1

TEMPERATURE AND LIGHT CONTROL OF GROWTH OF TEAK (*TECTONA GRANDIS* LINN.F.) SEEDLINGS

by

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STATEMENT OF ORIGINALITY

Except where specific acknowledgement is given, the research work reported in this thesis is entirely that of the author.

(Khongsak Pinyopusarerk)

ABSTRACT

Initial studies in this thesis attempted to delineate temperature response of teak seedlings of two different provenances under controlled environment conditions. These studies confirmed anomalous results reported earlier by other workers. The causes of the anomalies were considered. There was evidence that a light radiation x temperature interaction might have been involved.

Subsequent studies examined the effect of light radiation and temperature on teak seedlings of one of the provenances. The existence of a light radiation x temperature interaction has been demonstrated. Seedling growth (e.g. total leaf area, dry matter production and height) was better at higher temperature (33/28°C) than at lower temperature (33/25°C) under total radiation of 200 cal $cm^{-2}day^{-1}$. In contrast there were no differences in these parameters between temperatures under total radiation of 100 cal $cm^{-2}day^{-1}$. The results also showed very important effects of total daily radiation. Despite the interaction effect seedling growth was better at the higher total radiation level.

Growth analysis studies showed net assimilation rate and leaf area ratio were both affected by light radiation and temperature conditions. This suggested the controls might act through photosynthesis, respiration and leaf development.

Accordingly, the effects of light radiation and temperature on seedling photosynthesis, respiration and leaf structure were examined. The results showed:

(1) Rate of photosynthesis was increased with increased light intensity from 200 to 800 $\mu Em^{-2}sec^{-1}$. The light response

curve suggested the light compensation point would be at about 55 $\mu Em^{-2} sec^{-1}$ and the light saturation level at 900 $\mu Em^{-2} sec^{-1}$.

(2) The rates of photosynthesis and respiration increased with increasing temperature within the range 25 to 31°C.

(3) Teak seedlings produced more and larger leaves at high temperature and high light radiation conditions. Examination of epidermal cells on leaves indicated that at high temperature the larger leaves were due to both more and larger cells. At high light radiation level there were more but smaller cells in leaves.

The results of photosynthesis, respiration and leaf characteristics indicated the seedling performance recorded in the earlier studies could generally be explained in terms of responses in photosynthesis, respiration and leaf structure to different temperature and light radiation regimes. Interpretation in this way removed many of the anomalies noted in previous studies.

The importance of results of these studies for planning phytotron experiments is discussed.

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TABLE OF CONTENTS

INTRODUCTION

Provenance studies of teak seedlings under controlled environment conditions have demonstrated the existence of provenance variation in many growth characteristics, and have shown the importance of temperature as a control of teak seedling growth and development. Delineation of temperature responses of individual provenances has however not been possible because results obtained have been anomalous and confused by a provenance x temperature interaction.

The studies reported in this thesis attempted initially to clarify temperature response of teak seedlings of different provenances under controlled environment conditions. This objective was not achieved because the results were again anomalous. The causes were examined. There was evidence of a light radiation x temperature effect which could have been responsible for the anomalies.

Subsequent studies examined the effect of light radiation on temperature response of teak seedlings. These studies demonstrated the existence of a light radiation x temperature interaction and indicated total light radiation was an important control of teak seedling development.

There were indications from growth analysis studies that net assimilation rate and leaf area ratio were both affected by temperature and radiation conditions. This suggested these controls might act through photosynthesis, respiration and leaf development. The effect of temperature and light radiation on seedling photosynthesis, respiration and leaf development were therefore examined.

The results indicated the seedling performance in the earlier studies

of this thesis could generally be explained as simple responses of photosynthesis, respiration and leaf development under different temperature and radiation regimes. The implication for studies in the phytotron and for future provenance studies under controlled environment conditions are discussed.

The thesis has been divided into four parts.

Part I reviews the natural occurrence of teak and the studies of provenance variation and emphasises the need for further studies. Before detailing experimental studies, phytotron facilities and general experimental procedures used are outlined. This is followed by details of the initial studies with two teak provenances in which attempts were made to delineate the optimum temperature for each.

In Part II a brief review of the effect of light radiation on plant growth is presented followed by studies of the effect of light radiation and temperature together on teak seedlings. The relationship between total radiation and photoperiod is also examined.

Part III outlines studies determining the effect of temperature and radiation on photosynthesis, respiration and leaf development of teak seedlings.

Finally Part IV. The results obtained from the studies in Parts I and II are interpreted using the knowledge gained from Part III. Some wider implications of the results are discussed.

PART I

TEAK RESPONSE TO TEMPERATURE

OUTLINE OF PART I

Studies of provenance variation in teak under controlled environment conditions have confirmed field observations of provenance differences in many growth characteristics. Delineation of optimum temperatures for particular provenances has been attempted but the results obtained have been anomalous and confused by provenance x temperature interactions. In this part of the thesis, attempts have been made to clarify the temperature response of teak seedlings of two provenances under controlled environment conditions.

Initially (Chapter 1) the importance and natural occurrence of teak, and the studies of provenance variation are reviewed. The need for further study is considered based on the results of provenance studies under controlled environment conditions.

Chapter 2 outlines the controlled environment facilities and general experimental procedures used in the study.

Chapter 3 outlines a series of experiments conducted to determine optimal temperatures for growth of each of two Indian provenances. These objectives were not completely achieved as the results were also anomalous. Possible causes of these anomalies have been considered.

CHAPTER 1

THE OCCURRENCE OF TEAK (*TECTONA GRANDIS* LINN. f.) AND PROVENANCE VARIATION IN THE SPECIES

1.1 INTRODUCTION

Teak (*Tectona grandis* Linn. f.) is one of the most important tropical tree species. The species is a major commercial timber species in several Southeast Asian countries including Burma, Thailand and Indonesia, and occurs over a wide range of climatic conditions and various geological formations.

Tree species with a wide geographical distribution generally show marked differentiation. Hence the geographic origin or provenance of the seed source has a marked effect on the subsequent performance. Knowledge of variation pattern of the species is therefore essential background for any wide ranging commercially important species.

Provenance studies have shown the existence of variation in growth characteristics of teak but the detailed pattern is not well understood. Attempts have been made to examine the variation under controlled environment conditions as well as in the field. There were however no clearcut results from these studies and some results were anomalous.

This Chapter outlines the importance and natural occurrence of teak and reviews the studies of provenance variation. Particular emphasis is given to provenance variation displayed under controlled environment conditions. The need for further studies of this nature is emphasised.

1.2 THE IMPORTANCE OF TEAK WITH PARTICULAR REFERENCE TO SOUTHEAST ASIAN COUNTRIES

1.2.1 The Importance of Teak to the Economy

Teak is a major commercial timber tree in several countries in Southeast Asia including Burma, Thailand and Indonesia. Exports of teak are a major source of government revenue in these countries.

The production and export of teak from Burma, Thailand and Indonesia are shown in Table 1.1. The value of teak exports during the 1960s in Burma was approximately 20 million $US per annum, in Thailand approximately 10 million $US per annum. Indonesia began to export teak in 1970 (Samapuddhi, 1973) and earned about 3 million $US per annum during 1970-1972. The value of teak exports in 1974 doubled that of previous years although the quantity exported was less. This is due mainly to the marked increase in price associated with increased demand.

Teak exports from Burma and Thailand decreased from late 1960. A reduction in the material available in the natural teak forests accompanied by an increase in domestic consumption was largely responsible for the decrease.

1.2.2 The Role of Teak in Plantation Forestry

Since the world demand for teak continues to increase (Samapuddhi, 1973), the production from natural teak forests alone will not be sufficient to meet the demand. Future consumption of teak will therefore be heavily dependent on the production from plantations.

Teak planting programmes have been planned for many countries throughout the tropics. For example, on the Indian subcontinent alone

Table 1.1 Production and Exports of teak (log and sawn timber) from Burma, Thailand and Indonesia

Year	Burma[1]			Thailand[2]			Indonesia[3]		
	Production $x10^3$ cu.ton	Export $x10^3$ cu.ton	Value $x10^6$ \$US	Production $x10^3$ cu.ton	Export $x10^3$ cu.ton	Value $x10^6$ \$US	Production $x10^3$ cu.ton	Export $x10^3$ cu.ton	Value $x10^6$ \$US
1962	250	119	12.9	137	40	8.5	492		
1964	381	154	21.3	213	40	8.9	474		
1966	240	135	23.2	234	49	12.2	373		
1968	296	110	22.0	264	29	8.5	473		
1970	301	118	22.5	238	29	7.8	568	59	3.1
1972	291	-	-	178	40	10.4	597	45	2.9
1974	201	69	-	150	35	20.1	600	53	8.1

Source: [1] Report to the People, Burma, 1971-72, 1978-79

[2] Statistical Yearbook, Thailand 1974-75

[3] Statistical Yearbook, Indonesia, 1975

the annual planting target is 20,000 ha (Kelding, 1973), in Thailand 10,000 ha per annum (Anon., 1973) and in Burma 1,200 ha (Anon., 1979). Planting schemes on a smaller scale have also been carried out in West and East Africa (e.g. Kenya, Tanzania, Nigeria and Ghana), and in Central and South America (e.g. Trinidad, Puerto Rico and Brazil) (Wood, 1967; Kelding, 1973, 1977).

1.3 NATURAL DISTRIBUTION AND FACTORS RELEVANT TO THE OCCURRENCE OF THE SPECIES

1.3.1 Natural Distribution

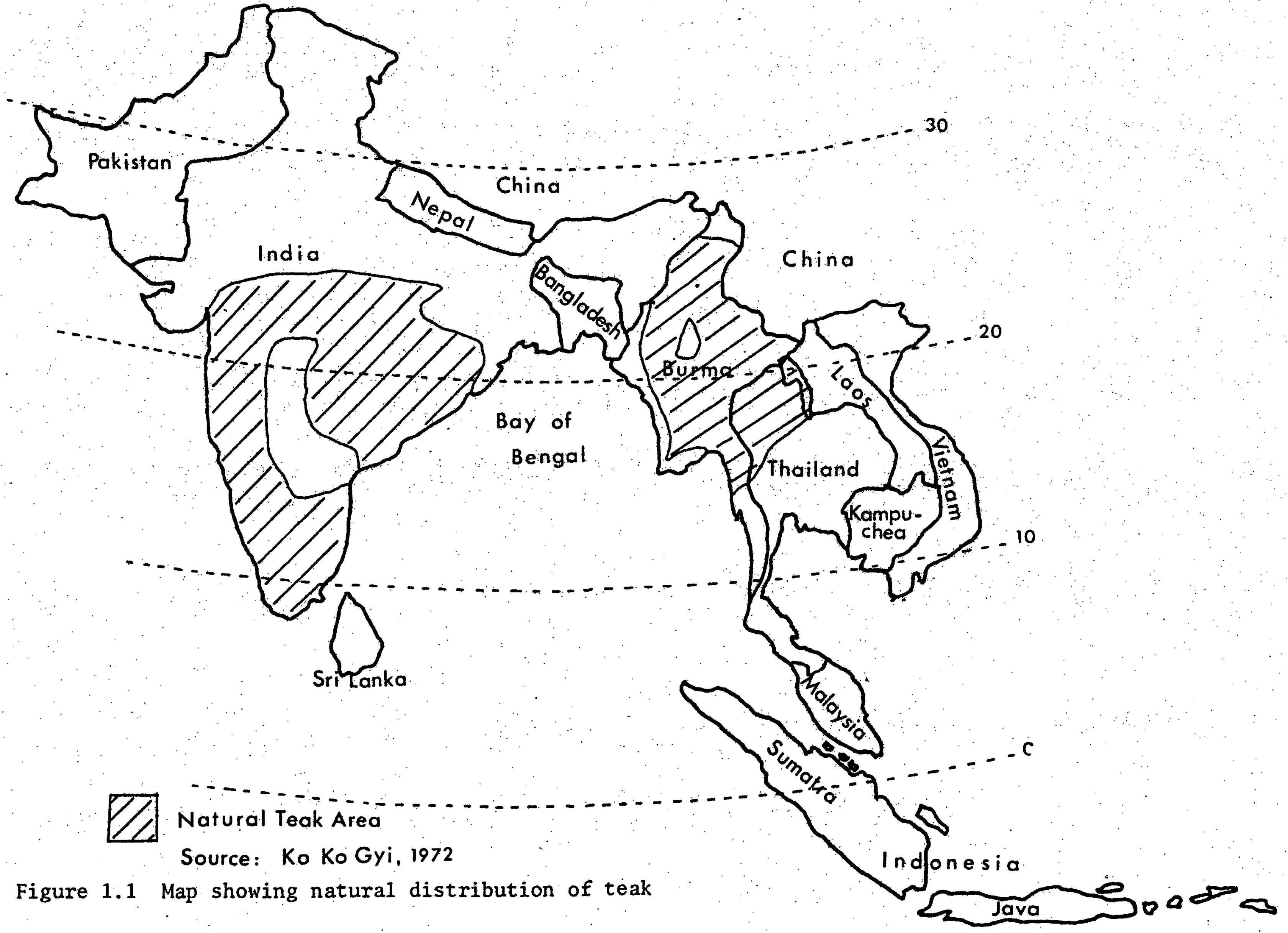
Teak has a scattered distribution throughout the Indian peninsula and much of Burma, northern Thailand and northwestern Laos (Figure 1.1) (Troup, 1921; Mahapol, 1954; Haig *et al.*, 1958; Streets, 1962). The species is also found in Java and some of the small islands of the Indonesian Archipelago, but is believed to have been introduced to these areas by the Hindus during the fourteenth and sixteenth centuries (Altona, 1922, 1923).

The northern limit of its distribution lies about latitude 25°30'N in Burma, and the southern limit about 9°N in India. On the east, it extends to a longitude of about 104° 31'E and on the west to 73°W (Troup, 1921; Kermode, 1957).

With regard to altitudinal limits, teak extends from sea level up to 1200 m or rather more as in Coorg, Central India (Streets, 1962). In Burma and Thailand, however, the species is limited to 885 m (Haig *et al.*, 1958; Iman, 1970).

1.3.2 Climatic Requirements

Teak can grow over a wide range of climatic conditions from dry to



Source: Ko Ko Gyi, 1972

Figure 1.1 Map showing natural distribution of teak moist tropical with annual rainfall varying from 625 mm, e.g. Madras and Bombay in India, to 5080 mm on the west coast of India (Troup, 1921; Anon., 1958). Teak also grows under a wide range of temperatures from as low as 2°C to as high as 46°C (Haig *et al*., 1958; Streets, 1962). However it cannot tolerate frost which causes it to die back (Troup, 1932; Kermode, 1964).

Teak reaches its largest dimension (average 25 to 30 m in height and 3 m in girth) in a fairly moist, warm tropical climate with annual rainfall of 1270 to 3800 mm, temperature range of 13 to 40°C and a marked dry season of 3 to 5 months' period (Troup, 1921; Mahapol, 1954; Haig *et al*., 1958; Streets, 1962). Unsatisfactory results of planting teak in regions without a well-marked dry season have been reported in areas of Malaysia and north Borneo (Streets, 1962).

1.3.3 Edaphic Requirements

Teak is found on various geological formations such as granite, gneiss, schist, calcareous crystalline rocks, limestone, some sandstone, conglomerate and shale (Kulkani, 1951; Puri, 1951, 1960; Banijbhatana, 1957; Takle and Mujumdar, 1957). In areas where conglomerate or sandstone underlies the soil, the species appears to be stunted in growth and may be absent from such localities (Hewetson, 1951; Kulkani, 1951; Kadambi, 1957; Seth and Yadav, 1959).

Teak grows best on deep, well-drained, moist, sandy loams of moderate to high fertility (Anon., 1958; Streets, 1962). It will not grow on waterlogged ground or on sites liable to prolonged inundation (Haig *et al*., 1958; Streets, 1962). Consequently, most teak forests are situated on slopes with good subsoil drainage, but the species will also grow well on flat alluvial ground provided the drainage is good.

Teak usually grows on soils within the pH range 6.5-7.5. Kulkani (1951) pointed out that the species is absent from natural forest where the soil pH is below 6.0. However, lower soil pH values have been reported in successful teak plantations in Nilambur, India where soil pH was 5.5-5.8 (Gupta, 1951), in Laos, 4.0-6.0 (Stevens, 1970) and in northern Thailand, 5.0 (Aksornkoae *et al.*, 1972).

Maximum soil pH suitable for teak growth is considered to be 8.5 (Kulkani, 1951).

1.4 PROVENANCE VARIATION IN TEAK

As teak can grow over a wide range of climatic conditions and various geological formations, variation in growth characteristics would be expected to occur in the species. Such variation has been recognised from several provenance trials e.g. in India (Mathauda, 1954), Indonesia (Coster and Eidmann, 1934; Beard, 1943; Becking, 1951; Alphen de Veer, 1957) and Burma (Maung Gale and Nyunt Naing, 1967). The results of these trials are detailed in the following sections.

1.4.1 India

Provenance trials of teak were established in 1930 at Nilambur and South Coimbatore using seed sources from Burma and India. The results after 15 years are shown in Tables 1.2 and 1.3.

The trial at Nilambur was assessed at the age of 4, 9 and 15 years. The materials from south Bombay and south Burma were superior to the others in height, diameter and volume production. The materials from Anamalais and north Burma were always the poorest in these parameters. The remaining provenance (Nilambur and Travancore) were intermediate (Table 1.2).

Table 1.2 Results of teak provenance trial in Nilambur, India

Provenance	4-year Height m	Diameter cm	Volume m^3/ha	9-year Height m	Diameter cm	Volume m^3/ha	15-year Height m	Diameter cm	Volume m^3/ha
Nilambur	6.4	5.6	15.6	11.0	9.4	50.0	15.5	14.7	59.1
Anamalais	6.4	5.3	14.8	10.1	8.9	41.3	14.0	13.5	54.3
Travancore	6.4	5.6	19.0	10.7	9.4	50.4	14.3	14.5	56.9
South Bombay	6.4	5.8	18.1	12.5	10.4	61.2	17.1	16.8	76.2
South Burma	6.4	6.1	18.3	11.6	9.9	52.1	16.5	16.8	77.7
North Burma	5.2	5.3	10.6	9.1	8.9	32.9	13.1	13.7	52.1

Source: Mathauda, 1954

Table 1.3 Results of teak provenance trial in South Coimbatore, India

Provenance	5-year			11-year		15-year
	Height m	Diameter cm	Volume m^3/ha	Height m	Diameter cm	Height m
Mount Stuart	7.9	7.9	46.7	13.1	14.7	16.2
Mysore	7.0	7.4	33.6	12.5	13.7	15.2
Nilambur	7.3	7.4	34.6	12.5	14.0	15.2
South Burma	6.1	6.4	20.3	10.1	11.9	12.5

Source: Mathauda, 1954

Another trial at South Coimbatore was assessed at 5, 11 and 15 years after outplanting. The material from Mount Stuart showed promising growth, being the best in all growth parameters measured. The South Burma provenance on the other hand was inferior to the other provenances (Table 1.3).

Thus the results of the trial at South Coimbatore indicated the local materials gave the most promising performances. The exotic seed source from South Burma showed the poorest result. This was contrary to its performance at Nilambur indicating the possible existence of provenance x site interaction.

Wood properties were also tested at age 36 years in the South Coimbatore trial (Purkayastha *et al.*, 1972). Assessment was made of wood density (weight/length). Wood from Mount Stuart and Mysore was significantly heavier than that from Nilambur and South Burma.

1.4.2 Indonesia

Provenance trials were established at several localities in Indonesia in 1932. Seven provenances from Indochina, Burma, Thailand, Malabar (India), Central Province (India), Godavari (India) and from local stands were included. The results have been reported by Coster and Eidmann (1934), Beard (1943), Becking (1951), Alphen de Veer (1957) and Anon. (1958).

There were marked differences in growth and tree form after 21 years. The local and Malabar (India) provenances showed the best height growth. The Thai provenance had the straightest stems with small branches and the Burmese provenance was only slightly inferior to the Thai in these characteristics. The trees from Central Province and Godavari (India) showed poor growth and bad shape with heavy branching.

1.4.3 Burma

Provenances from four exotic and nine Burmese seed sources were compared at three locations in South Burma (Zigon, Pyinmana and North Toungoo) (Maung Gale and Nyung Naing, 1967). The exotic materials were from Indonesia and India (locations unspecified) and also from Togo (Dahomey) and Papua New Guinea. The Burmese materials were from three northern provenances (Myitkyina, west Katha and Mongmit) and six southern provenances (Pyinmana, South Toungoo, Thayetmyo, Zigon, Tharrawaddy and Kawkareik).

At age six years, survival varied considerably between provenances at all test sites. The Burmese materials always had a higher survival percentage than the exotic materials. The southern Burmese provenances (local at the test sites) also had better survival rates than the northern provenances.

Height growth was not statistically analysed but there was evidence of differences between provenances and of provenance x site interaction. No details were reported.

1.4.4 Conclusion

The results from various provenance trials outlined above indicate the existence of provenance variation in teak. This variation has been found in volume production, tree form, wood property and survival. Although local provenances have generally proved to be superior to exotic sources, the existence of provenance x site interaction has been demonstrated particularly in India and Burma.

1.5 STUDIES OF PROVENANCE VARIATION UNDER CONTROLLED ENVIRONMENT CONDITIONS

There have been some studies of teak performance and variation pattern under controlled environment conditions.

Ko Ko Gyi (1972) and Kanchanaburangura (1976) both demonstrated the existence of provenance variation in teak seedlings in response to day/night temperatures under phytotron conditions. They also attempted to define optimal temperature and daylength conditions for the growth of teak seedlings. Effect of daylength was however found to be less important than temperature. Development of teak seedlings was generally not affected by daylength except at very short day (i.e. at 8 hours). This is well below the daylength under natural conditions in the tropics, i.e. about 12 hours.

Ko Ko Gyi (1972) compared seedlings of five provenances from

Pati (Indonesia), Toungoo (South Burma), Myitkyina (North Burma), Sungum, Kerala State (India) and Pakse (Laos) (see Figure 1.2) under six temperature regimes. The regimes were made up of the combination of three day temperatures (30, 33 and 36°C) and two night temperatures (22 and 31°C), and the seedlings were grown under these conditions for four weeks.

There was clear evidence of provenance differences. Myitkyina provenance (North Burma) was always amongst the best in height and diameter growth. The Indian provenance (Sungum) was always the poorest.

Even more importantly, provenance x temperature interaction effects were demonstrated in diameter and height increment. Typical figures for diameter increment are given in Figures 1.3A and B. In this example all provenances grew best at the highest day (36°C) and night (31°C) temperatures but there were significant differences in the rankings at other temperature regimes. The Indonesian provenance grew well at 33°C but relatively poorly at 30°C day temperature. The southern Burmese provenance (Toungoo) was as good as the northern Burmese provenance at 33 and 30°C but significantly poorer at 36°C. The Laotian provenance was amongst the best at 30 and 36°C but performed relatively poorly at 33°C. The Indian provenance was not poorer than the southern Burmese provenance at 36°C but was significantly poorer at the lower temperatures (30 and 33°C).

Similarly with night temperature (Figure 1.3B) the Indonesian and Laotian provenances were as good as the northern Burmese at 31°C but significantly poorer at 22°C. The southern Burmese provenance on the other hand exhibited a reverse trend. This provenance was not significantly poorer than the northern Burmese at 22°C but was at the higher night temperature. Furthermore the southern Burmese was poorer than the Indonesian and Laotian at the high night temperature (31°C) but better

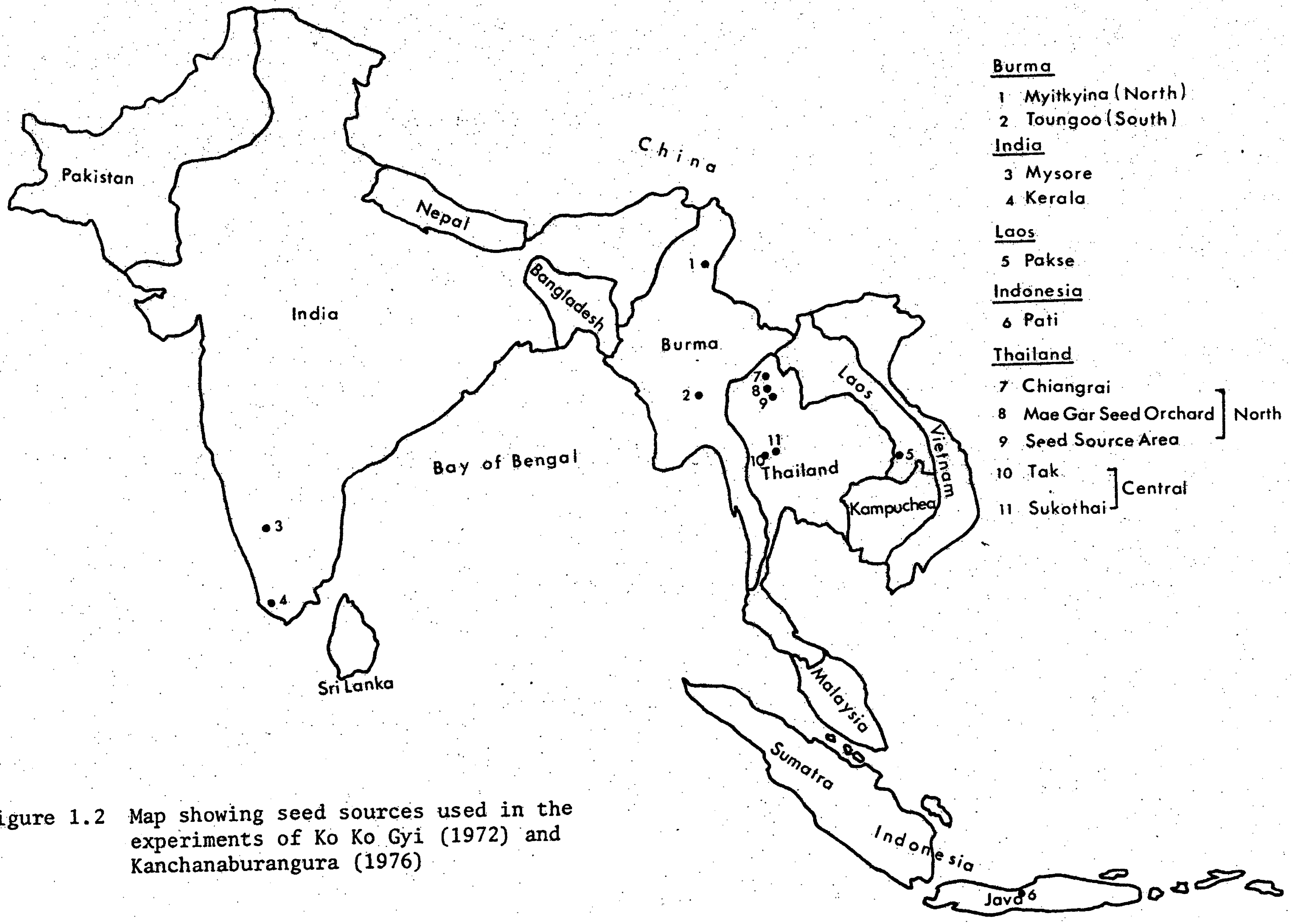


Figure 1.2 Map showing seed sources used in the experiments of Ko Ko Gyi (1972) and Kanchanaburangura (1976)

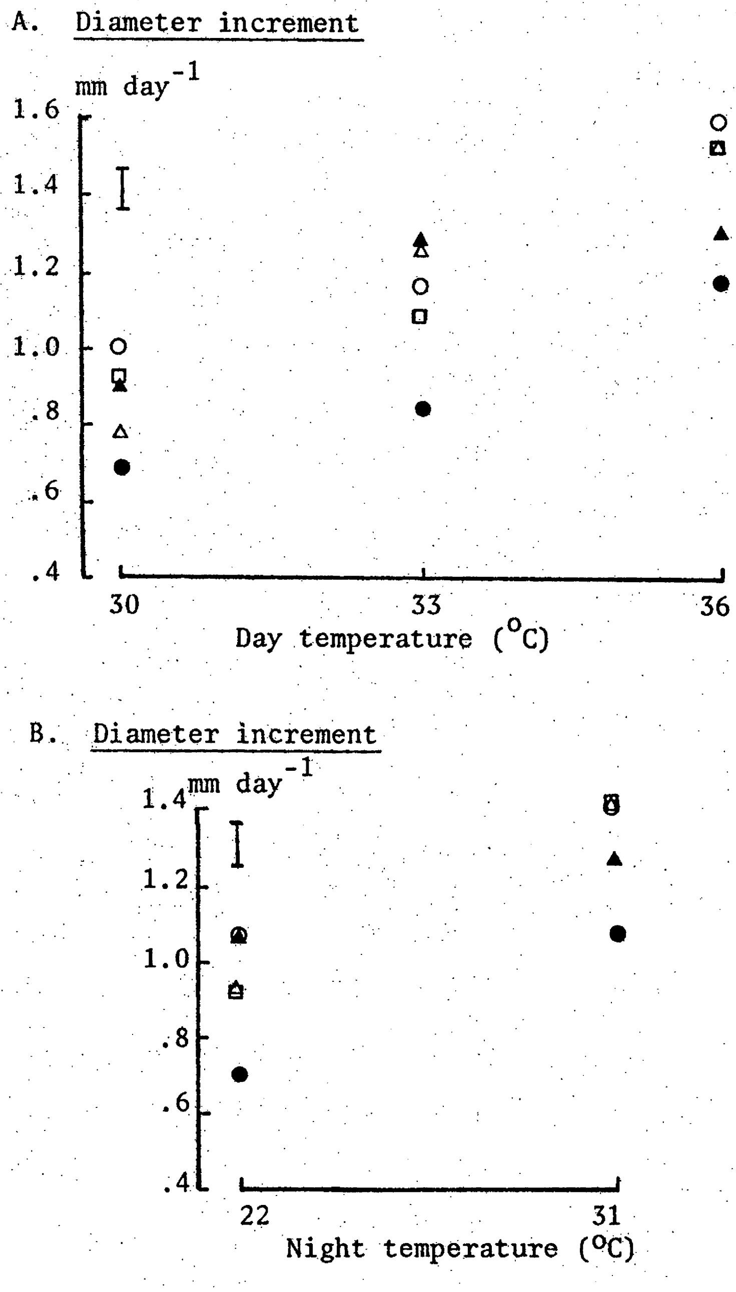


Figure 1.3 Effect of day and night temperatures on diameter increment of teak seedlings from North Burma (○), South Burma (▲), Laos (□), Indonesia (△) and India (●). (Source: Ko Ko Gyi (1972))

than these provenances at the low night temperature (22°C).

Kanchanaburangura (1976) investigated provenance variation using five Thai and two Indian provenances. Of the Thai provenances two came from the central region and three from the north. The two Indian provenances were Sungum, Kerala State (as also used by Ko Ko Gyi) and Masale Valley, Mysore State (see Figure 1.2). Development of seedlings of these provenances were compared in the phytotron glasshouse under various temperature regimes of 24/19, 30/25, 33/28 and 36/31°C; 30/13, 33/25 and 36/19°C; and 30/19, 30/22 and 30/26°C day/night temperatures.

There was clear evidence of provenance differences within the Thai materials. Significant differences were found in height growth, diameter growth, dry matter production and leaf area production. However, there was no clear regional differences and the northern provenances were not clearly differentiated from those of the central provenances.

There was however a clear difference between the Thai and Indian provenances. In most of the parameters studied the Thai provenances were superior to the Indian provenances.

The growth analysis studies of Kanchanaburangura (1976) were of interest because the Thai provenances had lower net assimilation rate but greater leaf area ratio than the Indian provenances. The greater leaf area gave the Thai materials an overall advantage in relative growth rate.

There was some evidence of provenance x temperature interaction in height and diameter growth. All provenances had best growth at day temperature between 30 and 33°C in combination with night temperature between 25 and 28°C. At the highest temperature applied (36/31^{C}C) the Thai provenances performed significantly better than the Indian provenances.

1.5.1 Conclusion

Studies of Ko Ko Gyi (1972) and Kanchanaburangura (1976) under controlled environment conditions confirmed the field observation of provenance variation in teak. This variation was found in height growth, diameter growth, leaf area production, dry matter production and growth analysis parameters.

Furthermore the provenance x temperature interaction displayed in the studies of Ko Ko Gyi was in accord with the results reported for the field trials in India by Mathauda (1954) (see Section 1.4.1).

The presence of provenance x temperature interaction in teak indicates it would be desirable to be able to specify optimum temperature ranges for individual provenances. For example this might have some direct practical benefit in allowing ranking of best suited provenances to higher temperatures. It may also give an indication of the physiological processes involved in the interaction.

1.6 TEMPERATURE ANOMALIES IN THE PROVENANCE RESPONSE

Delineation of optimum temperatures for particular provenances has not however been possible. Both Ko Ko Gyi (1972) and Kanchanaburangura (1976) demonstrated the importance of temperature as a control of the growth of teak seedlings but the results were not in accord.

The initial studies of Ko Ko Gyi (1972) using a single provenance (Papua New Guinea) found growth (e.g. height, leaf area production and dry matter production) was better at higher temperatures within the ranges 15/10 - 27/22^{o}C and 33/22 - 33/28^{o}C day/night temperature. In a later study with the additional provenances detailed in Section 1.5, all provenances showed an increase in these growth parameters with temperatures from 30 to 36°C day and 22 to 31°C night.

In Kanchanaburangura's study using materials from Thailand and India, growth (e.g. leaf area production and dry matter production) increased with an increase in temperature from 24/19°C to peak at 30/25 to 33/28°C but declined with further increase in temperature at 36/31°C. One of the provenances used by Kanchanaburangura was the same as used by Ko Ko Gyi. Indeed the material came from the same seed batch.

The temperature response of teak seedlings as defined by Ko Ko Gyi (1972) and Kanchanaburangura (1976) therefore did not agree although both pointed out the teak seedling preference for high temperatures in growth and development. In Ko Ko Gyi's studies growth increased steadily with increasing temperature within the range 15/10-36/31°C day/night temperature. In contrast in Kanchanaburangura's studies growth increased with temperature from 24/10 to peak at 30/25 to 33/28°C and declined at 36/31°C.

Thus, there was no clear agreement in the temperature response of teak seedlings. However, the temperature regimes used by Ko Ko Gyi and Kanchanaburangura did not allow precise interpretation of temperature effects. It is thus worthy of further study using a more precise range of day and night temperatures.

1.7 THE PUTATIVE IMPORTANCE OF LEAF AREA AND PHOTOSYNTHESIS

Growth analysis studies suggested leaf area ratio and net assimilation rate were important in determining provenance response to temperature in both Ko Ko Gyi's and Kanchanaburangura's studies. These parameters may be interpreted as indicating the area of photosynthetic material and the rate of photosynthesis are important determinants of the temperature response.

Ko Ko Gyi (1972) found growth of the provenance from India was significantly poorer than the provenance from Indonesia at 36°C day but was not significantly poorer at 30°C day temperature. Growth analysis studies showed leaf area ratio of the Indian provenance was significantly smaller than the Indonesian provenance at 36°C but not at 30°C. In contrast, net assimilation rate of the Indian provenance tended to be greater than the Indonesian provenance although the differences were not significant.

Similarly Kanchanaburangura (1976) found growth of the Indian provenances was poorer than the Thai provenances at 36/31°C but not at the lower temperatures (e.g. 24/19 and 30/25°C). Kanchanaburangura also found the Indian provenances had smaller leaf area ratio but greater net assimilation rate than the Thai provenances.

