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GROWTH AND PHOTOSYNTHETIC RESPONSES TO TEMPERATURE IN SEVERAL MALAYSIAN TREE SPECIES

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MORI, T., NAKASHIZUKA, T., SUMIZONO, T. & YAP, S.K. 1990. Growth and photosynthetic responses to temperature in several Malaysian tree species. Responses of seed germination, seedling growth, and photosynthesis to temperature regimes were determined in four dipterocarp, two non-dipterocarp and an exotic planting species from Peninsular Malaysia. All the seeds and seedlings showed chilling injuries below 15° *C*, although their occurrence time differed from species to species. Species such as *Shorea assamica* and *Duabanga grandifolia* which are found mainly in the monsoon forests of India and Myanmar could tolerate longer periods at 10 to 15° *C* than the species like *Shorea parvifolia* and *Dryobalanops aromatica* which are confined to the evergreen rain forests. The relative growth rate, net assimilation rate, net photosynthesis rates, and stomatal conductance of the tropical tree species were similar in magnitude to those of the temperate ones, while these rates for shade tolerant species like *D. aromatica* and *Neobalanocarpus heimii* tended to be lower than those for light demanding species such as *Du. grandifolia* and *Bombax valetonii.* Growth and photosynthetic characteristics of dipterocarp species, especially those in evergreen rain forests such as *S. parvifolia, N. heimii* and *D. aromatica* showed narrow plasticity to environmental temperature changes.

Key words: Tropical trees - dipterocarps - seed germination - seedling growth - photosynthesis - stomatal conductance - shade tolerance - temperature

Introduction

A great number of tree species grow in tropical rain forests, and their structures are extremely complex (Whitmore 1984). The dipterocarps are the main representative timber tree species in the southeast Asian tropical rain forests; in Peninsular Malaysia alone, there are 168 species in 14 genera (Symington 1943).

The ability of individual species to tolerate different environmental conditions of its distribution zone must reflect ecophysiological characteristics of the species. For example, Symington (1943) stated that dipterocarps like *Shorea assamica* which are found in greater abundance in monsoon forest areas in India and Myanmar generally have xerophytic characteristics. Being more tolerant to extremes in environmental conditions, they have greater potential in artificial planting compared with dipterocarp species like *Shorea parvifolia* and *Dryobalanops aromatica* which grow only in ever green rain forests (Mori 1980, 1981).

Within the distribution area of the species, one major strategy for individual species to compete successfully with others for a niche lies in its growth rate at the regenerating phase. A seedling's growth rate is largely related to the degree of light requirement of the seedling (Sasaki & Mori 1981, Whitmore 1984). At the seedling stage, tree species may be simply divided into two groups: those which regenerate in open land, or forest edge. These groups are "shade tolerant" and "light demanding" respectively, in their early stages of life. Most dipterocarp species in Malaysia are shade tolerant (Nicholson 1960, Mori 1980).

The difference in growth and photosynthetic characteristics between tropical tree species growing at high and low altitude, or in seasonal and humid rain forests and between light demanding and shade tolerant species or early and late succession species are little known (Okali 1971, Koyama 1981, Fetcher *et al.* 1983). Such information on the characteristics of the various tree species in the tropics is essential for improving management techniques of tropical rain forests and for the development of plantations (Mori 1981). Here, we compare seed germination and seedling growth and photosynthesis of selected tropical species under various temperature regimes.

Materials and methods

Plant material

The species used in this study and their habitats and some growth characteristics are listed in Table 1. The seeds were collected from Peninsular Malaysia in 1987 and 1988. *Acacia* seeds were from the Seed Centre, CSIRO, Canberra, Australia. The experiments were carried out in the phytotron of the Forestry and Forest Products Research Institute, Tsukuba, Japan.

Seed germination and growth conditions of seedlings

The seeds of *S. parvifolia*, *S. assamica*, and *Du. grandifolia* were placed on germinating beds of 0.8% agar in petri dishes and kept at different temperatures

(Table 2). The seeds were considered as germinated when the length of the radicals emerged and reached the length of the seed. These tests were concluded when all the remaining seeds did not respond a week after the last germination.

