

PHOTOSYNTHETIC RESPONSES TO LIGHT AND THE
ECOLOGICAL DOMINANCE OF *HOPEA FERREA*
(DIPTEROCARPACEAE) IN A SEMI-EVERGREEN FOREST
OF NORTHEASTERN THAILAND

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ABSTRACT

Semi-evergreen forests of Thailand have a high diversity of tree species, but commonly exhibit a strong ecological dominance by single species of Dipterocarpaceae. This situation is evident with *Hopea ferrea* in the semi-evergreen forest at the Sakaerat Environmental Research Station of northeastern Thailand where this species comprised 32.9% of all trees over 10 cm dbh and more than 50% of total tree basal area and biomass. The dominance of *H. ferrea* results from the ecological success of light-adapted seedlings and saplings which are able to utilize the frequent and long-lasting sunflecks which reach the forest floor below an inhomogeneous upper canopy. Extended seasonal drought in this monsoon climate of northeastern Thailand and high ambient air temperatures in the late dry season may restrict the use of a similar growth strategy by other potentially competing species. Saplings of *H. ferrea* were able to maintain significantly higher rates of net photosynthesis when light saturated ($5.4 \mu\text{mol m}^{-2} \text{s}^{-1}$) than other species with similar water use efficiencies. Access to soil water not readily available to these other species may allow this adaptive growth strategy to be successful for *H. ferrea*. Photosynthetic production in *H. ferrea* was also aided by a rapid triggering response to early morning sunflecks that allowed stomata to open more rapidly than those of other species. Limited water availability also represented a strong selective pressure on tree seedlings in the forest understory, particularly during April and May when ambient air temperatures became very high. Maximum rates of stomatal conductance of *H. ferrea* canopy leaves in the wet season ranged from 220–250 $\text{mmol m}^{-2} \text{s}^{-1}$, compared to maximum rates of only 40–110 $\text{mmol m}^{-2} \text{s}^{-1}$ in the dry season when midday water potentials dropped below -3.0 MPa. Full irradiance during sunflecks typically brought leaf temperatures of saplings of all species to 36–38°C in the late dry season, reducing maximum photosynthetic capacity through temperature effects as well. Inherent tolerance to high temperatures in many Dipterocarpaceae may provide a selective advantage to *H. ferrea*. Given the apparent sensitive balance between the light environment and regional climatic conditions on the ecological success of *H. ferrea*, small changes in forest canopy coverage or the seasonality and intensity of monsoon conditions could cause fundamental changes in the structure of semi-evergreen forest in Thailand.

Key words: Dipterocarpaceae, semi-evergreen forest, *Hopea ferrea*, photosynthesis, stomatal response, water relations

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INTRODUCTION

Tropical forest communities are characterized by high tree diversity with mixed species dominance (GENTRY, 1982; CONDIT *ET AL.*, 2002). Typically no single species is able to maintain strong ecological dominance. Clearly there are exceptions to this pattern (CONNELL & LOWMAN, 1989, HART *ET AL.*, 1989), but nevertheless there has been little study of the mechanisms that might allow such strong ecological dominance in the face of potentially strong biological competition.

Semi-evergreen forests of northeastern Thailand present an interesting case of single species dominance in high diversity stands. Here single species of Dipterocarpaceae frequently are overwhelming ecological dominants in forests where more than 50 tree species are present per hectare (BUNJAVEJCHEWIN 1986, 1999; KANZAKI *ET AL.*, 1995). Semi-evergreen forests are widespread in the Dangrek Range and areas of foothill regions around the Khorat Plateau in northeastern Thailand where they occur in a strongly seasonal monsoon climatic regime with 1200–1400 mm annual precipitation (THOMPSON & LANSBERG, 1975; RUNDEL & BOONPRAGOB, 1995). These semi-evergreen forests are tall, closed-canopy forests averaging 25–35 m in height with emergent trees to 40 m. However, environmental selection for drought-adapted species in the semi-evergreen forests of Thailand and Indochina differs from more mesic Indo-Malaysian elements of tropical rainforest to the south. As a result, endemism is relatively high at the species level.

In this paper we report on field studies of semi-evergreen forest at the Sakaerat Environmental Research Station in northeastern Thailand where *Hopea ferrea* Pierre (Dipterocarpaceae) is the strong ecological dominant in a highly diverse forest community. We use an ecophysiological approach to ask, What factors and adaptive traits allow this single species to maintain such dominance in the face of competition from so many other tree species? Our studies were focused on the late dry season of April and May when low soil water availability and high ambient air temperatures provide particularly strong environmental stress for plant growth, and thus strong selective pressures on demographic success.

STUDY SITE

Field studies were carried out at the Sakaerat Environmental Research Station near Pak Thong Chai, Nakhon Ratchasima Province, 60 km south of Khorat in northeastern Thailand (lat. 14°31'N, long. 101°55'E). This field station encompasses a research area of 81 km² on the northeastern slopes of the western Dangrek Range of Thailand, near their transition to the lower Khorat Plateau. The topography of the station is largely gentle slopes and rolling terrain at 300–560 m elevation. The shallow soils are sandy clay loams derived from sandstone parent material and are poor in available nutrients and soil water holding capacity. Semi-evergreen forest covers 36% of the Sakaerat reserve, with sharp transitions to deciduous dipterocarp woodland, forest plantations, and disturbed areas with swidden agriculture from local villages (TONGYAI, 1980; BUNJAVEJCHEWIN, 1986). Soils in this semi-evergreen forest are reported as acidic with a mean pH of 4.5 for surface mineral soils of 0–15 cm depth (BUNJAVEJCHEWIN, 1986). Cation exchange capacity of these soils was 7.0 meq 100 g⁻¹ and organic matter content was 3.2%.