Thus the studies of Ko Ko Gyi and Kanchanaburangura suggested leaf area might play an important part in determining the provenance performance. The results implied that the Thai and Indonesian provenances had a lower rate of photosynthesis than the Indian provenances. But the greater leaf area produced by the Thai and Indonesian gave these materials greater overall photosynthetic production than the Indian.

1.8 CONCLUSION

Both Ko Ko Gyi (1972) and Kanchanaburangura (1976) demonstrated the existence of provenance variation in teak under controlled environment conditions. This variation was found in a number of characters, e.g. height growth, diameter growth, leaf area production, dry matter production and growth analysis parameters.

There was also evidence of provenance x temperature interaction effects. Such effects were found in various growth parameters e.g. height growth and diameter growth.

Growth analysis studies suggested leaf area ratio and net assimilation rate were important in determining provenance performance. The results also suggested that seedlings with greater leaf surface area had greater overall photosynthetic production resulting in more dry matter accumulation.

The importance of temperature in the control of teak seedling growth and development was clearly demonstrated. However, there was no clear agreement in definition of the optimum temperature. The temperature ranges used in these studies were large and complex and did not allow precise interpretation of the temperature response.

From the above evidence, more detailed study is needed of teak provenance response to temperature and indeed of teak response to temperature in general.

As leaf area ratio and net assimilation rate have been shown to be important in determining the provenance performance, growth analysis parameters are therefore worthy of being included in such further investigations.

CHAPTER 2

AN OUTLINE OF GENERAL EXPERIMENTAL PROCEDURES

The experiments described in this thesis were conducted in the CSIRO 'CERES' phytotron in Canberra (Morse and Evans, 1962). Before detailing the experiments it is necessary to outline the facilities used. This Chapter describes these facilities and outlines the experimental methods and techniques generally used throughout the study. Where specific techniques were used these are dealt with in relevant sections.

2.1 PHYTOTRON FACILITIES

'CERES' phytotron contains glasshouses and cabinets in which temperature and photoperiod were controlled.

2.1.1 Glasshouses

In glasshouses day and night temperature regimes alternated in a square wave pattern with day temperature held at one level for eight hours (0830 to 1630 hours) and night temperature held for the remaining 16 hours. Temperatures were held within $\pm 1.5^{\circ}C$ of the specified levels. Relative humidity was maintained above 40%. The light source was natural daylight. Incandescent lamps provided illumination of about 5μE $m^{-2} sec^{-1}$ at plant height to extend the daylength to 16 hours (0400 to 2000 hours).

2.1.2 Growth Cabinets

Naturally lit BT cabinets and artificially lit LB cabinets (Morse and Evans, 1962) were used in some experiments.

Naturally lit BT cabinets were used inside the glasshouses. Temperatures were held within ±0.25°C of the specified levels. Photoperiod was 16 hours of which eight hours was from natural daylight (0830 to 1630 hours) and eight hours from low intensity incandescent light (1630 to 0030 hours). The time control settings for temperature, daylight and photoperiod light cycle were accurate to about ±3 minutes.

Artificially lit LB cabinets provided mean air temperature control to within ±0.25°C of the specified levels. Lighting was supplied by V.H.O. (140 watt) warm white fluorescent tubes, Philips T.L.M.F. 140/33 RS augmented by four incandescent lamps. Light intensity at the cabinet base was 850 $\mu E\ m^{-2} sec^{-1}$ (4000 f.c) and at mid-height 1065 $\mu E\ m^{-2} sec^{-1}$ (5000 f.c).

2.2 GENERAL EXPERIMENTAL PROCEDURES

2.2.1 Establishment of Seedlings

2.2.1.1 Pretreatment of seeds

Seeds were pretreated by alternate soaking in running tap water for 24 hours, followed by drying in a 33/28°C day/night temperature glasshouse for 48 hours. This process was repeated five times before the seeds were sown.

2.2.1.2 Sowing of seeds

Seeds were sown in shallow germination trays containing equal parts of perlite and vermiculite in a 30/25°C day/night temperature glasshouse. During germination the seeds were watered twice daily with tap water.

2.2.1.3 Transplanting of seedlings

When seedlings had two pairs of leaves above the cotyledon they were transplanted into 10 cm pots containing equal parts of perlite and vermiculite. The seedlings were watered with modified Hoagland's nutrient solution (Appendix I) in the morning and tap water in the afternoon. Additional mid-day application of tap water was necessary when the seedlings had reached the 5-6 leaf pair stage. The seedlings were maintained in a 30/25°C day/night temperature glasshouse until the experimental treatments were applied.

2.2.2 Grading of Seedlings for Experiments

The grading procedure used in all experiments was as follows. The most uniform seedlings based on height and number of leaf pairs were chosen from the seedling stock transplanted. These seedlings were subdivided into size classes based on height and size of leaves. Seedlings from each size class were randomly allocated so variation in seedling size was evenly distributed between treatments.

2.2.3 Maintenance of Seedlings

Regular checking was done for fungal or insect infestation. Seedlings were subjected to attack by two spotted mite (*Tetranychus urticae*) and aphid. Two spotted mite could cause severe damage to the seedlings resulting in abnormally poor development. Two spotted mite was controlled biologically within the phytotron using the predator mite (*Typhladromus occidentalis*) and chemically by spraying with omite and pirimor. Aphid was controlled by frequent spraying with DDT and Lindane.

Seedlings were re-potted into larger pots when they outgrew the pots used originally. Any sign of roots being exposed due to wash out of the perlite/vermiculite mixture during watering was quickly remedied by adding more of the same mixture. Position effect was minimized through periodic changing of pot position. In addition, seedlings were carefully spaced to avoid heavy mutual shading.

2.2.4 Harvests

In order to calculate growth analysis parameters two destructive harvests were carried out. The first harvest was two weeks after the seedlings had been under treatment; the second after a further two or more weeks. The diverse seedlings of each provenance and treatment were ranked for size at the first harvest. They were matched into the required number of pairs. One of each pair was selected at random for the first harvest, leaving the other to grow on to the second.

At each harvest, height, diameter, total leaf area and dry weight of leaves, stem and roots were recorded. In harvesting, the leaves were removed and leaf area measured, the stem was cut off at the cotyledon level, the roots were carefully washed free of the rooting medium. The various plant parts were dried in an oven at 80°C for at least 48 hours before weighing.

2.3 GENERAL PLANT PARAMETERS MEASURED

The parameters measured in most experiments are discussed here, while those specific to some experiments are discussed in the pertinent sections.

(i) <u>Seedling height</u>: Defined as the distance from the cotyledonary scar to the highest visible node on the stem.

(ii) Stem diameter: Measured with a Vernier caliper at mid-point between cotyledon and the first node. Two measurements were made at right angles and the mean calculated.

(iii) Dry weight: Leaves, stem and roots were weighed separately at room temperature after oven drying for at least 48 hours.

(iv) Leaf area: Measured with an 'Automatic Area Meter' Type AAM-5, Hayashi Denko Co. Ltd., Tokyo.

(v) Growth analysis parameters: Relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) were calculated using the usual formulae (see Sestak *et al.*, 1971; Evans, 1972 and Ledig, 1974) -

$$\mathrm{RGR} = \frac{L_n W_2 - L_n W_1}{t_2 - t_1}$$

$$\mathrm{NAR} = \frac{W_2 - W_1}{A_2 - A_1} \times \frac{L_n A_2 - L_n A_1}{t_2 - t_1}$$

$$\mathrm{LAR} = \frac{A_2}{W_2}$$

where 'W_1' and 'W_2' and 'A_1' and 'A_2' represent total plant dry weight and total leaf area at time 't_1' and 't_2' respectively. 't_2-t_1' is the time interval between harvests. 'L_n' indicates the natural logarithm.

2.4 ANALYSIS OF DATA

The data were subjected to standard analysis of variance. For the comparison of the significance of the differences between treatment means, Duncan's multiple range test (Duncan, 1955 outlined in Steel and Torrie, 1960) or the standard least significant difference (LSD) procedure

(Steel and Torrie, 1960) was used. Computation was conducted using programmes from SPSS (Statistical Package for the Social Science) by Nie *et al.*, 1972.

In the Figures throughout this thesis the differences necessary for significance at the 5% level are shown by means of a bar line.

CHAPTER 3

IDENTIFICATION OF ANOMALOUS RESULTS IN TEMPERATURE RESPONSE OF TEAK SEEDLINGS

3.1 INTRODUCTION

It is known (Chapter 1) that growth and development of teak seedlings are strongly controlled by day and night temperatures. The growth (e.g. height, diameter, leaf area and dry matter production) has been shown to be poor at both low day (e.g. 24°C) and low night (e.g. 19°C) temperatures. However, growth response under higher temperatures over the range 27 - 36°C day and 25 - 31°C night is unclear, and appears to be confused by a provenance x temperature interaction. The studies outlined in this Chapter have therefore examined the response of teak seedlings from two provenances over the ranges of day and night temperatures mentioned above. The objectives were:

(1) to determine the optimal day and night temperature for growth and development of seedlings of each provenance,

(2) to examine possible provenance differences in response to varying day and night temperatures.

As before, i.e. in the studies of Ko Ko Gyi (1972) and Kanchanaburangura (1976), the results were anomalous. In this Chapter the anomalies are detailed and possible causes considered.

3.2 PLANT MATERIALS AND EXPERIMENTAL PROCEDURE

3.2.1 Plant Materials

Two seed sources from India were used, Sungum, Kerala State and Masale Valley, Mysore State (see Figure 1.2). Details of the seed sources are given in Table 3.1.

Table 3.1 Information of seed sources

Provenance	Latitude Longitude	Altitude m	Annual rainfall mm	Seed stands
Sungum Kerala State (K)	8°N 76°31'E	700	2540	Plantation
Masale Valley Mysore State (M)	11°55'N 76°10'E	823	1270	Natural forest

The seed from Sungum, Kerala State had been used in the studies of Ko Ko Gyi (1972) and Kanchanaburangura (1976).

Establishment, maintenance and grading of seedlings for the experiments were as described in Sections 2.2.1-2.2.3. The number of seedlings used for each treatment varied with the experiments depending on the number of uniform seedlings available and also on space availability.

3.2.2 Experimental Procedure

Five experiments were conducted. Details of the experimental treatments are summarized in Table 3.2.

The first experiment examined the growth of seedlings of both provenances under four night temperature regimes (19, 25, 28 and 31°C) with a common day temperature (33°C). The second examined the response of

Table 3.2 Summarized details of the experiments conducted to determine growth response of teak seedlings to temperature

BT = Naturally lit BT Cabinet, GH = Glasshouse

Experiment No.	Provenances used	Temperature regimes ^{o}C day/night	Growth room	Period of experiment	No. of harvests	Harvest interval (week)	No. plants harvest/ treatment	Total No. of seedlings
1	K,M	33/19,33/25,33/28 and 33/31	BT	May-June (early winter)	2	4	3	48
2	K,M	24/28,27/28,33/28 and 36/28	GH	June-July (winter)	2	2	3	48
3	K	33/25,33/28 and 33/31	GH	July-August (winter)	2	2	5	30
4	K,M	33/25 and 36/31	GH	Sept.-Nov. (spring)	1	-	10	40
5	K,M	33/25,33/28 and 36/31	GH	Jan.-Mar. (summer)	2	2	7	84

of seedlings also from both provenances under a range of day temperatures of 24, 27, 33 and 36°C, each with a common night temperature of 28°C. As one treatment in the first experiment (Kerala provenance under 33/28°C) was destroyed by insect (*Tetranychus urticae*) attack, a portion of the experiment was repeated as a third experiment using the three night temperatures 25, 28 and 31°C with a 33°C day temperature.

These experiments indicated a provenance x temperature interaction was present with the Mysore provenance performing best at 33/25°C and the Kerala provenance at 36/31°C. To verify the presence of this interaction, development of the two provenances was examined (Experiment 4) under the two temperature regimes considered optimum for each provenance, 33/25 and 36/31°C. Surprisingly, the results differed from those obtained in the earlier experiments. Both provenances grew better at 36/31 than at 33/25°C. Consequently, this experiment was repeated including an intermediate temperature regime of 33/28°C but with the same result.

The experiments outlined above (except Experiment 4) included growth analysis studies. The first harvest occurred after the seedlings had been under treatment for two weeks, and the second two to four weeks after the first. At harvest, seedling height, stem diameter, total leaf area and dry weight of leaves, stem and roots were noted.

3.2.3 Statistical Analysis

Data were subjected to standard analysis of variance. Duncan's multiple range test was used to determine the significance of the differences between treatment means.

In Experiments 1 and 2 there were definite differences between uniform seedling blocks created in establishing the experiments. These were therefore included as a main source of variation in the analysis. In later experiments more seedlings were used giving much smaller differences between blocks and thus block-block variation was disregarded.

In Experiment 1 the Kerala seedlings at 33/28°C were destroyed. The 33/28°C treatments were therefore not included in the statistical analysis, and the experiment was analysed on three temperature regimes x two provenances. However, data were obtained from the four temperature regimes for the Mysore seedlings and these were also analysed and separately summarized in Appendix II.

3.3 RESULTS

There were significant differences between provenances and temperature treatments for many growth parameters (Table 3.3). Critical study of individual results using Duncan's multiple range test indicated a trend toward a provenance x temperature interaction. This is considered in more detail in discussion of each parameter.

The first three experiments indicated the presence of a provenance x temperature interaction in many growth parameters e.g. diameter, dry matter production and total leaf area. Growth of the material from the Mysore provenance generally peaked at about 33/~~35~~25 to 33/28°C whilst that of the Kerala provenance was greater with the higher temperature, with no indication of a peak being present over the range used (Table 3.4; Figure 3.1).

The results obtained in Experiments 4 and 5 were very different. In these experiments both provenances showed a tendency for increased growth of all parameters with increasing temperature despite the significant interaction (i.e. in Experiment 4) (Table 3.4; Figure 3.1).

The response of height growth was however similar for both provenances in all experiments, and appeared to be favoured by high temperature rather than low temperature (Table 3.5; Figure 3.2).

3.3.1 Effect of Temperature - the presence of provenance x temperature interaction

3.3.1.1 Diameter growth, dry matter production, total leaf area, RGR, NAR and LAR

3.3.1.1.1 Experiments 1-3

For the Mysore provenance, the pattern demonstrated (Table 3.4, Figure 3.1) (see also Appendices II and III) was for increased diameter, dry matter production, total leaf area, RGR amd NAR with increased temperature up to a peak at 33/25°C (Experiment 1) and 33/28°C (Experiment 2). At higher temperatures values recorded were less. Thus in Experiment 1, the values recorded for diameter growth, dry matter production and total leaf area were 5.3 mm, 3.88 g and 6.10 dm^2 respectively at 33/19°C, significantly higher at 33/25°C (7.5 mm, 9.29 g and 18.41 dm^2) and lower at 33/31°C (6.7 mm, 6.48 g and 14.08 dm^2) (Figure 3.1). Similarly in Experiment 2 the values recorded for diameter growth, dry matter production and total leaf area were significantly greater at 33/28°C than at 24/28°C (11.2 mm, 18.08 g and 27.47 dm^2 vs. 9.1 mm, 14.19 g and 20.10 dm^2 respectively), and lower at 36/28°C (9.9 mm, 15.49 g and 24.30 dm^2) (Figure 3.1).

Similarly there was an increase in RGR and NAR with temperature from 33/19°C (Experiment 1) and 24/28°C (Experiment 2) to a peak at 33/25°C and 33/28°C respectively. At higher temperatures the rates were lower (Table 3.4, Figure 3.1).

In contrast to the patterns of RGR and NAR, LAR of the Mysore provenance increased with increasing temperature in all experiments (Table 3.4, Figure 3.1).

In the Kerala provenance, the values recorded for all parameters were generally greater the higher the temperature (Table 3.4, Figure 3.1). In

Table 3.3 Summarized results of analysis of variance of the data presented in Tables 3.4 and 3.5 showing degree of freedom, mean squares values and significance levels
*, **, *** indicate significance at the 5, 1 and 0.1% levels respectively; ns indicates 'not significant' at the 5% level

Expt. No.	Source of variation	Degree of freedom	Height	Diameter	Dry matter production	Total leaf area	RGR	NAR	LAR
	Block	2	6.635^{***}	3.087^{ns}	3.162^{ns}	18.131^{***}	$.008^{**}$	$.002^{*}$	$.023^{ns}$
	Provenance (P)	1	91.576^{***}	$.436^{ns}$	12.785^{**}	44.494^{**}	$.005^{*}$	$.003^{*}$	$.005^{ns}$
1	Night temperature (T)	2	960.296^{***}	4.312^{**}	34.384^{***}	178.589^{***}	$.026^{***}$	$.007^{***}$	$.463^{***}$
	P x T	2	5.896^{*}	$.751^{*}$	1.666^{ns}	22.219^{***}	$.004^{ns}$	$.001^{ns}$	$.068^{ns}$
	Error	10	.514	.105	.895	.142	.001	.0004	.027
	Block	2	101.254^{***}	5.941^{***}	24.175^{***}	51.767^{***}	$.003^{*}$	$.001^{*}$	$.002^{ns}$
	Provenance (P)	1	6.934^{ns}	$.540^{*}$	4.735^{*}	$.025^{ns}$	$.008^{***}$	$.004^{***}$	$.031^{**}$
2	Day temperature (T)	3	232.134^{***}	2.670^{***}	11.794^{***}	51.382^{***}	$.004^{**}$	$.001^{*}$	$.023^{**}$
	P x T	3	11.464^{*}	1.690^{***}	5.965^{**}	12.524^{***}	$.001^{ns}$	$.000^{ns}$	$.001^{ns}$
	Error	14	2.440	.073	.636	1.642	.0005	.0002	.003
3	Night temperature	2	205.665^{***}	$.459^{ns}$	3.410^{ns}	34.125^{*}	$.012^{ns}$	$.001^{ns}$	$.053^{ns}$
	Error	16	18.377	.559	1.375	5.259	.005	.002	.016
	Provenance (P)	1	621.730^{***}	10.816^{***}	191.060^{***}	337.870^{***}			
4	Temperature (T)	1	436.260^{***}	33.124^{***}	280.380^{***}	541.380^{***}			
	P x T	1	78.120^{*}	$.900^{ns}$	53.696^{*}	79.791^{*}			
	Error	36	11.389	.706	7.991	11.620			

Table 3.3 (cont.)

Expt. No.	Source of variation	Degree of freedom	Height	Diameter	Dry matter production	Total leaf area	RGR	NAR	LAR
	Provenance (P)	1	977.824***	12.161***	79.578***	200.928***	.021*	.020*	.035^{ns}
5	Temperature (T)	2	4.542^{ns}	7.536***	15.143**	38.877***	.067***	.006^{ns}	.083**
	P x T	2	2.945^{ns}	.562^{ns}	2.888^{ns}	5.575^{ns}	.006^{ns}	.006^{ns}	.002
	Error	36	5.836	.389	.978	3.140	.004	.003	.010

(n.b. For Experiments 1 and 2, block variation was included in the analysis of variance. There were no significant interactions of block x provenance and block x temperature. The values of these terms were therefore pooled with the main error term to give error values shown here).

Table 3.4 Effects of temperature on diameter growth, dry matter production, total leaf area, RGR, NAR and LAR of teak seedlings. Within each experiment data which do not have the same affix are significantly different at the 5% level according to Duncan's new multiple range test

Experiment No.	Temperature regime (°C day/night temperature)							
	33/19	24/28	27/28	33/25	33/28	33/31	36/28	36/31
Mysore Provenance								
Diameter (mm)								
1	5.3			7.5		6.7		
2		9.1^{a}	9.2^{a}		11.2		9.9	
4				5.8				7.3
5				5.5^{a}	6.1^{a}			7.3
Dry Matter Production (g)								
1	3.88			9.29		6.48		
2		14.19^{a}	17.88^{b}		18.08^{b}		15.49^{a}	
4				6.33				9.30
5				5.30^{a}	5.91^{a}			7.90
Total Leaf Area (dm^2)								
1	6.10			18.41		14.08		
2		20.10	27.20^{b}		27.47^{b}		24.30	
4				8.40				12.93
5				7.53^{a}	8.69^{a}			12.32
RGR (gg^{-1}week^{-1})								
1	0.29			0.46		0.35		
2		0.20^{a}	$0.\overset{a}{2}3^{b}$		0.25^{b}		$0.23^{a,b}$	
5				0.53^{a}	0.59^{a}			0.69
NAR (gdm^{-1}week^{-1})								
1	0.18^{a}			0.25		0.17^{a}		
2		0.15^{a}	0.16^{a}		0.17^{a}		0.16^{a}	
5				0.36^{a}	$0.40^{a,b}$			$.44^{b}$
LAR (dm^2 g^{-1})								
1	1.57			1.98^{a}		2.20^{a}		
2		1.41^{a}	$1.50^{a,b}$		1.52^{b}		1.56^{b}	
5				1.42^{a}	$1.47^{a,b}$			1.57^{b}

Table 3.4 (cont.)

Experiment No.	Temperature regime (°C day/night temperature) 33/19	24/28	27/28	33/25	33/28	33/31	36/28	36/31
Kerala Provenance								
Diameter (mm)								
1	6.1			7.0^{a}		7.3^{a}		
2		9.6^{a}	9.8^{a}		10.0^{a}		11.2	
3				8.1^{a}	8.6^{a}	8.6^{a}		
4				6.6				8.7
5				6.8^{a}	$7.4^{a,b}$			7.9^{b}
Dry Matter Production (g)								
1	5.77			9.83^{a}		9.10^{a}		
2		15.36	$17.66^{a,b}$		17.11^{a}		19.06^{b}	
3				12.28^{a}	13.00^{a}	13.92^{a}		
4				8.38				15.99
5				7.96	9.20^{a}			9.98^{a}
Total Leaf Area (dm^2)								
1	10.19			17.32		20.51		
2		20.60	25.12^{a}		25.00^{a}		28.10	
3				16.68^{a}	18.46^{a}	21.83		
4				11.39				21.57
5				11.14	13.34^{a}			15.20^{a}
RGR ($gg^{-1}week^{-1}$)								
1	0.27			0.37^{a}		0.36^{a}		
2		0.22^{a}	$0.26^{a,b}$		0.27^{b}		0.31	
3				0.31^{a}	0.33^{a}	0.40^{a}		
5				0.59^{a}	$0.65^{a,b}$			0.71^{b}
NAR ($gdm^{-1}week^{-1}$)								
1	0.16^{a}			0.20^{a}		0.16^{a}		
2		0.17^{a}	$0.18^{a,b}$		$0.20^{b,c}$		0.21^{c}	
3				0.21^{a}	0.22^{a}	0.24^{a}		
5				0.42^{a}	0.45^{a}			0.47
LAR (dm^2g^{-1})								
1	1.67^{a}			1.77^{a}		2.28		
2		1.34^{a}	$1.44^{a,b}$		1.46^{b}		1.57	
3				1.37^{a}	$1.42^{a,b}$	1.57^{b}		
5				1.40^{a}	1.45^{a}			1.58

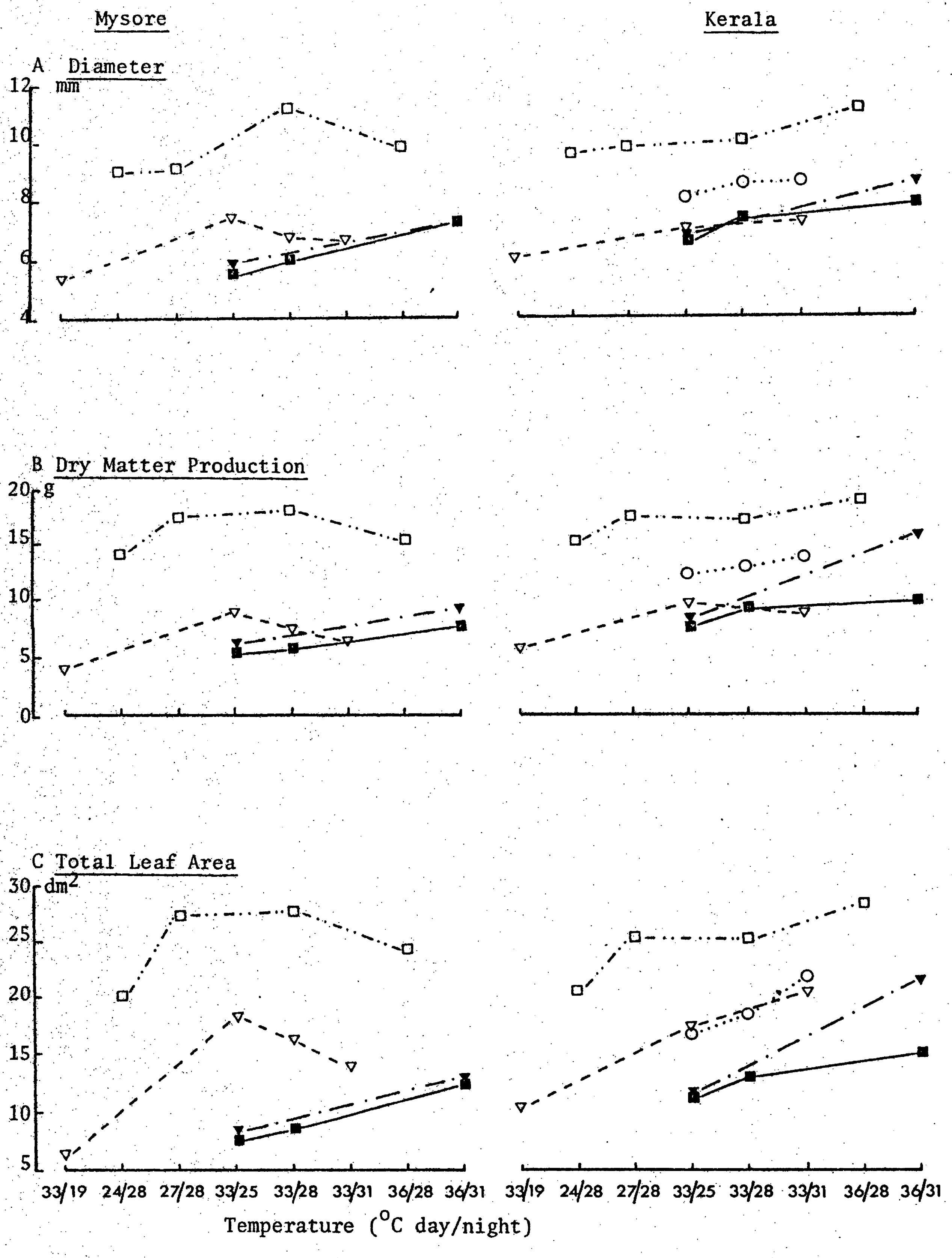


Figure 3.1 Effect of temperature on the growth and development of teak seedlings of Mysore and Kerala provenances.
Symbols ▽, □, ○, ▼ and ■ represent Experiments 1-5 respectively

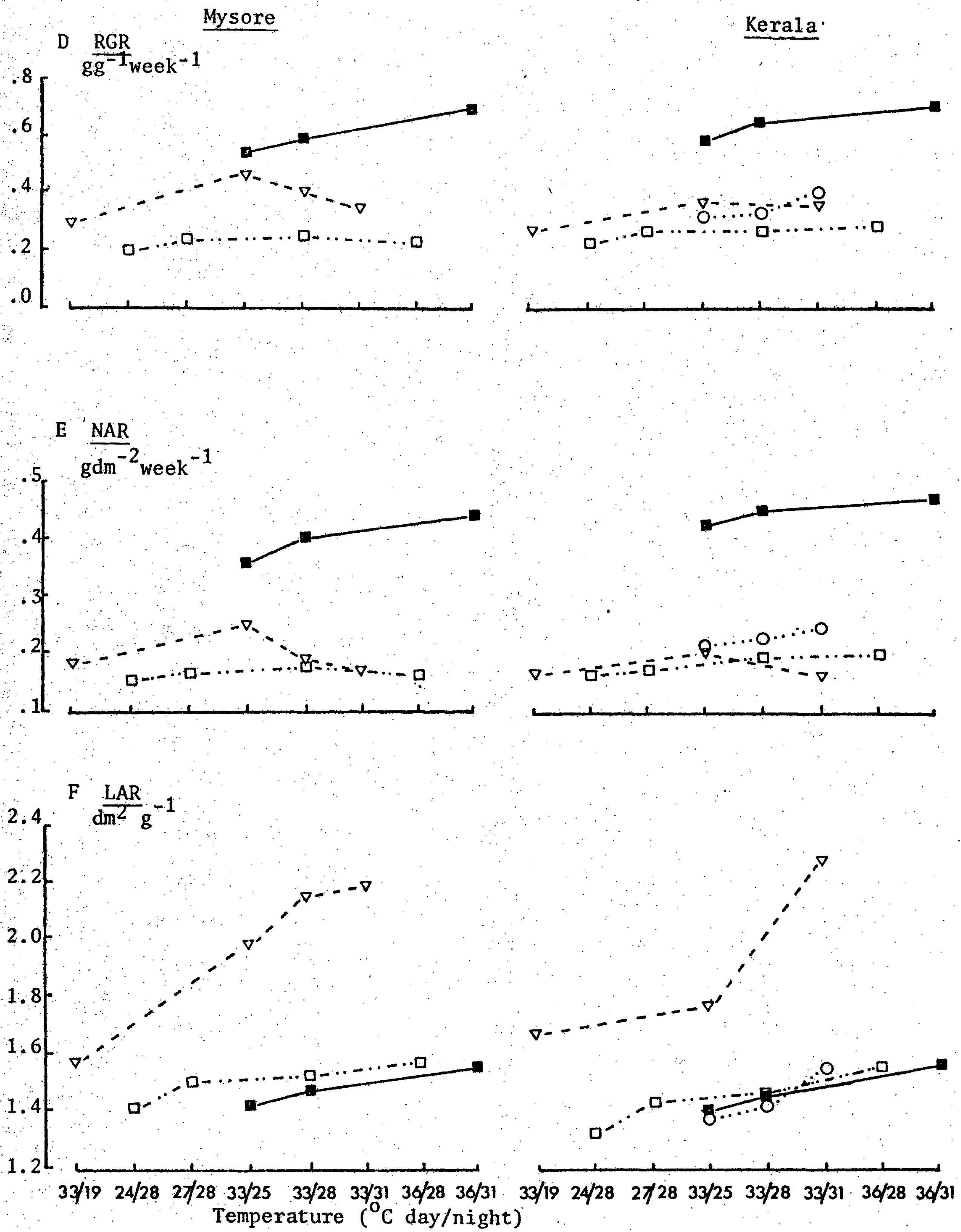


Figure 3.1 (cont.)

Experiment 1 growth of these parameters at the lowest temperature, 33/19°C, averaging 6.1 mm, 5.77 g and 10.19 dm^2 for diameter, dry matter production and total leaf area respectively was lower than at 33/25°C (7.0 mm, 9.83 g and 17.32 dm^2 respectively) and at 33/31°C (7.3 mm, 9.10 g and 20.31 dm^2 respectively).

The temperature response of the Kerala provenance over the range 33/25 - 33/31°C examined in Experiment 3 supported the results obtained for Experiment 1. The values recorded for these parameters increased with an increase in temperature from 33/25 to 33/31°C (Table 3.4, Figure 3.1). Similarly in Experiment 2 diameter, dry matter production and total leaf area were greatest at 36/28°C (11.2 mm, 19.06 g and 28.10 dm^2) and poorest at 24/28°C (9.6 mm, 15.36 g and 20.60 dm^2). The growth at 33/28 and 27/28°C was also better than that at the lower temperature except for diameter where the values recorded at 24/28 and 27/28°C did not differ significantly (Table 3.4, Figure 3.1).

RGR, NAR and LAR were greater at the higher temperature in all experiments although the pattern in Experiment 1 was somewhat confused (Table 3.4, Figure 3.1). The increase in NAR with temperature was however slight. For example in Experiment 3 the values of NAR recorded at 33/25, 33/28 and 33/31°C were 0.21, 0.22 and 0.24 $gdm^{-2}week^{-1}$ respectively.

3.3.1.1.2 Experiments 4 and 5

The pattern demonstrated in Experiments 4 and 5 was for an increase in all growth parameters with increasing temperature in both Kerala and Mysore provenances (Table 3.4, Figure 3.1).

In both experiments the two provenances exhibited significantly greater diameter growth, dry matter production, total leaf area, RGR, NAR and LAR at 36/31 than at 33/25°C. In Experiment 5 the values recorded at 33/28°C were intermediate between those at 36/31 and 33/25°C (Table 3.4, Figure 3.1).

In the Kerala provenance the differences in these growth parameters between 33/28 and 33/25°C and between 33/28 and 36/31°C were generally not significant, the exception being dry matter production and total leaf area.

In the case of the Mysore provenance there were no significant differences between 33/28 and 33/25°C but significant differences between 33/28 and 36/31°C except in NAR and LAR (Table 3.4, Figure 3.1).

3.3.1.2 Height Growth

Seedling height was favoured by higher temperature for both provenances in all experiments up to 33/28°C with no significant decline at higher temperatures (i.e. 36/28 and 36/31°C) (Table 3.5, Figure 3.2). In Experiments 1 and 3 height growth increased with increasing night temperature within the range 19, 25, 28 and 31°C. Similarly in Experiment 4 height growth at 36/31°C was markedly better than at 33/25°C.

In Experiment 2 although seedling height increased from 39.1 cm (Mysore) and 36.8 cm (Kerala) at 24/28°C to reach the peak, 50.3 cm (Mysore) and 53.5 cm (Kerala) at 33/28°C, the values recorded at 36/28°C (48.3 and 50.8 cm for Mysore and Kerala respectively) were not significantly poorer (Table 3.5, Figure 3.2).

There were no significant differences in height growth between the temperature regimes in Experiment 5. However, the values recorded for both provenances tended to be greater at 33/28°C and this was followed by the values recorded at 36/31 and 33/25°C respectively (Table 3.5, Figure 3.2).