Table 1. List of species used, their habitats in Peninsular Malaysia and some ecological characteristics (based on Symington 1943, Whitmore 1972, Yap 1986)

Species	Habitat			Light requirement	Growth
	Forest type*	Elevation(*m*)	Distribution		
Shorea assamica	LDF	Up to 300(500)	India (Assam) to Borneo	Medium	Fast-Medium
Dryobalanops aromatica	LDF	Up to 400	Malaya to Borneo	Low	Slow
Shorea parvifolia	LDF to HDF	Up to 750	Malaya to Borneo	Low	Medium
Bombax valetonii	LDF to HDF	Up to 600	Thailand to Java	High	Fast
Neobalanocarpus heimii	LDF to UDF	Up to 1000	Malaya	Very low	Very slow
Duabanga grandifolia	LDF to UDF	Up to 1000	India to Malaya	High	Fast
Acacia auriculiformis	Exotic species		Australia, PNG	High	Very fast

*LDF-Lowland dipterocarp forest; HDF-Hill dipterocarp forest; UDF-Upper hill dipterocarp forest

The germinated seeds were placed in plastic pots filled with vermiculite. The pots were placed in a culture box in which nutrient solution was supplied automatically once a day. The seedlings were left at 25°*C*, 12 *h* day length for about one month and then transferred to the growth chambers with different experimental temperature regimes (Table 3). Day length was 12 *h* and photon flux density (LI-190S) was 400 $\mu mole\ m^{-2}\ s^{-1}$; the artificial light source consisted of Yoko (Toshiba), BOC (Mitsubishi), and fluorescent lamps. The composition of culture solution was the same as that reported by Koffa and Mori (1986). The seedling height and diameter were measured every week and at the end of the experiment, the dry weight of the seedlings was determined. One treatment for growth analysis consisted of ten seedlings for each species.

Photosynthesis measurement

The seedlings grown at 32/23°*C* (day/night) or 30/25°*C* were used for the determination of photosynthetic characteristics. The CO_2 exchange rates of leaves were measured with an infra-red gas analyser (Fuji Z500) using a gas open system under different light and temperature conditions. A full-expanded and uppermost leaf was used for the measurement. Light source was the same as those of growth experiments mentioned above. An assimilation chamber was equipped with water jacket circulating temperature controlled water to keep the leaf temperature constant.

For the determination of light-photosynthesis relationships, the leaf temperature was kept at 28° *C* and photon flux densities were changed from 0 to 800 $\mu mole\ m^{-2}\ s^{-1}$, covering the assimilation chamber with light absorbing plastic films. In the determination of leaf temperature effects on photosynthesis, the leaf temperature was controlled between 15 and 35° *C* and photon flux densities were maintained at optimum condition in the range of 400 to 800 $\mu mole\ m^{-2}\ s^{-1}$ depending on the species (Table 4). Stomatal conductance was measured with a super porometer (LI-1600) at 50% relative humidity, 30°*C* leaf temperature, and 130 to 300 $\mu mole\ m^{-2}\ s^{-1}$ photon flux density.

Results and discussion

Seed germination

Final germination rates of the dipterocarp seeds tested were not affected by the imbibition temperature between 16 and 30° *C*. But *Du. grandifolia* seeds showed a slight decline in germination rate with decreasing imbibition temperature. In general lower temperatures, between 16 and 30° *C*, reduced the germination speed (Table 2). Below 16° *C*, all the seeds suffered chilling injury during imbibition, although the occurrence time of their injury varied from species to species. For example, seeds of *S. assamica* at 10 and 13° *C* could produce the radicles and grow slowly for three weeks, but the cotyledons did not open. After three weeks in these temperatures, the tips of radicles turned dark brown or black as a result of chilling injury (Figure 1).