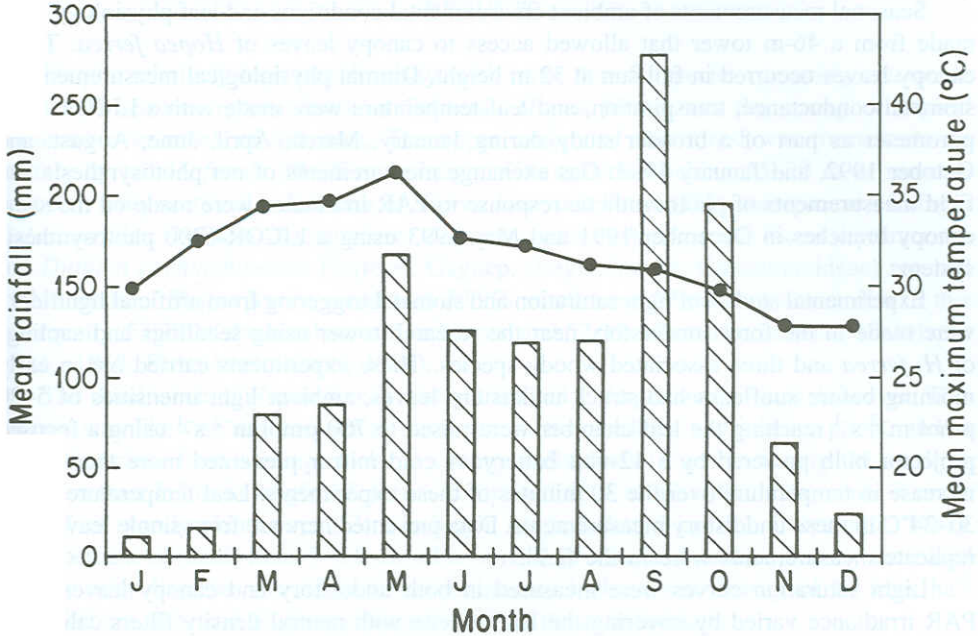


Figure 1. Seasonal pattern of mean monthly rainfall and monthly mean maximum temperature at the Sakaerat Environmental Research Station in northeastern Thailand. Mean rainfall data is for 1969–1979. Mean maximum temperatures are 1969 data taken from Sukapanpotharam (1979).

Mean annual precipitation at Sakaerat from 1969–1982 was 1240 mm (BUNJAVEJCHEWIN, 1986). Peak monthly rainfall is present from May through October, but begins to decline in November with the transition to the dry season (Fig. 1). The early dry season from December through February is almost totally without rain, but moderate rainfall typically returns in the late dry season well before the beginning of the wet season in late May or June. Mean maximum air temperatures are 30–35°C in the early dry season, but rise sharply to 38–40°C in April and May. As the wet season begins in late May and June, mean maximum temperatures steadily decline from these high levels to 25–26°C in November and December.

MATERIALS AND METHODS

The population structure of the semi-evergreen forest at Sakaerat was extracted from data collected by other researchers in previous studies. The size distribution of *Hopea ferrea* and other tree species, the relative distribution of basal area, and biomass distribution in this community were taken from BUNJAVEJCHEWIN (1986) and SABHASRI ET AL. (1968), while population data on saplings and seedlings at this site were measured by Jantane (1987).

Seasonal measurements of ambient environmental conditions and leaf physiology were made from a 46-m tower that allowed access to canopy leaves of *Hopea ferrea*. These canopy leaves occurred in full sun at 32 m height. Diurnal physiological measurements of stomatal conductance, transpiration, and leaf temperature were made with a LICOR-1600 porometer as part of a broader study during January, March, April, June, August, and October 1992, and January 1993. Gas exchange measurements of net photosynthesis and field measurements of photosynthetic response to PAR irradiance were made on the same canopy branches in December 1991 and May 1993 using a LICOR-6200 photosynthesis system.

Experimental studies of light saturation and stomatal triggering from artificial lightflecks were made in the forest understory near the research tower using seedlings and saplings of *H. ferrea* and three associated woody species. These experiments carried out in early morning before sunflecks had struck understory leaves, ambient light intensities of 5–20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ reaching the leaf chamber were raised to 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ using a focused projector bulb powered by a 12-volt battery. A cold mirror prevented more than a 2°C increase in temperature over the 30 minutes of these experiments. Leaf temperatures were 30–34°C in these understory measurements. Data presented here are from single leaves, but replicate measurements were in the field.

Light saturation curves were measured in both understory and canopy leaves, with PAR irradiance varied by covering the leaf cuvette with neutral density filters calibrated to remove a fixed percentage of incoming irradiance. Natural irradiance in midmorning was used in canopy leaf experiments, while PAR irradiance provided by artificial illumination from a projector bulb was used in the understory. Leaves were allowed to reach a stable photosynthetic rate for at least 5 min at each light level before photosynthetic rates were recorded. Replicate measurements were made for each of two leaves on two plants at each level of PAR intensity. Leaf areas of plant tissues used for photosynthetic studies were marked in the field and measured using a LICOR portable leaf area meter on the same day so that shrinkage would not occur with drying.

Leaf temperatures and leaf-air temperature gradients were determined using an Everest Instruments infra-red thermometer, focused to measure mean leaf surface temperature over a 1 cm² area. Leaf water potentials were measured on freshly cut branch tips using a Scholander-type pressure chamber.

Mean leaf angles were measured on populations of seedling (0.5 m), sapling (2.0 m) and canopy leaves (32 m) of *Hopea ferrea* using a Suunto inclinometer. Fifty leaves of each population were used for measurements.

Stable carbon isotope analyses were carried out using pooled samples of 3–5 mature leaves from each study population. Analyses were made using standard technique with a Finnigan isotope ratio mass spectrometer at the Stable Isotope Laboratory of the Department of Biology, Boston University. Carbon isotope ratios can be used as a measure of integrated water use efficiency over the period of time in which carbon was sequestered in leaf structures (see RUNDEL *ET AL.*, 1989 and EHLERINGER *ET AL.*, 1993 for reviews of stable isotope physiology). A higher (less negative) value of carbon isotope ratio, measured in units of parts per thousand (‰), indicates higher water use efficiency than a leaf with a lower (more negative) value.

