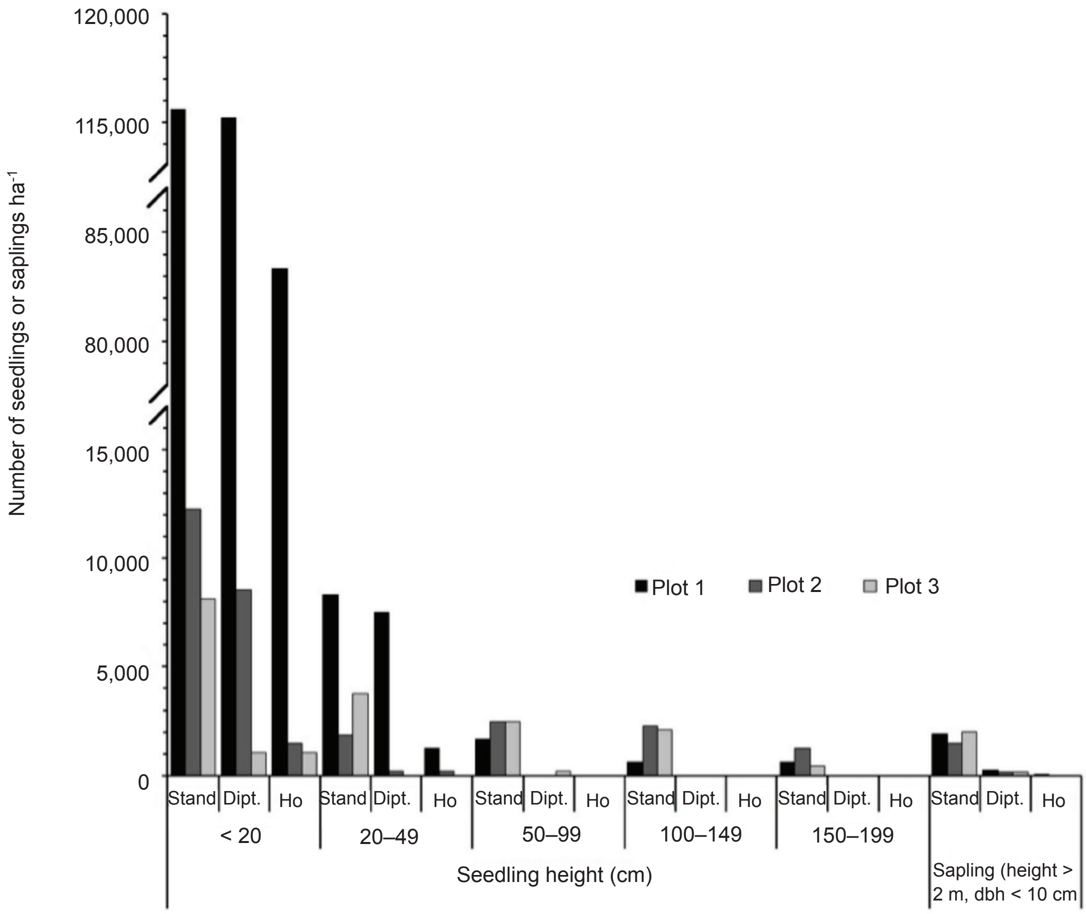

Figure 2 Numbers of naturally-regenerated seedlings and saplings per hectare in different height classes; Dipt. = dipterocarp, Ho = *Hopea odorata,* dbh = diameter at breast height

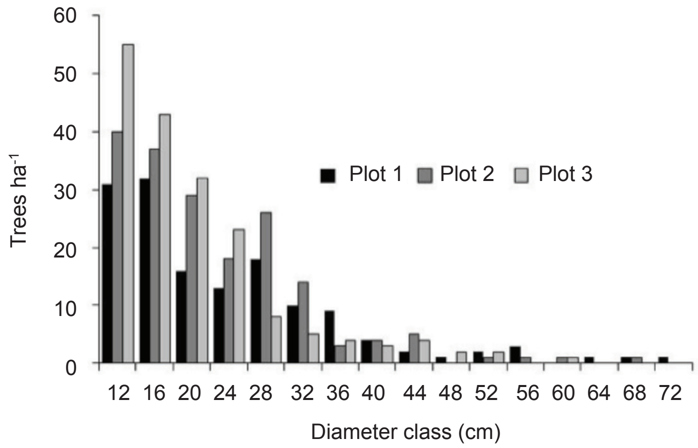

Figure 3 Diameter distribution of trees ≥ 10 cm diameter at breast height

Table 4 Mean values ± standard deviation of canopy openness, leaf area index (LAI), per cent transmitted photosynthetically active radiation (PAR) at 1.5-m height above ground and number of regenerated *Hopea odorata* seedlings along three transects where the mother trees were presented