Table 3.5 Effect of temperature on height growth of teak seedlings. Within each experiment, figures that do not have the same affix are significantly different at the 5% level according to Duncan's new multiple range test

Expt.	Temperature regime (^{o}C day/night temperature)							
No.	33/19	24/28	27/28	33/25	33/28	33/31	36/28	36/31
Mysore Provenance								
1	11.5			25.8		37.6		
2		39.1	46.8^{a}		50.3^{b}		$48.3^{a,b}$	
4				9.9				13.7
5				13.0^{a}	14.3^{a}			13.5^{a}
Kerala Provenance								
1	17.8			28.2		42.4		
2		36.8	46.9		53.5^{a}		50.8^{a}	
3				26.9^{a}	32.4^{a}	39.7		
4				15.0				24.4
5				21.9^{a}	24.6^{a}			23.0^{a}

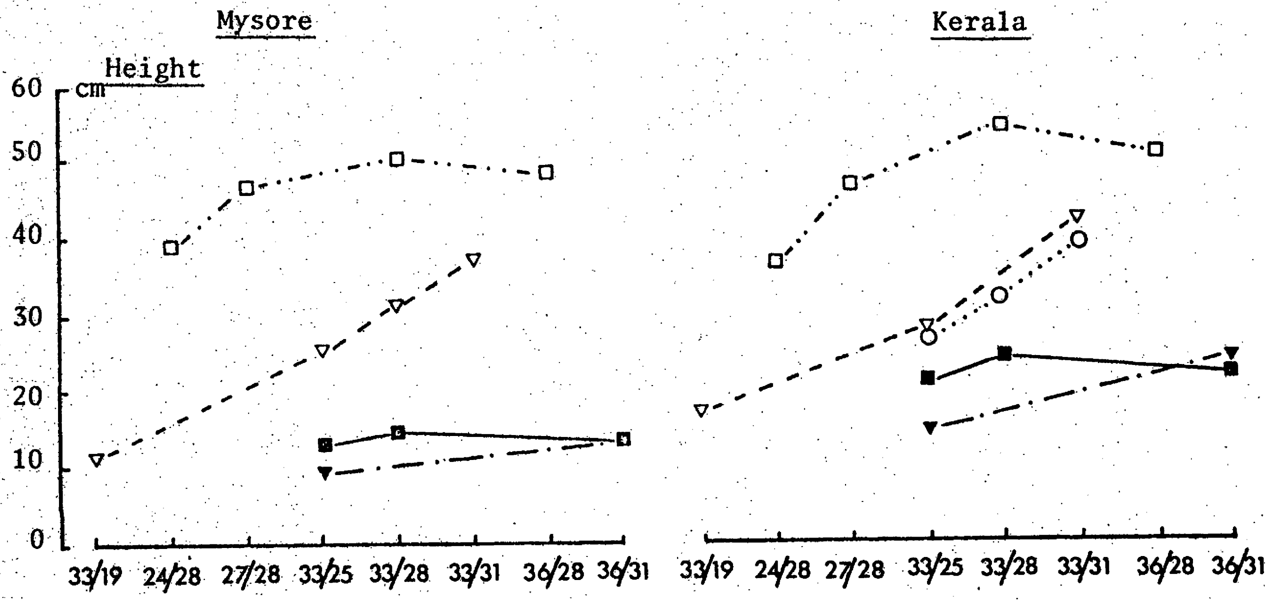


Figure 3.2 Effect of temperature on height growth of teak seedlings of two provenances.

Symbols ▽, □, ○, ▼ and ■ represent Experiments 1-5 respectively.

3.3.2 Provenance Differences

There were significant differences in the growth parameters studied between the two provenances with the Kerala provenance generally being better than the Mysore provenance. However, there were exceptions e.g. RGR and NAR in Experiment 1 and LAR in Experiment 2 in which the values of these parameters recorded for the Mysore provenance were greater (Tables 3.3 and 3.6).

Analysis of variance did show significant provenance x temperature interaction occurred in some parameters. Despite the interaction, growth of these parameters in the Kerala provenance was always superior to the Mysore provenance.

Diameter growth, dry matter production, total leaf area and height growth of the Kerala seedlings were generally significantly greater than the Mysore provenance (Table 3.6). The differences in diameter in Experiment 1, and in total leaf area and height growth in Experiment 2 were not significant, but nevertheless the values of these parameters recorded for the Kerala provenance were always greater than those for the Mysore provenance. For example in Experiment 1 the pooled value of diameter growth for the Kerala provenance was 6.8 mm as compared with 6.5 mm for the Mysore provenance. Similarly in Experiment 2 the pooled value of height growth for the Kerala provenance was 47.0 cm and for the Mysore provenance was 46.1 cm.

RGR and NAR of the Kerala seedlings were generally greater than those of the Mysore seedlings. In Experiment 1, however, the values of these parameters recorded for the Mysore provenance were greater than those for the Kerala provenance.

LAR tended to be greater in the material from Mysore provenance than

Table 3.6 Comparison of provenance differences showing pooled values for each parameter. Within each experiment, figures not connected by a vertical line are significantly different at the 5% level according to Duncan's multiple range test

Expt. No.	Provenance	Diameter mm	Dry matter production g	Total leaf area dm^2	Height cm	RGR $gg^{-1}week^{-1}$	NAR $gdm^{-2}week^{-1}$	LAR dm^2g^{-1}
1	Mysore	6.5	6.55	12.86	25.0	0.37	0.20	1.93
	Kerala	6.8	8.23	16.01	29.5	0.33	0.17	1.90
2	Mysore	9.0	16.41	24.71	46.1	0.23	0.16	1.50
	Kerala	10.2	17.30	24.77	47.0	0.27	0.19	1.45
4	Mysore	6.6	7.82	10.66	11.8			
	Kerala	7.7	12.19	16.48	19.7			
5	Mysore	6.3	6.37	9.51	13.6	0.60	0.40	1.49
	Kerala	7.4	9.05	13.23	23.2	0.65	0.45	1.48

that from the Kerala provenance. In Experiment 2, the values of LAR recorded for the Mysore provenance were significantly greater than those for the Kerala provenance. The differences in LAR in other experiments were not significant but the pooled values for the Mysore provenance were slightly greater than those for the Kerala provenance. In Experiment 1 however the ratios at the lowest temperature (33/19°C) and at the highest temperature (33/31°C) of the Kerala provenance were greater than the Mysore provenance.

3.4 DISCUSSION

3.4.1 The Anomalous Results in the Determination of Provenance Response to Temperature

The results indicate a pattern of provenance x temperature interaction in the first three experiments. Both provenances showed increased values of diameter, dry matter production, total leaf area, RGR and NAR up to 33/25 to 33/28°C. Above these temperatures the Mysore provenance showed a tendency for decreased growth of these parameters whilst similar values for the Kerala provenance increased.

The above pattern was, however, not repeated in the last two experiments where no decline at high temperatures occurred in the Mysore provenance. In both provenances the values recorded for diameter, dry matter production, total leaf area, RGR and NAR increased with increase in temperature.

The contrasting response of the Mysore material between the experiments is of interest. The discrepancies could have been due to the fact that the experiments were conducted at different times of the year (see Table 3.2). Although most environmental factors (e.g. temperature, photoperiod and nutrition) were controlled in the phytotron others, such as the quantity of light radiation, could not be controlled.

Incident light radiation received daily on the roof of the Canberra phytotron varies seasonally (Figure 3.3). Experiments 1, 2 and 3 conducted during May to August coincided with the period of low radiation, averaging about 300 cal $cm^{-2}day^{-1}$ whilst Experiments 4 and 5 conducted during September to March coincided with the period of high radiation, averaging about 400-600 cal $cm^{-2}day^{-1}$. It was thus possible that the different response patterns between experiments were due to the variation in the supply of light energy to the glasshouses.

Anomalous results between experiments in the Canberra phytotron have been reported in studies of Hamzah (1975) and Awang (1977). Hamzah (1975) grew seedlings of *Eucalyptus decaisneana* Blake under three day (24, 27 and 30°C) and three night (18, 21 and 24°C) temperatures under glasshouse facilities in January and in July. Despite similar experimental procedure, there were differences in the growth response of the seedlings between experiments. Similarly, Awang (1977) found growth response to temperature shown by seedlings of *Eucalyptus pilularis* Sm. varied considerably between experiments. Both Hamzah and Awang suggested that seasonal variation in total daily radiation could be responsible for these differences.

The existence of light x temperature interaction would make it difficult to delineate optimum temperatures for particular provenances and would hinder comparison of provenance performances unless the pattern of the interaction is understood. Therefore, before further study of temperature effect of teak seedlings it is essential to clarify the effect of light radiation on the temperature response.

3.4.2 Effect of Temperature

Despite the possibility of a light radiation x temperature interaction

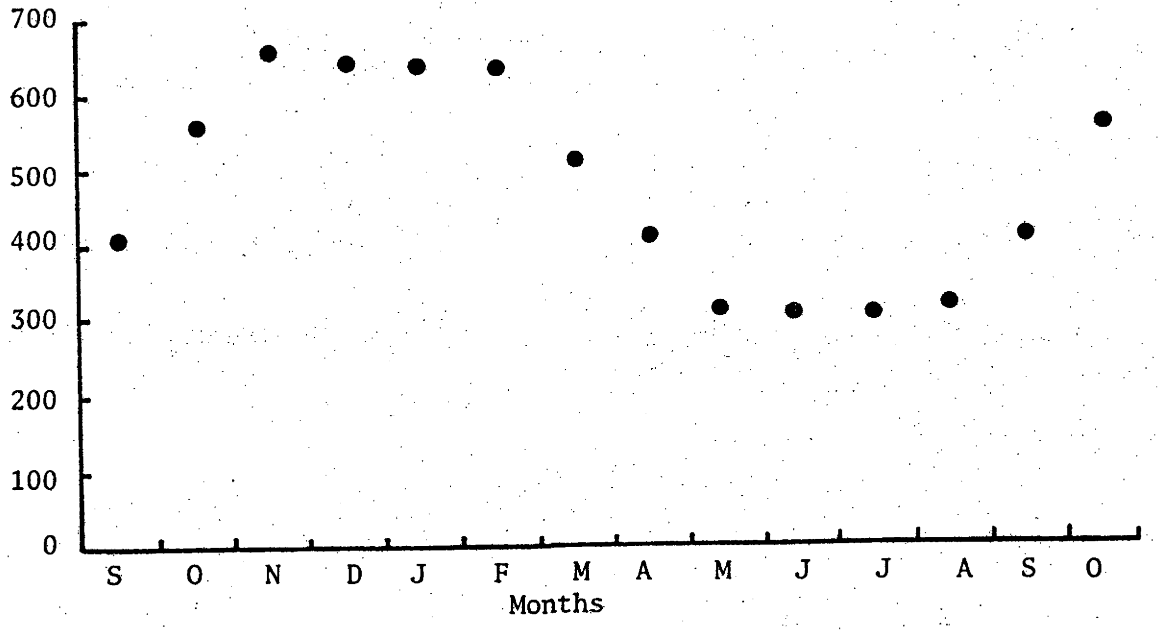


Figure 3.3 Mean daily radiation (cal $cm^{-2}day^{-1}$) over Canberra CSIRO phytotron calculated on a monthly basis - mean of 5 years.

it is possible to draw some conclusion as to the effect of temperature on teak seedling development.

It has been shown in the studies of Ko Ko Gyi (1972) and Kanchanaburangura (1976) that low day and low night temperatures inhibited height growth, diameter growth, dry matter production and total leaf area. This is confirmed by the results from the present study. The results clearly indicate the seedlings of the two provenances grew best under warm to hot day and night temperatures. A warm day associated with a cool night (e.g. 33/19°C) or vice versa (e.g. 24/28°C) resulted in poor growth.

Best growth was attained at the temperature range 33-36°C day and 28-31°C night despite the anomalous results between the experiments. The present study thus confirms the temperature suitable for good growth and development of teak seedlings in the phytotron be within the range 33-36°C day and 28-31°C night.

3.4.3 Growth Analysis Parameters

RGR is an important index of productivity. It is a function of both the physiological and structural components of plant growth. The physiological component is measured in terms of net assimilation rate (NAR). The structural component is measured in terms of leaf area ratio (LAR). The components, NAR and LAR are related to RGR as $RGR = NAR \times LAR$. These components may operate independently. Consideration of the response of NAR and LAR in the different temperature regimes may indicate whether the causes of growth differences are due to physiological or structural differences.

The pattern of variation of NAR with temperature was similar to that recorded for diameter growth and dry matter production although the differences were generally not statistically significant. In the Mysore provenance the values recorded peaked at 33/25 to 33/28°C and were lower at higher temperatures in Experiments 1 and 2, whilst in the Kerala provenance the values showed a steady increase with temperature in all experiments except Experiment 1. In later experiments the values for the Mysore material increased throughout at higher temperatures and there was no decline.

The pattern of variation in LAR did not vary. In all experiments and for both provenances the values recorded were greater the higher the temperature.

These results suggest the main agency causing the patterns observed is NAR or putting it another way, variations in the rate of photosynthesis may be an important determinant of teak seedling response to temperature variations.

The variation of LAR with temperature may however also be important in explaining the response patterns observed. Although in both provenances there was an increase in LAR with temperature, the increase recorded for the Kerala material was much greater at high temperatures than for the Mysore material. This suggests the Kerala provenance may be better suited to higher temperatures than the Mysore material because it produces proportionately more leaf area at high temperatures. Therefore in explaining the response patterns observed the rate of the area of photosynthetic material produced should not be overlooked.

3.4.4 Provenance Difference

There was evidence of provenance differences despite the significant provenance x temperature interaction. These differences were found in height growth, diameter growth, dry matter production, leaf area production and growth analysis parameters. In general, the material from Kerala provenance proved to be superior to that from Mysore provenance.

3.4.5 Conclusion

The results obtained from the present studies suggest that temperature may not operate independently of other environmental factors in controlling the growth and development of teak seedlings and that the effect of light is important. There is some evidence that seasonal variation in light radiation could be involved in the anomalous results recorded for provenance x temperature response. Thus the role of light in the control of teak seedling development is worthy of detailed study. In any further studies it will be important to examine seedling photosynthesis and leaf growth.

PART II

DEMONSTRATION OF THE EXISTENCE OF A RADIATION X TEMPERATURE INTERACTION IN THE CONTROL OF TEAK SEEDLING DEVELOPMENT

OUTLINE OF PART II

The studies reported in Part I indicated that temperature might not operate independently of other environmental factors in influencing teak seedling growth and development. Indeed the effect of light radiation might be important and there was some evidence from Part I that a radiation x temperature interaction might exist.

In this section of the thesis total daily radiation is shown to be an important control of teak seedling growth and the existence of a radiation x temperature interaction is demonstrated.

Initially (Chapter 4), the general influence of light on plant growth is briefly reviewed with particular emphasis given to the effects of total radiation as well as light intensity and duration on (a) photosynthesis, (b) leaf growth and development, and (c) shoot growth and dry matter production. Available information on the effect of light on growth of teak is included.

The first experiment reported (Chapter 5) examined teak seedling development under two different conditions of total daily radiation (100 and 200 cal $cm^{-2}day^{-1}$) at two different temperature regimes (33/25 and 33/28^{o}C). There was a common photoperiod of 16 hours for all treatments.

Subsequent studies (Chapter 6) extended the coverage to include a lower level of total radiation (50 cal $cm^{-2}day^{-1}$) in comparison with one previously used (100 cal $cm^{-2}day^{-1}$). The relationship between total radiation and photoperiod was also examined because earlier reports of photoperiodic effects on teak seedlings (Ko Ko Gyi, 1972; Kanchanaburangura, 1976) had taken no account of possible seasonal variations caused by variations in total radiation.

CHAPTER 4

THE INFLUENCE OF LIGHT ON PLANT GROWTH

4.1 INTRODUCTION

Light is an important environmental factor influencing the growth and development of plants. Light performs two functions for plants; firstly it provides the fundamental source of energy for photosynthesis, and secondly it regulates plant activity and development (Treshow, 1970).

The influence of light on plant growth and development may be categorised as the effect respectively of intensity, duration and quality. These three parameters are all vital to normal plant development. Under natural conditions, however, the influence of light quality appears to be less important than intensity and duration of illumination (Kozlowski, 1971). In addition, many studies have emphasized the effect of light intensity and duration more than that of light quality.

In natural conditions the intensity of daylight, together with the period of daylight, produce the total daily light radiation the plants receive. The total daily radiation has also been shown to be an important parameter in influencing plant growth and development regardless of actual intensity levels or periods of illumination producing it.

In this Chapter the general influences of light intensity, daylength and total radiation on plant growth and development are reviewed with particular reference to photosynthesis, leaf growth and development, shoot growth and dry matter production. Finally and separately, the influence of light on growth of teak is discussed.

Much of the reported work on light intensity has used the measurement unit foot-candle (f.c.). This unit cannot be converted to the units, e.g. Watt/m^2 (Wm^{-2}) or Joule/m^2/sec (Jm^{-2}sec^{-1}) used at the present time due to insufficient information of the light source. Thus the original units by the various workers have been retained in this review.

4.2 PHOTOSYNTHESIS

4.2.1 Effect of Light Intensity

The effect of light intensity on photosynthesis is complicated because of the fact that in nature an increase in light intensity is usually accompanied by an increase in temperature and consequently by an increase in respiration and transpiration (Kozlowski, 1971; Zelitch, 1971).

However, measurements of photosynthesis by gas exchange procedures under controlled environment conditions with light the only variable have been able to demonstrate the important effects of light intensity. The rate of net photosynthesis (gross photosynthesis minus respiration) is generally limited by low light intensities or by shading, and is increased by high light intensities (Treshow, 1970).

Low light intensity has been shown to result in a low rate of photosynthesis in many species. For example, Kramer and Decker (1944) determined the rates of photosynthesis in seedlings of *Quercus alba* L., *Q. rubra* L., *Cornus florida* L. and *Pinus taeda* L. at light intensities varying from 300 to 10,000 f.c. provided by projector-type Mazda lamps. All species showed the lowest rates of photosynthesis at the lowest light intensity. Similarly and more recently, Woledge (1971) found that within the range 10 to 121 Wm^{-2} the rates of net photosynthesis of plants of *Festuca arundinacea* Schreb. were lowest at 10 Wm^{-2} and highest at 121 Wm^{-2}. Awang (1977) also obtained similar results for seedlings of several eucalypt species including *Eucalyptus microcorys* F. Muell., *E. pilularis* Sm., *E. acmenioides* Schau., *E. paniculata* Sm. and *E.saligna* Sm. within the range of light intensities 125 to 685 $\mu E\ m^{-2} sec^{-1}$.

However, plants may perform differently at low light intensities. Schaedale (1975) points out that light compensation point (i.e. light intensity at which photosynthesis and respiration balance each other) is a useful index of the ability of plants to maintain net photosynthetic rate at low light intensities. Characteristically, shade tolerant plants usually have lower light compensation points than shade intolerant plants (Baker, 1950). Bohning and Burnside (1956) showed that net photosynthesis of shade tolerant herbaceous species e.g. *Oxalis rubra, Nephrolepis exaltata* var. *bostoniensis, Saintpaulia ionantha* Wendl. and *Philodendron cordatum* Koch. was not zero until a light intensity as low as 50 f.c. was reached. In shade intolerant species e.g. *Phaseolus vulgaris* L., *Lycopersicon esculentum* Mill., *Helianthus annuus* L., *Nicotiana tabacum* L., *Glycine max (*L.) Merr., *Ricinus communis* L., *Gossypium hirsutum* L. and *Coleus blumei* Benth., photosynthesis was zero at higher light intensity levels (100 - 150 f.c.) (Bohning and Burnside, 1956).

Loach (1967) reported similar results for woody plant species e.g. shade tolerance and low compensation points in *Fagus grandifolia* Ehrh., *Acer rubrum* L. and *Quercus rubra* L., and shade intolerance and high compensation points in *Liriodendron tulipifera* L., and *Populus tremuloides* Michx. Bourdeau and Laverick (1958) found the light compensation points of the two strong light demanding species of *Pinus strobus* L. and *P.resinosa* Ait. to be at about 175 and 215 f.c. respectively.

The level of light intensity at which the maximum rate of photosynthesis is attained varies greatly with species. Maximum photosynthesis at low light levels is another characteristic of shade tolerant species (Bourdeau and Laverick, 1958; Loach, 1967). For example seedlings of *Acer saccharum* Marsh and *Quercus macrocarpa* Michx., both shade tolerant, attained their maximum rate of photosynthesis at light intensities below 2000 f.c. (Wuenscher and Kozlowski, 1970). Kramer and Decker (1944) showed that seedlings of *Quercus rubra* and *Cornus florida* attained maximum photosynthesis at light intensities about 3000 f.c. whereas *Pinus taeda,* shade intolerant, did not show light saturation even at 10,000 f.c. Ronco (1970) found *Picea engelmannii* Parry seedlings reached a maximum rate at about 5000 f.c. while in *Pinus contorta* Dougl. the rate of photosynthesis increased rapidly as light intensity increased from 1000 to 7000 f.c. The increase continued but more slowly with increasing light intensities above 7000 f.c. The maximum rate did not appear to be attained even at 12,000 f.c.

The measurements mentioned above also indicate that broadleaf species (e.g. *Acer saccharum, Quercus rubra* and *Cornus florida*) may attain maximum rates of photosynthesis at lower light intensities than pine (e.g. *Pinus taeda* and *P. contorta*). This is in accord with the measurements obtained for other broadleaf species e.g. *Acer rubrum* L. and *Liquidambar styraciflua* L. (Kozlowski, 1949; Bormann, 1953).

It is also noteworthy that the broadleaf species listed above attain maximum photosynthesis at light intensity levels (i.e. at 3000 f.c. and less) which are well below that of natural full daylight (about 10,000 f.c.). Thus under natural conditions photosynthesis will not generally be limiting to fully exposed leaves.

Effects of light intensity on individual plants may be confused by the shading effects of the plants themselves. Treshow (1970) has pointed out that whilst optimal intensity may be known for individual leaves, the actual requirements of whole plants are more complex. In extreme cases, the outer canopy of leaves may be receiving ample light whilst at the same time photosynthesis of the inner, shaded leaves is limited by inadequate light. In contrast, under very bright natural conditions the inner leaves may be receiving optimal light whilst the light received by the outside leaves is so intense that it decomposes the chlorophyll and suppresses photosynthesis.

4.2.2 Effect of Daylength

Daylength does not appear to affect rate of photosynthesis. There have been few studies of this but results have been clearly demonstrated. Bohning (1949) exposed young plants of *Malus pumila* Mill. to continuous illumination at a light intensity of 3,200 f.c. He found that the rate of photosynthesis was fairly uniform for a period of 18 days.

Muller (1928) has reported that at Godhavn, Greenland (latitude 69°N) arctic plants e.g. *Salix glauca* L. and *Chambaenerium latifolium* (L.) Spach carry on photosynthesis throughout the 24 hours in summer.

The above evidence thus suggests that trees will accumulate more total photosynthate if exposed to a long day than if exposed to a short day.

4.2.3 Effect of Total Daily Radiation

No information has been reported dealing with the direct effect of total daily radiation on photosynthesis. Total daily radiation varies seasonally as light intensity and photoperiod vary greatly from season to season. Thus overall photosynthesis (i.e. the rate of net photosynthesis x the period of light available for photosynthesis) would be expected to vary with seasonal variation in total daily radiation.

There is evidence of seasonal variation in photosynthesis. Under field conditions in Japan, Negisi (1966) noted that photosynthesis of seedlings of *Pinus densiflora* Sieb., *Cryptomeria japonica* D.Don and *Chamaecyparis obtusa* Sieb. was higher in the spring than in the winter. The effect of these differences in production of photosynthate would be magnified by the seasonal difference in daylength. Thus the overall effect would be substantially lower growth in the winter due to the low total radiation as well as the low photosynthetic rate.

4.3 LEAF GROWTH AND DEVELOPMENT

4.3.1 Effect of Light Intensity

Light intensity influences the growth and development of leaves. High light intensities encourage growth of smaller but denser and heavier leaves whilst low light intensities produce larger and thinner leaves (Milthorpe, 1956).

The growth of leaves is determined by the two fundamental processes of cell division and cell expansion which dictate the number and size of cells present (Sunderland, 1960). However, Ashby and Wangermann (1950) suggest that leaf area is related more closely to the number of cells produ rather than to the size of cells.

High light intensities result in a greater number of cells of leaf blades. Milthorpe and Newton (1963) studied the change in the rate of production of cells in leaves of a variety of *Cucumis sativus* under three light intensities of 1, 3 and 7 cal $cm^{-2}hr^{-1}$. The plants were initially in darkness so that cell production in all developing leaves was very similar. After being exposed to light there were marked differences with a greater number of cells being produced at the higher light intensity. Milthorpe and Newton (1963) also agreed with Ashby and Wangermann (1950) that the number rather than the size of cells was the chief determinant of leaf size.

There are, however, important effects of cell size difference. At high light intensities, individual cells of the leaf blade are smaller than at low light intensities (Treshow, 1970). Production of small cells results in smaller but harder textured and thicker leaf blades with denser and smaller stomata, a thicker cuticle, smaller vein islets, and more conducting and mechanical tissue. The individual cell walls are generally thicker and intercellular spaces are smaller. Treshow (1970) points out that these morphological modifications help make the plant more resistant to extreme environmental conditions, including high temperatures.

Although surface area of individual leaves is smaller under high light intensities, total leaf area produced per plant is generally larger. This is due to plants growing under high light intensities producing substantially more leaves than those growing under low light intensities. This was evident in the study of Milthorpe and Newton (1963) who found that plants of *Cucumis sativus* produced more leaves at a faster rate under high light intensities. The rates of leaf production recorded were 0.66, 1.00 and 1.14 leaves per day at intensities of 1,3 and 7 cal $cm^{-2}hr^{-1}$ respectively.

4.3.2 Effect of Daylength

Daylength markedly influences leaf development (Milthorpe, 1956).

Individual leaf area and total leaf area of plants are affected by change in daylength.

Newton (1963) compared individual leaf area produced by *Cucumis sativus* grown under four different daylengths of 7.5, 10, 15 and 20 hours. Final areas of leaves observed were generally smallest at 7.5 hours and largest at either 10 or 15 hours. The area at 20 hours was smaller than at 10 or 15 hours although larger than at 7.5 hours. Newton also observed that there was a tendency for fewer leaves to be produced under the longer days.

Total leaf area of plants appears to be increased by long days under conditions of the same total daily radiation. Awang (1977) compared total leaf area produced by seedlings of several *Eucalyptus* species under the range of daylength of 8 to 16 hours. Total leaf area was generally greater at 14 and 16 hour days.

Leaf abscission is also regulated by length of day. Downs and Borthwick (1956) have reported that under long day conditions some deciduous plants e.g. *Salix glauca* L. and *Syringa vulgaris* L. keep their leaves almost all winter and become essentially evergreen. Kramer and Kozlowski (1960) have pointed out that leaf abscission in deciduous trees is delayed when normal daylength is supplemented by added light. When exposed to shorter daylength than normal these species shed their leaves earlier.

4.3.3 Effect of Total Daily Radiation

Total daily radiation has been shown to be more important than its components, light intensity and daylength, in controlling leaf growth and development. Newton (1963) grew plants of *Cucumis sativus* under various light intensities of 2,3,4 and 6 cal $cm^{-2}hr^{-1}$ for different photoperiod (7.5, 10, 15 and 20 hours) giving a range of total daily radiation from 15 to 120 cal $cm^{-2}day^{-1}$. The rate of leaf production was greatest with the highest amounts of total daily radiation but the rates of expansion of individual leaves and maximum area each attained were greatest with intermediate amounts of total radiation. Newton (1963) suggested the inhibitory effect on leaf expansion and size of high total radiation could be due to inadequate supplies of nutrient available for large plants in small pots.

In a consequent study, Milthorpe and Newton (1963) therefore examined the development of leaves under three different amounts of total radiation (15, 45 and 105 cal $cm^{-2}day^{-1}$) and two conditions of nutrient supply. It was found that the rate of expansion and maximum area of individual leaves occurred with the greatest amount of total radiation provided the nutrient supply was not limiting. When nutrient supply was restricted the division and expansion of cells were reduced considerably. The smaller leaves on plants receiving high rather than medium radiation were due to their cells being much smaller and fewer.

4.4 SHOOT GROWTH AND DRY MATTER PRODUCTION

4.4.1 Effect of Light Intensity

Low light intensities generally retard stem elongation and reduce dry matter production. Numerous studies, some of which are outlined below, have shown that shoot growth and dry matter production of several tree species are better at high light intensity than at low light intensity.

Shirley (1929) examined the effect of shading on growth of seedlings of *Sequoia sempervirens* (D.Con) Endl. and *Pinus taeda* L. Dry matter production was almost directly proportional to the light intensity, there being an increase in dry matter production with an increase in the proportion of total sunlight available to the plants from 1 to 70%. Strothmann (1967) working with *Pinus resinosa* Ait. found height growth and dry weight of unshaded seedlings was far better than heavy shaded (8% of full light) seedlings. Prajapati (1977) with *Pinus roxburghii* Sarg. reported that there was a 470% increase in total dry weight when light intensity was increased from 0.9 to 5.4 mW cm^{-2}. Similar results have been observed for other species e.g. *Quercus lyrata* Walt. (Kozlowski, 1949), *Pinus strobus* L. (Logan, 1966) and *Pinus ponderosa* Laws (Treshow, 1970).

The effects of light intensity on dry matter production however varies with species and, as would be expected, appear to act in a similar manner to those recorded for photosynthesis. Some species grow satisfactorily under very low light levels or heavy shading whilst others need substantially higher levels. Bates and Roeser (1928) grew coniferous seedlings for a period of nine months under artificial illumination and 10 hour photoperiod. Variation in light intensity was effected by having the plants at varying distances from the light source. *Picea engelmanni* Parry and *Pseudotsuga menziesii* (Mirb.) Franco were found to require twice as much light to produce the same dry weight as *Sequoia sempervirens*. Similarly, Shirley (1945) reported that *Pinus virginiana* Mill. and *Pinus strobus* L. attained maximum dry weight in 45% of full sun while *Pinus resinosa* and *Picea glauca* (Moench.) Vosa required 98%.

Some species are capable of tolerating very low light levels whilst others will die at the same levels. Shirley (1929) reported that under a very low light intensity of 40 f.c. seedlings of *Sequoia sempervirens* and *Pinus taeda* were able to survive for a period of six months although failing to increase in dry weight during this time. In contrast, *Helianthus cucumerifolius* Torr. & Gray died within three weeks under the same conditions.

4.4.2 Effect of Daylength

Vegetative growth of many woody plants is known to be controlled by the relative lengths of daily light and dark periods.

There may be a direct control of shoot growth and dry matter production and also an indirect control of bud and shoot dormancy. Dormancy control is a complex topic (e.g. Romberger, 1963) and is irrelevant to the studies in this thesis and has thus not been discussed further here.

Shoot growth and dry matter production have been shown to be generally better at long than at short days (Kozlowski, 1971). Downs and Piringer (1958) reported height and dry matter production of *Pinus virginiana* and *Pinus ponderosa* increased markedly with increasing daylength from 8 to 16 hours. Seedlings of *Acer rubrum* L. and *Pinus sylvestris* L. made continuous shoot growth at 14 and 16 hour daylength but stem elongation ceased after two to four weeks under an 8-hour daylength (Downs and Borthwick, 1956). Similar results have also been reported for other species e.g. *Pinus elliottii* Englm. (Downs, 1962), *Sequoia sempervirens* (Hellmers and Pharis, 1968), *Pinus roxburghii* (Bhatnagar *et al.*, 1970) and *Eucalyptus acmenioides* (Awang, 1977).

In some species growth increased with daylength up to a particular level and did not increase further at higher levels. Longman (1972) has shown that height growth of the tropical species e.g. *Terminalia superta* Engl. and Diels., *Ceiba pentandra* (Linn.) Gaertn., *Chlorophora excelsa* (Welw.) Benth and *Bombax buonopozense* P. Beauv. increased markedly (up to 200%) when daylength was increased from 9 to 13 hours. With further increase in daylength to 17 hours *Chlorophora excelsa* was greatly stimulated, there being a 355% increase. *Terminalia superta* was also stimulated showing a 59% increase. *Ceiba pentandra* and *Bombax buonopozense*, on the other hand, showed no further response.

Thus in tropical regions where variation in daylength is relatively small, there are a number of species (i.e. *Terminalia* superba, *Ceiba pentandra, Chlorophora excelsa* and *Bombax buonopozense*) which have been shown to be sensitive to change in daylength. However, the response varies greatly with species.

4.4.3 Effect of Total Daily Radiation

A number of studies have shown that variation in shoot growth and dry matter production may be attributed to the amount of total daily radiation present irrespective of light intensity and length of daylight. Newton (1963) demonstrated that dry matter production of the plant of *Cucumis sativus* was influenced most by the amount of radiation received per day.

The findings of Newton (1963) were confirmed by the work of Hughes and Cockshull (1971) and Hughes (1973). Hughes and Cockshull initially found growth of *Chrysanthemum morifolium* cv. Bright Golden Anne. under constant light intensity did not differ from growth under fluctuating light intensity but with the same total daily radiation. Hughes (1973) then compared growth in two light intensities (22 and 33 $Jm^{-2}sec^{-1}$) and 8- and 12-hour days giving three levels of total radiation of 63, 95 and 142 $J\ cm^{-2}day^{-1}$. Total plant dry weight was markedly better at the higher total radiation irrespective of the daylength being 8 or 12 hours.

Newton (1963) with *Cucumis sativus* and Hughes (1973) with *Chrysanthemum morifolium* found net assimilation rate was a linear function of total radiation. In contrast, leaf area ratio was greater at the lower total radiation.

4.5 THE INFLUENCE OF LIGHT ON GROWTH OF TEAK

Teak is a strong light demanding species (Troup, 1921; Anon., 1958). But surprisingly, information dealing with the effect of light on the species is very limited. Available information of the effect of light appears to be limited to the reports of Bhatnagar (1966), Ko Ko Gyi (1972), Nwoboshi (1972) and Kanchanaburangura (1976).

Variation of light intensity by shading has been shown to affect growth of teak. Bhatnagar (1966) grew germinated teak seedlings under various light intensities at Dehra Dun in India. He found height growth was greatest at 94% of full sunlight (14.3 cm) followed by 100% (13.0 cm), 22% (10.8 cm) and 9% (7.8 cm) respectively.

Nwoboshi (1972) also studied the effect of shading on growth of teak but the results were ambiguous. He compared plants raised from stump planting with those from direct seed sowing grown at various light intensities of 25, 53, 75 and 100% of full sunlight in Ibadan, Nigeria. Different responses were recorded in different growth parameters. Total dry weight of both seedlings and stumps increased with an increase in light intensity to peak at 75% and declined with further increase to 100%. Height of teak stump material was best at 53% whilst for seedlings, it was best at 100%. Maximum leaf area of teak stump material was produced at 53% whilst there was no definite response in the leaf area of seedlings although the smallest area was recorded at 25% of full sunlight.

The effect of shading may be of particular importance in the young seedling when the plant has to outgrow weed competition. Negligence of this fact has caused failure for teak plantation establishment. In Thailand, young teak plants in many plantations have failed to thrive and, in some cases, died primarily because of heavy shading by weeds.

Ko Ko Gyi (1972) and Kanchanaburangura (1976) studied the effect of photoperiod on teak seedling growth in naturally lit cabinets type C (Morse and Evans, 1962) at the Canberra phytotron.

Relative growth rate of the whole plant was not affected by photoperiod over the range 8 to 16 hours. Net assimilation rate was greater at the longer days whilst leaf area ratio exhibited a reverse trend.

Height growth was greater at the longer days. However the differences were demonstrated between 8 and 12 hours and between 9.5 and 14 hours. There were no differences in the response above 12 hours. Furthermore differences in height growth were evident only when long days were associated with warm night temperatures (i.e. 22°C and above).

No other information has been reported.

It has been shown in the studies described in Chapter 3 that the response of teak seedlings to varying temperature conditions differed considerably between experiments. Ko Ko Gyi (1972) and Kanchanaburangura (1976) reported similar results. It was suggested that seasonal variation of light, particularly in total daily radiation, could have caused the anomalies since the experiments were conducted at different times of the year.

4.6 THE NEED FOR FURTHER INVESTIGATION OF THE EFFECT OF TOTAL DAILY RADIATION ON THE GROWTH OF TEAK

This review shows that the effect of light on plant growth and development can be caused by light intensity, daylength and total daily radiation. All these parameters are important in influencing life functions of plants.

The influence of light on the growth of teak has received little attention. The results of previous studies and of those outlined in Chapter 3 indicate light may substantially affect development of teak seedlings and there may be the existence of light x temperature interaction. The effect of light on the growth and development of teak is thus worthy of further investigation in order to achieve a better understanding of climatic requirements of the species.