RESULTS

Despite relatively high tree diversity, with more than 50 species occurring in a single hectare of semi-evergreen forest at Sakaerat, *Hopea ferrea* was the strong ecological dominant over much of this area. The upper canopy of this forest was formed almost entirely by tall *H. ferrea* 30–35 m in height with crowns reaching 15–20 m or more in diameter. Only scattered individuals of *Shorea henryana* Pierre (Dipterocarpaceae), *Irvingia malayana* Oliv. Ex Benn. (Iringiaceae), *Lagerstroemia cochinchinensis* Pierre (Lythraceae), and *Dialium cochinchinensis* Pierre ex Gagnep. (Leguminosae: Caesalpinoideae) reached to this stratum. *Hopea ferrea* comprised 32.9% of all trees 10 cm or more in dbh in this community, 53.7% of the basal area of such trees, and 57.0% of total tree biomass (SABHASRI ET AL., 1968, BUNYAVEJCHEWIN, 1986).

The dominance of *Hopea ferrea* was not limited to large canopy trees, however. This species was likewise the ecological dominant in the seedling and sapling pools, and at every size class from saplings to large canopy individuals (Fig. 2). Among the seedling pool less than 1.3 m in height, *H. ferrea* comprised 68% of all individuals, while it made up 44% of woody plants over 1.3 m in height but less than 5 cm dbh (JANTANEE, 1987). Forty percent of small trees 5–9.9 cm dbh were *H. ferrea*, and relative density increased steadily with diameter size. This forest community had a mean density of 14 trees ha⁻¹ above 60 cm dbh, and *H. ferrea* formed 64% of these individuals.

Stomatal conductance in *Hopea ferrea* was strongly impacted by seasonal changes in leaf water potential. Wet season rates of maximum stomatal conductance for canopy leaves ranged from 220 to 250 mmol m⁻² s⁻¹, when midday leaf water potentials reached no lower than -1.5 MPa. Dry season maximum rates of stomatal conductance were 40–110 mmol

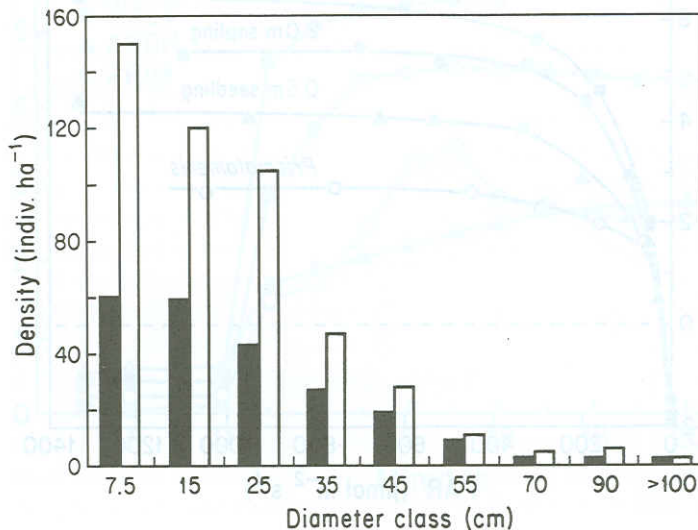


Figure 2. Densities (individuals ha⁻¹) by diameter class for *Hopea ferrea* and all trees in the semi-evergreen forest of the Sakaerat Environmental Research Station in northeastern Thailand. Data from BUNYAVEJCHEWIN (1986) and JANTANEE (1987). Open squares - all trees; closed squares - *H. ferrea*

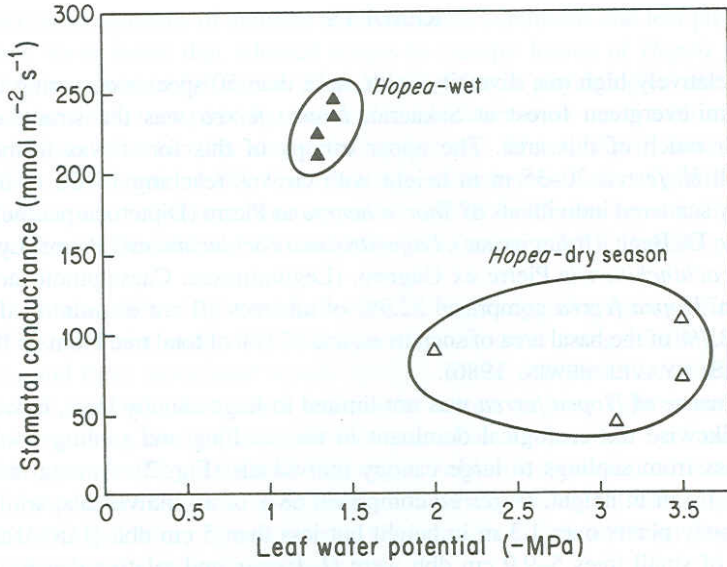


Figure 3. Seasonal distribution of minimum midday water potential (MPa) and maximum stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$) in canopy leaves of *Hopea ferrea*.