Table 2. Seed germination rates at various temperatures

	S. assamica						
Temperature (° *C*)	30/25	25/20	20	18	16	13	10
Final germination (%)	100	-	92	92	100	88*	0
Last germination (day)	2	-	5	10	10	13	21
	Du. grandifolia						
Temperature (° *C*)	30/25	25/20	20	18	16	13	10
Final germination (%)	73	68	64	41	45	0**	0**
Last germination (day)	3	5	8	15	25	50	60
	*S. parvifolia****						
Temperature (° *C*)	33	28	23	18	13		
Final germination (%)	13	13	13	17	0		
Last germination (day)	6	12	14	20	21		

*Radicle emerged but cotyledon did not and root tips were injured by chilling after three weeks; **About 20% of seeds were stil alive (see text); ***Many seeds were probably injured during transportation period

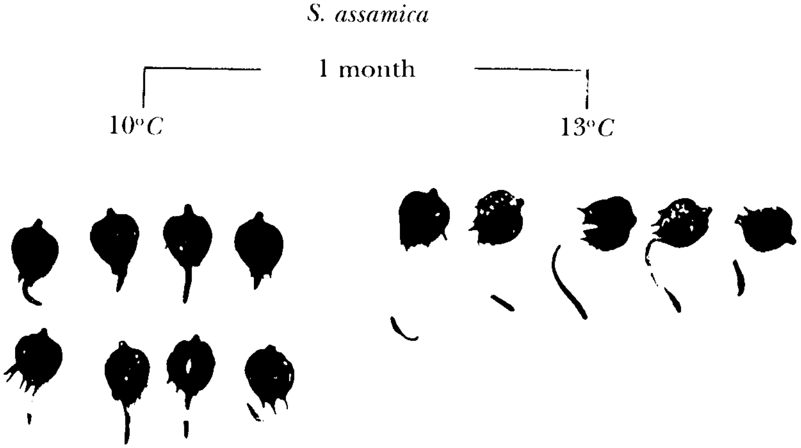

Figure 1. Seeds imbibed on 0.8% agar bed at 10 and 13°*C* for a month (Root tips of radicles that emerged turned black from chilling injuries after 3 weeks imbibition)

When such seeds were transferred to higher germination temperatures (30/20°*C*, day/night) after cutting off the injured part of root tip on the thirtieth day, more than 50% of the seeds still had the ability to produce shoots slowly and then grew normally. About 20% of *Du. grandifolia* seeds also kept their germination ability up to seven weeks of imbibition at 10 and 13°*C*. In contrast, *S. parvifolia* seeds at 13°*C* did not germinate and the colour of their embryos turned dark within two weeks. Low germination rates in *S. parvifolia* appeared to be due to the partial loss of viability during the transportation period from Malaysia to Japan in March 1987. Similar phenomenon was observed for *D. aromatica* seeds which were reported as one of the most sensitive seeds among dipterocarps to low temperatures (Sasaki 1979, Mori 1980).

Our findings on the response of dipterocarp seed germination to temperatures agree with that of Sasaki (1977, 1979), Mori (1980) and Yap (1981), who showed that many seeds of white meranti group of *Shorea*, for example *S. assamica*, could tolerate low temperature for a little longer than those of red meranti group such as *S. parvifolia*. Sasaki (1977) has generalised that critical temperature for inducing chilling injury is about 15°*C* in the seeds of many tropical lowland tree species. This temperature approximately coincides with the minimum temperature at the altitudinal upper limit (1200 *m*) of dipterocarp distribution (Burgess 1975). Also average minimum weekly temperature at 1160 *m* in the slopes of Genting Highlands was between 16 and 19°*C* from 1988 to 1989 (Nakashizuka *et al.* 1990).

Growth of seedlings

The seedlings were grown under various room temperatures as shown in Table 3. These temperature regimes roughly represent the temperature range at different forest types at different altitudes in Peninsular Malaysia (Symington 1943): 32/23°*C* (day/night) for lowland dipterocarp (0-300 *m* above sea level); 28/23 or 28/20°*C* for hill dipterocarp (300-750 *m*); 25/18 or 23/18°*C* for upper hill dipterocarp (750-1200 *m*); 21/15°*C* for oak-laurel (1200-1500 *m*) and 18/13°*C* for montane ericaceous (above 1500 *m*). The highest room temperature, 33/28°*C* and 35/28°*C* were nearly the same as the temperature range from 9:00 to 20:00 at the exposed lowland area (Bee & Sien 1974).