CHAPTER 5

EFFECT OF TOTAL RADIATION ON THE TEMPERATURE RESPONSE OF TEAK SEEDLINGS

5.1 INTRODUCTION

The studies in Chapter 3 suggested that total radiation might be important in the control of teak seedling growth and development and a total radiation x temperature interaction might exist.

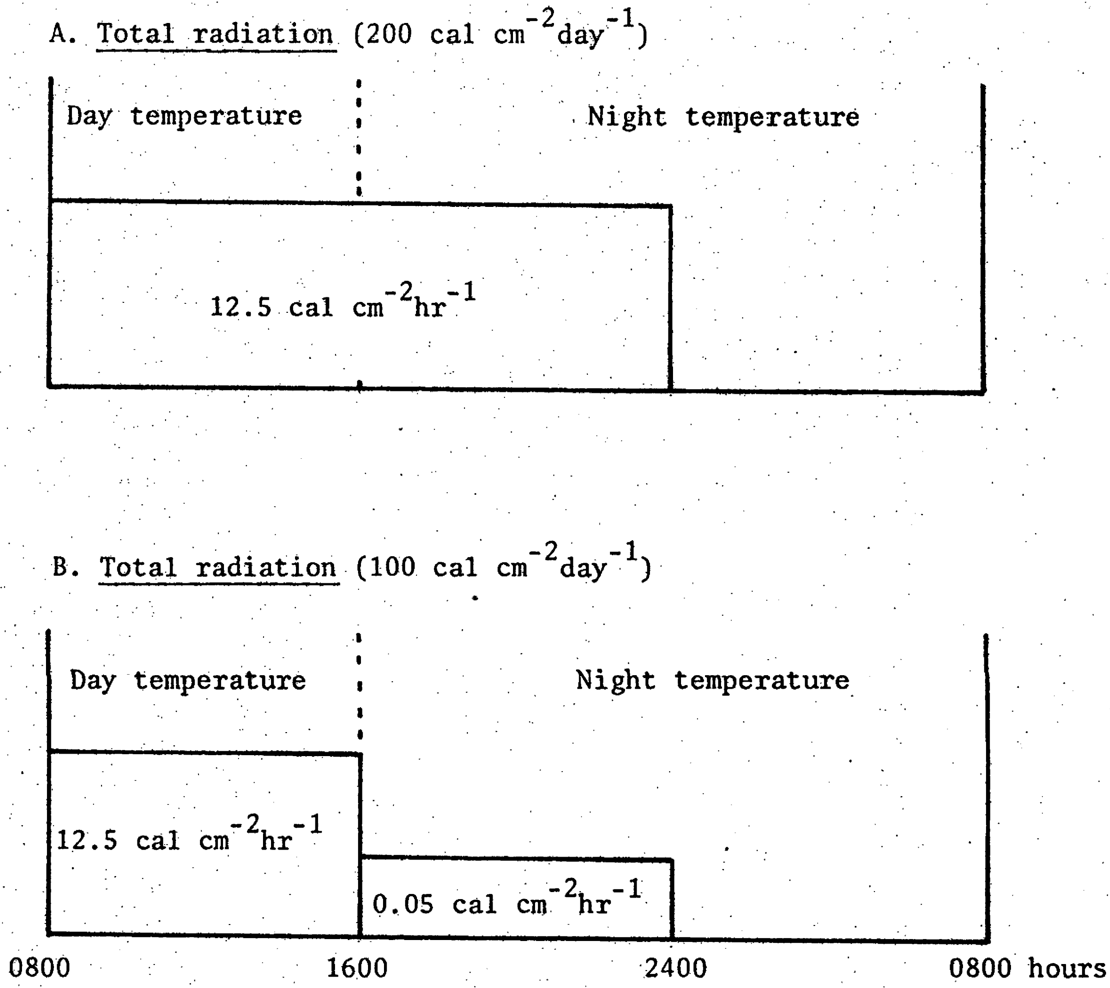
The experiment outlined in this chapter demonstrates the effect of total radiation as a control of the growth and development of teak seedlings. The importance of total radiation levels in determining temperature response is also shown.

5.2 MATERIALS AND METHODS

The experiment was conducted in artificially lit cabinets (LB type, Morse and Evans, 1962) using two temperature regimes (33/25, 33/28°C) and two levels of total radiation (200 and 100 cal cm^{-2}day^{-1}) with a common photoperiod of 16 hours. The light cycles used to achieve the desired radiation levels are illustrated in Figure 5.1.

Day temperature was held for eight hours (0800-1600) and night temperature for the remaining 16 hours.

The measurements of total radiation in the cabinets were made with a Kipp solarimeter. The light levels were maintained by frequent checking with a Li-Cor quantum meter which had been calibrated under this light source with the solarimeter (i.e. about 800 μEm^{-2}sec^{-1} for irradiance of 12.5 cal cm^{-2}hr^{-1} and 5 μEm^{-2}sec^{-1} for 0.05 cal cm^{-2}hr^{-1}).



A. Total radiation (200 cal $cm^{-2} day^{-1}$)

B. Total radiation (100 cal $cm^{-2} day^{-1}$)

Figure 5.1 Diagrams showing temperature and light-dark cycles in the experiment

The higher total radiation level (200 cal $cm^{-2}day^{-1}$) used in the experiment was considered the maximum possible in standard LB cabinets under a 16-hour photoperiod. At this level fluorescent tubes had to be replaced frequently (often weekly) to maintain the light level.

Seedlings of the Kerala provenance were used in the experiment. Six weeks after germination, forty selected seedlings were divided into four groups of ten. Each group was allocated at random to one of the four treatments.

Two harvests were carried out, the first after two weeks in treatments and the second three weeks after the first. Five seedlings from each treatment were included in each harvest. Assessments were made of height, diameter, leaf area and dry weight of leaves, stem and roots. In addition, at the second harvest five leaf discs of about 1 cm^2 each were taken at the tip, middle and base of the last fully expanded leaves and used to estimate chlorophyll concentration. Procedure for chlorophyll extraction and estimation of chlorophyll concentration is summarized in Appendix IV.

Data were subjected to analysis of variance with total radiation x temperature being the major sources of variation. Duncan's multiple range test was used to determine the significance of difference between treatment means.

5.3 RESULTS

There were marked differences in the plant appearance between light treatments (see Plate 5.1). Plants grown under the higher total daily radiation were taller than those grown under the lower total daily radiation, and their leaves were abnormal, in comparison with usual field grown plants. They were very thick, very dark green in colour and wrinkled at the margin. This contrasted with the leaves of the plants grown under the lower radiation. These were a lighter green in colour

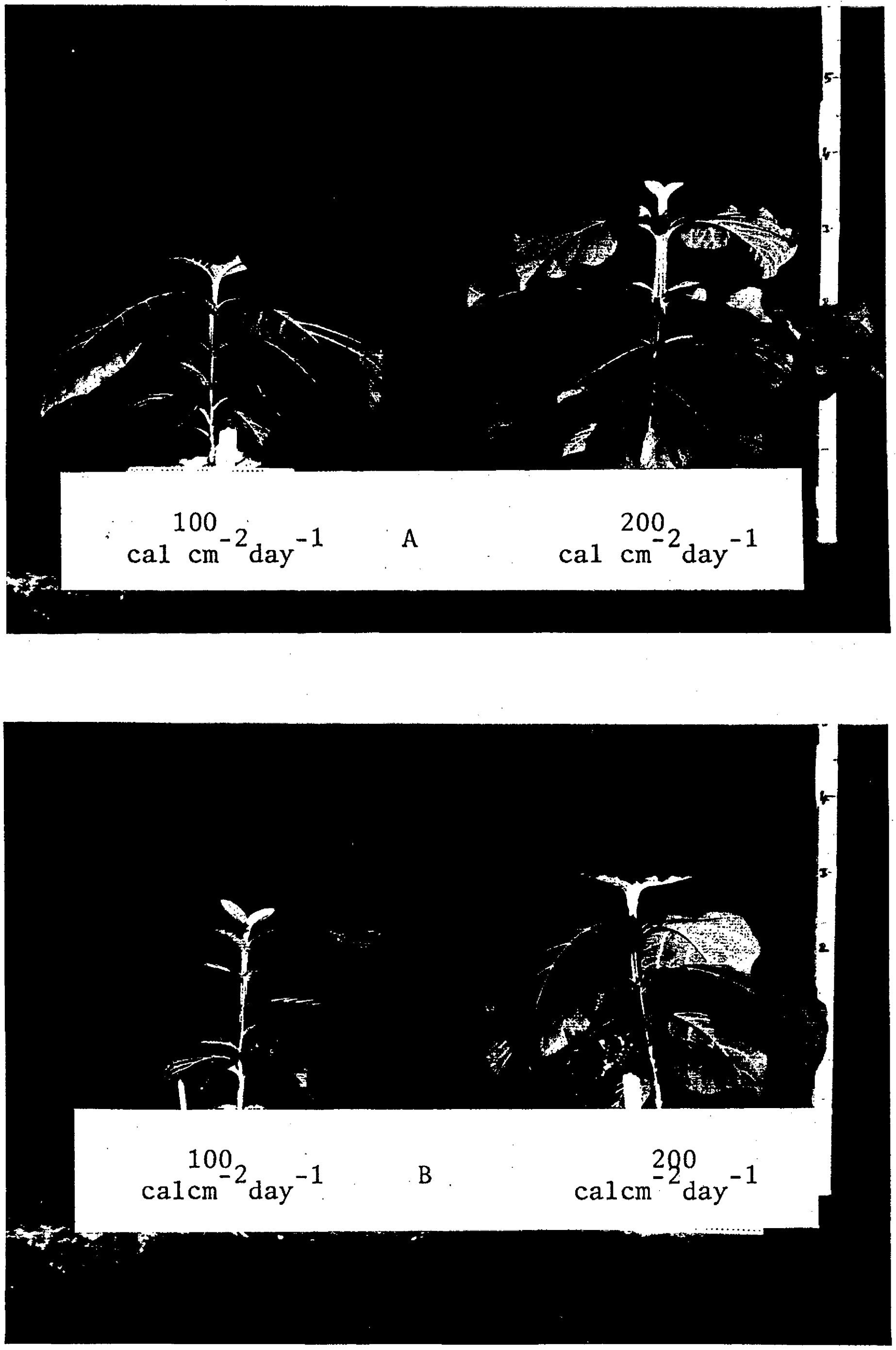


Plate 5.1 Effect of total radiation on the growth of teak seedlings grown at (A) 33/28°C and (B) 33/25°C

with flat unwrinkled leaf blade and appeared similar to teak in natural conditions in the field in Thailand.

There was no difference in those characteristics between the temperature treatments.

There were indications of a temperature x total radiation interaction. The statistical analysis revealed significant interaction only in total leaf area but the F values recorded for the interaction term for height and dry matter production were high (Table 5.1). Application of Duncan's multiple range test can be used without a significant F value (Street and Torrie, 1960). This test indicated that under the total radiation level of 200 cal $cm^{-2}day^{-1}$ the values recorded for total leaf area, height growth and dry matter production differed significantly in the different temperature regimes (33/25 and 33/28°C). In contrast, under total radiation of 100 cal $cm^{-2}day^{-1}$ the values of these parameters were very similar between the two temperature regimes (Table 5.2, Figure 5.2).

5.3.1 Effect of Total Radiation

There were marked differences in all growth parameters studied between the two levels of total radiation. In general, despite the interaction effect the values recorded were significantly greater at the higher total radiation level than at the lower. The exception was LAR which exhibited a reverse trend (Tables 5.2, 5.3; Figures 5.2A-H).

The values recorded for total leaf area, height, dry matter production, diameter, RGR, NAR and chlorophyll content were significantly greater at 200 cal $cm^{-2}day^{-1}$ than at 100 cal $cm^{-2}day^{-1}$, and this was evident at both temperature regimes. For example total leaf area under 200 cal $cm^{-2}day^{-1}$ was 26.39 and 35.98 cm^2 at 33/25 and 33/28°C respectively as compared with 20.69 and 21.27 dm^2 at the same temperatures under 100 cal $cm^{-2}day^{-1}$.

Table 5.1 Summarized results of analysis of variance of the data in Tables 6.2 and 6.3. *, ** and *** indicate significance at the 5, 1 and 0.1% levels respectively. ns indicates 'not significant' at the 5% level

Source of variation	Degrees of freedom	Mean squares	F ratio
<u>Height</u>			
Temperature (T)	1	44.105	3.377^{ns}
Radiation (R)	1	358.705	27.462***
T x R	1	50.880	3.895^{ns}
Error	16	13.062	
<u>Diameter</u>			
Temperature (T)	1	5.724	7.522*
Radiation (R)	1	55.445	72.857***
T x R	1	.005	$.006^{ns}$
Error	16	.761	
<u>Dry matter production</u>			
Temperature (T)	1	70.876	3.979^{ns}
Radiation (R)	1	1669.513	93.738***
T x R	1	60.448	3.394^{ns}
Error	16	17.810	
<u>Total leaf area</u>			
Temperature (T)	1	129.134	6.293*
Radiation (R)	1	520.608	25.370***
T x R	1	101.700	4.956*
Error	16	20.521	
<u>Relative growth rate</u>			
Temperature (T)	1	.006	1.083^{ns}
Radiation (R)	1	.052	8.695**
T x R	1	.004	$.752^{ns}$
Error	16	.006	
<u>Net assimilation rate</u>			
Temperature (T)	1	.001	$.199^{ns}$
Radiation (R)	1	.328	51.001***
T x R	1	.000	$.050^{ns}$
Error	16	.006	

Table 5.1 (cont)

Source of variation	Degrees of freedom	Mean squares	F ratio
Leaf area ratio			
Temperature (T)	1	.016	1.635^{ns}
Radiation (R)	1	1.008	101.434***
T x R	1	.002	$.222^{ns}$
Error	16	.010	
Chlorophyll content			
Temperature (T)	1	9.316×10^{-6}	20.151***
Radiation (R)	1	38.226×10^{-6}	82.685***
T x R	1	1.275×10^{-6}	2.758^{ns}
Error	16	4.62×10^{-5}	

Table 5.2 Effect of temperature and total daily radiation on total leaf area, height growth and dry matter production of teak seedlings. Within each parameter figures that do not have the same affix are significantly different at the 5% level according to Duncan's multiple range test

Parameter	Temperature ^{o}C	Total daily radiation cal $cm^{-2}day^{-1}$		Mean
		100	200	
Total leaf area dm^2	33/25	20.69^a	26.39^a	23.54
	33/28	21.29^a	35.98	28.63
	Mean	20.98	31.19	
Height cm	33/25	22.0^a	27.3	24.7
	33/28	21.8^a	33.4	27.6
	Mean	21.9	30.4	
Dry matter production g	33/25	15.26^a	30.06	22.66
	33/28	15.55^a	37.30	26.43
	Mean	15.41	33.68	
Diameter mm	33/25	7.5^a	10.8^b	9.2
	33/28	8.5^a	11.9^b	10.2
	Mean	8.0	11.4	
RGR $gg^{-1}week^{-1}$	33/25	0.50^a	$0.58^{a,b}$	0.54
	33/28	0.51^a	0.64^b	0.58
	Mean	0.51	0.61	
NAR $gdm^{-2}week^{-1}$	33/25	0.35^a	0.59^b	0.47
	33/28	0.36^a	0.63^b	0.50
	Mean	0.36	0.61	
LAR dm^2g^{-1}	33/25	1.36^a	0.89^b	1.13
	33/28	1.39^a	0.97^b	1.18
	Mean	1.38	0.93	
Chlorophyll mg $cm^{-2}x10^{-3}$	33/25	4.01^a	7.28	5.65
	33/28	3.15^a	5.41	4.28
	Mean	3.58	6.35	

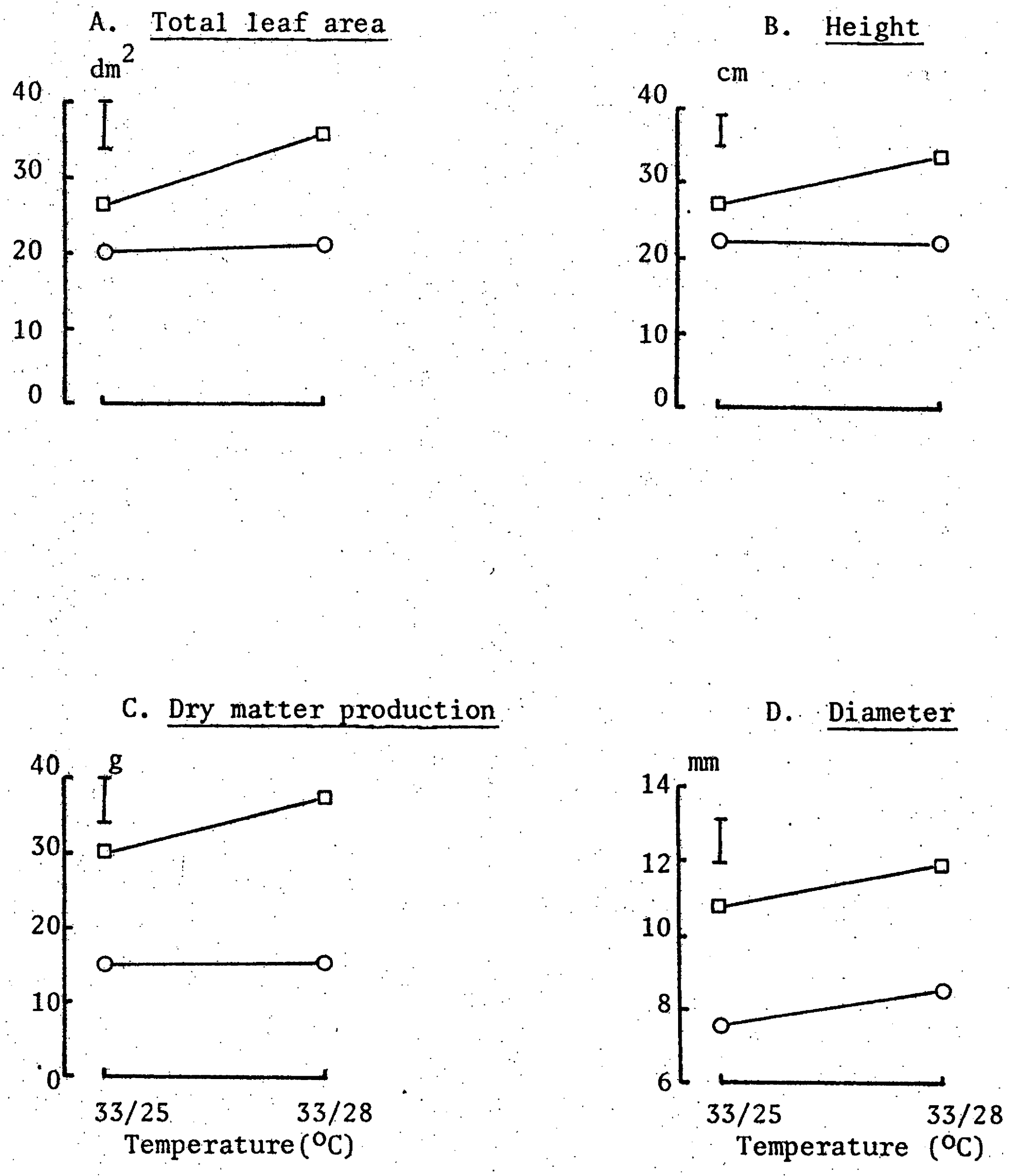


Figure 5.2 (a) Effect of total radiation and temperature on the growth and development of teak seedlings.

□——□ 200 cal $cm^{-2}day^{-1}$

o——o 100 cal $cm^{-2}day^{-1}$

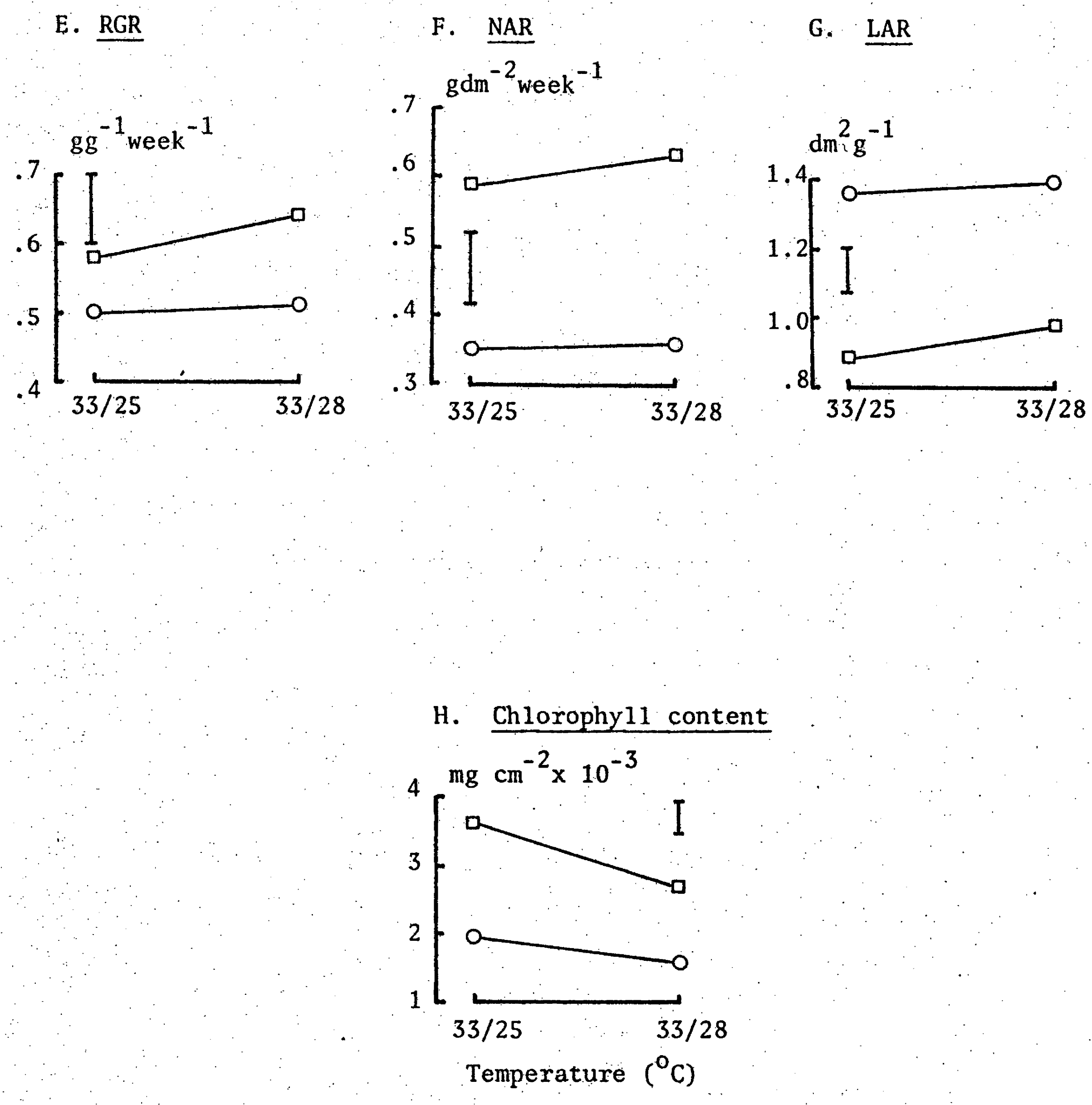


Figure 5.2 (b) Effect of total radiation and temperature on the growth and development of teak seedlings.

□——□ 200 cal $cm^{-2}day^{-1}$

o——o 100 cal $cm^{-2}day^{-1}$

In contrast to the other parameters, LAR was greater at the lower total radiation. The values were 1.35 and 1.39 dm^2g^{-1} at 33/25 and 33/28°C respectively under 100 cal $cm^{-2}day^{-1}$, and were significantly smaller under 200 cal $cm^{-2}day^{-1}$ (0.89 and 0.97 dm^2g^{-1} at 33/25 and 33/28°C respectively).

5.3.2 Effect of Temperature

5.3.2.1 Overall growth

5.3.2.1.1 Total leaf area, height and dry matter production

The pattern demonstrated under 200 cal $cm^{-2}day^{-1}$ was for increased total leaf area, height growth and dry matter production with an increase in temperature from 33/25 to 33/28°C. In contrast the values of these parameters were very similar between the two temperature regimes under 100 cal $cm^{-2}day^{-1}$ (Table 5.2, Figures 5.2A-C).

Thus, under total radiation 200 cal $cm^{-2}day^{-1}$ the values of total leaf area, height and dry matter production recorded at 33/25°C were 26.39 dm^2, 27.3 cm and 30.06 g respectively, and were significantly greater at 33/28°C (33.98 dm^2, 33.4 cm and 37.30 g respectively) (Figures 5.2A-C).

Under total radiation of 100 cal $cm^{-2}day^{-1}$ the values recorded at 33/25°C (20.69 dm^2, 22.0 cm and 15.26 g for total leaf area, height and dry matter production respectively) were not significantly different from those at 33/28°C (21.27 dm^2, 21.8 cm and 15.55 g respectively) (Figures 5.2A-C).

5.3.1.1.2 Diameter growth

Diameter growth was better at the higher temperature under both total radiation conditions (Table 5.2, Figure 5.2D).

Under 200 cal cm^{-2}day^{-1} diameter at 33/28°C (11.9 mm) was significantly greater than at 33/25°C (10.8 mm). Similarly under 100 cal cm^{-2} day^{-1} the value recorded at 33/28°C (8.5 mm) was significantly greater than at 33/25°C (7.5 mm).

5.3.2.2 Growth analysis parameters

RGR, NAR and LAR were not significantly affected by temperature, but nevertheless the temperature response followed a pattern similar to that in total leaf area, height and dry matter production (Table 5.2, Figures 5.2E-G).

Thus under total radiation 200 cal cm^{-2}day^{-1} the values of RGR, NAR and LAR recorded at 33/28°C (0.64 gg^{-1}week^{-1}, 0.63 gdm^{2}week^{-1} and 0.97 dm^{2}g^{-1} respectively) tended to be greater than those at 33/25°C (0.58 gg^{-1}week^{-1}, 0.59 gdm^{2}week^{-1} and 0.89 dm^{2}g^{-1} respectively) (Figures 5.2E-G).

Under total radiation of 100 cal cm^{-2}day^{-1} the values of these parameters recorded at 33/25 and 33/28°C were very similar (Table 5.2, Figure 5.2E-G).

5.3.2.3 Chlorophyll content

Chorophyll content was greater at the lower than the higher temperature (Table 5.2, Figure 5.2H).

Under both radiation levels chorophyll content at 33/25°C was greater than at 33/28°C. The decreased chlorophyll at higher temperature was however more pronounced under higher total radiation.

5.4 DISCUSSION

5.4.1 Effect of Total Radiation

It is clear that height growth, diameter growth, dry matter production and total leaf area of teak seedlings were better at the higher total radiation. Indeed, the response to variations in total radiation was so large as to suggest that this factor may be a very important control of teak seedling development.

The results are in agreement with those reported for other species e.g. *Sequoia sempervirens* (Hellmers and Pharis, 1968), *Chrysanthemum morifolium* (Hughes, 1973) and *Helianthus annuus* cv Pole Star and *Phaseolus vulgaris* cv Canadian Wonder (Eze, 1973). Height growth and dry matter production of these species were found to be greater at the higher total radiation than at the lower.

5.4.2 Differences in Temperature Response under Differing Amounts of Total Daily Radiation

The results indicate a marked difference in the temperature response with different amounts of total daily radiation. Under 200 cal $cm^{-2}day^{-1}$, the growth (e.g. total leaf area, height and dry matter production) of teak seedlings increased with an increase in temperature from 33/25 to 33/28°C. In contrast under 100 cal $cm^{-2}day^{-1}$ the values of these parameters were very similar between the temperature regimes.

The results thus indicate that variation in total radiation has a marked effect on the temperature response of teak seedlings. This supports the suggestion made previously (Chapter 3) that seasonal variation in total radiation could have caused the anomalous results in earlier studies.

5.4.3 Growth Analysis Parameters

Variation in total radiation has a marked effect on the growth analysis parameters of teak seedlings. For RGR, the rates were greater at the higher total radiation. Of the components of RGR, NAR was greater at the higher total radiation whilst the position was reversed for LAR. Thus the higher RGR at the higher total radiation was due to the higher value of NAR.

These results are in accord with those observed both under controlled environment conditions and in the field for other species. Newton (1963) with *Cucumis sativus* and Hughes with *Chrysanthemum morifolium*, under controlled environment conditions, found NAR was proportional to the amount of total radiation whilst the reverse was true for LAR. RGR was found to be favoured by the higher amounts of total radiation.

Eze (1973) examined the effect of seasonal variation in total radiation on the vegetative growth of *Helianthus annuus* and *Phaseolus vulgaris* under natural conditions in Freetown, Sierra Leone (West Africa). There was a definite seasonal pattern of variation in RGR, NAR and LAR. In both species the values of RGR and NAR obtained during the dry season (total radiation 400-500 cal $cm^{-2}day^{-1}$) were much greater than those obtained during the rainy season (total radiation 100-200 cal $cm^{-2}day^{-1}$). The values of LAR on the other hand were greater during the rainy season. Similar results have also been reported for the *Helianthus* species under natural conditions in Ibadan, Nigeria (Njoku, 1959) and in Accra, Ghana (Okali, 1971).

The results suggest that the plants grown under higher total radiation may have an advantage due to their having a more efficient means of capturing, converting and conserving energy in the process of photosynthesis than those grown under lower radiation. Accordingly this results in the greater photosynthetic production by the plants receiving the higher total radiation.

The plants receiving higher radiation produced much greater leaf area than those receiving lower radiation although LAR was smaller. The smaller LAR at higher radiation was largely due to the heavier plants and to thicker and heavier leaves (small leaf area/leaf weight). The higher radiation grown plants therefore also benefit from the larger leaf area giving them a substantially larger assimilatory surface.

5.4.4 Chlorophyll Content

As noted previously the leaves of seedlings receiving the higher radiation were very dark green in colour but those receiving the lower radiation were lighter in colour. This was due to the higher amount of chlorophyll present in the leaves of the higher-radiation seedlings.

Chlorophyll plays a vital role by enabling plants to absorb light for photosynthesis. The greater amount of chlorophyll under the higher total radiation could therefore reflect in more photosynthesis. This was evident in the higher NAR at the higher radiation.

5.5 CONCLUSION

The effect of total radiation on teak seedling growth was quite dramatic. In general, the growth was better at the higher total radiation. The growth analysis studies indicated this could be due primarily to an overall greater rate of photosynthesis. Also leaf chlorophyll content was increased at high light levels and this could be part of the mechanism by which photosynthesis was increased at these levels. But there were also differences in leaf appearance and possibly structure.

An effect of variation in total radiation on the temperature response of teak seedlings was also demonstrated through a total radiation x temperature interaction. Better growth (e.g. height, diameter and dry matter production) at the higher temperature was observed under the total radiation of 200 cal $cm^{-2}day^{-1}$ but not under 100 cal $cm^{-2}day^{-1}$.

CHAPTER 6

EFFECT OF TOTAL RADIATION AND DAYLENGTH ON TEAK SEEDLING GROWTH AND DEVELOPMENT

6.1 INTRODUCTION

In Chapter 5 total radiation was shown to be an important control of teak seedling growth and development. In general, growth (e.g. height, diameter, dry matter production and total leaf area) was better the higher the total radiation.

Total radiation varies greatly with season and the variation is determined by the period of daylength, together with irradiance levels. This effect of total daily radiation could modify photoperiodic effects and vice versa. Ko Ko Gyi (1972) and Kanchanaburangura (1976) have reported effects of photoperiods on teak seedlings between 8 and 12 hours when the total daily radiation level approximated to 8 hours of natural daylight in each treatment. However, the effects might have been different with different radiation levels. In this Chapter the relationship between total radiation and photoperiod is examined. Seedling growth was determined under a total radiation level lower than those used in the previous experiment (Chapter 5).

6.2 MATERIALS AND METHODS

The experiment was conducted in artificially lit cabinets, LB type. Six combinations of daylength and irradiance made up two groups of total radiation. These are summarized in Table 6.1.

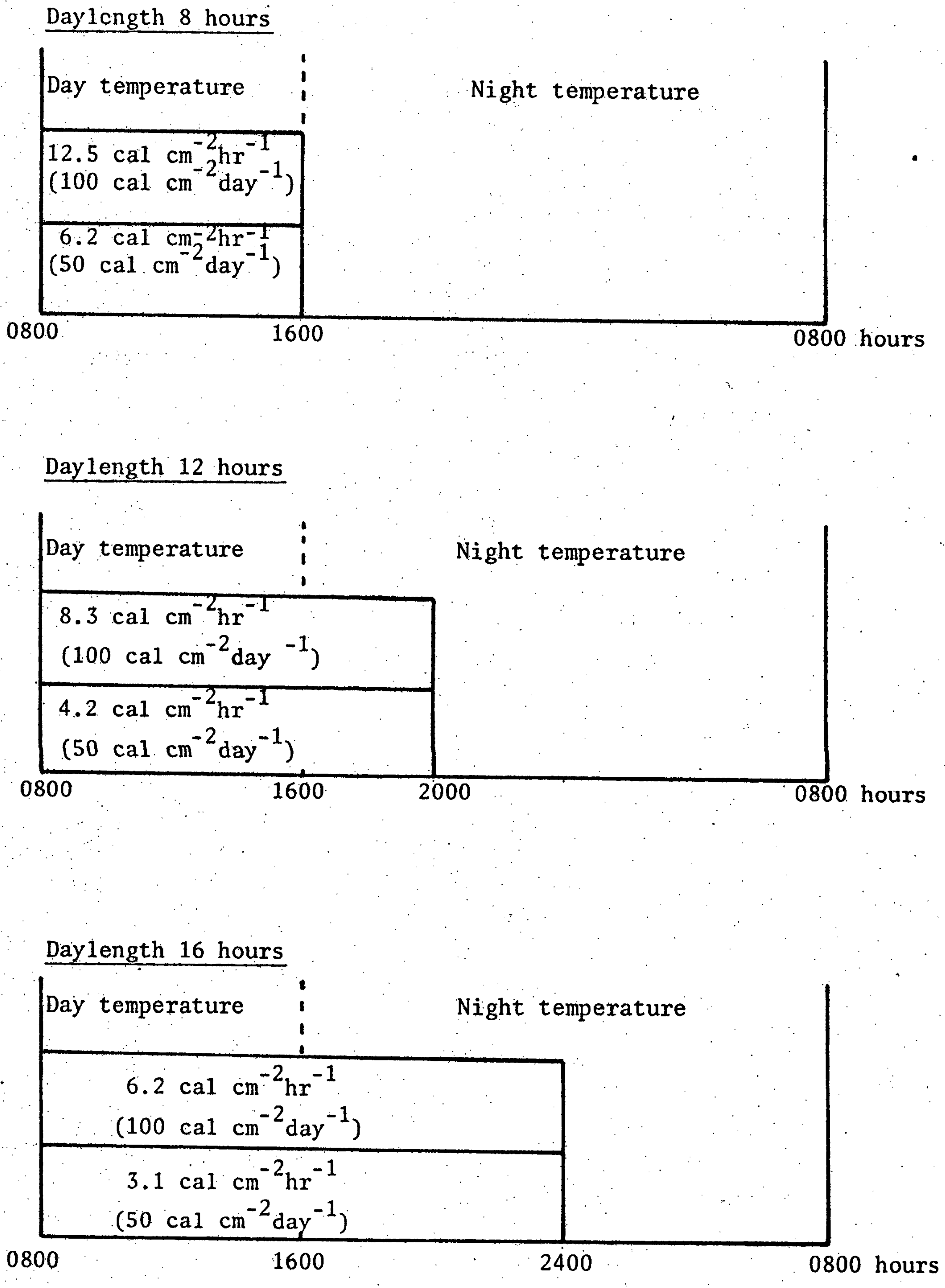


Figure 6.1 Diagram showing details of experimental treatments.