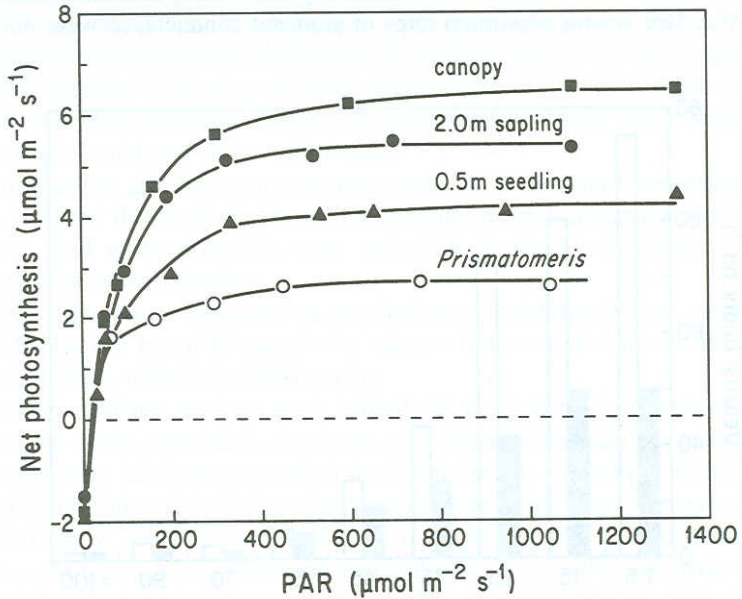


Figure 4. Light response curve of photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for field seedlings, saplings, and canopy leaves of *Hopea ferrea*, and understory leaves of *Prismaomeris memecyloides*. Data were collected in the late dry season on April 30 and May 1, 1993.

$\text{m}^{-2} \text{s}^{-1}$ at a time when midday water potentials fell below -3.0 MPa (Fig. 3). Data reported here were collected in early May of 1993 under late dry season conditions of low maximum conductance and moderate water stress.

Photosynthetic rates in canopy leaves of *H. ferrea* peaked at a mean level of $6.4 \mu\text{mol m}^{-2} \text{s}^{-1}$, although individual leaves had rates as high as $8.0 \mu\text{mol m}^{-2} \text{s}^{-1}$. Stomatal conductance in these leaves was $85 \text{ mmol m}^{-2} \text{s}^{-1}$. Light response curves showed that these leaves reached light saturation at a PAR irradiance of about $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 4).

Leaf photosynthesis in seedlings and saplings of *Hopea ferrea* did not exhibit strong adaptations to low light intensity in the understory in comparison to the canopy leaves. In a forest understory with typical midday PAR irradiance of only $5\text{--}20 \mu\text{mol m}^{-2} \text{s}^{-1}$, light saturation was reached in leaves of saplings at 2 m height at about $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, and at about $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ for seedlings at 0.5 m height. Light saturated rates of net photosynthesis were $5.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the sapling leaves and $4.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the seedlings. By comparison, a common shade-adapted shrub in this understory, *Prismatomeris memecyloides* (Rubiaceae), had a maximum photosynthetic rate of only $3.2 \mu\text{mol m}^{-2} \text{s}^{-1}$, and also became light saturated at a relatively high PAR irradiance of about $450 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Under morning PAR irradiance of $7\text{--}20 \mu\text{mol m}^{-2} \text{s}^{-1}$ the forest understory saplings of *Hopea ferrea* and three associated woody species, *Walsura trichostemon* Miq. (Meliaceae) and *Ardisia helferi* Kurz (Myrsinaceae), and *P. memecyloides*, exhibited low rates of net photosynthesis of only $0.2\text{--}0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 5). *Hopea ferrea* was intermediate at

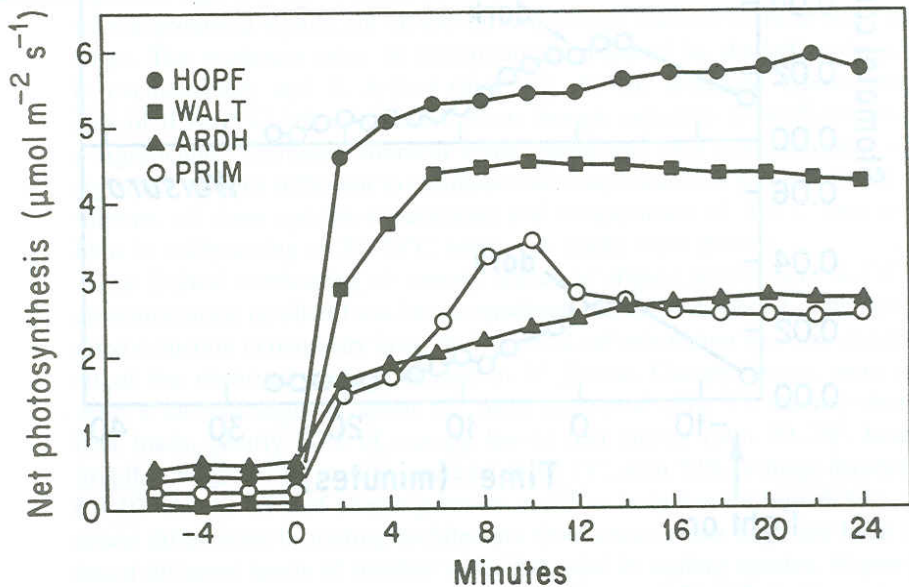


Figure 5. Stomatal triggering in response to artificial light flecks in saplings of *Hopea ferrea*, *Walsura trichostemon*, *Ardisia helferi*, and *Prismatomeris memecyloides*. Net photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured continuously over the period of these experiments during the late dry season from May 1–3, 1993. Leaves were exposed to saturating light intensities at time zero.