Under the growth temperature of 13°*C* at night, young leaves of *S. assamica, D. aromatica,* and *Bombax valetonii* showed chlorosis and shoot tops of *S. parvifolia* showed necrosis. These chilling injuries were clearly observed after two weeks of temperature treatments. In contrast, *Du. grandifolia* did not show any apparent injury at 13°*C* night temperature for four weeks, although the leaf colour changed to reddish green in the low temperatures. A temperature of 13°*C* coincides with the minimum temperature at about 1600 to 1800 *m* above sea level in the Genting Highlands forest area (Nakashizuka *et al.* 1990).

Table 3. Seedling growth under various growth temperatures

Growth temp. (D/N °C)*	Height (*cm*)	Diameter (*mm*)	Dry weight (dw.) (*g*)	% to max. dw.	RGR of dw. ($week^{-1}$)
S. assamica (7 weeks)**:					
35/28	22.2	2.6	1.72	74	0.21
32/23	28.7	3.0	2.31	100	0.24
28/20	27.4	2.7	2.08	90	0.23
25/18	11.0	2.1	1.06	46	0.16
21/15	3.0	1.2	0.51	22	0.10
18/13	1.7	0.5	0.14	6	0.03
Du. grandifolia (4 weeks):					
35/28	26.9	4.7	10.94	94	0.74
32/23	23.8	4.8	11.61	100	0.75
28/20	22.9	4.6	8.94	77	0.69
25/18	10.2	3.4	8.24	71	0.68
21/15	6.0	2.3	4.56	39	0.55
18/13	1.7	0.5	1.97	17	0.37
B. valetonii (7 weeks):					
33/28	16.1	4.6	8.41	84	0.50
28/23	13.2	4.2	10.02	100	0.52
23/18	5.9	3.3	6.30	63	0.46
18/13	1.3	1.1	0.06	6	0.16
S. parvifolia (5 weeks):					
33/28	11.2	1.3	-	-	-
28/23	19.7	1.3	-	-	-
23/18	5.0	0.8	-	-	-
18/13	dead of shoot top		-	-	-

(* Day/night temperature; ** Growth treatment period; dw. - dry weight; RGR - relative growth rate)

In all the species tested, the chlorosis or necrosis induced by low temperatures were not observed above 18°*C* night temperature. This is nearly equal to minimum daily temperature at about 1000 to 1200 *m* above sea level in the

Genting Highlands forests. As mentioned before, this elevation is very close to the upper limit (1200 *m*) of vertical distribution of dipterocarps (Symington 1943).

The quantitative growth analysis of seedlings in relation to variation in environmental temperatures is shown in Figure 2. The height growth of the seedlings were largely inhibited at day time temperatures below 25° *C*. Maximum height growth of *Du. grandifolia* and *B. valetonii* were observed above 30° *C*, but that of *Shorea* species were slightly inhibited above 30° *C*. The increase in dry weight growth of the seedlings was highest at temperature conditions represented by 30/23° *C* which corresponded with that in the lowlands (Table 3).