Treatment	Canopy openness (%)	LAI	PAR (%)	Number of *H. odorata* seedlings		
				< 20 cm	20–49 cm	50–99 cm
Abandoned logging track (n = 8)	20.4 ± 4.0	4.0 ± 0.7	11.4 ± 8.9	3000	7500	1100
Closed forest in Plot 1 (n = 4)	11.4 ± 3.5	5.9 ± 0.5	6.6 ± 6.9	83,300	1250	0
Closed forest north of track (n = 4)	6.6 ± 2.1	6.6 ± 0.6	2.2 ± 3.1	0	0	0
Open area (n = 3)	100	0	100 ± 1.5			

0.07–0.16 cmol Ex-Ca kg^{-1}, 0.052–0.137 cmol Ex-Mg kg^{-1} and 0.014–0.037 cmol Ex-Na kg^{-1}. Soil particles were high in sand (77.2–91.3%) and low in clay (5.5–18.2%) contents; BD ranged from 1.17–1.26 g cm^{-3}. Clay content and many other properties were highest in Plot 2. In the 20–40 cm layer, concentrations of TC, TN and Ext-P were about half those in the 0–20 cm layer; exchangeable cation levels were either similar to the 0–20 cm layer or lower; pH and EC were lower; bulk densities were marginally higher but sand and clay levels similar.

DISCUSSION

This study has shown that a healthy natural secondary forest dominated by evergreen dipterocarp species, including *H. odorata*, produces a rich reproductive resource for regeneration. This was shown by the substantial number of seedlings in the < 20-cm height class. However, their rapid disappearance with increasing height class indicated that the current site condition did not support seedling development. The major factor restricting their development was low levels of transmitted light.

Stand structure vs regeneration of *H. odorata*

The stand structure indicated that the forest was in the mature phase when dipterocarps form a potential reproductive resource for regeneration. Dipterocarps dominated the seedling but not the sapling layer, indicating that this forest is mid-successional. At this closed-forest stage, light conditions can support the formation of a seedling layer, but a sapling layer will only form when the canopy starts to break up (Ashton et al. 2001). The inverted J-shaped distribution of tree number with dbh class indicated previous disturbance, possibly caused by selective logging, but at levels insufficient to support seedling development, particularly of *H. odorata*.

The difference in IVI of dipterocarp species among the three plots is probably related to their spatial distribution. *Hopea odorata* usually grows in the lower and wetter parts of the landscape, its distribution overlapping with *A. costata* and *S. roxburghii* (Bunyavejchewin et al. 2003). Plot 1 was at the base of a slope and the IVI of all three species was high. Conversely, *D. alatus* is usually distributed in the upper and drier part of the landscape (Bunyavejchewin et al. 2003) where it was predominant in Plot 3. There is no evidence of strong segregation among these dipterocarps and they are often found clumped together (Bunyavejchewin et al. 2003). This may have led to the negative association between dipterocarp and non-dipterocarp species found in this study where the higher IVI of dipterocarps in Plots 1 and 2 than Plot 3 was linked to lower species diversity index.

Abundance of *H. odorata* in the adult and seedling layers differed among the three plots. Many mid- and late-successional dominants of dipterocarp forest are site-restricted, their distribution being related to seed dispersal characteristics, elevation, soil moisture and nutrients (Ashton et al. 2001, Bunyavejchewin et al. 2003). Dispersal of most dipterocarp species is by wind in which seeds gyrate slowly towards the ground on wings modified from sepals (Bawa 1998). Species with large seeds like *Dipterocarpus globosus* (Nakagawa et al. 2005) and *Shorea beccariana* (Krishnapillay & Tompsett 1998) can disperse seeds 15–24 m and 12–16 m respectively, from mother trees (Takeuchi et al. 2005). As *H. odorata* seed is much smaller (Krishnapillay & Tompsett 1998), it is expected to disperse further. However, as its development is restricted by soil water availability (Bunyavejchewin et al. 2003), its dispersal may not be represented by its abundance. The abundance of *H. odorata* was highest in Plot 1 which was permanently wet and close to a small creek.

There was a sharp decrease in the seedling number at height classes ≥ 20 cm. Seedling recruitment consists of seed production, germination and seedling establishment (Clark et al. 1998). The substantial numbers of dipterocarp seedlings in the < 20 cm height class indicated that seed production and germination were not an issue. Under the warm and moist conditions common at this site, dipterocarp seeds will germinate quickly (Tompsett 1998). However, the subsequent limitations to seedling establishment indicate a strong filter in the recruitment process and transition from germination to development (Clark 2009, James et al. 2011). This is linked to niche condition and resource supply (Kettle 2009).