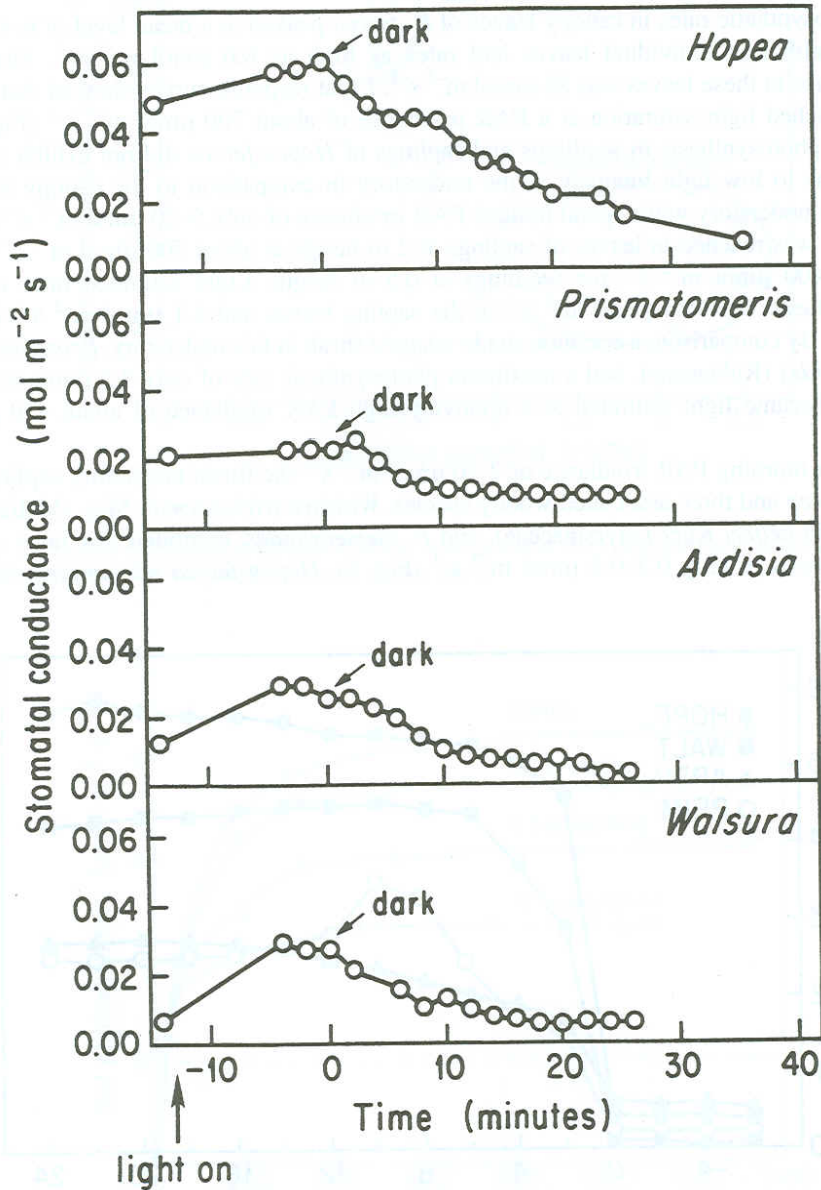


Figure 6. Response of stomatal conductance to the end of artificial lightflecks in saplings of *Hopea ferrea*, *Walsura trichostemon*, *Ardisia helferi*, and *Prismaomeris memecyloides*. These experiments were carried out under field conditions during the late dry season from May 1–3, 1993. Light-saturated leaves were placed into complete darkness at time zero.

$0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$. These species exhibited very different responses, however, to triggering by a continuous artificial sunfleck of $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR irradiance. Within 2 minutes of exposure, *H. ferrea* leaves reached a photosynthetic rate of $4.7 \mu\text{mol m}^{-2} \text{s}^{-1}$, more than 80% of their maximum rate. The three associated species all responded more slowly to a simulated sun fleck and had significantly lower rates of light-saturated net photosynthesis than *H. ferrea*. After a 2-minute exposure to saturating light, *W. trichostemon* and *A. helferi* had reached only about 60% of their maximum rates of net photosynthesis at 4.3 and $2.7 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. *Prismatomeris memecyloides* was even more sluggish in its stomatal response, reaching less than 50% of its steady-state maximum rate of photosynthesis after 2 min. Photosynthesis in this shrub species rose to a peak of $3.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ after 10 min and then dropped to a lower steady-state rate of $2.5 \mu\text{mol m}^{-2} \text{s}^{-1}$.

The response of light saturated leaves to sudden darkness, simulating the end of a sunfleck, was investigated in saplings of *H. ferrea* and the same three associated species by illuminating understory leaves to a point where maximum rates of photosynthesis were reached and then covering the leaf chamber to reduce all incoming PAR irradiance. All four species showed similar temporal responses in their rates of stomatal closure under these experiments. While net photosynthesis rates dropped to negative levels almost immediately, stomatal conductance dropped to only 70–80% of maximum rates after 4 min and remained at 20–32% of maximum after 20 min in the dark (Fig. 6). Moderate rates of stomatal conductance of 25 – $42 \text{ mmol m}^{-2} \text{s}^{-1}$ were present at midmorning in all of these species under shaded understory conditions with PAR irradiance below $20 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Leaf temperatures of canopy leaves ranged from 35 – 40°C during canopy measurements, never rising more than 3°C above ambient temperatures. However, exposure to full sun in a long sunfleck produced significant effects on leaf energy balance in understory saplings and seedlings. The moderate rates of transpiration measured in shaded saplings of *H. ferrea*, *W. trichostemon*, and *A. helferi* (data not shown) produced midmorning leaf temperatures of 0.5 – 1.5°C below ambient. Even though exposure to sunflecks with full irradiance significantly increased stomatal conductance and thus transpirational cooling, this cooling effect was not sufficient to maintain leaf temperatures at ambient levels. Under these conditions, all three species experienced leaf temperatures of 4 – 5°C over ambient, heating them in midmorning to 36 – 38°C when sun flecks were present.

The more limited overheating of canopy leaves of *Hopea ferrea*, only 2 – 3°C above ambient air temperature resulted from low to moderate winds at this level in the forest and the associated reduction in boundary layer resistances. Leaf orientation was also an important component of the observed energy balance in *H. ferrea*. Canopy leaves were sharply inclined with a median angle of about 55° from horizontal (Fig. 7), thereby decreasing midday heat loads. Nearly 50% of canopy leaves had angles from 50 – 70° . Leaves of saplings at 2.0 m height had a median angle of about 15° , with 70% of these leaves having angles of 0 – 0° . Nearly 80% of seedling leaves at 0.5 m height were horizontal.