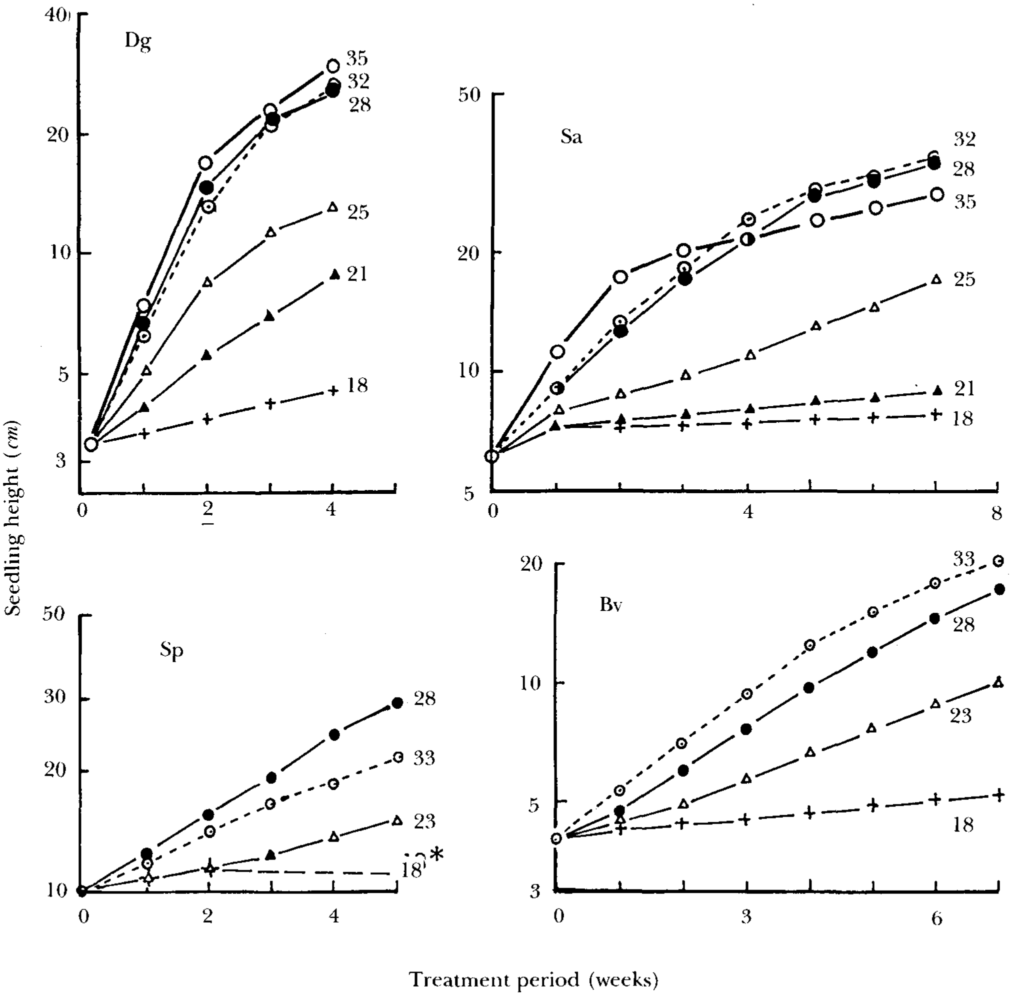

Figure 2. Height growth of the seedlings of *Du. grandifolia* (Dg), *S. assamica* (Sa), *S. parvifolia* (Sp) and *B. valetonii* (Bv), grown under various growth temperatures (Numbers in figure are day time growth temperatures)

The dry weight and relative growth rate (RGR) were reduced with increase or decrease of the temperature from 32/23 or 28/23°*C*. The reduction of RGR in *S. assamica* and *B. valetonii* with change of growth temperatures were mostly due to the reduction of net assimilation rate (NAR). But in *Du. grandifolia* it is due to the changes in NAR and leaf area rate (LAR) (Figure 3). The degree of growth reduction at low or high temperatures was highest in *S. parvifolia* followed by *S. assamica, B. valetonii* and *Du. grandifolia. S. parvifolia* was most sensitive to the low and high temperature conditions even though its vertical range of altitudinal distribution in Peninsular Malaysia is almost the same as *S. assamica* and *B. valetonii.*