Light condition vs regeneration of *H. odorata*

In general, the later the species in the succession, the higher is its shade tolerance (Strugnell 1936). Late successional dipterocarps tolerate shade (Appanah 1998). How this tolerance changes with seedling development remains unquantified though high rates of growth and survival are often associated with partial shading (Weinland 1998). The relationship between growth rate and levels of chlorophylls a and b of 6- and 18-month-old seedlings raised across a light gradient showed that while *H. odorata* was shade tolerant, its demand for light increased with age (Thao 1995).

Low light intensity was the major factor limiting *H. odorata* seedling development. Germination and establishment were high where relative canopy openness and incident PAR were respectively 20.4 and 11.4%, limited to germination where they were 11.4 and 6.6%, and absent where they were 6.6 and 2.2%. Similarly, in secondary forest in Borneo, rates of survival and growth of seedlings of four dipterocarp species were lower in closed forest where relative incident PAR at 1.5-m height was 2.4% than in artificially created gaps where PAR was 11.4% (Romell et al. 2008, 2009). In shade-house trials, 15 tropical shade-tolerant species were able to survive but not grow at levels of transmitted PAR as low as 0.8% (Bloor & Grubb 2003). In this study, there was more rapid reduction in the number of seedlings in the smallest size classes along the track than in Plot 1 as seedling development inevitably led to greater levels of self-thinning. Thus low light intensity stimulates early establishment of *H. odorata* (Kettle 2009) whereas deep shade is associated with its poor growth and/or survival (Kamaluddin & Grace 1993, Appanah 1998). Dipterocarp seedlings can remain in low light condition for long periods as 'advanced regeneration' but will then perish if there is no canopy disturbance to initiate rapid height growth (Ashton et al. 2001). For *H. odorata* in this study, poor growth was associated with the transmission of 6.6% of PAR; the track, which had reduced LAI by about one-third and which initiated rapid height growth, was associated with an approximate doubling of the transmission of PAR.

In a shade-house experiment, Lee et al. (1997) found that *H. odorata* seedling growth and photosynthetic rate can respond positively up to PAR levels of 40% of that experienced in an open area. Thus while *H. odorata* requires a relative incident PAR of around 11% to initiate active growth in its natural environment, greater levels of disturbance may lead to its more rapid development. Vigorous seedling growth in treatments receiving up to 87.5% full sunlight has been observed for other dipterocarp species (Nicholson 1960); in *H. odorata* similar responses observed by Lee et al. (2000) are linked to plasticity of leaf structure and function. However, if this information is to be applied in plantations, survival and growth rate may be insufficient for an assessment of successful establishment, as vigour, morphology and stem form may also be affected by light condition (Weinland 1998). There is an inevitable compromise between growth rate and stem quality when growing shade-tolerant species in commercial silvicultural systems (Medhurst et al. 2003).

Soil condition vs regeneration of *H. odorata*

The soils were low in element concentrations and this was associated with low clay and high sand contents. Evergreen dipterocarp forests are found in environments with both low (Grubb et al. 1994) and high (Baillie et al. 2006, Zaidey et al. 2010) soil nutrient concentrations. In a species mixture, resources are efficiently exploited over time, so soil nutrient levels may be low if no disturbance occurs (Ashton 1999). The response of dipterocarp seedlings to nutrient supply may also depend on light availability (Sundralingam 1983, Ang et al. 1992). In gap and closed forest, fertiliser application had no effect on the growth of *S. curtisii* and *H. beccarriana* seedlings respectively (Turner et al. 1993); in full sunlight, that of *Dryobalanops lanceolata* and *S. leprosula* was significantly increased, suggesting the primary factor determining growth was light (Nussbaum et al. 1995). In this study, in spite of low soil nutrient concentrations, there was good adaptation and growth of *H. odorata* seedlings on the old logging track and the basal areas of the main plots indicated productive forest. Thus, nutrient supply was probably a secondary factor determining seedling growth as long as other resources were sufficient. The success of dipterocarp forest was not correlated with soil nutrient concentration but rather with topography, soil depth and water availability (Ashton & Hall 1992).

The soils were slightly acidic and pH was higher than found previously in evergreen dipterocarp forest (Grubb et al. 1994, Baillie et al. 2006, Zaidey et al. 2010). Under acidic conditions (pH_{KCl} = 3.9–4.7), plantations of *H. odorata* grow well in Vietnam and can achieve MAI of 7.5–13.3 m^3 ha^{-1} (Que et al. 2010). Thus, it would appear that this species is well-adapted to a wide range of soil pH.

As the soils were dominated by sand and mean BD was low, they were not compacted. Soil compaction can impair rooting behaviour at germination (Dabral et al. 1984, Zainudin 2000) and seedling growth (Nussbaum et al. 1995) of dipterocarps. However, while a BD > 1.6 g cm^{-3} significantly restricted rooting of 3-month-old *H. odorata*, there was no significant effect when seedlings were over 6 months old, suggesting that this species can adapt to soil compaction (Zainudin 2000).

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