Presumed differences in rooting architecture (root excavations have not been carried out) produced different levels of midday water potential in sapling species. *Hopea ferrea* reached -1.71 MPa, compared to a more negative -2.28 and -2.78 MPa in *W. trichostemon* and *A. helferi*, respectively (Table 1). The shade-adapted *P. memecyloides* reached only -1.37 MPa. Seedlings of *H. ferrea*, presumably with shallow root systems, reached -2.51 MPa at midday, while upper canopy leaves at 29 m height dropped to -2.01 MPa even though moderately high conductance rates of 60 – 90 mmol m^{-1} were maintained.

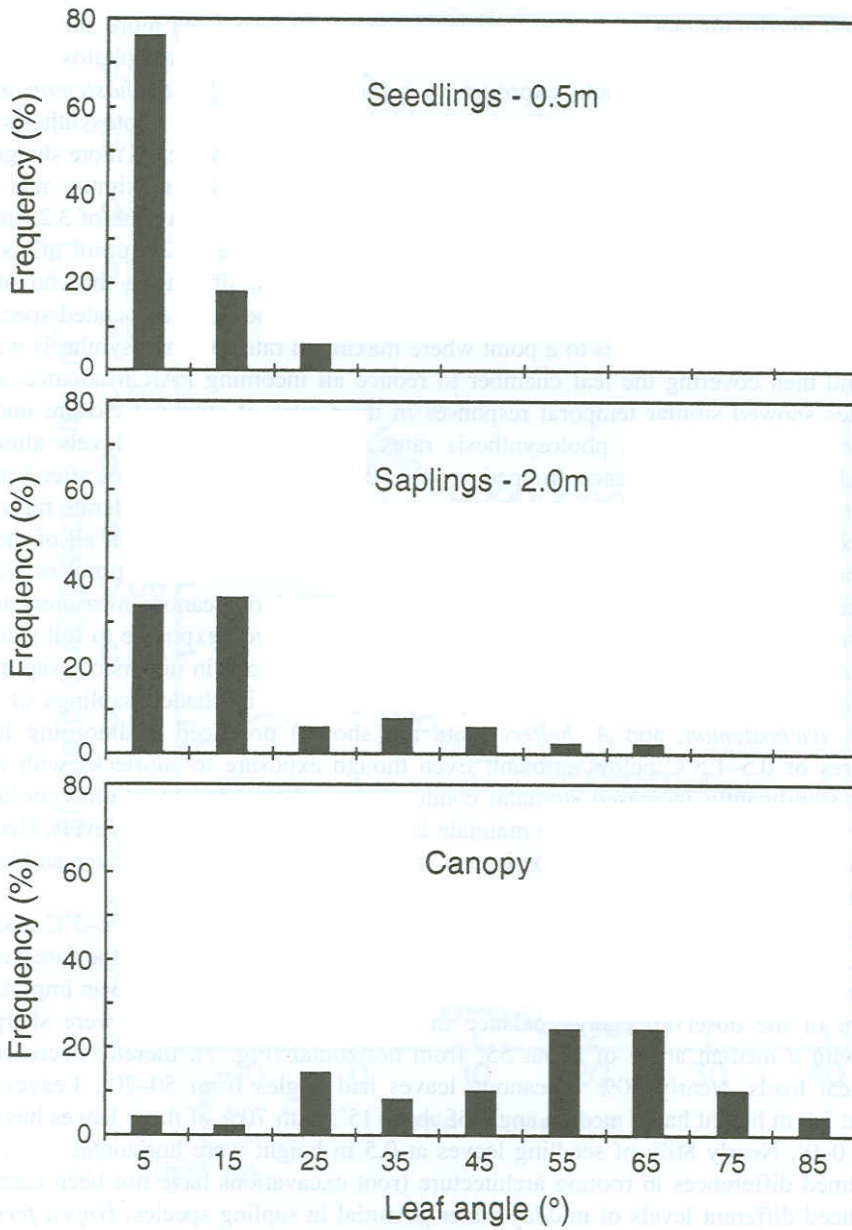


Figure 7. Relative distribution of leaf angles ($^{\circ}$ from horizontal) in seedlings (0.5 m), sapling (2.0 m), and canopy leaves (32 m) of *Hopea ferrea* in the semi-evergreen forest of the Sakaerat Environmental Research Station in northeastern Thailand.

Table 1. Ecophysiological characteristics of midday water potential, maximum photosynthetic rate, leaf nitrogen content, and carbon isotope ratio of study species in the semi-evergreen forest of the Sakaerat Environmental Research Station, northeastern Thailand. Data here were collected in the late dry season from April 30 to May 6, 1993. ND = no data.

Species	Midday ψ (MPa)	P-max ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Leaf nitrogen (mg g^{-1})	$\delta^{13}\text{C}$ (o/oo)
Canopy <i>Hopea ferrea</i>	-2.01	6.7	14.4	-27.5
Sapling <i>Hopea ferrea</i>	-1.71	5.5	27.8	-32.2
<i>Walsura trichostemon</i>	-2.28	4.4	28.2	-31.9
<i>Ardisia helferi</i>	-2.78	3.2	14.3	-32.2
Understory shrub <i>Prismatomeris memecyloides</i>	-1.37	3.2	19.6	-30.0
Seedling <i>Hopea ferrea</i>	-2.51	4.1	ND	ND

Despite the different levels of photosynthetic rate and midday water potential in the three sapling species studied, the integrated water use efficiency as indicated from carbon isotope ratios of leaf tissue was virtually identical (Table 1). For *H. ferrea*, *W. trichostemon*, and *A. helferi* these values were -32.2, -31.9, and -32.2 o/oo, respectively. Better stomatal control and the maintenance of higher water potentials were reflected in a higher water use efficiency for the shade-adapted *P. memecyloides*, as indicated by its $\delta^{13}\text{C}$ of -30.0 o/oo. The $\delta^{13}\text{C}$ for canopy leaves of *Hopea ferrea* was -27.5 o/oo, but this value was not directly comparable with the understory leaves since respired CO_2 undoubtedly affected the $\delta^{13}\text{C}$ of the latter.