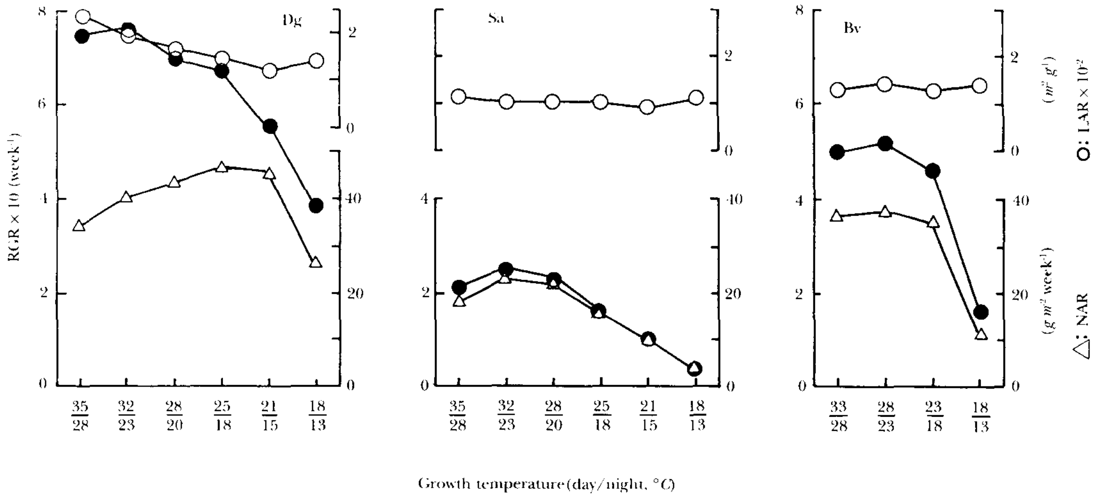

Figure 3. RGR (•), NAR (▲) and LAR (o) of the seedlings of *Du. grandifolia* (Dg), *S. assamica* (Sa) and *B. valetonii* (Bv), grown under various growth temperatures

Whitmore (1984) gives the NAR of woody plants at 20 to 60 *g* dry weight m^{-2} wk^{-1}, mostly 30 *g* m^{-2} wk^{-1}. In this experiment, the NAR at optimum temperature condition was within this range (Figure 3). Consequently, NAR of many tropical tree seedlings should be similar to those in temperate tree species, although the maximum NAR obtained from some fast growing *Acacia* spp. in our phytotron was 70 to 90 *g* m^{-2} wk^{-1} (Mori *et al.* unpublished data). This range is the lowest level of those for herbaceous plants reported by Jarvis and Jarvis (1964) and Okali (1971).

Decreasing the growth temperature induced an increase in the distribution ratio of dry weight of the shoots, especially to the stem and branches, and a decrease in the roots (Figure 4), excepting for 18/13°*C* where the growth of seedlings was so small that ratios of dry weight of a part of seedling to total weight might not be altered from that at pretreatment time. A high amount of dry weight accumulation was observed in the roots of *B. valetonii*, indicating the characteristic of deciduous tree species. Such trees store large amounts

The Pn of *A. auriculiformis* was about double that of *B. valetonii* and *Du. grandifolia* (Figure 6). The stomata of *A. auriculiformis* are on the adaxial and abaxial sides of the phyllode. In this study, only one side of the leaf area was used for calculation of Pn; thus in reality the rate for *A. auriculiformis* is similar to that of *Du. grandifolia* and *B. valetonii.*

The Pn values obtained in the present study at light saturated conditions were similar in magnitude to those of other tropical trees (Pearcy 1983, Langenheim *et al.* 1984, Kwesiga *et al.* 1986) and deciduous temperate trees (Koike 1985). In contrast, Koyama (1981) reported very high Pn in the leaves collected from mature trees of *Shorea leprosula* and other fast growing species in Malaysia whose level was similar to that of *A. auriculiformis,* expressed by one side of leaf area. The difference may be caused by the lower Pn of leaves of young seedlings than those from mature trees (Koike 1985). In general, the maximum Pn of tropical trees seldom exceed those of deciduous temperate trees (Kwesiga *et al.* 1986), the same as NAR of seedlings mentioned before.

In the light saturated condition, the optimum leaf temperatures for maximum Pn of the seven species was between 27 and 32°C. The highest temperature was observed for *Du. grandifolia* and the lowest for *N. heimii* (Figure 7). The reduction of Pn by increasing or decreasing leaf temperatures from the optimum conditions was smaller for light demanding or fast growing species than for dipterocarp species (Figure 7 & Table 4). Within dipterocarp species, this reduction was smallest in *S. assamica* and biggest in *N. heimii.* The former species is relatively more light demanding among dipterocarps, and the latter is typically shade tolerant and slow growing (Symington 1943).