Table 6.1 Details of Experimental Treatments

Total radiation cal $cm^{-2}day^{-1}$	Daylength hours	Irradiance cal $cm^{-2}hr^{-1}$	Quantum Flux $\mu Em^{-2}sec^{-1}$
50	8	6.2	400
50	12	4.2	265
50	16	3.1	200
100	8	12.5	800
100	12	8.3	530
100	16	6.2	400

The light cycles used are shown in Figure 6.1. In all treatments light periods commenced at 0800 hours and were held for 8, 12 and 16 hours at varying irradiance to produce two levels of total radiation of 50 and 100 cal $cm^{-2}day^{-1}$.

As before the light levels were maintained by frequent checking with the quantum meter. In this experiment the quantum meter readings ranged from 200 to 800 $\mu Em^{-2}sec^{-1}$ (Table 6.1). There was a common day/night temperature regime of 30/25°C in all cabinets.

Seedlings of the Kerala provenance were used. 132 uniform seedlings at six weeks old were divided into six groups each of 22 seedlings. The seedling groups were allocated at random to the six treatments.

For each treatment six seedlings were harvested at weeks 2 and 4 after transfer to treatments for growth analysis studies. The remaining ten seedlings were harvested at week 6. Height, diameter, leaf area and dry weight of leaves, stem and roots were noted at the harvest.

Data were subjected to analysis of variance as total radiation x daylength. Comparison of the significance of the difference between treatments was made using Duncan's multiple range test.

6.3 RESULTS

There were significant differences in several growth parameters among the different total radiation and daylength treatments. Statistical analyses also showe significant interaction effects between total radiation and daylength in some parameters (Table 6.2). Despite the interaction effect, the values recorded at the higher total radiation were always greater than those at the lower (Table 6.3, Figure 6.2).

6.3.1 Effect of Total Radiation

6.3.1.1 Diameter, dry matter production, total leaf area and height

The results indicated growth of diameter, dry matter production, total leaf area and height was generally better at the higher radiation despite the significant interaction effect in diameter and dry matter production (Table 6.3, Figure 6.2).

The values of diameter, dry matter production and total leaf area recorded for 100 cal $cm^{-2}day^{-1}$ were generally significantly greater than those recorded for 50 cal $cm^{-2}day^{-1}$.

The differences in height growth between the two levels of radiation were however not significant but the values were always greater at the higher radiation (Table 6.3, Figure 6.2).

6.3.1.2 Growth analysis parameters

RGR and NAR were significantly greater at the higher total radiation whilst LAR showed a reverse trend (Table 6.4, Figure 6.3). NAR and LAR were also affected by significant interaction between daylength and total

Table 6.2 Summarized results of analysis of variance of the data in Tables 6.3 and 6.4. *, ** and *** indicate significance at the 5, 1 and 0.1% levels respectively. ns indicates 'Not significant' at the 5% level

Source of variation	Degrees of freedom	Mean squares	F ratio
Height			
Radiation (R)	1	22.571	1.935^{ns}
Daylength (D)	2	118.001	10.117***
R x D	2	.366	$.031^{ns}$
Error	54	11.663	
Diameter			
Radiation (R)	1	68.054	155.604***
Daylength (D)	2	7.413	16.950***
R x D	2	2.026	4.634***
Error	54	.437	
Dry matter production			
Radiation (R)	1	815.049	159.835***
Daylength (D)	2	65.354	12.816***
R x D	2	26.518	5.200**
Error	54	5.099	
Total leaf area			
Radiation (R)	1	180.822	16.949***
Daylength (D)	2	16.651	1.561^{ns}
R x D	2	14.498	1.359^{ns}
Error	54	10.668	
Relative growth rate			
Radiation (R)	1	.146	25.639***
Daylength (D)	2	.006	1.051^{ns}
R x D	2	.003	$.526^{ns}$
Error	30	.006	
Net assimilation rate			
Radiation (R)	1	.253	198.962***
Daylength (D)	2	.044	34.374***
R x D	2	.015	11.848***
Error	30	.001	
Leaf area ratio			
Radiation (R)	1	2.040	199.719***
Daylength (D)	2	.386	37.801***
R x D	2	.088	8.636***
Error	30	.010	

Table 6.3 Effect of total daily radiation and daylength on diameter, dry matter production, total leaf area and height of teak seedlings. Within each parameter, figures that do not have the same affix are significantly different at the 5% level according to Duncan's multiple range test

Parameter	Total radiation cal $cm^{-2}day^{-1}$	Daylength (hours)			Mean
		8	12	16	
Diameter (mm)	50	6.5^a	6.9^a	7.1^a	6.8
	100	7.9	9.5^b	9.5^b	9.0
	mean	7.2	8.2	8.3	
Dry matter production (g)	50	8.04^a	9.12^a	9.30^a	8.83
	100	12.81	18.33^b	17.56^b	16.20
	mean	10.43	13.68	13.43	
Total leaf area (dm^2)	50	17.45^a	17.56^a	17.69^a	17.57
	100	$19.20^{a,b}$	22.71^c	$21.20^{b,c}$	21.04
	mean	18.23	20.15	19.95	
Height (cm)	50	15.1^a	$17.8^{a,b}$	19.7^b	17.5
	100	16.0^a	19.6^b	21.0^b	18.5
	mean	15.6	18.7	20.4	

Table 6.4 Effect of total radiation and daylength on RGR, NAR and LAR of teak seedlings. Within each parameter, figures that do not have the same affix are significantly different at the 5% level according to Duncan's multiple range test

Parameter	Total radiation	Daylength (hours)			Mean
	cal cm^{-2}day^{-1}	8	12	16	
RGR (gg^{-1}week^{-1})	50	0.57^{a}	0.59^{a}	$0.62^{a,b}$	0.50
	100	$0.70^{b,c}$	0.76^{c}	0.74^{c}	0.73
	mean	0.64	0.68	0.68	
NAR (gdm^{-2}week^{-1})	50	0.26^{a}	$0.30^{a,b}$	0.31^{b}	0.29
	100	0.36	0.47	0.55	0.46
	mean	0.31	0.39	0.43	
LAR (dm^{2}g^{-1})	50	2.17	2.04^{a}	$1.98^{a,b}$	1.99
	100	1.87^{b}	1.55	1.35	1.59
	mean	2.02	1.80	1.67	

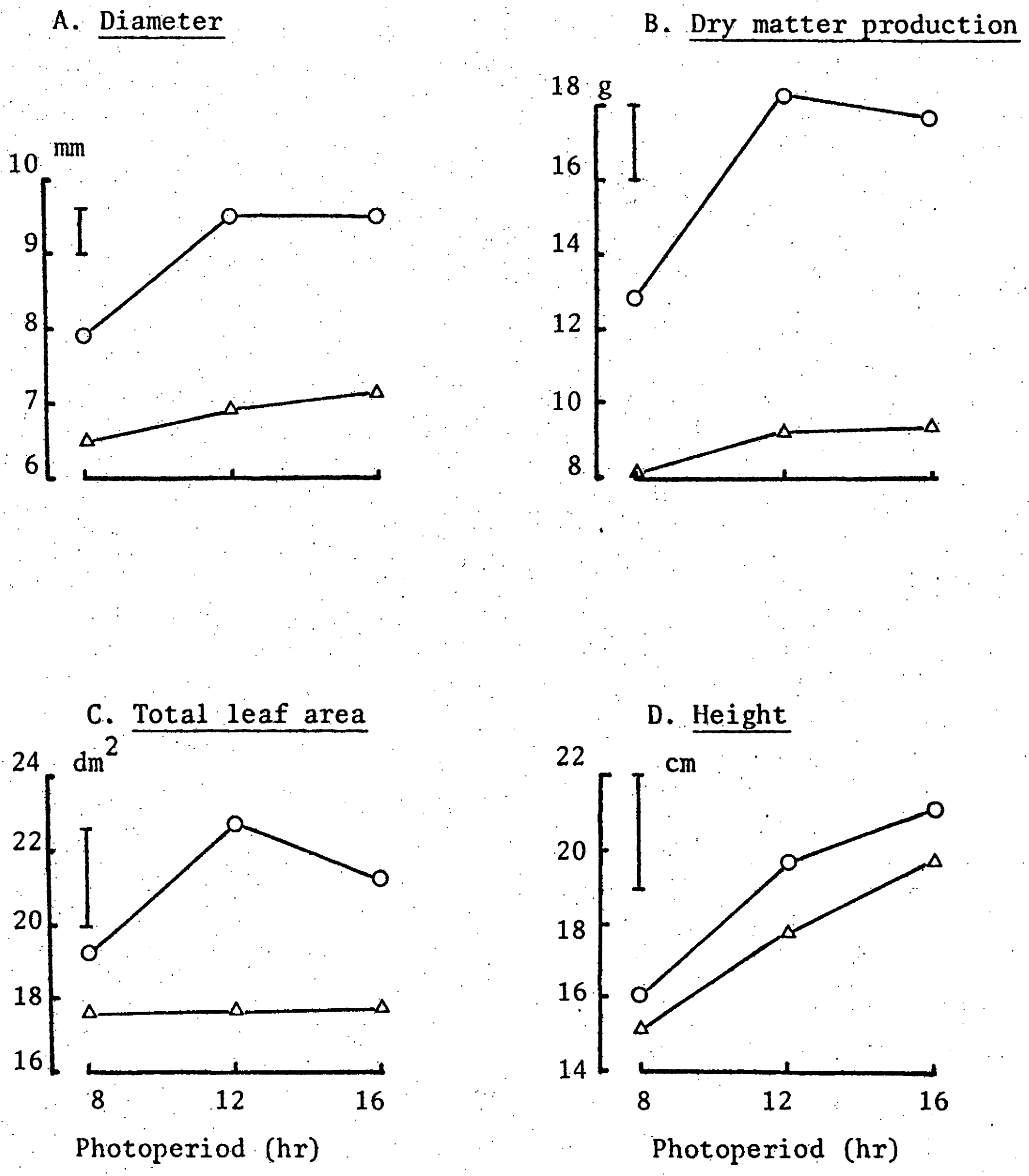


Figure 6.2 Effect of total radiation and photoperiod on (A) diameter, (B) dry matter production, (C) total leaf area, and (D) height of teak seedlings

o _____o 100 cal cm^{-2}day^{-1}

Δ______Δ 50 cal cm^{-2}day^{-1}

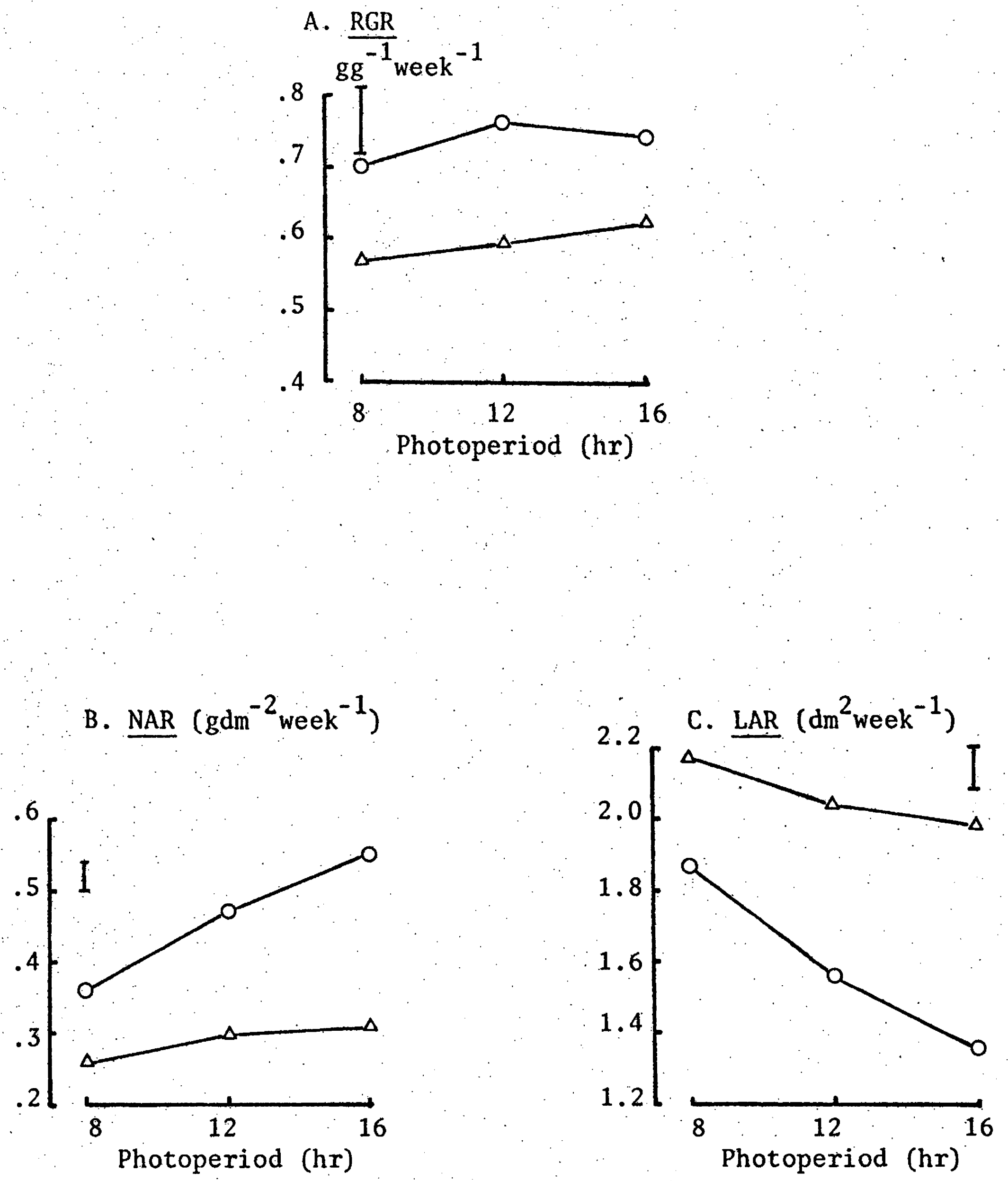


Figure 6.3 Effect of total radiation and photoperiod on (A) RGR, (B) NAR, and (C) LAR of teak seedlings

o————o 100 cal $cm^{-2}day^{-1}$

Δ————Δ 50 cal $cm^{-2}day^{-1}$

radiation. The values recorded however were never poorer at the higher total radiation at all daylengths.

For RGR pooled values for 100 and 50 cal $cm^{-2}day^{-1}$ were 0.73 and 0.59 $gg^{-1}week^{-1}$ respectively. Similarly for NAR the values were 0.46 and 0.29 $gdm^{-2}week^{-1}$ respectively (Figure 6.3).

LAR on the other hand was always greater at the lower radiation. Pooled values were 1.99 and 1.59 dm^2g^{-1} for 100 and 50 cal $cm^{-2}day^{-1}$ respectively (Figure 6.3).

6.3.2 Effect of Daylength with the Same Total Radiation

6.3.2.1 Diameter, dry matter production and total leaf area

The pattern demonstrated under 100 cal $cm^{-2}day^{-1}$ was for increased diameter, dry matter production and total leaf area with an increase in daylength from 8 to 12 hours with no significant decrease at 16 hours. In contrast under 50 cal $cm^{-2}day^{-1}$, there were no significant differences in the values of these parameters over the range of daylengths used (Table 6.3, Figure 6.2).

Thus under total radiation of 100 cal $cm^{-2}day^{-1}$ the values recorded for diameter, dry matter production and total leaf area at 8-hour day (7.9 mm, 12.81 g and 19.20 dm^2 respectively) were poorer than those at 12-hour day (9.5 mm, 18.23 g and 22.73 dm^2 respectively). The values recorded at 16-hour day were smaller, but not significantly, than at 12-hour day (Table 6.3, Figure 6.2).

In contrast, under total radiation of 50 cal $cm^{-2}day^{-1}$ the values of the three parameters were very similar over the daylength range 8 - 16 hours. For example the values recorded at 8, 12 and 16 hour day for diameter were 6.5, 6.9 and 7.1 mm respectively, and for total leaf area were 17.45, 17.56 and 17.69 dm^2 respectively (Figure 6.2).

6.3.2.2 Height growth

Height growth increased with an increase in daylength from 8 to 16 hours under both total radiation conditions (Table 6.3, Figure 6.2).

Response of height to daylength was the same for both 100 and 50 cal $cm^{-2}day^{-1}$. The values recorded were greatest at 16 hour day followed in decreasing order of magnitude by those recorded at 12-and 8-hour day respectively. The differences between daylengths of 12 and 16 hours were however not significant.

6.3.2.3 Growth analysis parameters

RGR was not affected by daylength but its components, NAR and LAR were (Table 6.2). The response of NAR and LAR was also affected by a significant daylength x radiation interaction.

Despite a non-significant difference, the response of RGR followed a pattern similar to that for dry matter production. Under 100 cal cm^{-2} day^{-1}, RGR tended to increase from daylength 8 to 12 hours and decrease at 16 hours. Similarly under 50 cal $cm^{-2}day^{-1}$ there were no differences in the values recorded over the daylength range 8-16hrs (Table 6.4,Figure 6.3).

NAR was greater at long day than at short day but the variation with daylength was more pronounced under 100 than 50 cal $cm^{-2}day^{-1}$. The values recorded were 0.36, 0.47 and 0.55 $gdm^{-2}week^{-1}$ compared to 0.26, 0.30 and 0.31 dm^2g^{-1} respectively under 50 cal $cm^{-2}day^{-1}$ (Figure 6.3).

In contrast to NAR, LAR was greater at short day rather than at long day. The variation with daylength was however similar to that for NAR. There was a marked decrease in LAR at each longer day under 100 cal cm^{-2} day^{-1} and the decrease was slight under 50 cal $cm^{-2}day^{-1}$ (Table 6.4,

Figure 6.3).

6.4 DISCUSSION

6.4.1 Effect of Total Radiation

It is clear the growth (e.g. diameter, dry matter production and total leaf area) of teak seedlings is better the higher the total radiation level irrespective of varying daylengths. It was shown in Chapter 5 that growth was much better at 200 cal $cm^{-2}day^{-1}$ than at 100 cal $cm^{-2}day^{-1}$ but with the same photoperiod of 16 hours. In the present study using two levels of total radiation of 100 and 50 cal $cm^{-2}day^{-1}$ over a range of daylengths of 8 to 16 hours, seedling growth was always better at the higher total radiation regardless of the length of day.

The results thus indicate total radiation effect is important, and that the growth and development of teak seedlings are better the higher the total radiation within the range tested (i.e. 50-200 cal $cm^{-2}day^{-1}$).

6.4.2 Effect of Daylength

There were differences in the daylength response with the same total radiation. The values recorded at 50 cal $cm^{-2}day^{-1}$ were not significantly different over the range of daylength used. This contrasted with the pattern observed at radiation of 100 cal $cm^{-2}day^{-1}$. At this level the values of all parameters recorded at the shortest day (8 hours) were generally significantly poorer than that recorded at the longer days. There were however no significant differences between values recorded at daylengths 12 and 16 hours although the values at 12 hours were greater than at 16 hours.

The results indicated growth of teak seedlings was not affected by daylength at a low level of total radiation (50 cal $cm^{-2}day^{-1}$) but there was an effect at 100 cal $cm^{-2}day^{-1}$. This effect of daylength was however pronounced only at very short days (i.e. 8 hours).

Thus photoperiodic effect may be important only above critical levels of total radiation. However, the daylength in natural teak zones normally exceeds 12 hours. Under natural conditions therefore daylength appears to be of minor importance as a control of growth of teak.

6.4.3 Growth Analysis Parameters

RGR was significantly greater the higher the total radiation, indicating that the seedlings receiving higher radiation were growing at a faster rate than those receiving lower radiation. The greater RGR at the higher radiation was due mainly to the higher NAR under the same conditions. This confirms the results obtained from the study outlined in Chapter 5.

Effect of daylength was less marked in influencing teak seedling growth rate. RGR was not affected by daylength but the components, NAR and LAR were. The response of NAR and LAR were opposite and appeared to be in balance thereby maintaining RGR at a relatively uniform level. Ko Ko Gyi (1970) and Kanchanaburangura (1976) obtained similar results.

6.4.4 Conclusion

The study outlined in Chapter 5 indicated total radiation was a very important control of teak seedling development. In this study of the effect of differing total radiation levels over a range of photoperiods has confirmed this importance.

Photoperiod appears to be less important than total radiation in the control of teak seedling development. Photoperiodic effects may only be important above critical levels of total radiation.

There was an indication from both studies that photosynthesis (as shown by NAR) might play an important role in determining the response of teak seedling development to total radiation. There was also an indication (Chapter 5) that variation in leaf structure might be associated with these putative differences in photosynthesis.

PART III

THE STUDY OF PHOTOSYNTHESIS, RESPIRATION AND LEAF DEVELOPMENT OF TEAK SEEDLINGS

OUTLINE OF PART III

The studies reported in Part II indicated the rate of photosynthesis and the type of leaf development under various conditions of temperature and radiation were important determinants of the response of teak seedlings to these conditions. The effect of temperature and radiation levels on teak seedling photosynthesis and leaf development is studied in this part of the thesis.

Initially in Chapter 7 the apparatus used for measurement of photosynthesis is described and details given of the preliminary studies which showed the importance of leaf age on the rate of photosynthesis. The results of this study aided selection of the leaves to be used for the later studies.

Chapter 8 outlines the studies of effect of light intensity on the rate of photosynthesis, including determination of the light compensation point and the light saturation level for teak.

Chapter 9 compares the rates of photosynthesis and respiration of teak seedlings under differing levels of total radiation and temperature.

The leaf structure (i.e. cell size and number) of teak seedlings are examined under different temperature conditions (Chapter 10) and different levels of total radiation and daylength (Chapter 11).

CHAPTER 7

AN OUTLINE OF MEASUREMENT OF PHOTOSYNTHESIS AND RESPIRATION

7.1 INTRODUCTION

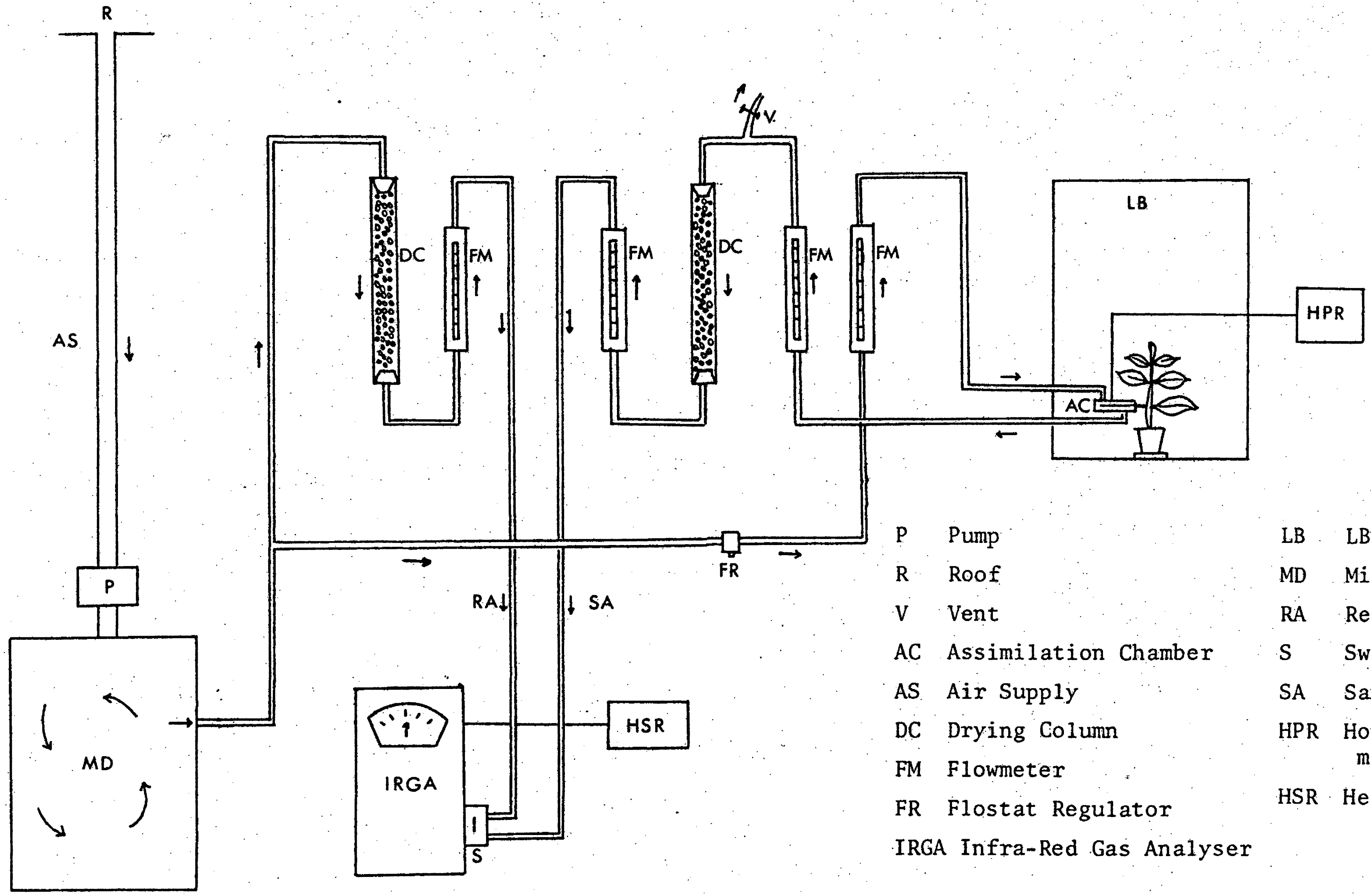
This Chapter outlines the procedures used for the measurement of photosynthesis and respiration reported in Chapters 8 and 9. The importance of leaf age in selecting material for measurement is demonstrated.

7.2 MEASUREMENT OF PHOTOSYNTHESIS AND RESPIRATION

7.2.1 Apparatus

The rates of photosynthesis and respiration were measured using the apparatus shown in Figure 7.1. Air was drawn into the system from the roof of the phytotron building and short term fluctuations in CO_2 concentration were eliminated by passing the air through a large (200 ℓ) stirred mixing drum. The air coming from the drum was split into two streams. One was passed through a calcium chloride drying column and a 'Gapmeter' 2 ℓ flowmeter to a Grubb Parsons SB2 Infra Red Gas Analyser (IRGA) and used as reference air. The other stream was passed through a 'Flostat' regulator and a 12 ℓ flowmeter to the perspex assimilation chamber. The air returning from the assimilation chamber was passed through a 12 ℓ flowmeter, a calcium chloride drying column and a 2 ℓ flowmeter to the IRGA as sample air. Return air not being passed through the IRGA was vented to the atmosphere. The air flow rates used varied from 6 ℓ/min. to 12 ℓ/min.

The assimilation chamber (18 cm x 56 cm x 2 cm) was in an artificially lit LB growth cabinet. Temperature inside the assimilation chamber was



P	Pump	LB	LB Growth Cabinet
R	Roof	MD	Mixing Drum
V	Vent	RA	Reference Air
AC	Assimilation Chamber	S	Switch
AS	Air Supply	SA	Sample Air
DC	Drying Column	HPR	Honeywell Potentiometric Recorder
FM	Flowmeter	HSR	Heath Servo Recorde
FR	Flostat Regulator		
IRGA	Infra-Red Gas Analyser		

Figure 7.1 Apparatus used in the measurement of photosynthesis and respiration

regulated by manipulating the temperature control of the LB Cabinet and inside the chamber was measured underneath the leaf with a thermocouple connected to a Honeywell potentiometric recorder.

The IRGA was calibrated to measure the CO_2 differential between the sample air and reference air against a background of 300 ppm CO_2 in nitrogen. The switch on the IRGA was arranged so that the incoming air subsample could be split to pass through both tubes of the IRGA to give a zero. With the switch in this position the air continued to move through the assimilation chamber in a normal manner so that the equilibrium of the leaf to the conditions in the assimilation chamber was not disturbed while the zero was being taken. During measurement, the IRGA reading was relayed onto a Heath Servo-Recorder (Model EUW-2 OA). This aided in determining the steady position before the final reading was taken.

7.2.2 Calculation of Photosynthetic and Respiratory Rates

The rates of photosynthesis and respiration were calculated using the formulae modified from Sestak *et al*. (1972).

$$\text{PH, RS} = \frac{\Delta C \times F \times 44 \times 273 \times P \times 10^{3}}{A \times 22.414 \times T \times 1013 \times 10^{6}} \quad \text{mg } CO_2 dm^{-2} hr^{-1}$$

where PH, RS = rate of photosynthesis and respiration

ΔC = the difference in CO_2 concentration of the air stream before and after the assimilation chamber measured at the same temperature and pressure (ppm)

F = air flow rate through the assimilation chamber (ℓ/min)

A = leaf area (cm^2)

T = absolute temperature (K) at which the flowmeter was calibrated and the temperature of the flowmeter at time of measurement

P = barometric pressure (mb) at the time of measurement, usually the same as normal atmospheric pressure (1013 mb).

7.3 LEAF AGE

The rate of photosynthesis varies considerably with age of leaves (Kramer and Kozlowski, 1960). The rate generally increases with increasing leaf age up to some critical level of maturity, and then declines. In order to obtain uniformity for the measurements in the experiments, the pattern of change in rates of photosynthesis with leaf age of teak seedlings was determined.

Five seedlings on which the sixth leaves had just unfolded were selected from the seedling stock for the measurements of photosynthesis and leaf area development. Photosynthesis was measured on single intact leaves at a temperature of 33°C and a level of light intensity of 800 μEm^{-2} sec^{-1}(3700 fc). The measurements were made daily over a period of 30 days.

Changes in net photosynthetic rate and leaf area over the period are plotted in Figure 7.2. The rate of photosynthesis increased as leaf area increased and reached a maximum when the leaves fully expanded, about days 13-14. The rate then declined at day 15 and remained fairly constant until day 20 before beginning to drop off substantially.

The results indicated the rate of net photosynthesis in teak seedlings varied with age of leaves. However, the rate was fairly stable for 4-5 days after the leaves attained their final size.

On the basis of the above evidence, all measurements of photosynthesis and respiration reported in Chapters 8 and 9 were made on leaves within five days of their becoming fully expanded.

The sixth to eighth leaf pairs above the cotyledon were used for the measurements. For the experiment reported in Chapter 8 leaves of the seventh pairs were used. In Chapter 9, those of the sixth pair were used in Experiment 1 and the eighth pair in Experiment 2.

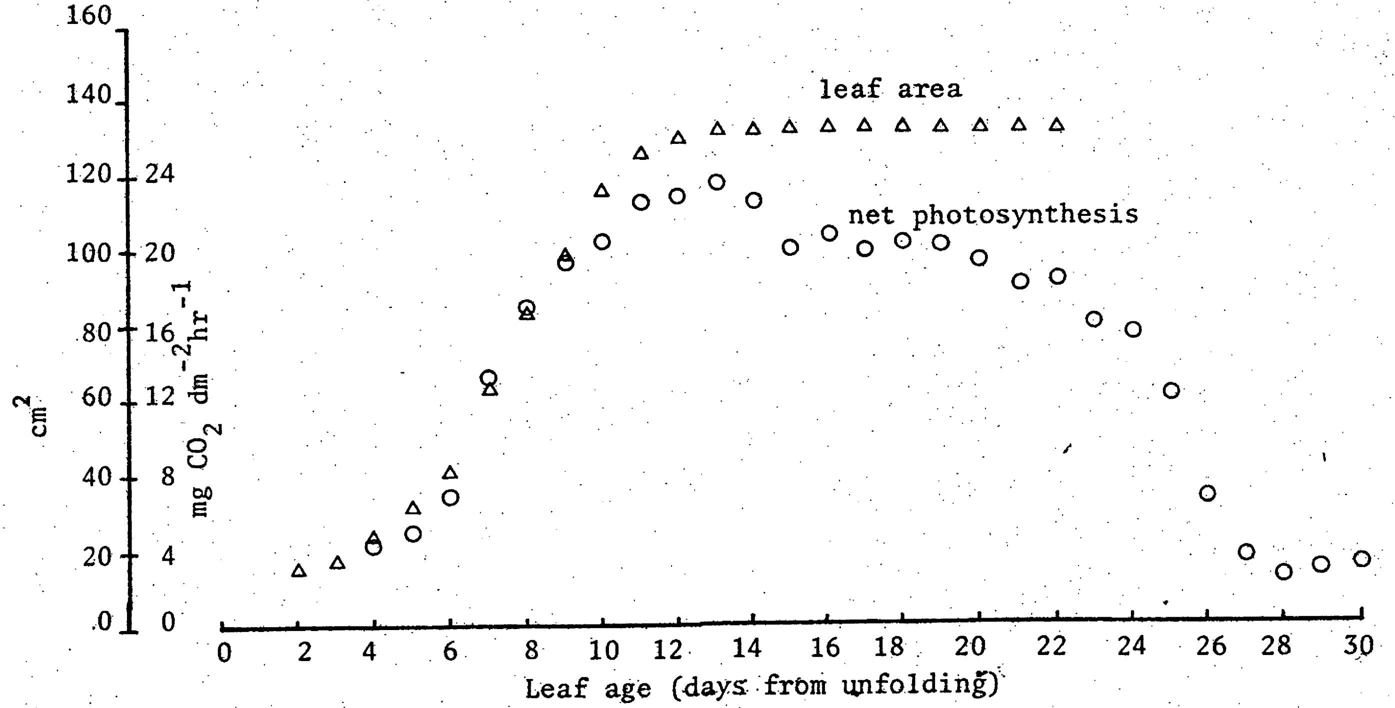


Figure 7.2 Change in the rate of net photosynthesis with leaf age of teak seedlings. Each point is mean of five seedlings

CHAPTER 8

EFFECT OF LIGHT INTENSITY ON THE RATE OF PHOTOSYNTHESIS OF TEAK SEEDLINGS

8.1 INTRODUCTION

In the earlier studies reported in this thesis (Parts I and II) there were indications that responses to variations in light radiation could be caused by differences in rates of photosynthesis at different levels of light intensity. The evidence was circumstantial and based primarily on calculation of net assimilation rate.

The study reported in this chapter has (i) determined the rate of photosynthesis of teak seedlings at different levels of light intensity; (ii) determined respiration rate in the dark and (iii) established approximate light compensation point and light saturation level for photosynthesis in the species. The relevance of this to teak seedling performance is discussed. Its relevance to the interpretation of the results of the controlled environment studies will be discussed later in Chapter 12.

8.2 MATERIALS AND METHODS

Seedlings used were part of the experiment outlined in Chapter 6 in which the seedlings were grown at various light intensities, i.e. 200, 265, 400, 530 and 800 $\mu Em^{-2} sec^{-1}$. (There were two treatments at 400 $\mu Em^{-2} sec^{-1}$ under the two different total radiation conditions, 50 and 100 cal $cm^{-2} day^{-1}$) (see Table 6.1). Measurements of photosynthesis and respiration were made under all six conditions.