DISCUSSION

Tree species diversity in the semi-evergreen forest of Sakaerat is high. A complete census of woody plants for a 1.0-hectare quadrat at this site found 55 tree species reaching 5 cm or more in dbh (SMITINAND *ET AL.*, 1968). Samples of 20 1000- m^2 plots in the same area by BUNYAVEJCHEWIN (1986) reported 59 woody species of this size. An adjacent semi-evergreen forest community dominated by another Dipterocarpaceae, *Shorea henryana*, had 75 woody species, with 92 woody species in the two communities combined. Nevertheless, single species dominance was a characteristic feature of both community types. *Hopea ferrea* made up 54% of the basal area of trees over 10 cm dbh in its community, while *S. henryana* comprised 25% of basal area in the adjacent community where *H. ferrea* was absent.

How then is a single species such as *H. ferrea* able to attain such ecological dominance over its potential competitors? One explanation put forth by KANZAKI *ET AL.* (1995) is that *H. ferrea* is highly shade-tolerant and thus able to maintain its position in small forest gaps.

This explanation is inconsistent with our ecophysiological observations on seedlings and saplings of *H. ferrea*, which appear highly adapted to using relatively long-lasting sunflecks on the forest floor.

Our explanation for this monodominance lies in the relatively open canopy structure of this forest that allows the light-adapted seedlings and saplings of *H. ferrea* to efficiently utilize frequent sunflecks for growth. High ambient air temperatures and low water availability during the dry season may restrict the ability of other light-adapted tree species to effectively compete with *H. ferrea*. Although the aspect of ecological dominance and drought tolerance is very different, this situation with *H. ferrea* is analogous in many respects to a light-adapted C_4 tree species that utilizes sunflecks to grow successfully in the understory of Hawaiian forests (PEARCY, 1983).

Canopy structure of the semi-evergreen forest at Sakaerat is notably separable into two strata. The large canopy trees produce dense foliage cover at about 20–30 m height which intercept 80–90% of incoming radiation (YODA ET AL., 1983). Smaller trees form an irregular second canopy stratum centered 5–15 m above the ground. The density of large trees (over 60 cm dbh) of only 14 individuals ha^{-1} in the semi-evergreen forest is not sufficient to allow a closed coverage of leaves in the upper canopy of the forest. Large tree crowns more than 10 m in diameter covered only about 60–70% of the upper canopy (Fig. 8). Similar results were found by KANZAKI ET AL. (1995) who determined that 74% of the *H. ferrea* forest canopy was mature, compared to 20% in a building stage and 6% in gaps and

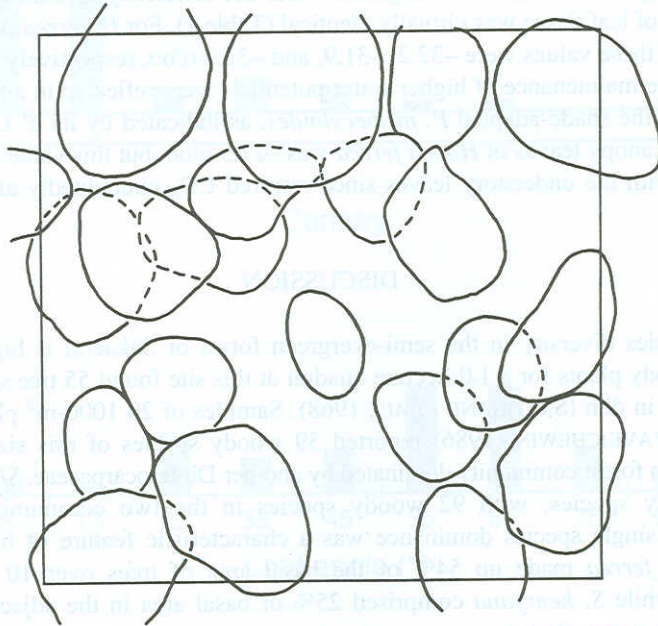


Figure 8. Horizontal profile of canopy trees with maximum crown width of 10 m or more in the SW quadrant of a surveyed 1-hectare in the semi-evergreen forest at the Sakaerat Environmental Research Station in northeastern Thailand. Redrawn from SMITINAND ET AL. (1968).

This broken upper canopy and irregular coverage by the lower tree strata allowed frequent sunflecks of relatively long duration to penetrate to ground level. Although the shaded forest understory typically experienced only 5–20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of PAR irradiance, sunflecks occurred with sufficient frequency and intensity to allow an average of 7–8% of total solar irradiance to penetrate to saplings at 5 m height (YODA *ET AL.* 1983). This understory light environment was thus significantly more open than that described for wet lowland rainforest communities such as those in Costa Rica (CHAZDON & FETCHER, 1984; MONTGOMERY & CHAZDON, 2002).

Our seasonal data on plant water potential clearly demonstrated a strong influence of this factor on operational limits for leaf stomatal conductance. These results are consistent with the findings of Pitman (1996) who reported that water potential was second only to incident solar radiation as an environmental variable influencing stomatal conductance of *H. ferrea*. He found only a small influence of temperature and vapor pressure deficit.

Canopy leaves of *H. ferrea* became light saturated at a PAR irradiance of about 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 4). The canopy leaves of some early successional tropical trees have been reported to saturate at more than 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (HOGAN *ET AL.*, 1995). However, the low light saturation point of *H. ferrea* is not unexpected, as it is similar to low light saturation levels that we have measured in dominant *Shorea* species from the adjacent deciduous dipterocarp forest at Sakaerat (RUNDEL *ET AL.*, unpublished data), and in canopy leaves of *Pentaclethra macroloba* in Costa Rica (OBERBAUER & STRAIN 1986). These data suggest that the dipterocarp canopy leaves are adapted for the cloudy wet season conditions of relatively low solar irradiance rather than for the clear sky conditions of the dry season.