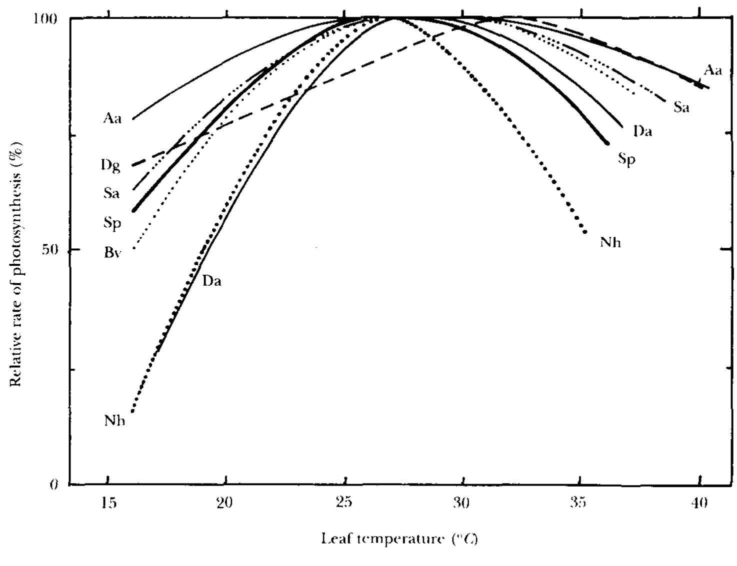

Figure 7. Changes of relative rates of net photosynthesis with leaf temperatures (Symbols in figure similar to that in Figure 6)

The stomatal conductance was higher in light demanding or fast growing species than those species that are shade tolerant or slow growing, indicating a similar tendency to that of photosynthesis. This relation between stomatal conductance and growing speed of seedlings was also obtained by one of our co-authors (Nakashizuka unpublished) who did measurements for many dipterocarp seedlings in the nursery of Forest Research Institute Malaysia (FRIM). Consequently, our findings showed that light demanding or fast growing species have higher maximum Pn and stomatal conductance and wider adaptability for changing leaf temperature than shade tolerant or slow growing species. Bazzaz and Carlson (1982), Fetcher *et al.* (1983), and Koike (1988) reported similar results of greater plasticity in photosynthetic parameters for early successional species than for late successional species. Generally, those in the former category are light demanding and the latter ones are shade tolerant.

Low stomatal conductance may induce easy increase of leaf temperature under high light irradiation. For example, during photosynthesis measurement of *N. heimii* and *D. aromatica,* leaf temperatures above 30°*C* could be attained easily by the temperature-controlled water circulating around the chamber. To achieve the same temperature for *A. auriculiformis* and *Du. grandifolia* the circulating water had to be raised to above 40°*C* as their leaves were cooled down by vigorous transpiration at the higher temperature conditions. The leaves of the former groups drooped during day time even in the growth chamber with a relatively low light intensity. These phenomena are apparently effective for leaves with low stomatal conductance to escape from excessive heating caused by strong sunlight irradiation. This may also explain the absence of these seedlings in open areas (Symington 1943).

Conclusion

The chilling injuries of seeds and seedlings occurred below 15°*C* in tropical species found in lowland and hill forests (below 1000 *m*). This temperature was close to the minimum temperature at the altitudinal upper limit of dipterocarp distribution. The susceptibility of seeds and seedlings to low temperatures was higher in tree species such as *S. parvifolia* and *D. aromatica* which are found in the moist tropical forest when compared with species distributed in the more seasonal forests of the northern areas.

The relative growth rate (RGR), net assimilation rate (NAR) and net photosynthesis rate (Pn) of the seedlings of tropical species which were grown under controlled temperatures were within a similar range to those of temperate tree species. These rates also show the dependence on the degree of light requirement in their early growth stages. The higher the light requirement, the bigger the rates of growth, net photosynthetic rate, and stomatal conductance. Light demanding species such as *A. auriculiformis, Du. grandifolia,* and *B. valetonii* had higher plasticity in photosynthetic parameters to variation in temperatures. The narrower plasticity of shade tolerant species like *N. heimii* may be due to the stable natural environment of these species, being sheltered under the high canopy.

From these characteristics in growth and photosynthesis of the seedlings, the degree of light requirement of the species appears to be in decreasing order: *A. auriculiformis, Du. grandifolia, B. valetonii, S. assamica, S. parvifolia, D. aromatica,* and *N. heimii.* Handling of the seedlings for reforestation purposes should be easier with species of the early plant succession stage, with high light demand or with species that are naturally distributed in the northern, more seasonal area. They have a greater plasticity to change in temperatures as well as higher tolerance to water and transplanting stresses, as reported by Mori (1980) and Sasaki (1980).

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