The measurements commenced when the seedlings had been in the treatments for four weeks. At this stage the seedlings had developed approximately nine pairs of leaves. Six seedlings with the seventh leaf pair just fully expanded were selected in each treatment.

The measurements of photosynthesis and respiration were made on the seventh pair of leaves of the selected seedlings using the apparatus outlined in Figure 7.1 (Chapter 7). Photosynthetic rates were determined at a temperature of 30°C, and dark respiration rate at a temperature of 25°C. These were the day and night temperatures at which the seedlings were growing. The seedlings were well watered before being taken to the measurement chamber.

Data were subjected to a simple analysis of variance with six seedlings at each light intensity level. Comparison of the significance of the mean differences between photosynthetic rates and between respiration rates were made using Duncan's multiple range test.

8.3 RESULTS

The rates of photosynthesis were significantly affected by differing levels of light intensity but there were no differences in the dark respiration rates between the seedlings (Table 8.1).

The light response curve of photosynthesis is illustrated in Figure 8.1. In general, the rates of photosynthesis increased with an increase in light intensity within the range 200-800 $\mu Em^{-2}sec^{-1}$ (Table 8.2, Figure 8.1).

The response however showed a tendency for rapid rise in photosynthetic rate with increased light intensity at low levels of light

Table 8.1 Summarized result of analysis of variance of the data presented in Table 8.2.
*** indicates significance at the 1% level
ns indicates not significant at the 5% level

Source of variation	Degrees of freedom	Mean squares	F-ratio
Net photosynthesis			
Light intensity	5	126.296	109.140***
Error	30	1.157	
Dark respiration			
Light intensity	5	.0028	.733^{ns}
Error	30	.0038	

Table 8.2 Effect of light intensity on the rate of photosynthesis and respiration. Data connected with a vertical line are not significantly different at the 5% level

Light intensity μEm^{-2}sec^{-1}	Net photosynthesis Mg CO$_2$dm^{-2}hr^{-1}	Dark respiration Mg CO$_2$dm^{-2}hr^{-1}
200	4.55	1.29
265	7.19	1.25
400	10.76	1.31
400	11.63	1.30
530	14.64	1.27
800	17.36	1.29

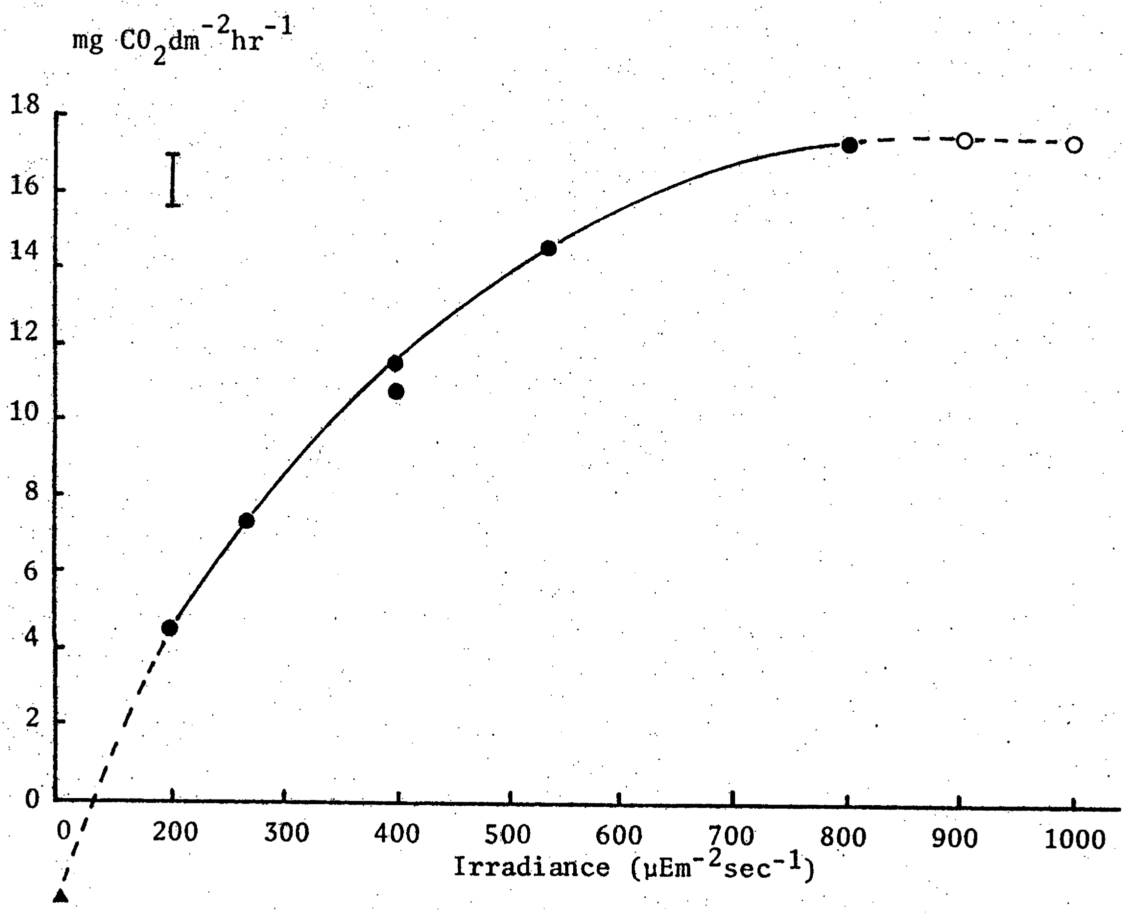


Figure 8.1 Values for net photosynthesis of teak seedlings recorded at different irradiance levels.

○ represents estimated values

▲ represents mean respiration of the six treatments intensity easing to a more gradual rate of increase at the higher intensities. An increase in light intensity from 200 to 265 $\mu Em^{-2}sec^{-1}$ (33%) increased the rate of photosynthesis by 58% whilst a larger (51%) increase in the light level from 530 to 800 $\mu Em^{2}sec^{-1}$ resulted in only a 19% increase in the rate of photosynthesis.

The maximum light intensity possible in the experimental apparatus was insufficient to maximize the rate of photosynthesis, indicating that the light saturation point for the species is above 800 $\mu Em^{-2}sec^{-1}$. (N.B. This is about 3700 f.c. under the light source in the LB cabinets). Extrapolation of the curve in Figure 8.1 indicates light saturation would occur at approximately 900 μEm^{-2} sec^{-1} (4000 f.c.).

Light compensation point, as estimated by interpolation was reached at about 55 $\mu Em^{-2}sec^{-1}$ (200 f.c.) (Figure 8.1).

There were no differences in dark respiration rate between the seedlings grown at differing levels of light intensity. The rate recorded varied slightly from 1.25 to 1.31 mg $CO_2dm^{-2}hr^{-1}$ (Table 8.2).

8.4 DISCUSSION

The results demonstrate a marked effect of light intensity on the rate of photosynthesis of teak seedlings. The rates of photosynthesis increased with increasing light intensities within the range 200-800 μEm^{-2} sec^{-1}.

Similar results in which plants showed increased photosynthesis with increased light intensity within the same range as that used here have been reported in Chapter 4, e.g. *Pinus taeda*, 300-10000 f.c. (Kramer and Dicker, 1944; Bormann, 1956), *Festuca arundinacea*, 10-121 Wm^{-2} (Woledge, 1971), *Trificum boeoticum* Boiss., *T. spelta* L and *T. aestivum* L., 50-350 Wm^{-2} (Dunstone *et al.*, 1973) and several eucalypt species, 125-685 $\mu Em^{-2}sec^{-1}$ (Awang, 1977).

The results indicate that the maximum light intensity, 800 $\mu Em^{-2}sec^{-1}$ (3700 f.c.) possible in the experimental conditions was insufficient for the seedlings to attain their maximum rate of photosynthesis. The The putative saturation level of light intensity for teak, 4000 f.c., is higher than that of some other broadleaf species such as *Acer saccharum, A. rubrum, Quercus macrocarpa* Michx., *Q. velutina* Lam., *Q. alba* L. and *Fagus grandifolia*. These species have saturation light intensities below 3000 f.c., and are classified as shade tolerant species (Kramer and Dicker, 1944; Loach, 1967; Wuenscher and Kozlowski, 1971). The higher level in teak seems to confirm that the species is light demanding.

The putative light compensation point for teak (200 f.c.) is higher than that generally observed for shade tolerant species which have been shown to be as low as 50 f.c. (section 4.2.1, Chapter 4). This again confirms that teak is a shade intolerant species.

However, there was some evidence that the species could tolerate some degree of shading. The results showed a relatively steep rise in the rate of photosynthesis at low light intensities. A steep rise of photosynthetic rate at low light intensities indicates a high efficiency of light absorption and utilization by leaves at low light intensities (Loach, 1967). The results thus suggest that teak seedlings could grow and survive under some degree of shading despite its light demanding characteristics. This agrees with the observations in the field (Kadambi, 1957; Takle and Mujumdar, 1957; Wyatt-Smith, 1967).

8.5 CONCLUSION

An important effect of light intensity on the rate of photosynthesis of teak seedlings has been demonstrated. The rate of photosynthesis increased with increasing light intensity within the range 200-800 $\mu Em^{-2}sec^{-1}$ (800-3700 f.c.).

There were indications that light compensation point would be at about 55 $\mu Em^{-2}sec^{-1}$ (200 f.c.) and light saturation would occur at about 900 $\mu Em^{-2}sec^{-1}$ (4000 f.c.). The light compensation point and light saturation level confirm that teak is a light demander. However there is evidence that the species can grow under some degree of shading.

Throughout this chapter the term 'Light Respiration' is used. This refers to the respiration occurring during the period when the cabinets have closed and the only illumination is provided by low intensity incandescent lights which continu the illumination to provide the necessary length of photoperiod. Thus during this period there will be a net loss of energy due to respiration even though the trees are illuminated and this has been referred to as 'Light Respiration'. This should not be confused with 'Photorespiration', ie. the respiration which occurs during periods of active photosynthesis.

CHAPTER 9

EFFECT OF TOTAL RADIATION AND TEMPERATURE ON TEAK SEEDLING PHOTOSYNTHESIS AND RESPIRATION

9.1 INTRODUCTION

The study outlined in Chapter 5 indicated the presence of an interaction between total light radiation and temperature as controls of teak seedling growth. The growth analysis studies in the same experiment indicated differences in net assimilation rate and thus suggested the effects could have been caused primarily by variations in rate of photosynthesis at different light and temperature levels.

The experiments reported in this Chapter have compared the rate of photosynthesis and respiration of teak seedlings under differing levels of total radiation and temperature.

9.2 MATERIALS AND METHODS

Two experiments were conducted in artificially lit LB cabinets. The first compared performance of teak seedlings under total radiation of 100 cal $cm^{-2}day^{-1}$, and the second under 200 cal $cm^{-2}day^{-1}$. The light levels were the same as for the experiment reported in Chapter 5. The photoperiod in both experiments was 16 hours. Three temperature regimes were used for both experiments (33/25, 33/28 and 33/31°C).

The timing of the temperature and daily light/dark cycles differed slightly from that normally used in the phytotron. This was possible because artificially lit cabinets were used and facilitated measurement of photosynthesis and respiration. Thus these parameters could be recorded for each seedling on the same day. Timing details of the regimes are illustrated in Figure 9.1.

9.2.1 Experiment 1

Thirty seedlings at the fourth-leaf pair stage were selected for uniformity and divided into three groups of ten. Each group was allocated at random to one of the temperature regimes. The seedlings were grown under these conditions until the sixth leaf pair had fully expanded, about four weeks after transfer.

In each temperature regime, five seedlings each with the sixth leaf pair just fully expanded were selected. Measurements of photosynthesis and respiration were made on these seedlings on the leaves of the sixth pair.

Net photosynthesis was measured during period 1 (day temperature - full light) and light and dark respiration during period 2 (night temperature - low light) and period 3 (night temperature - dark) respectively (see Figure 9.1A).

9.2.2 Experiment 2

Following Experiment 1, a further 24 uniform seedlings from the same sowing and at the sixth-leaf pair stage were selected. Eight seedlings were placed in each temperature treatment under 200 cal cm^{-2} day^{-1} conditions. These seedlings were allowed to grow for about four weeks at which four seedlings with the eighth leaf pair just fully expanded were selected for photosynthesis and respiration measurements.

Net photosynthesis and respiration rates were determined during the

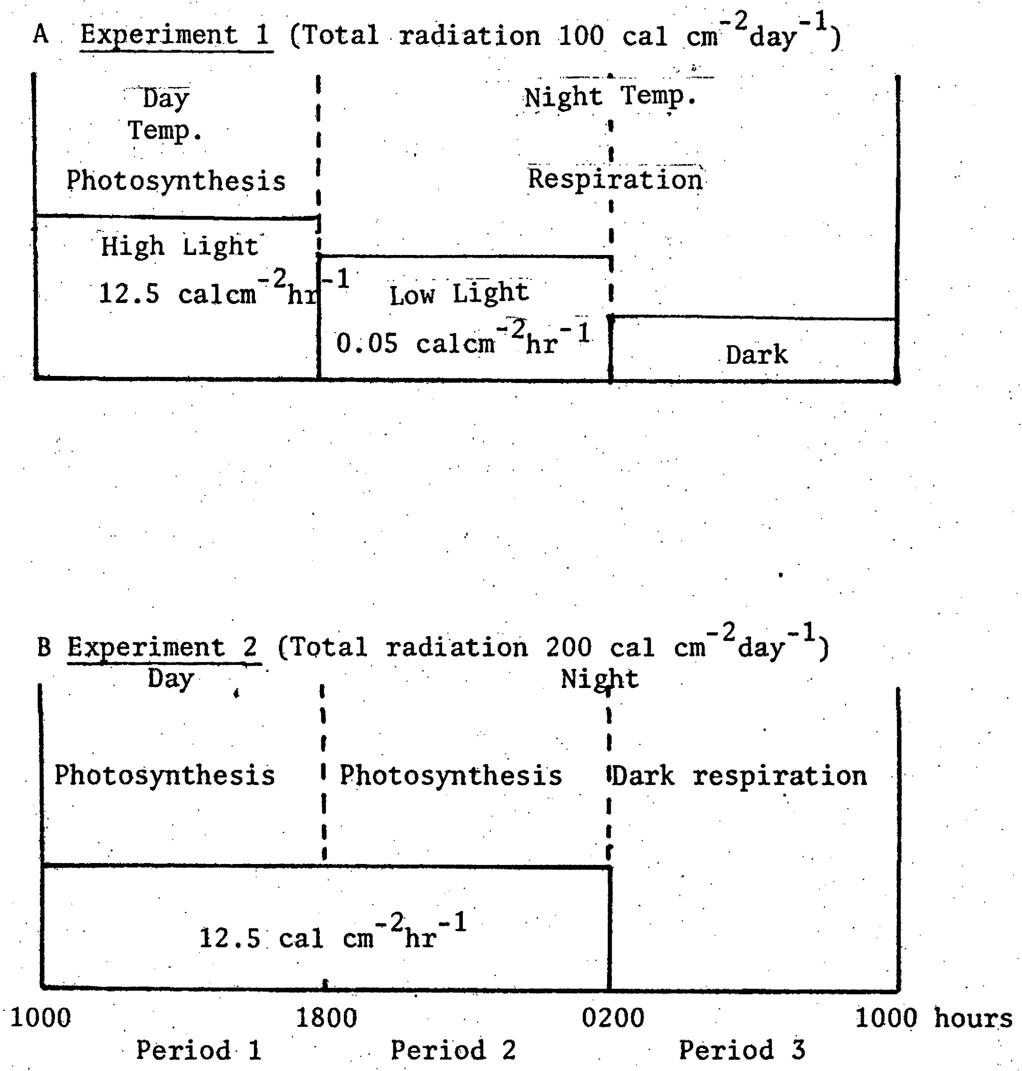


Figure 9.1 Timing details of temperature and light-dark cycles used for the measurements of photosynthesis and respiration

same periods as in the first experiment. However, the light level in period 2 was much higher than in the corresponding period in the first experiment (see Figure 9.1B).

The data for each of the three periods in each experiment were subjected to standard analysis of variance. There were five seedlings in each treatment in Experiment 1, and four each in Experiment 2. Duncan's multiple range test was used to determine the significance of the difference between the temperature treatment means.

9.3 RESULTS

There were no significant differences in the rates of photosynthesis measured during the period of day temperature, presumably because all material was at the same day temperature (33^{o}C). The rates during the period of 'night' temperature, and light and dark respiration rates differed significantly at the different temperatures (Table 9.1).

9.3.1 Photosynthesis

There were no differences in the rates of photosynthesis measured at the common day temperature of 33^{o}C in both experiments. The values recorded were 18.11, 17.86 and 18.51 mg $CO_2 dm^{-2}hr^{-1}$ in Experiment 1, and were 18.56, 18.01 and 17.98 mg CO_2 $dm^{-2}hr^{-1}$ in Experiment 2 (Table 9.2, Figures 9.2 and 9.3). Thus the different night temperatures had no effect on the rate of photosynthesis during the day.

The rates of photosynthesis measured during the period of night temperature (i.e. Period 2 of Figure 9.1B) were greater the higher the temperature (Table 9.2, Figure 9.3). The values recorded were greatest at 31^{o}C (18.21 mg CO_2 $dm^{-2}hr^{-1}$) and significantly lower at 25^{o}C (16.09 mg CO_2 $dm^{-2}hr^{-1}$). The values recorded at 28^{o}C were intermediate

Table 9.1 Summarized results of analysis of variance of the data presented in Table 9.2.
*. **, *** indicate significance at the 5, 1 and 0.1% levels respectively; ns indicates 'not significant at the 5% level'

Source of variation	Degrees of freedom	Mean squares	F-ratio
	EXPERIMENT 1		
Photosynthesis (day temperature)			
Temperature	2	2.490	1.770^{ns}
Error	12	1.409	
Light respiration			
Temperature	2	.057	5.70*
Error	12	.010	
Dark Respiration			
Temperature	2	.170	7.731*
Error	12	.022	
	EXPERIMENT 2		
Photosynthesis (day temperature)			
Temperature	2	.615	.562^{ns}
Error	9	1.094	
Photosynthesis (night temperature)			
Temperature	2	4.495	5.619*
Error	9	.800	
Dark respiration			
Temperature	2	.211	13.854**
Error	9	.015	

Table 9.2 Effect of total radiation and temperature on photosynthesis and respiration of teak seedlings; the data not connected with a vertical line are significantly different at the 5% level according to Duncan's multiple range test

Expt. No.	Total radiation cal $cm^{-2} day^{-1}$	Temperature ^oC day/night	Photosynthesis (mg $CO_2 dm^{-2} hr^{-1}$)		Respiration (mg $CO_2 dm^{-2} hr^{-1}$)	
			Day temp.	Night temp.	Light	Dark
1	100	33/25	18.11		0.20	1.44
		33/28	17.86		0.26	1.49
		33/31	18.51		0.41	1.79
2	200	33/25	18.56	16.00		1.25
		33/28	18.01	17.13		1.35
		33/31	18.98	18.21		1.69

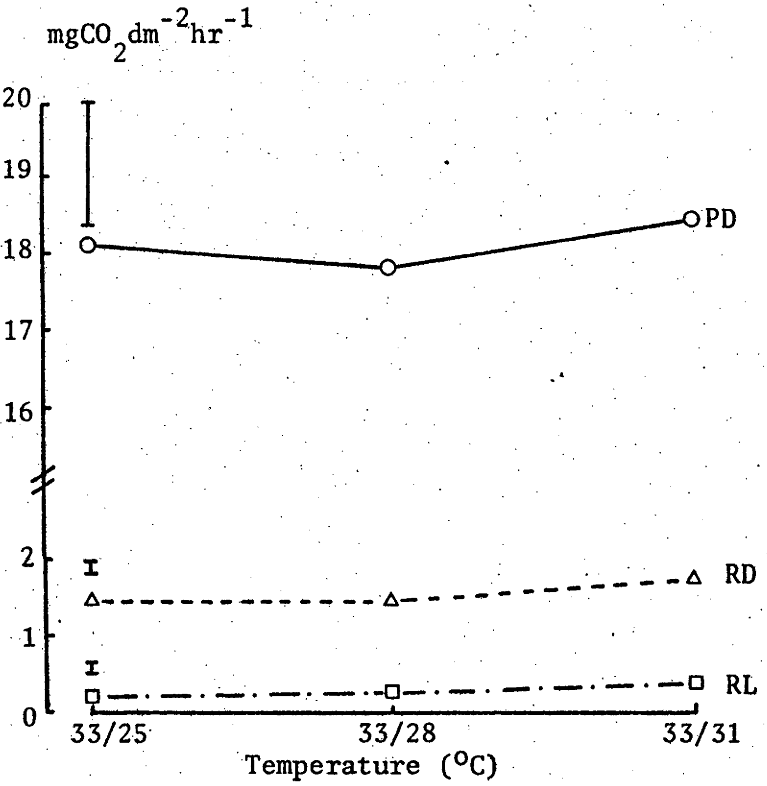


Figure 9.2 Effect of temperature on the rates of photosynthesis and respiration of teak seedlings grown under total radiation of 100 calcm^{-2}day^{-1} conditions (Experiment 1).

PD = Photosynthesis during day temperature (period 1)
RL = Light respiration (period 2)
RD = Dark respiration (period 3)

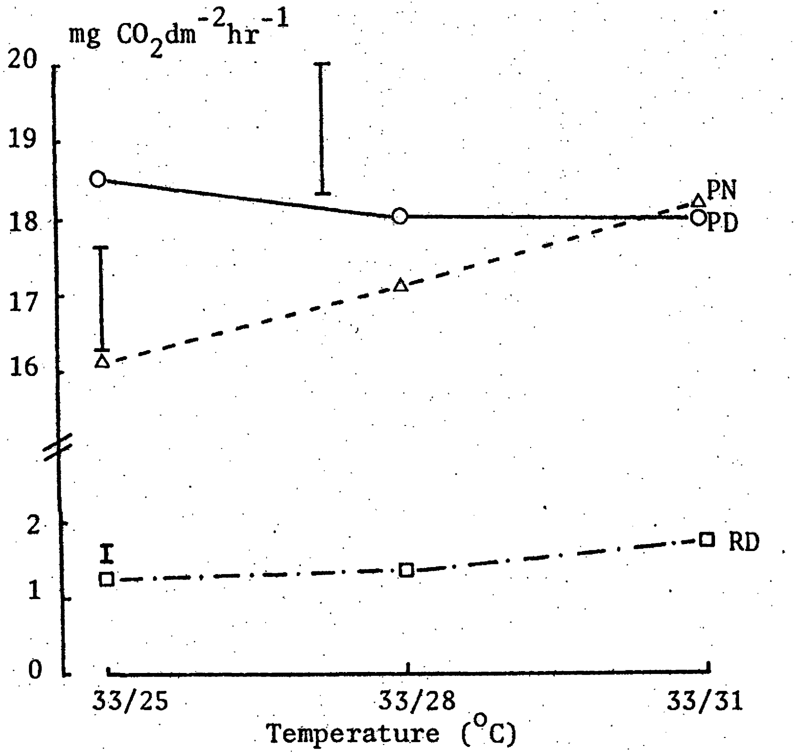


Figure 9.3 Effect of temperature on the rates of photosynthesis and respiration of teak seedlings grown under total radiation of 200 cal $cm^{-2}day^{-1}$ conditions (Experiment 2).
PD = Photosynthesis during day temperature (period 1)
PN = Photosynthesis during night temperature (period 2)
RD = Dark respiration (period 3)

(17.13 mg $CO_2dm^{-2}hr^{-1}$) and did not differ significantly from those at 25 and 31°C.

9.3.2 Respiration

The rates of light respiration (Period 2, Experiment 1) and dark respiration (Period 3, Experiments 1 and 2) were greater at the higher temperature (Table 9.2, Figures 9.2 and 9.3).

In Experiment 1, the rates of light and dark respiration recorded at 31°C were significantly greater than those at 28 and 25°C. There were no significant differences between the values recorded at 25 and 28°C, but the values at 28°C were always greater than at 25°C (Table 9.2, Figure 9.2).

Similarly in Experiment 2, dark respiration rate at 31°C was higher than at 28 and 25°C. Again, although the difference between the values recorded at 25 and 28°C was not significant, the rate at the higher temperature tended to be higher (Table 9.2, Figure 9.3).

9.4 DISCUSSION

The results demonstrate an important effect of temperature on the rates of photosynthesis and respiration of teak seedlings. The rates of photosynthesis and respiration increase at higher temperatures within the range 25 to 31°C.

The rates of photosynthesis determined at the day temperature of 33°C were very similar in both experiments. Although there was no direct comparison between experiments, indications are that the different levels of total daily radiation had no effect on rate of photosynthesis.

The results suggest seedlings receiving higher total radiation (Experiment 2) would have greater overall photosynthetic production than those receiving lower radiation (Experiment 1) solely because the lighting arrangement permitted photosynthesis to be maintained longer.

Furthermore, in Experiment 2 although the seedlings experienced the same total radiation of 200 cal $cm^{-2}day^{-1}$, those grown at the higher 'night' temperatures (e.g. 31°C) would have greater photosynthetic production than those grown at the lower 'night' temperature (e.g. 25°C). This obviously had important implications for interpretation of the results of the other experiments. This is discussed in more detail in Chapter 12.

CHAPTER 10

EFFECT OF TEMPERATURE ON THE GROWTH AND DEVELOPMENT OF LEAVES OF TEAK SEEDLINGS

10.1 INTRODUCTION

The experiments reported in this chapter have examined the growth and development of leaves of teak seedlings grown under different temperature regimes, and the effect of a change in temperature on later leaf development.

10.2 MATERIALS AND METHODS

Two experiments were conducted in artificially lit LB cabinets. The first experiment examined the effect of three temperature regimes (33/25, 33/28 and 33/31°C) on the leaf development of seedlings. In this experiment there was a common photoperiod of 16 hours made up of eight hours of high intensity (800 $\mu Em^{-2}sec^{-1}$) and eight hours of low intensity (5 $\mu Em^{-2}sec^{-1}$). Temperature and light/dark cycles were as shown in Figure 5.1B,Chapter 5, with day temperature held for the period of high intensity light. Night temperature was held for the remainder of the 24 hour period, i.e. the period of low intensity light and the dark period.

The second experiment examined the effect of a change in temperature from the higher regimes (33/28 and 33/31°C) to the lower regime of 33/25°C on later leaf development under the same light conditions.

N.B. This experiment as reported was all that could be salvaged from a more detailed study intended to compare leaf characteristics under different temperature regimes of 33/25, 33/28 and 33/31^{o}C. The experiment could not be proceeded with because the seedlings kept under the 33/25^{o}C regime were destroyed from a severe shock at 4^{o}C overnight due to a breakdown of temperature control in the cabinet.

10.2.1 Experiment 1

Twentyone uniform seedlings (Kerala provenance) germinated and grown in a phytotron glasshouse at a 30/25^{o}C temperature regime were selected on each of which the fifth leaf pair had just unfolded. The seedlings were transferred to grow under three temperature regimes (33/25, 33/28 and 33/31^{o}C), i.e. seven seedlings to each regime. The seedlings were grown under these conditions for a period of six weeks. Measurements of the following leaf growth characteristics were made on the seven seedlings during this period.

(1) Development of individual leaf area;
(2) Rate of leaf expansion;
(3) Number of epidermal cells in leaves;
(4) Mean epidermal cell size;
(5) Frequency of leaf production.

10.2.1.1 Development in area of leaves of the seventh pair

Development of individual leaf area was determined using leaves of the seventh pair. Measurements commenced immediately after the lamina had fully unfolded from the apical bud, and continued daily until final leaf size was attained after about two weeks. The length and width of the lamina of each leaf in the pair was recorded and the mean of each pair on each seedling calculated. Leaf length was defined as the distance from stem to leaf apex including petiole, and leaf width was taken at the widest part across the lamina at right angles to the mid rib.

The mean area of each leaf pair was calculated using a simple correlation equation established by measurements of leaf area, leaf length and leaf width over a previous sample of fifty leaves. The equation used was

$$Y = 0.5697 + 0.6432X$$

where Y = leaf area

X = leaf length x leaf width product.

Details of the establishment of this correlation are given in Appendix V.

10.2.1.2 Rate of leaf expansion

The rate of leaf expansion was calculated from daily increment of the mean area of the seventh leaf pair. Data were recorded for each seedling over the period of leaf development (i.e. 15 days).

10.2.1.3 Epidermal cell number and dimension

The total number of epidermal cells on the upper surface of leaves and the mean size of these epidermal cells were determined at three different stages of leaf development for the seventh pair of leaves of each seedling. Data were obtained

(i) during the period of rapid leaf growth (day 5);

(ii) as the leaves approached full expansion (day 10); and

(iii) when leaves were fully expanded (day 15).

The technique for cell-number estimation was adapted from that described by Sampson (1961) and modified by Dunstone (1972). The procedure was as follows.

Impressions about 1 cm^2 in area were made at the base, middle and tip of the upper surface of leaves with a fast setting, low viscosity silicon rubber compound (Dow Corning RTV 583 with No.4 catalyst).

Replicas of the rubber impressions were made by painting the rubber with clear nail polish and allowing it to dry. The dry lacquer was peeled off using a piece of clear cellulose tape mounted on a microscope slide.

Cell counts were taken directly from the screen of a 'Reichhart' lanameter (screen microscope). The scales or fields used were calibrated with a 'Zeiss' stage micrometer.

Counts were made of the number of epidermal cells falling within a measured field of 0.15 mm diameter (0.02 mm^2). Ten fields were counted from each sampling and the mean number of cells per mm^2 calculated from three samplings (base, middle and tip) for each leaf. For each stage of leaf development total number of cells in each leaf was calculated from the mean number of cells per mm^2 of the lamina. Mean size of cells (square micron - μ^2) was calculated directly from the number of cells falling in the measured field of 0.02 mm^2.

10.2.1.4 Frequency of leaf production

The time interval between each successive leaf pair commencing to unfold was noted for each seedling over the period of six weeks. Mean values were calculated for each seedling from this period.

10.2.2 Experiment 2

Seedlings used in this experiment were from the same stock as those used for Experiment 1. Twenty seedlings of uniform development in which the fourth leaf pair had just unfolded were divided into two groups, each of ten seedlings, and placed in LB cabinets under the two temperature regimes of 33/28 and 33/31°C. The seedlings remained under these conditions for four weeks until they had developed approximately seven pairs of leaves.

After the four-week period five seedlings from each regime were transferred to a 33/25°C regime. Over a four week period the same leaf data were recorded as in Experiment 1. Leaves of the eighth pair were used for details of leaf development and epidermal cell data.

10.2.3 Statistical Analysis

The data were subjected to analysis of variance. Individual leaf area and rate of leaf expansion had temperature and leaf age over a period of 15 days from leaf unfolding as the major source of variation. Epidermal cell number and size had temperature and three stages of leaf development (days 5, 10 and 15) as the major sources of variation. The data for frequency of leaf production had temperature as the only major source of variation. Duncan's multiple range test was used to determine the significance of differences between treatment means.

10.3 RESULTS

10.3.1 Experiment 1

There were significant effects of temperature on leaf size, rate of leaf development and the number of epidermal cells per leaf and mean size of the epidermal cells (Table 10.1).

10.3.1.1 Individual leaf area development and rate of leaf expansion

The change in leaf area and the rate of expansion of leaves of the

Table 10.1 Summarized results of analysis of variance of the data recorded in Experiment 1 and presented in Tables 10.2 - 10.4.
*, ** and *** indicate significance at the 5, 1 and 0.1% levels respectively. Ns indicates not significant at the 5% level

Source of variation	Degrees of freedom	Mean squares	F-ratio
The seventh leaf area development			
Temperature (T)	2	2187.417	4.110***
Leaf age (A)	14	45808.775	86.062***
T x A	28	636.462	1.196 ns
Error	270	532.279	
Rate of leaf expansion			
Temperature (T)	2	252.060	14.895***
Leaf age (A)	14	1095.122	64.712***
T x A	28	34.670	2.049**
Error	270	16.923	
Number of cells			
Temperature (T)	2	12.773×10^{12}	224.088***
Leaf age (A)	2	16.46×10^{12}	288.772***
T x A	4	3.26×10^{11}	5.719**
Error	54	5.7×10^{10}	
Epidermal cell size			
Temperature (T)	2	206588.713	115.204***
Leaf age	2	2875672.344	1603.612***
T x A	4	12305.759	6.862***
Error	54	1793.247	
Frequency of leaf production			
Temperature	2	3.964	5.115*
Error	18	0.775	

seventh pair with age are plotted in Figures 10.1 and 10.2. For all three treatments, the graphical curves followed very similar courses. Leaf expansion and growth rate in the early stages of development, days 1-2 after leaves unfolded, were comparatively low. This was followed by a period of rapid growth until days 7-8. After this the leaves continued to increase in size but at a very much lower rate until the final size was attained, about 13-14 days from unfolding.

The final size attained was larger at the higher temperatures (Table 10.2). The area of leaves grown at 33/31°C was significantly larger than those grown at 33/28 and 33/25°C. The area recorded at 33/28°C was also larger than at 33/25°C although this difference was not significant.

The rate of leaf expansion was greater at the higher temperatures despite a significant interaction between temperature and leaf age (Table 10.2, Figure 10.2). The leaves at 33/25 and 33/28°C attained the maximum rate of expansion at day 6 and those at 33/31°C at day 7. The expansion rate was similar at all temperatures after day 9 with the leaves at 33/28 and 33/31°C fully expanded at day 13 and those at 33/25°C at day 14.

It was evident that the larger leaf area at the higher temperatures was due primarily to the higher rate of expansion during the rapid growth period and not to expansion being continued for a longer period.

10.3.1.2 Number and size of epidermal cells

The number and size of cells was greater at the higher temperatures (Table 10.3, Figure 10.3).

At all stages of leaf development, the number of cells was greatest at 33/31°C followed in decreasing order of magnitude by those at 33/28 and 33/25°C respectively (Table 10.3, Figure 10.3).