None of the four species that we studied in the understory demonstrated strong selection of photosynthetic traits for extreme shade tolerance. Even *Prismatomeris memecyloides*, an obligate understory shrub, light saturated at 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in our studies, compared to light saturation at PAR irradiances of 200–350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in shade-adapted tropical species (OBERBAUER & STRAIN, 1986; CHAZDON, 1986; RUNDEL *ET AL.*, 1998). Other shade adaptations were present in *P. memecyloides*, however, in its selection of shaded microsites where low rates of stomatal conductance conserved water supplies and restricted the occurrence of low midday water potentials during the dry season. Stable carbon isotope ratios demonstrated that this species had a higher water use efficiency (less negative $\delta^{13}\text{C}$ value) than the other species studied (Table 1).

Seedlings and saplings of *Hopea ferrea* achieved moderately high rates of net photosynthesis in comparison to other species in the understory when sunflecks brought high solar irradiance (Table 1, Fig. 5). The high frequency and long average duration of such sunflecks (personal observations) would be expected to allow a significantly higher daily carbon gain for *H. ferrea* than competing species. Since the water use efficiency of this species was no higher than that of typical sapling competitors such of *Walsura trichostemon* and *Ardisia helferi* (Table 1), higher photosynthetic rate must come at the cost of greater water use. Midday water potentials measured in these saplings during the late dry season established that *H. ferrea* was able to find the necessary water resources to maintain such a strategy of higher photosynthetic capacity (Table 1).

Previous studies of *Hopea ferrea* at Sakaerat have reported significantly higher rates of about 300–500 for midday stomatal conductance of canopy leaves during the wet season (PITMAN, 1996). These high rates may be a function differing conditions of measurement or may have resulted from the nature of the instrumentation used in this earlier study.

Measurements with a null balance porometer such as we used are generally considered more accurate than those made with a transient porometer as used by PITMAN (1996).

Photosynthetic responses to light variation in the understory is an important component of adaptation in rainforest species (PEARCY 1987; CHAZDON & PEARCY 1991; ALLEN & PEARCY 2000). In understory environments where a large proportion of the total daily irradiance comes in the form of short sunflecks, morphological and physiological adaptations to effectively utilize such irradiance are important components of species adaptation (VALLADARES *ET AL.*, 2000, 2002). Photosynthetic production in saplings of *H. ferrea* was aided by its rapid stomatal response to sunflecks. Stomata opened faster in this species than in the other saplings studied (Fig. 5), allowing a more efficient use of short duration sunflecks. These rates of stomatal induction in *Hopea* are more rapid than the highest rates reported in previous studies with understory saplings in tropical forest trees from Central America (KURSAR & COLEY, 1993; POORTER & OBERBAUER, 1993; ALLEN & PEARCY, 2000).

Adaptation to forest understory environments could potentially involve not only stomatal induction in the morning by sunflecks, but the stomatal response of light-saturated leaves to a sudden reduction in PAR irradiance as sunflecks end. No significant difference was observed in relative rates of stomatal closure among *H. ferrea* and other understory species studied, suggesting that this response has not been subject to differential selection between tree saplings and obligate understory species in the semi-evergreen forest community. The rates of stomatal closure observed here for *H. ferrea* and other species were similar to those reported previously for saplings of two tree species in Costa Rica (POORTER & OBERBAUER 1993).

Limited water availability in the dry season may also represent a strong selective pressure on tree seedlings. PITMAN (1996) reported mean soil water potentials at 30–47 cm soil depth to reach about -3.0 MPa under unusually dry August conditions at Sakaerat. These are consistent with our measured water potentials of -2.5 MPa in seedlings of *Hopea ferrea*. Full irradiance of seedlings at midday under the high ambient air temperature that typically occur in April in May in this forest produced leaf temperatures that reached 36 – 38°C in *H. ferrea* in the forest understory. Such temperatures likely reduce maximum photosynthetic capacity. Transpirational cooling to prevent heat damage to leaves under such conditions requires water resources and *H. ferrea* seedlings were more limited in water availability than saplings in our study (Table 1). It would be interesting to investigate tolerance to high temperature in *H. ferrea* in relation to other species. A study of photosynthetic response to temperature in a related genus in the deciduous dipterocarp forest at Sakaerat, *Shorea siamensis*, has shown good tolerance to high temperatures (RUNDEL *ET AL.*, unpublished data).

Our ecophysiological approach, of course, does not consider life history traits that may be important in determining the ecological success of *H. ferrea*. Fecundity, seed dispersal, predation levels, and other demographic traits may also be components of this success.

Our data on *Hopea ferrea* are not yet sufficient to parameterize ecophysiological models of tree growth and development, but they do allow us to raise significant questions relevant to considerations of the effects of global change and biodiversity in semi-evergreen forests. While the semi-evergreen forest of Sakaerat is relatively undisturbed, selective logging of large trees has occurred in the past. Is the open upper canopy structure at Sakaerat and perhaps the dominance of *H. ferrea* an artifact of such disturbance? A closed

upper canopy might well provide a very different light environment in the understory and select against the current ecological success of the light-adapted seedlings and saplings of *H. ferrea*. Such a change would be expected to promote more mixed ecological dominance, and perhaps higher biological diversity. Would global changes resulting in shorter or less arid dry seasons favor competing species by reducing the drought stress present in the understory and thus eliminate some of the advantages of *H. ferrea* over its competitors in water relations characteristics? Would longer or more severe dry seasons likely stress the semi-evergreen community overall and allow movements of ground fires from adjacent communities into the understory and thus promote replacement by deciduous dipterocarp forest species? The present community structure of dry dipterocarp forests may well be highly sensitive to small changes in forest canopy structure or regional climatic conditions. Future studies will hopefully allow more direct consideration of such questions.

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