The epidermal cell size was generally significantly larger at higher

Table 10.2 Change in leaf area and rate of leaf expansion with age of leaves of the seventh pair

Temperature	Leaf age (days from unfolding)															LSD
°C	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
Leaf 7 area (cm^2)																
33/25	1.54	3.32	6.91	13.32	23.55	35.75	52.08	67.26	81.02	89.91	93.58	95.37	96.38	97.17	97.24	
33/28	1.55	3.36	7.31	15.31	28.41	45.15	63.14	79.24	91.65	99.67	105.81	108.41	109.54	109.88	109.88	24.17 (TxA)
33/31	1.69	3.79	9.30	20.27	37.56	58.91	82.75	107.84	126.86	133.05	136.99	139.35	140.50	141.05	141.05	
Rate of leaf expansion (cm^2/day)																
33/25		1.78	3.59	6.41	10.23	12.20	16.33	15.18	13.76	8.89	3.67	1.79	1.01	0.79	0.07	
33/28		1.81	3.95	8.00	13.10	16.74	17.99	16.10	12.41	8.02	6.14	2.60	1.13	0.34	-	4.31 (TxA)
33/31		2.10	5.51	10.97	17.29	21.35	23.84	25.29	19.02	6.19	3.94	2.36	0.95	0.55	-	

Table 10.3 Effect of temperature and leaf age on the number and mean size of epidermal cells of leaves of the seventh pair of teak seedlings. Within each parameter the data that do not have the same affix are significantly different at the 5% level according to Duncan's multiple range test

Parameter	Temperature °C	Leaf age (day)		
		5	10	15
Number of cells per leaf x 10^b	33/25	4.3	6.2^b	$6.1^{a.b}$
	33/28	5.4	6.6^c	6.5^c
	33/31	5.9^a	7.6^d	7.6^d
Mean epidermal cell size μ^2	33/25	607	1188	1242^b
	33/28	700^a	$1274^{b,c}$	1305^c
	33/31	729^a	1418	1482

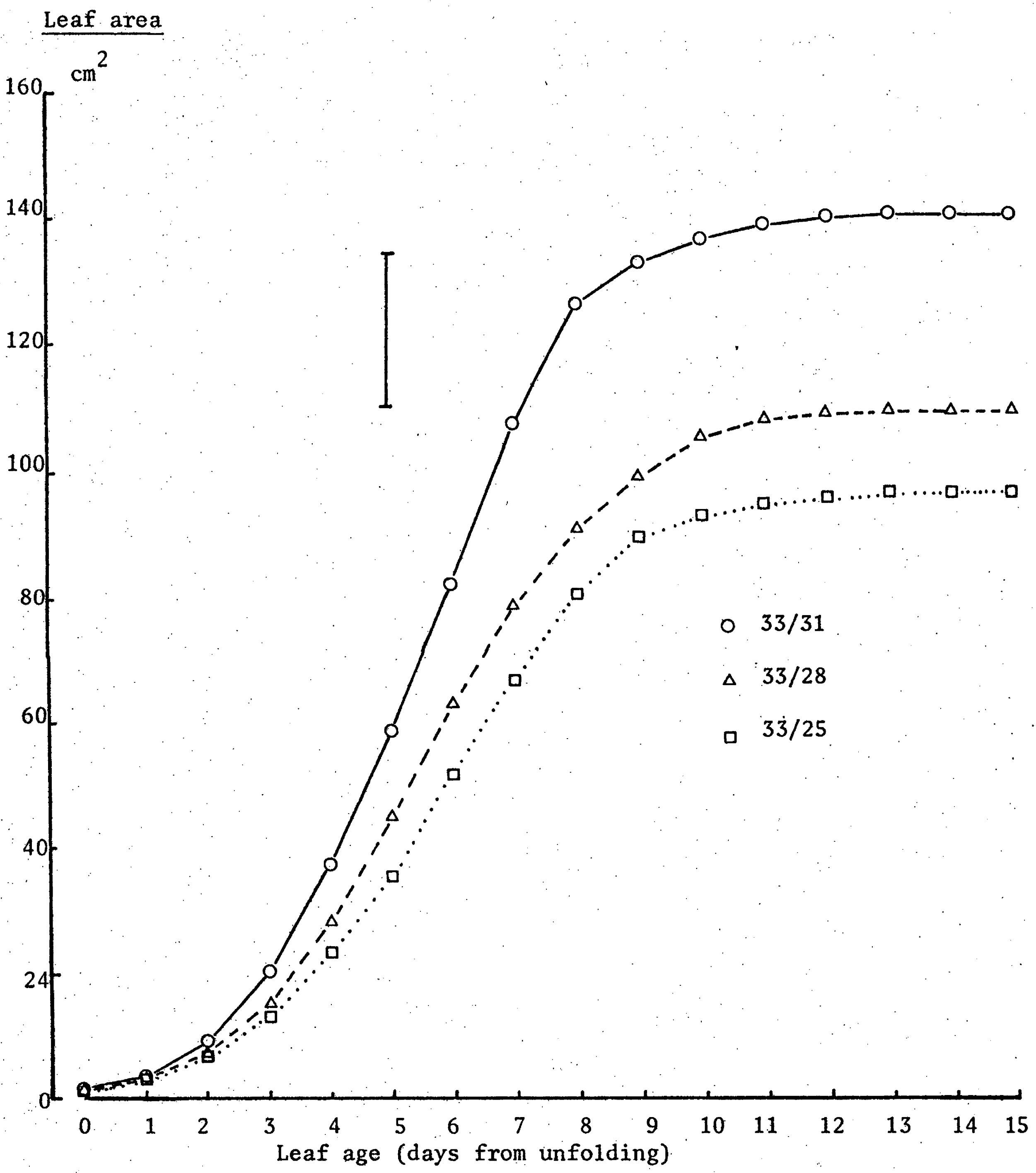


Figure 10.1 Change in leaf area with age of leaves of the seventh pair of teak seedlings grown at different temperatures

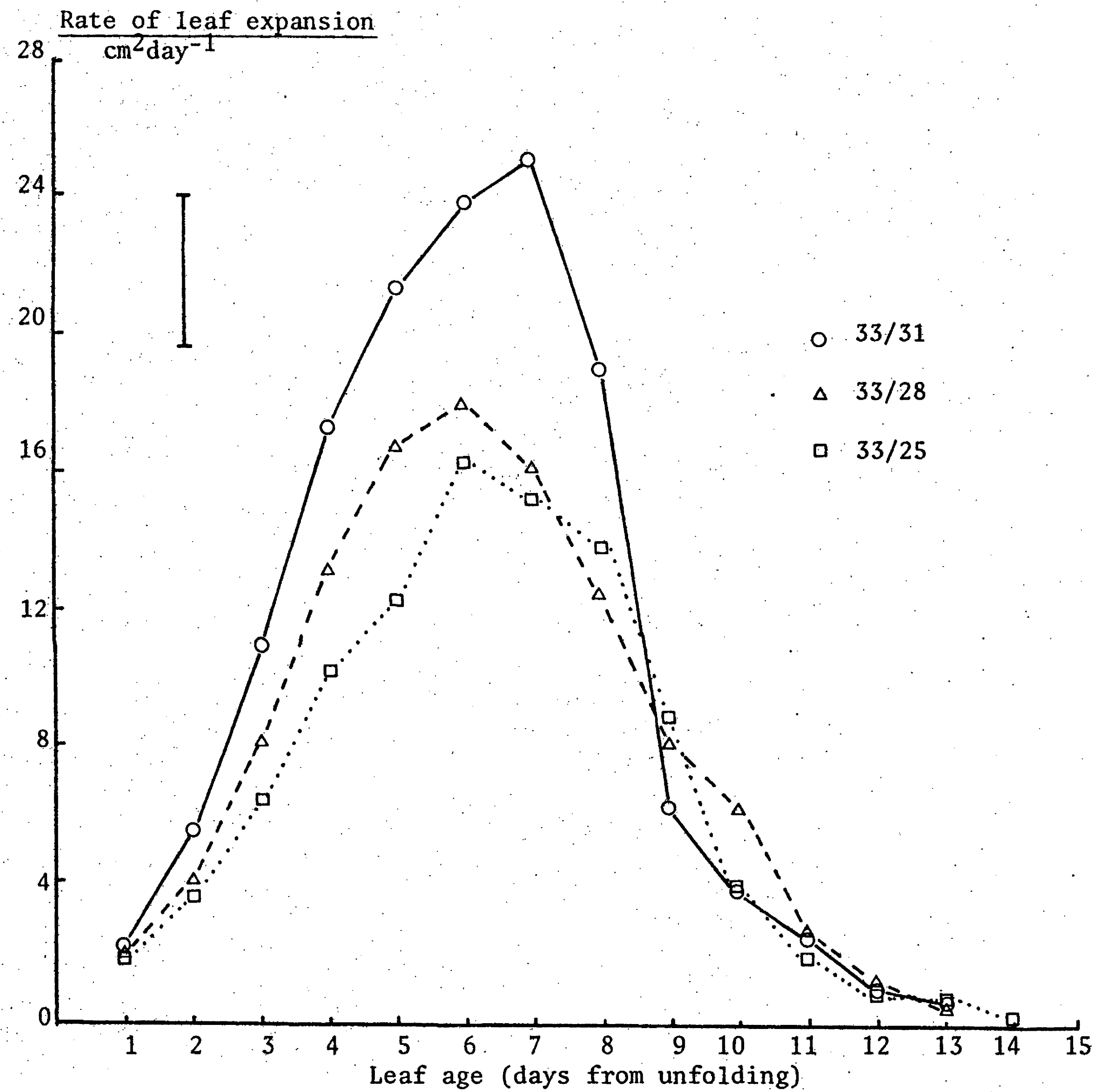


Figure 10.2 Change in rate of leaf expansion with age of leaves of the seventh pair of teak seedlings grown at different temperatures

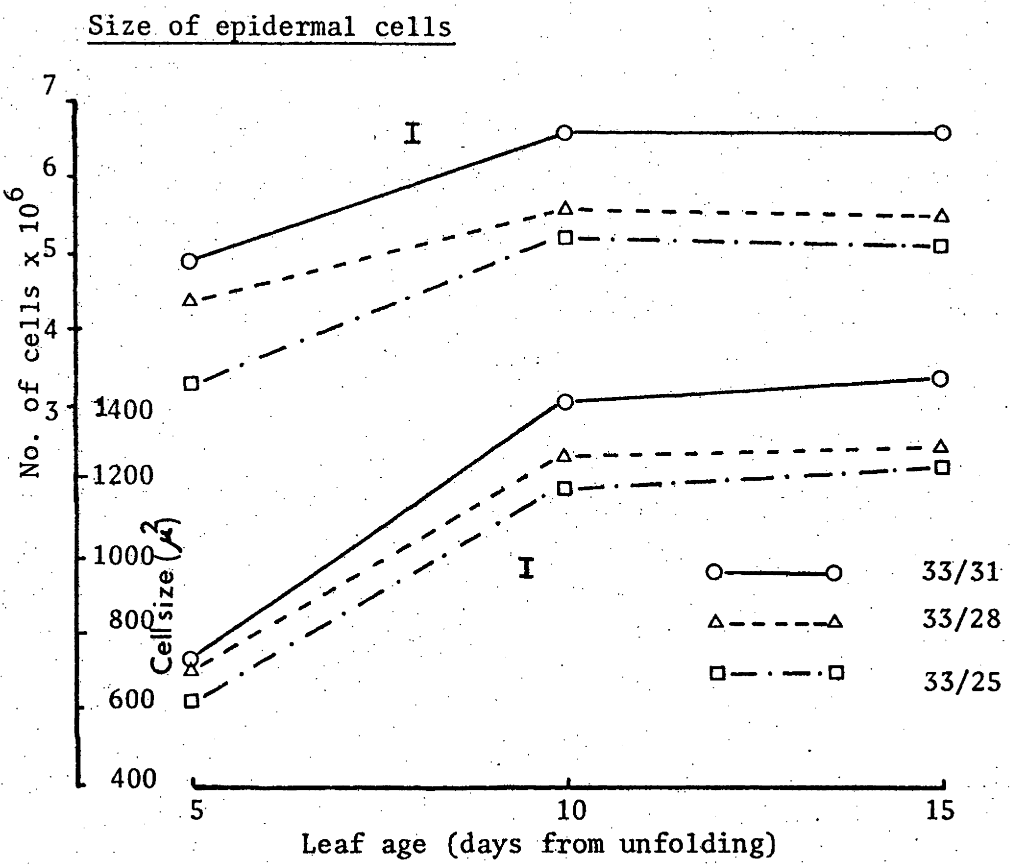


Figure 10.3 Change in number and size of epidermal cells with age of leaves of the seventh pair of teak seedlings grown at different temperatures

temperatures than at lower temperatures. The only exception was the difference at the early stage (day 5) between 33/28 and 33/31°C where although the cell size at 33/31°C was larger the difference was not statistically significant (Table 10.3, Figure 10.3).

Changes in the number and size of cells with leaf age indicated that cell division was complete well before leaf expansion was complete. There was a considerable increase in both the number and size of cells from day 5 to day 10. After day 10, the number of cells was unchanged but individual cells continued to expand.

Analysis of variance revealed a significant interaction between temperature and leaf age. It was noted that the increased size of cells from day 10 to day 15 in the leaves grown at 33/28 was slight and not significant compared with those grown at 33/25 and 33/31°C (Table 10.3, Figure 10.3).

10.3.1.3 Frequency of leaf production

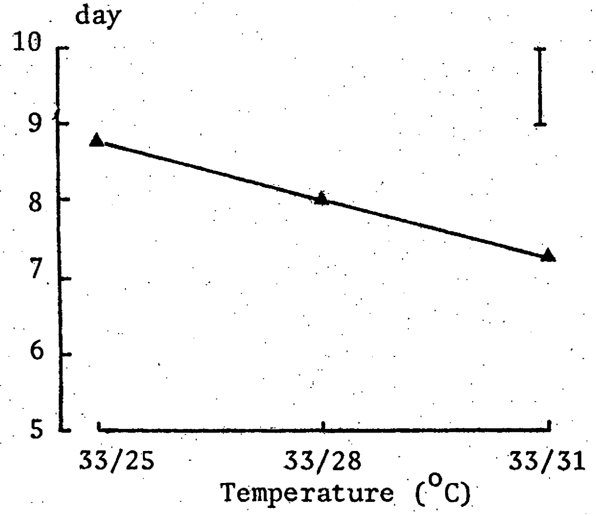
Seedlings grown at higher temperatures produced leaves at a faster rate than those grown at lower temperatures. The time interval between the commencement of unfolding of successive leaves was shorter at 33/31°C (7.3 days) and significantly longer at 33/25°C (8.8 days). The value recorded at the intermediate temperature, 33/28°C was intermediate (8.0 days) but did not differ significantly from each of the other temperatures (Table 10.4, Figure 10.4).

10.3.2 Experiment 2

Leaf growth of teak seedlings was changed after the seedlings had been transferred from both 33/28 and 33/31°C to 33/25°C (Table 10.5). Statistical analysis also revealed a significant interaction between the

Table 10.4 Effect of temperature on frequency of leaf production of teak seedlings. The data which do not have the same affix are significantly different at the 5% level according to Duncan's multiple range test

Parameter	Temperature (^{o}C) 33/25	 33/28	 33/31
Frequency of leaf production (day)	8.8^{a}	8.0^{a,b}	7.3^{b}



Frequency of leaf production

Figure 10.4 Effect of temperature on frequency of leaf production growing temperature and leaf age in some leaf characteristics but nevertheless, there was a tendency for the growth to be depressed as a result of decreased temperature (Tables 10.6 - 10.8).

10.3.2.1 Individual leaf area development and rate of leaf expansion

The patterns of the eighth leaf area development and the rate of expansion are shown in Figure 10.5.

There was a significant interaction between the growing temperature and leaf age. Although the growth curves of leaves followed a similar pattern, they differed in the steepness of slope. Leaves kept under 33/28 and 33/31°C throughout developed faster than those transferred to 33/25°C during the early stages. While the leaves kept under constant temperature conditions approached the fully expanded stage and the growth rate began to decline (at days 6-7) those transferred to 33/25°C just entered the most rapid growth period.

The decreased temperature resulted in a lower rate of development and the subsequent leaf area was smaller than under their original temperature conditions. The area of leaves kept continually at 33/31°C was 432.72 cm^2 and was reduced to 347.79 cm^2 at 33/25°C. Similarly, the area of leaves kept continually at 33/28°C was 326.62 cm^2 and was smaller at 33/25°C (302.54 cm^2). It was noted that the area recorded for leaves transferred from 33/31 to 33/25°C was still larger than that for leaves kept under 33/28°C throughout.

As for Experiment 1, the larger leaf area produced was due primarily to the higher rate of expansion (Table 10.6, Figure 10.6).

Table 10.5 Summarized results of analysis of variance of the data recorded in Experiment 2 and presented in 10.6-10.8. *,** and *** indicate significance at the 5,1 and 0.1% levels; ns indicates not significant at the 5% level.

Source of variation	Degrees of freedom	Mean squares	F-ratio
Leaf 8 area development			
Established tem. (ET)	1	136517.791	40.957***
Growing temp. (GT)	1	284608.965	85.387**
Leaf age (A)	14	408194.332	122.465***
ET x GT	1	17677.317	5.303*
ET x A	14	5064.902	1.520$^{\text{ns}}$
GT x A	14	6596.308	1.979*
ET x GT x A	14	1113.818	.334$^{\text{ns}}$
Error	240	3333.164	
Rate of leaf expansion			
Established temp. (ET)	1	2008.555	18.299***
Growing temp. (GT)	1	1062.833	9.683**
Leaf age (A)	14	9392.480	85.570***
ET x GT	1	249.725	2.275$^{\text{ns}}$
ET x A	14	144.824	1.319$^{\text{ns}}$
GT x A	14	1128.080	10.277***
ET x GT x A	14	107.403	.978$^{\text{ns}}$
Error	240	109.764	
Number of cells			
Established temp. (ET)	1	156.494×10^{12}	300.228***
Growing temp. (GT)	1	80.042×10^{12}	153.631***
Leaf Age (A)	2	141.681×10^{12}	271.940***
ET x GT	1	26.799×10^{12}	51.438***
ET x A	2	11.06×10^{11}	2.123$^{\text{ns}}$
GT x A	2	6.54×10^{11}	1.255$^{\text{ns}}$
ET x GT x A	2	3.4×10^{10}	.065$^{\text{ns}}$
Error	48	5.21×10^{11}	

Table 10.5 (cont)

Source of variation	Degrees of freedom	Mean squares	F-ratio
Epidermal cell size			
Established temp (ET)	1	20451.067	12.603***
Growing temp. (GT)	1	151403.266	93.255***
Leaf age (A)	2	2926850.937	1802.759***
ET x GT	1	3168.267	1.951 ns
ET x A	2	1293.017	.796 ns
GT x A	2	27806.517	17.127***
ET x GT x A	2	280.717	.173 ns
Error	48	1623.540	
Frequency of leaf production			
Established temp. (ET)	1	1.058	2.103 ns
Growing temp. (GT)	1	13.778	27.392***
ET x GT	1	.242	.481 ns
Error	16	.503	

Table 10.6 Effect of temperature and leaf age on leaf area development and rate of leaf expansion of leaves of the eighth pair. TT = Temperature throughout; TC = Temperature changed to 33/25°C

Estab. temp. °C	Growing temp.	Leaf age (days from unfolding)															LSD
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	(P=.05
Leaf 8 area development																	
33/28	TT	4.48	10.02	24.97	57.52	103.87	163.87	222.02	272.54	299.86	315.52	320.38	324.13	325.59	326.05	326.62	
	TC	3.22	6.19	12.29	25.56	49.90	86.50	134.80	187.40	232.40	266.36	284.35	293.79	298.24	302.34	302.54	
33/31	TT	5.46	4.61	25.82	60.15	114.54	193.78	271.46	340.34	380.97	411.51	422.46	432.45	432.56	432.72	432.72	50.61 (GTxA
	TC	3.71	6.79	12.78	28.26	56.06	96.66	149.50	205.08	256.19	196.39	324.56	327.75	345.00	347.79	347.79	
Rate of leaf expansion																	
33/28	TT		5.54	14.95	32.55	46.35	60.00	58.15	50.52	27.32	15.66	4.86	3.75	1.46	0.46	0.57	
	TC		2.97	6.10	13.27	24.34	36.60	48.30	52.60	45.00	23.96	17.99	9.44	4.45	4.10	0.20	
33/31	TT		6.15	14.21	34.33	54.39	79.24	77.68	68.88	40.63	30.54	10.95	9.99	0.11	0.16	-	9.18 (GTxA
	TC		3.08	5.99	15.48	27.80	40.60	52.24	55.58	51.11	40.20	28.17	13.19	7.25	2.79	-	

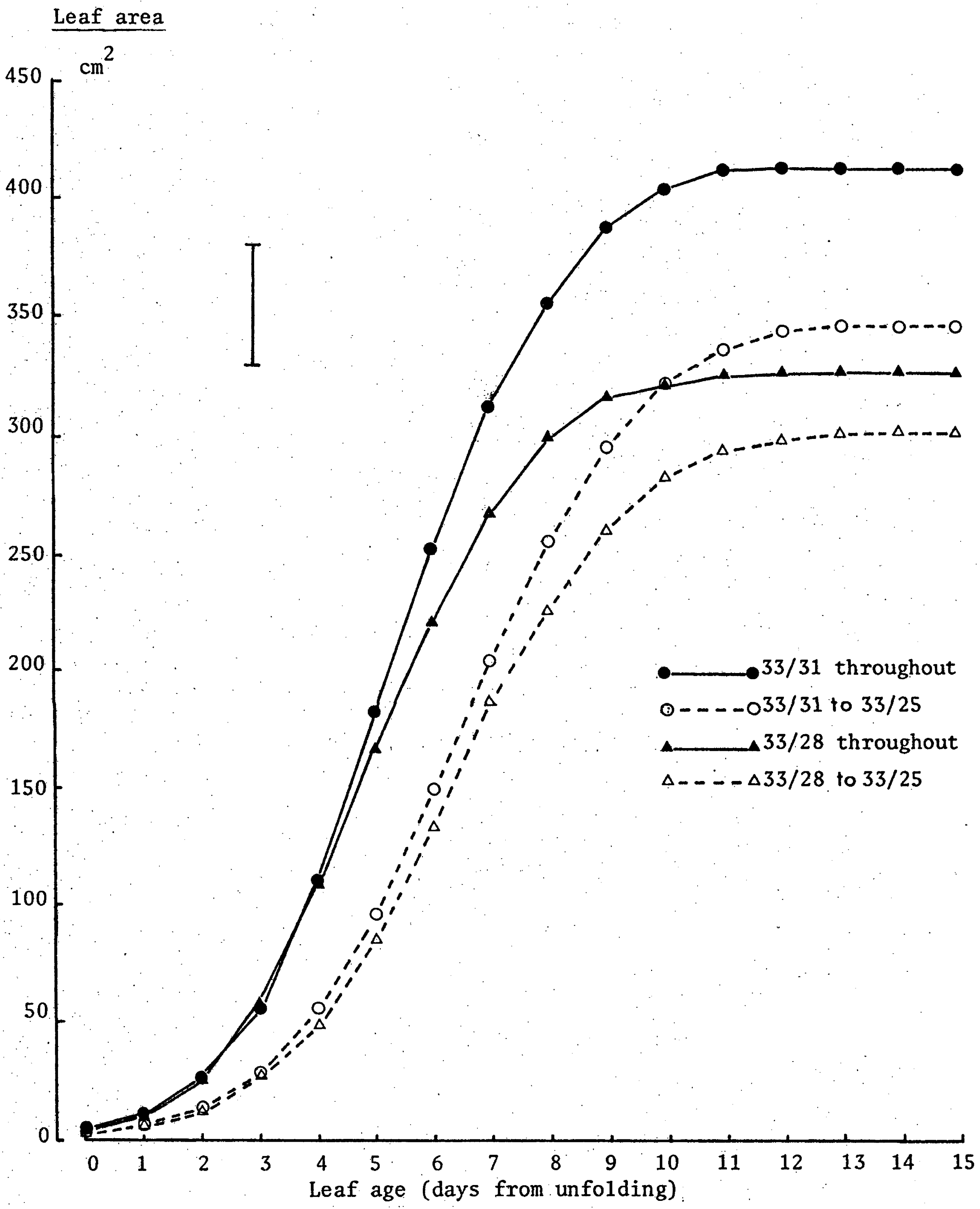


Figure 10.5 Effect of change in temperature from 33/28 and 33/31°C to 33/25°C on leaf area of the eighth pair of teak seedlings

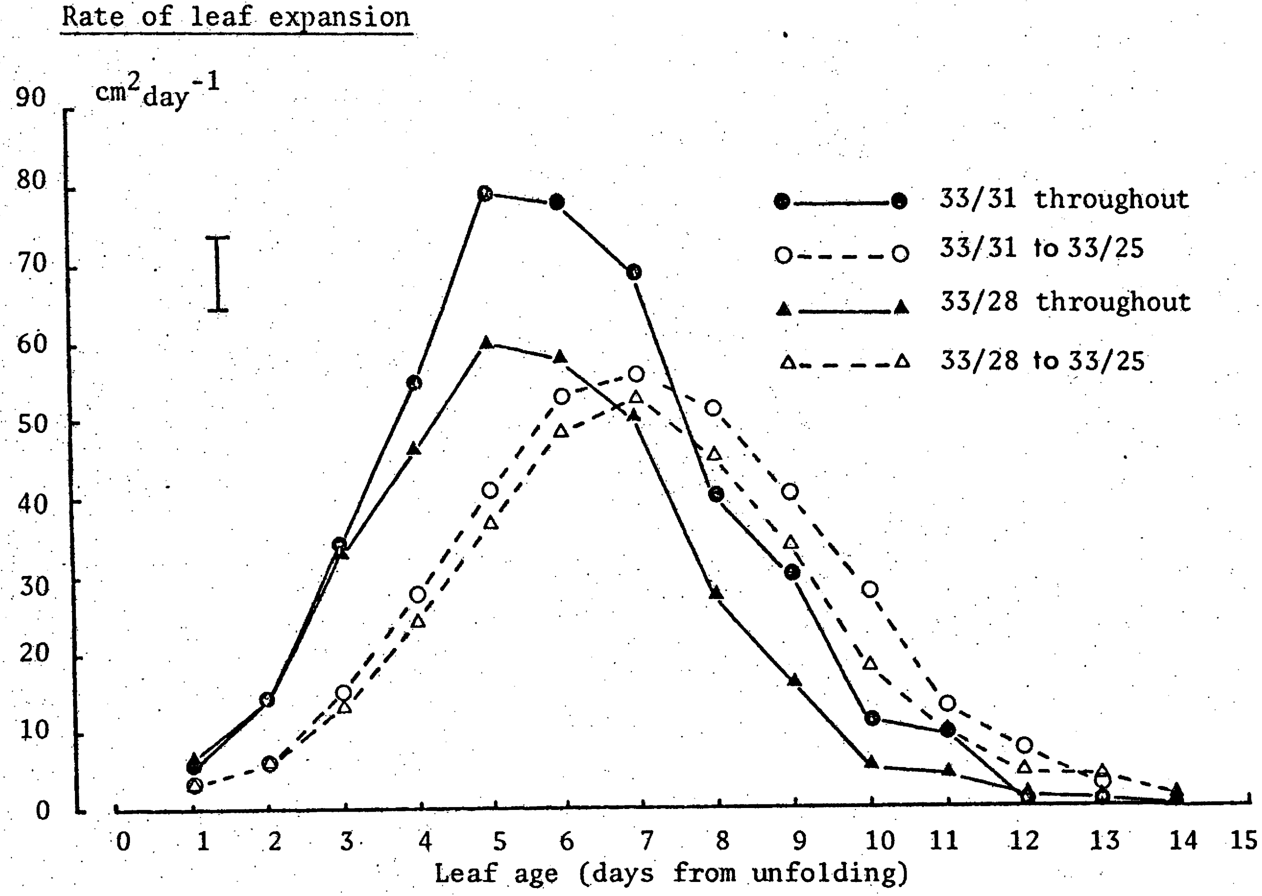


Figure 10.6 Effect of change in temperature from 33/28 and 33/31°C to 33/25°C on rate of leaf expansion of leaves of the eighth pair of teak seedlings

10.3.2.2 Number and size of epidermal cells

The decreases in temperature reduced the number and size of epidermal cells in the leaves (Table 10.7, Figure 10.7).

Despite the significant interaction effect, the number of cells was reduced on leaves transferred to the lower growing temperatures. For example, the number of cells recorded on leaves retained at 33/31°C were 18.6, 23.1 and 23.3 million over days 5, 10 and 15 respectively, and were reduced to 14.4, 19.9 and 19.8 million respectively at 33/25°C (Table 10.7, Figure 10.7). It was noted that the reduction in material subject to a change from 33/31 to 33/25°C was greater than that from 33/28 to 33/25°C.

Mean epidermal cell size was also reduced in seedlings transferred to 33/25°C. The size of cells recorded on leaves retained at 33/31°C throughout was 810, 1385 and 1456 μ^2 at days 5, 10 and 15 respectively, and was smaller at the same days, 620, 1283 and 1400 μ^2 when transferred to 33/25°C. There were no differences in the cell size of the leaves at 33/25°C between those transferred from 33/28 and 33/31°C (Table 10.7, Figure 10.7).

10.3.2.3 Frequency of leaf production

The frequency of leaf production was delayed as a result of the decreased temperature. Under 33/28 and 33/31°C throughout, the time interval between two successive leaves becoming unfolded was 8.7 and 8.0 days respectively, and was longer after transfer to 33/25°C (10.1 and 9.9 days respectively) (Figure 10.8).

Table 10.7 Effect of change in temperature and leaf age on number and size of cells of the eighth leaves of teak seedlings. The data which do not have the same affix are significantly different at the 5% level according to Duncan's multiple range test. TT = Temperature throughout; TC = Temperature changed to 33/25°C

Parameters	Established temp. (°C)	Growing temp. (°C)	Leaf age (day)		
			5	10	15
No. of cells x 10^6	33/28	TT	14.4^{a}	$18.4^{b,c}$	$18.5^{b,c}$
		TC	13.2	$17.7^{b,c}$	17.5^{b}
	33/31	TT	18.6^{c}	23.1^{e}	23.3^{e}
		TC	14.4^{a}	19.9^{d}	19.8^{d}
Cell size(μ^2)	33/28	TT	774^{b}	1345^{d}	1377^{d}
		TC	602^{a}	1269^{c}	1367^{d}
	33/31	TT	810^{b}	1385^{d}	1456
		TC	620^{a}	1286^{c}	1400^{d}

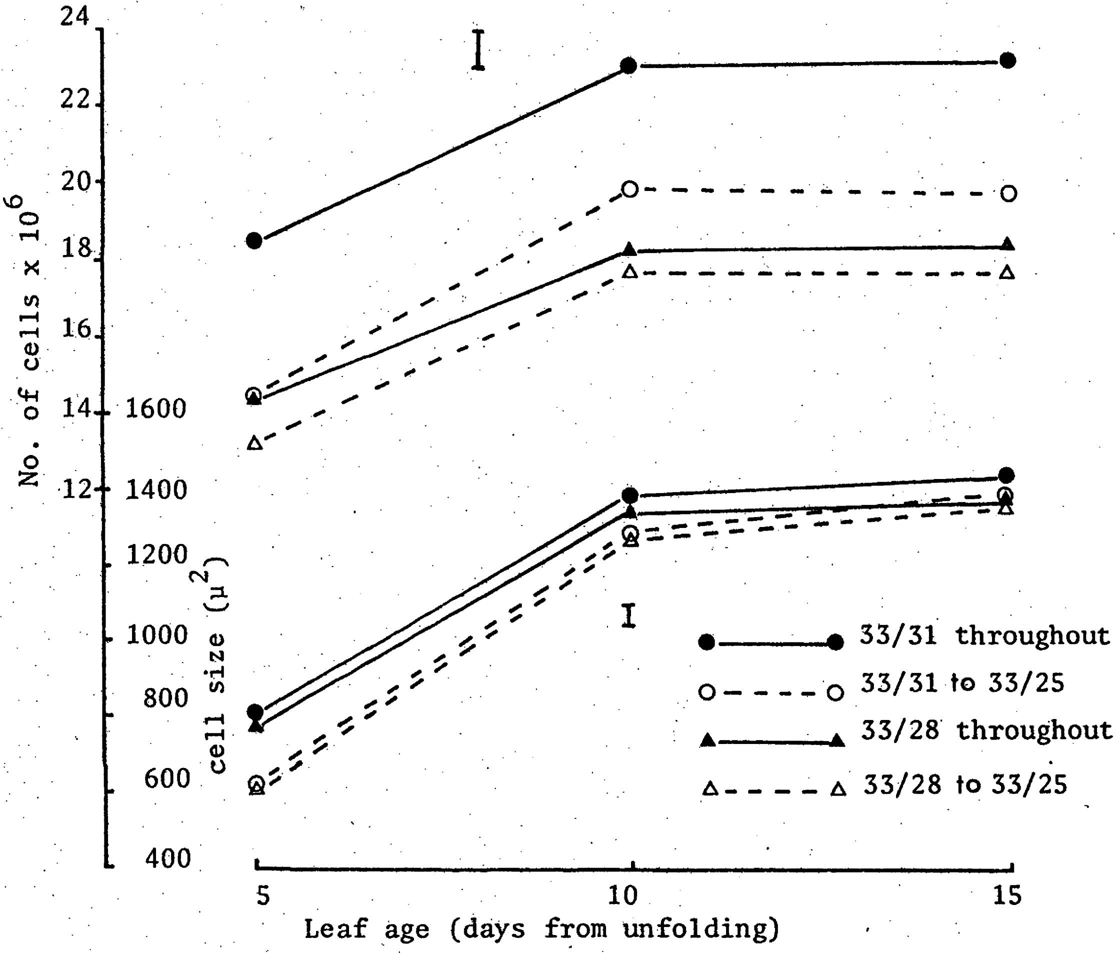


Figure 10.7 Effect of change in temperature from 33/28 and 33/31°C to 33/25°C on number and size of epidermal cells of leaves of the eighth pair of teak seedlings

Table 10.8 Effect of change in temperature on frequency of leaf production of teak seedlings. Data which do not have the same affix are significantly different at the 5% level according to Duncan's multiple range test.
TT = Temperature throughout; TC = Temperature changed to 33/25°C

Parameter	Established temp. °C	Growing temp. °C TT	TC	Mean
Frequency of leaf production (day)	33/28	8.7^{a}	10.1^{b}	9.4
	33/31	8.0^{a}	9.9^{b}	9.0
	Mean	8.4	10.0	

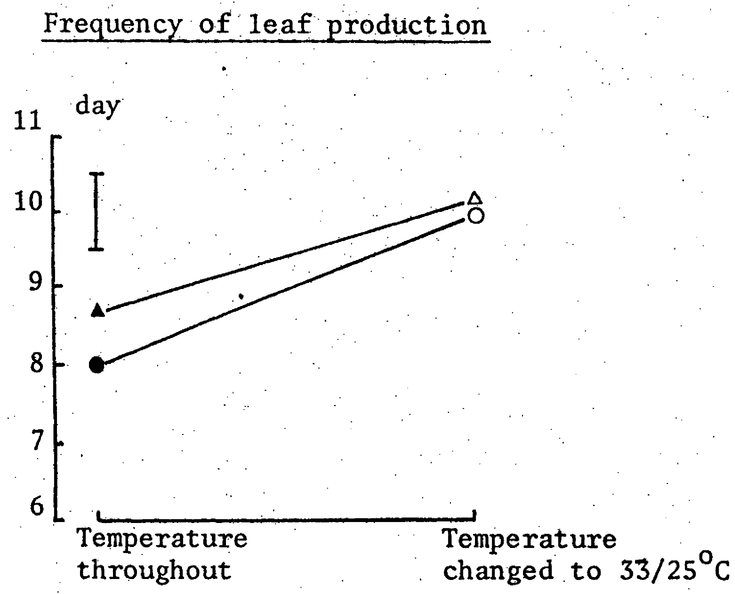

Frequency of leaf production

Figure 10.8 Effect of change in temperature from 33/28 and 33/31°C to 33/25°C on frequency of leaf production of teak seedlings

- ● 33/31 throughout
- ○ 33/31 to 33/25
- ▲ 33/28 throughout
- △ 33/28 to 33/25

10.4 DISCUSSION

The results obtained from the two experiments indicate an important effect of temperature in influencing the growth and development of leaves of teak seedlings. Within the temperature range studied (33/25, 33/28 and 33/31°C) individual leaf area, rate of leaf expansion, number and size of cells, and rate of leaf production appeared to be favoured by higher temperatures rather than lower temperatures.

Lowering the temperature from 33/28 and 33/31 to 33/25°C resulted in poorer development. The decreased growth was more pronounced in the seedlings transferred from 33/31°C than those from 33/28°C. However the area of the leaves originally at 33/31°C was still larger than that at 33/28°C. This indicates high temperatures stimulate leaf growth and development, and that leaves of teak seedlings are sensitive to change in temperature.

Temperature does not appear to affect the period of leaf development. In both experiments and at all temperature regimes, the period of leaf development from unfolding to final size was about 13-14 days. However, temperature does seem to affect emergence of new leaves as shown by the frequency of leaf production. The higher the temperature, the higher the frequency of leaf production.

Individual leaf area was greater at the higher temperatures. Estimation of the number and size of epidermal cells present in the leaves indicate that the larger area of leaves at higher temperatures was largely due to increased cell number and increased cell size.

The pattern of change with time in individual leaf area showed the rate of leaf expansion during the rapid growth period was important in determining the final area. The rate of expansion during this period was greater at higher temperatures than at lower temperatures and there were only small differences at other stages of development.

Total leaf area of individual seedlings would be larger at the higher temperatures. There were more leaves produced and these individual leaves were larger.

Leaves are the most important photosynthetic material of a plant. Greater leaf area generally provides more photosynthetic material which in turn generates higher photosynthetic production. Thus leaf area production may be of particular importance in determining teak seedling performance particularly at high temperatures.

Changes in cell size and number with leaf age were similar in all temperatures despite the significant interaction effect. The results indicated that cell division and cell expansion were concurrent in the early stages of leaf development; there was increase in both size and number of cells with leaf age. Cell production ceased before leaves attained final area but expansion continued. The increase in cell size after the cessation of division was however comparatively small.

Effect of temperature on the growth and development of leaves of teak seedlings appears to be similar to that generally observed for other species. Milthorpe (1959) reported that rate of leaf expansion and number of leaves produced by plants of *Cucumis sativus* were generally greater at the higher temperature within the range 12-24^{o}C. When the plants were transferred from 24^{o}C to a lower temperature of 18^{o}C, the rate of leaf expansion decreased substantially. Blackman (1956) reported that leaves of plants of *Helianthus annuus, Lemna minor* and *Salvinia natans* developed better at the higher temperature within the range 20-30^{o}C.

Njoku (1957) compared the development of leaves of *Ipomoea caerulea* grown at low (22^{o}C) and high (30^{o}C) night temperatures. The area of individual leaves was found to be larger at the higher night temperature. He pointed out that the occurrence of larger leaves at the higher night temperature was due to both more and larger epidermal cells. Milthorpe (1956) also found cell expansion in leaves of *Cucumis sativus* was retarded by low temperature (12°C).

10.5 CONCLUSION

The importance of temperature as a control of leaf growth and development of teak seedlings has been demonstrated. Within the temperature range studied (33/25, 33/28 and 33/31°C) teak seedlings produce larger and more leaves with more and larger-sized cells at higher temperatures than at lower temperatures. The larger leaves at higher temperatures were due to the higher rate of leaf expansion during the rapid growth period and not to expansion being continued for a longer period.

CHAPTER 11

EFFECT OF TOTAL RADIATION AND DAYLENGTH ON THE GROWTH AND DEVELOPMENT OF LEAVES OF TEAK SEEDLINGS

11.1 INTRODUCTION

In this chapter, the effect of total radiation and daylength on leaf growth is examined.

11.2 MATERIALS AND METHODS

The seedlings used were part of the experiment outlined in Chapter 6. There were two levels of total radiation (50 and 100 cal $cm^{-2}day^{-1}$) and three daylengths (8, 12 and 16 hours) with a common temperature regime of 30/25°C. Details of the light levels in these treatments are shown in Figure 11.1 (Figure 6.1 repeated for convenience of reference).

Measurements of leaf growth were made on ten seedlings from each treatment. These were germinated and grown in a 30/25°C day/night temperature glasshouse. The seedlings had developed three pairs of leaves when the experimental treatments commenced. Frequency of leaf production was noted for each seedling over a period of six weeks.

The leaves in the eighth pair were used for the study of individual leaf development. As before, measurements commenced when the lamina unfolded from the terminal bud and continued for 15 days when the leaves had attained their final size. Leaf length and width were recorded daily and mean leaf area of each pair calculated using the procedure outlined in section 10.2.1.1. Data for rate of leaf expansion were obtained from

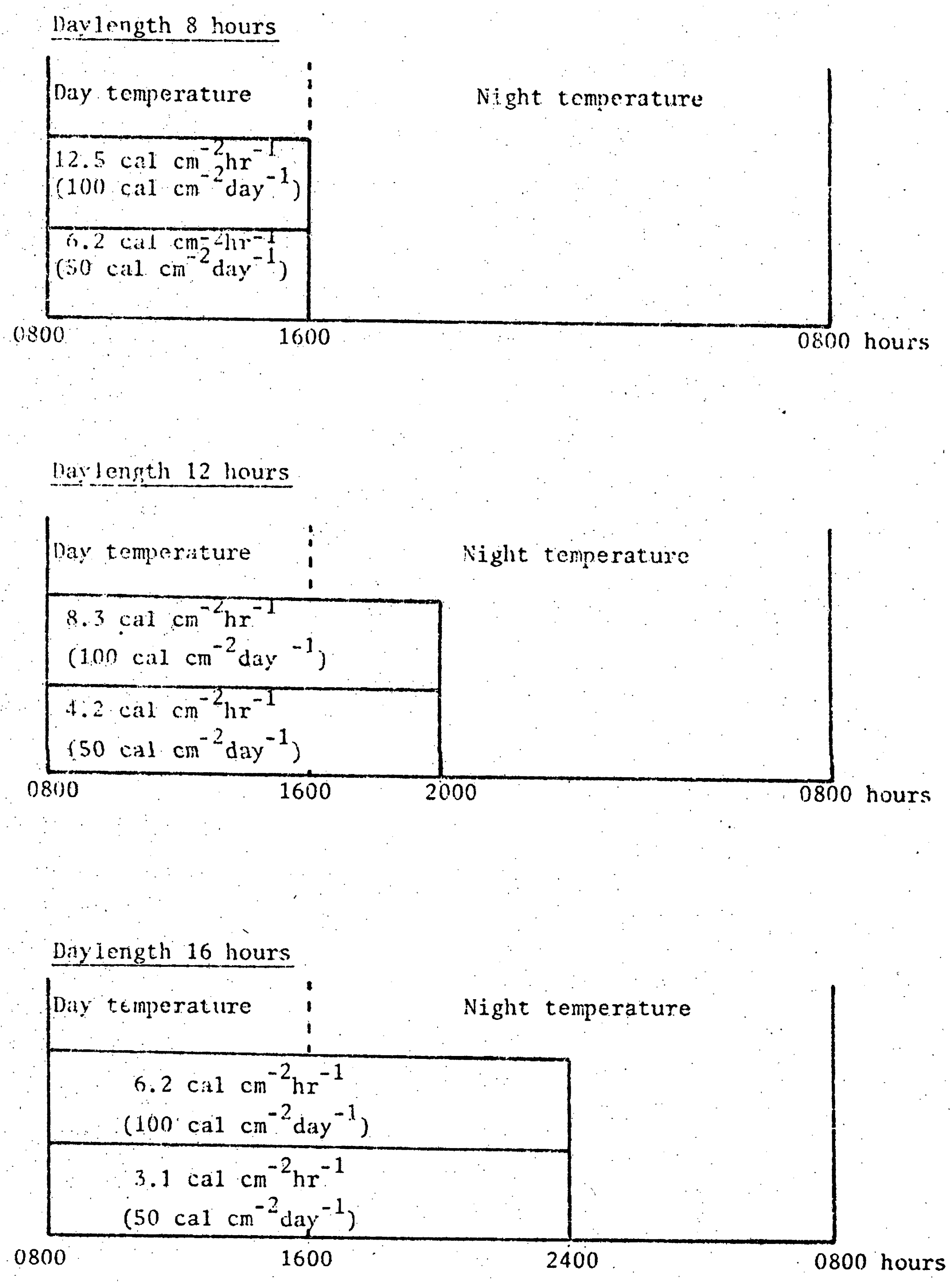


Figure 11.1 Diagram showing details of experimental treatments.

daily increment of the mean leaf area over the period of leaf development.

Epidermal cell number and size in the eighth leaf pair were determined at day 15. Leaves of six seedlings were taken at random for these impressions. The procedure used was identical with that described in section 10.2.1.3 except that the data were collected once only. Number of cells in each leaf was calculated from the mean number of cells per mm^2 of the lamina, and mean size of cells obtained from the number of cells in the measured field of 0.02 mm^2.

All data were subjected to analysis of variance. Daily figures were available for leaf area and for rate of expansion. These were analysed with total radiation x daylength x leaf age at the major sources of variation. The data for the final area of leaves of the eighth pair, cell number and size and for frequency of leaf production had total radiation and daylength as the major sources of variation. Duncan's multiple range test was used to determine the significance of differences between treatment means.

11.3 RESULTS

Growth of leaves was affected by total radiation and daylength. Values for rate of development of individual leaves showed a significant total radiation x daylength interaction (Table 11.1).

11.3.1 Effect of Total Radiation

11.3.1.1 Individual leaf area and rate of leaf expansion

Effect of total radiation on development of individual leaves appeared to be masked by a significant and confusing total radiation x daylength interaction. There was a tendency for the leaves at 100 cal $cm^{-2}day^{-1}$ to be larger than those at 50 cal $cm^{-2}day^{-1}$ levels. This was due to these leaves having a slightly greater rate of expansion and maintaining development for slightly longer (i.e. after day 10) (Table 11.2, Figures 11.2, 11.3). This resulted in a slightly greater final area of these leaves (Table 11.3).

11.3.1.2 Number of cells and mean epidermal cell size

Leaves of seedlings growing at the higher total radiation had more but smaller cells than those growing at the lower total radiation (Table 11.8, Figures 11.4A-B).

Pooled values for the number of cells of leaves growing at 100 cal $cm^{-2}day^{-1}$ was 20.3 million and was significantly greater than at 50 cal $cm^{-2}day^{-1}$, 15.8 million (Table 11.3, Figure 11.4A).

In contrast to the number of cells, mean epidermal cell size was smaller at the higher total radiation. The pooled values were 1335 and 1551 μ^2 for 100 and 50 cal $cm^{-2}day^{-1}$ respectively (Table 11.3, Figure 11.4B).

11.3.1.3 Frequency of leaf production

The time interval between two successive leaves unfolding was shorter at the higher total radiation than at the lower (Table 11.3, Figure 11.5). Thus there were more leaves produced by seedlings grown at the higher total radiation.

11.3.2 Effect of Daylength

11.3.2.1 Number of cells and mean epidermal cell size

The number of cells in the leaves did not differ significantly between daylengths with the same total radiation. However the values recorded at daylength 16 hours tended to be greater than those at 8 hours.

Table 11.1 Summarized results of analysis of variance of the data presented in Table 11.2.
*, ** and *** indicate significance at the 5, 1 and 0.1% levels respectively; ns indicates not significant at the 5% level

Source of variation	Degrees of freedom	Mean squares	F-ratio
Leaf 8 area development			
Total radiation (R)	1	4864.295	2.741^{ns}
Daylength (D)	2	7116.715	4.010*
Leaf age (A)	14	651521.383	367.111***
R x D	2	9902.844	5.580**
R x A	14	988.583	.557^{ns}
D x A	28	378.328	.213^{ns}
R x D x A	28	276.307	.156^{ns}
Error	810	1774.728	
Rate of leaf expansion			
Total radiation (R)	1	319.211	4.397*
Daylength (D)	2	18.121	.250^{ns}
Leaf age (A)	14	11528.810	108.786***
R x D	2	82.256	1.133^{ns}
R x A	14	83.311	1.147^{ns}
D x A	28	89.833	1.237^{ns}
R x D x A	28	44.558	.614^{ns}
Error	810	72.606	

Table 11.1 (cont)

Source of variation	Degrees of freedom	Mean squares	F-ratio
Leaf 8 area			
Total radiation (R)	1	4324.64	1.05^{ns}
Daylength (D)	2	95.835	$.023^{ns}$
R x D	2	781.27	$.190^{ns}$
Error	54	4117.035	
Number of cells			
Total radiation (R)	1	17.689×10^{13}	13.223***
Daylength (D)	2	28.511×10^{12}	2.131^{ns}
R x D	2	18.126×10^{12}	$.981^{ns}$
Error	54	13.377×10^{12}	
Mean epidermal cell size			
Total radiation (R)	1	418606.996	33.988***
Daylength (D)	2	148989.086	12.097***
R x D	2	553.083	$.045^{ns}$
Error	54	12316.153	
Frequency of leaf production			
Total radiation (R)	1	2.773	5.416*
Daylength (D)	2	1.350	2.637^{ns}
R x D	2	.066	$.129^{ns}$
Error	54	.512	

Table 11.2 Effect of total radiation, daylength and leaf age on leaf area development and rate of leaf expansion of the eighth pair of teak seedlings

Tot. radiation cal cm^{-2} day^{-1}	Daylength hr.	Leaf age (days from unfolding)															Mean	LSD P=.05
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14		
Leaf 8 area development cm^2																		
	8	2.73	4.98	9.71	20.64	38.90	65.82	98.88	138.27	178.32	209.50	229.52	246.00	252.85	255.69	256.26	133.87	
50	12	2.56	4.61	8.57	16.73	21.82	54.51	54.06	117.30	150.50	183.48	205.63	227.71	239.07	243.07	244.29	120.95	
	16	2.61	5.16	10.11	21.60	41.55	67.54	107.74	147.07	179.99	205.65	226.00	239.78	248.86	253.04	254.30	134.07	
	8	2.38	4.32	7.74	15.51	27.73	50.37	80.00	116.84	157.18	193.83	221.79	241.35	254.29	258.82	260.93	126.21	9.5
100	12	2.95	5.84	10.14	18.96	37.09	62.91	95.40	134.02	170.61	205.78	231.77	253.51	264.51	271.41	273.95	135.92	(RxD)
	16	2.62	4.70	8.77	18.58	37.81	68.59	103.11	145.48	188.88	220.67	247.68	259.87	367.02	270.04	270.93	140.98	
Rate of leaf expansion cm^2/day																		
	8		2.25	4.73	11.43	17.76	26.92	33.06	40.38	40.05	32.18	18.99	16.48	6.85	2.56	0.57		
50	12		2.05	3.86	8.16	15.09	22.69	29.55	33.24	33.50	22.68	22.15	22.08	11.36	4.0	1.22		
	16		2.55	4.95	11.49	19.95	25.99	40.20	39.33	32.92	25.66	20.35	13.78	9.8	4.18	1.26		4.3
	Mean		2.28	4.51	10.36	17.60	25.20	34.60	37.35	35.49	30.17	20.50	19.45	9.10	3.58	1.02		(RxA)
	8		1.94	3.42	7.77	12.22	22.64	29.63	36.84	40.34	36.65	27.96	19.56	12.94	4.53	2.11		
100	12		2.89	4.30	8.82	18.13	25.82	32.49	30.62	36.59	35.17	25.99	21.74	11.00	6.90	2.54		
	16		2.08	4.07	9.81	19.23	30.78	34.52	42.37	43.40	31.79	27.01	12.19	7.15	3.02	0.89		
	Mean		2.3	2:03	8.08	16.53	26.41	32.21	39.28	40.11	34.54	26.99	17.88	10.36	4.82	1.85		

Table 11.3 Effect of total radiation and daylength on leaf 8 area, number of cells, mean epidermal cell size, and frequency of leaf production of teak seedlings.
Within each parameter, the data which do not have the same affix are significantly different at the 5% level according to Duncan's multiple range test

Parameter	Total radiation cal $cm^{-2}day^{-1}$	Daylength (hr) 8	12	16	Mean
Leaf 8 area (cm^2)	50	256.26^{a}	244.29^{a}	254.30^{a}	251.62
	100	260.93^{a}	273.95^{a}	270.93^{a}	268.60
	Mean	258.60	259.12	262.62	
Number of cells $x10^6$	50	15.2^{a}	15.1^{a}	17.1^{a}	15.8
	100	$17.5^{a,b}$	21.7^{b}	21.6^{b}	20.3
	Mean	16.4	18.4	19.4	
Mean epidermal cell size (μ^2)	50	1657^{a}	$1560^{a,b}$	$1435^{b,c}$	1551
	100	$1450^{b,c}$	$1329^{c,d}$	1226^{d}	1335
	Mean	1554	1445	1330	
Frequency of leaf production (day)	50	7.9^{a}	$7.5^{a,b}$	$7.5^{a,b}$	7.6
	100	$7.5^{a,b}$	7.0^{b}	7.2^{b}	7.2
	Mean	7.7	7.3	7.4	

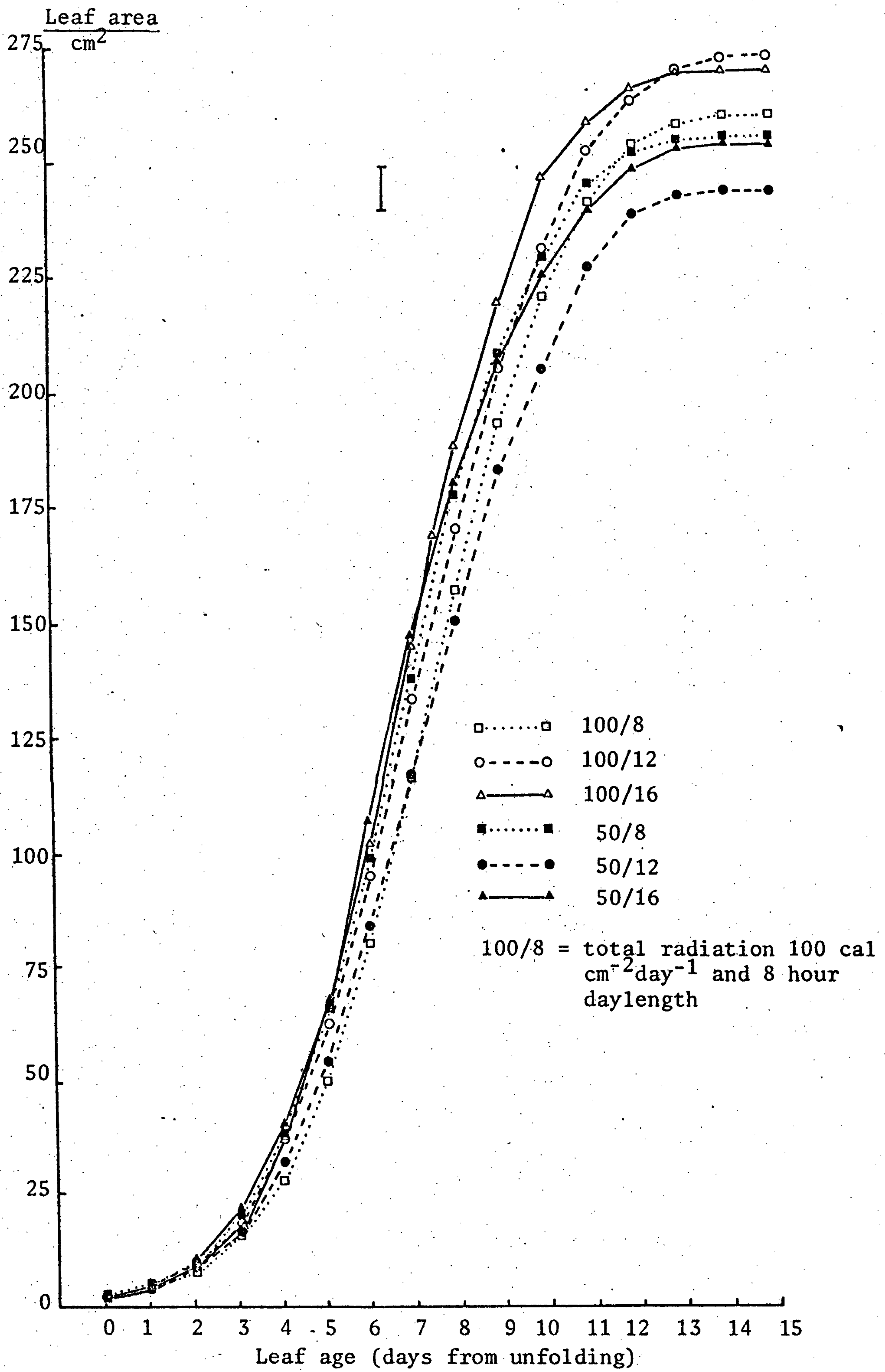


Figure 11.2 Change in leaf area with age of leaves of the eighth pair of teak seedlings grown under different conditions of total radiation and daylength

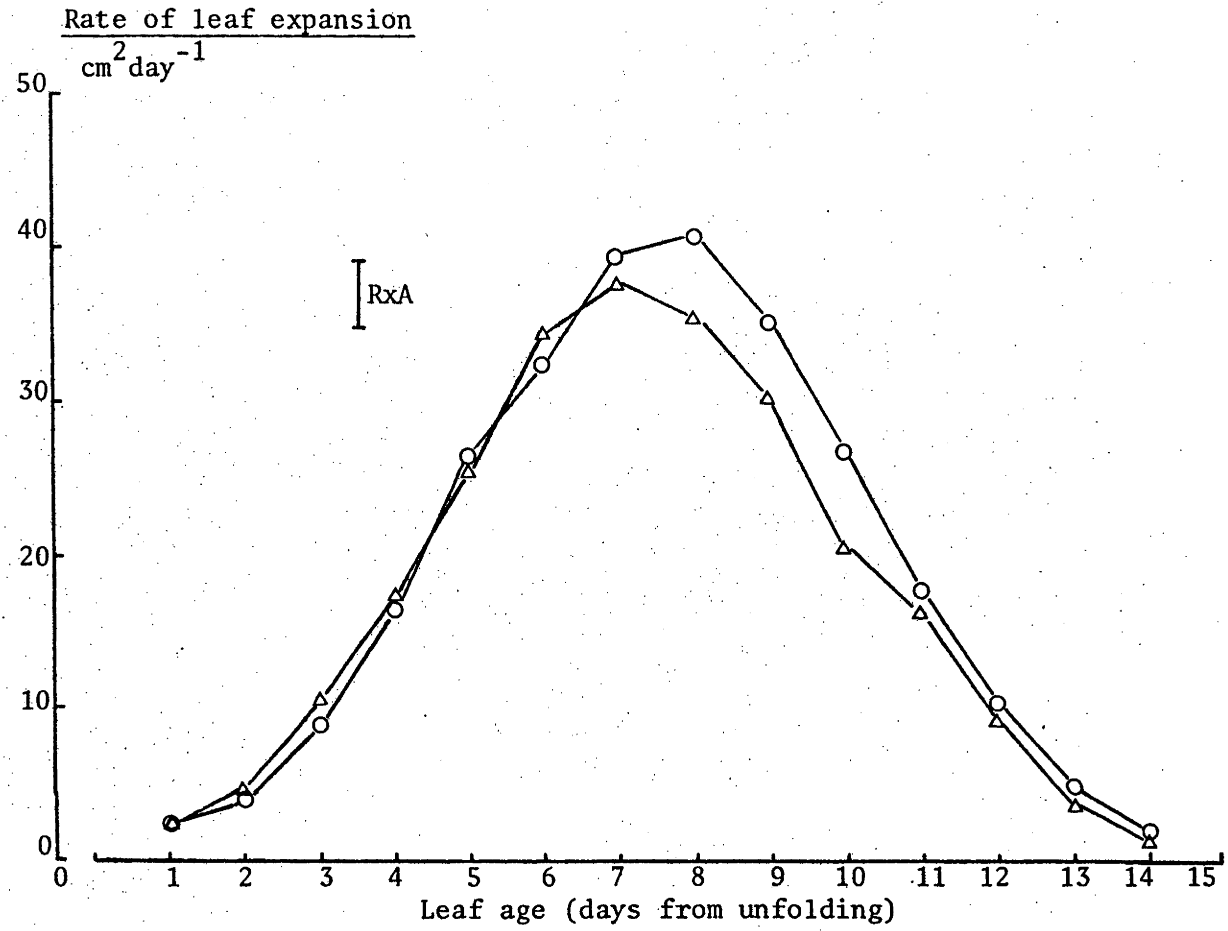


Figure 11.3 Change in rate of leaf expansion with age of leaves of the eighth pair of teak seedlings grown under different total radiation levels
o___o 100 cal $cm^{-2}day^{-1}$
Δ___Δ 50 cal $cm^{-2}day^{-1}$

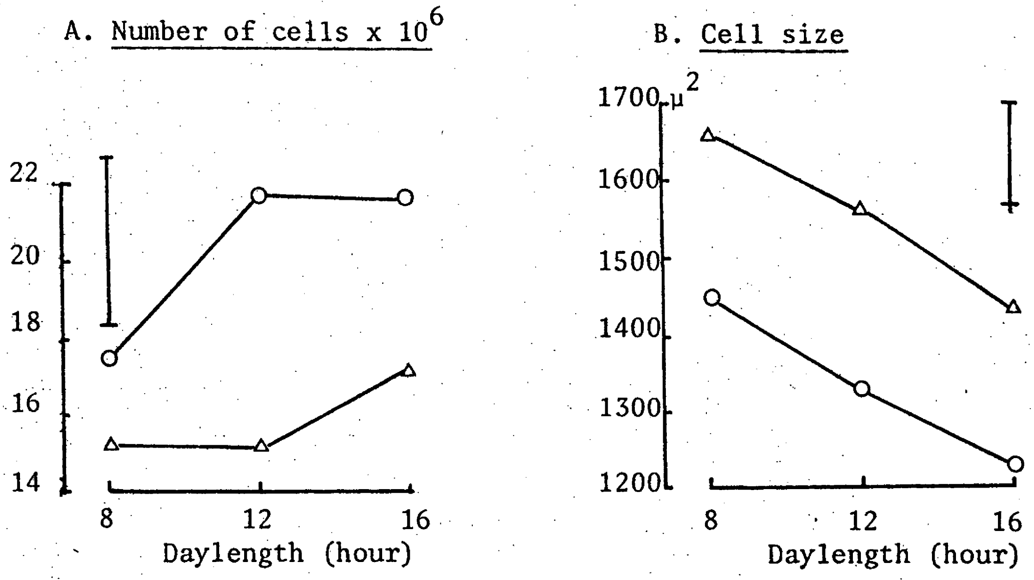


Figure 11.4 Effect of total radiation and daylength on number and size of cells of leaves of the eighth pair of teak seedlings
o——o 100 cal cm^{-2}day^{-1}
Δ——Δ 50 cal cm^{-2}day^{-1}

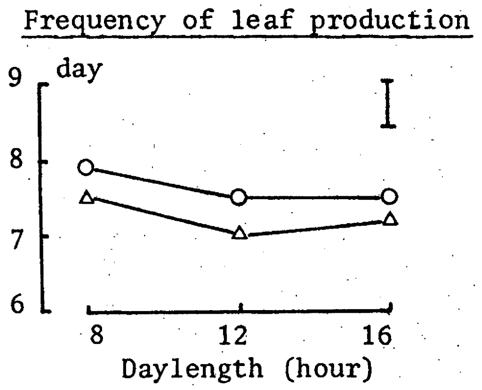


Figure 11.5 Effect of total radiation and daylength on frequency of leaf production of teak seedlings
o——o 100 cal cm^{-2}day^{-1}
Δ——Δ 50 cal cm^{-2}day^{-1}

For example, under 50 cal $cm^{-2}day^{-1}$, there were 17.1 million cells in the leaves at 16 hours and 15.2 million cells at 8 hours. Similarly under 100 cal $cm^{-2}day^{-1}$ there were 21.6 million cells at 16 hours compared with 17.5 million cells at 8 hours (Table 11.3, Figure 11.4A).

There were significant differences in the size of cells between daylengths. Under both total radiation levels, cells were smaller at longer day than at shorter day. The values recorded were 1657, 1560 and 1435 μ^2 at 8, 12 and 16 hours respectively under 50 cal $cm^{-2}day^{-1}$, and were 1450, 1329 and 1226 μ^2 respectively under 100 cal $cm^{-2}day^{-1}$ (Figure 11.4B).

11.3.2.3 Frequency of leaf production

There were no differences in the frequency of leaf production between daylengths. However there was a tendency for the seedlings grown at the shortest day (8 hours) to produce fewer leaves than those grown at the longer days. For example under total radiation 50 cal $cm^{-2}day^{-1}$, the time interval required for two successive leaves to unfold was 7.9 days at 8 hours compared with 7.5 days at 12 and 16 hours (Table 11.3, Figure 11.5).

11.4 DISCUSSION

The results showed both total radiation and daylength had a small effect on the growth of leaves of teak seedlings.

There was no clear difference in the development of individual leaves of seedlings grown under different light conditions. However there was a tendency for the leaves growing at the higher total radiation to be slightly larger. This was due to these leaves having a slightly greater expansion rate and maintaining development for a slightly longer period.

A count of epidermal cells present in each leaf suggested that variations in leaf size were due to both number and size of cells. At higher total radiation there were more but smaller cells in the leaves. Similarly, the size of cells was much smaller at longer days giving more cells in the leaves.

The larger number but smaller size of cells present in the leaves at higher total radiation found in this study is in accord with the findings of Milthorpe and Newton (1963) in the study of expansion of leaves of *Cucumis sativus*. Milthorpe and Newton reported that cell division was greater at higher total radiation, and accordingly number of cells increased sharply as leaf area increased. These cells were still in the early stages of expansion at the time cell division stopped. Because the rate of cell expansion was low after the cessation of cell division, these cells still remained at a small size by which time the leaf reached the fully expanded stage.

11.5 CONCLUSION OF PART III

The studies reported in Chapters 8-11 have demonstrated that

(1) The rate of photosynthesis of teak seedlings is increased by an increase in light intensity within the range 200-800 $\mu Em^{-2}sec^{-1}$ (800-3700 f.c.). It appears light compensation point and light saturation level are 55 $\mu Em^{-2}sec^{-1}$ (200 f.c.) and 900 $\mu Em^{-2}sec^{-1}$ (4000 f.c.) respectively (Chapter 8).

(2) The rate of photosynthesis and respiration of teak seedlings increase with an increase in temperature within the range 25-31^{o}C (Chapter 9).

(3) Within a day temperature of 33^{o}C and night temperatures of 25, 28 and 31^{o}C the teak seedlings at the higher night temperatures produced more and larger leaves with a faster rate of expansion than those at the lower night temperatures. These larger leaves contained more and larger cells (Chapter 10).

(4) Teak seedlings grown at total radiation of 100 cal cm^{-2}day^{-1}and at 16 hour day produced more and slightly larger leaves than those grown at total radiation of 50 cal cm^{-2}sec^{-1} at 8 hour day. There were more but smaller cells in the leaves at the higher total radiation level and at the longer day (Chapter 11).

PART IV

GENERAL DISCUSSION AND CONCLUSION

The studies in Part III have demonstrated how broad ranges of temperature and light radiation affect photosynthesis, respiration and leaf development of teak seedlings. In this part of the thesis, the performance of seedlings recorded in the earlier studies in Parts I and II are interpreted based on knowledge obtained from the studies in Part III.

Chapter 12 outlines interpretation of the results of the studies in Parts I and II using the results of photosynthesis, respiration and leaf development in Part III.

A conclusion of the studies in this thesis is given in Chapter 13.

CHAPTER 12

GENERAL DISCUSSION

12.1 INTERPRETATION OF THE RESULTS OF THE STUDIES IN PARTS I AND II

The studies reported in Part III have demonstrated how broad ranges of temperature and radiation affect the photosynthesis, respiration and leaf structure and development of teak seedlings. The performance of the seedlings in the studies detailed earlier in Parts I and II can now largely be explained in terms of simple response to temperature and radiation effects under phytotron conditions. Interpretation in this way removes many of the anomalies noted previously.

The results of the experiments detailed in Parts I and II have been summarized in Tables 12.1-12.11. These tables include estimates of results which would be anticipated on the basis of the knowledge of variation of photosynthesis, respiration and leaf characteristics gained in Part III.

In presenting the summaries account has been taken of the seasonal variation of photoperiod in the open glasshouses. In summer, the natural photoperiod is about 14-15 hours and sufficient light for photosynthesis is maintained well into the period of night temperature (1630 - 0830 hours). In contrast in winter daylengths are shorter and much less photosynthesis will take place during the period of night temperature. These seasonal differences would be accentuated particularly during the period of night temperature by the lower light intensities prevalent in winter.

Table 12.1 Interpretation of the results of the studies detailed in Parts I and II using the results of photosynthesis, respiration and leaf characteristics outlined in Part III.
DMP = Dry matter production; LA = Leaf area

CHAPTER 3	DMP	LA	LAR	NAR
MYSORE AND KERALA PROVENANCES UNDER SUMMER CONDITIONS - OPEN GLASSHOUSE				
33/25 36/31 (Exp. 4)	Greater at higher temperature	As DMP	As DMP	As DMP
33/25 33/28 36/31 (Exp.5)	"	"	"	"

PREDICTED EFFECT		INTERPRETATION	COMMENT
Net photosynthesis	increase with temperature up to 31°C. Rate at higher temperature is unknown.	(1) NAR will increase with night temperature (2) Effect of 36°C day temperature unknown	NAR does increase with increased temperature
Respiration	Increase with increased temperature		
No. of leaves	More at higher temperature	(1) LA will increase with temperature	Confirmed by LA pattern
Cell No.	More at higher temperature	(2) LAR may increase with temperature depending on overall photosynthetic production and allocation to plant parts	LAR does increase with temperature
Cell size	Larger at higher "		
OVERALL INTERPRETATION	The production of photosynthate must have been maintained at 36/31°C to give the increased DMP and leaf production at this temperature despite the higher respiration losses at night		

Table 12.2 Interpretation of the results of the studies detailed in Parts I and II using the results of photosynthesis, respiration and leaf characteristics outlined in Part III.
DMP = Dry matter production; LA = Leaf area

CHAPTER 3	DMP	LA	LAR	NAR
MYSORE PROVENANCE UNDER WINTER CONDITIONS - BT CABINET (NIGHT TEMPERATURE VARIES)				
33/19 33/25 33/28 33/31 (Expt. 1)	Increase with temperature up to 33/25°C and decrease at higher temperatures	As DMP	Increase with increased temperature	As DMP

	PREDICTED EFFECT	INTERPRETATION	COMMENT
Net Photo-synthesis	No effect - day temperatures are all the same	NAR will decrease with temperature	Incorrect, NAR peaks at 33/25°C
Respiration	Increase with night temperature		
No. of leaves	More at higher temperature	LA will increase with temperature	Incorrect, LA peaks at 33/25°C
Cell No.	More at higher temperature	LAR may increase with temperature depending on overall photosynthate production and allocation to different parts of the plant	LAR does increase with temperature
Cell size	Larger at higher temperature		

OVERALL INTERPRETATION

(1) The increased DMP from 33/19 to 33/25°C could be largely due to the increased LAR

(2) The decrease at temperatures above 33/25°C could be due to greater respiration losses at these temperatures

(3) The decline in leaf area at 33/28 and 36/31°C despite the expected increase at these temperatures confirms photosynthate losses must be high at these temperatures

(4) Despite the decline in LA at high temperature the LAR increases. This indicates proportion of photosynthate allocated to leaf production must have been increased at these temperatures

Table 12.3 Interpretation of the results of the studies detailed in Parts I and II using the results of photosynthesis, respiration and leaf characteristics outlined in Part III.
DMP = Dry matter production; LA = Leaf area

CHAPTER 3	DMP	LA	LAR	NAR
MYSORE PROVENANCE UNDER WINTER CONDITIONS - OPEN GLASSHOUSE (DAY TEMPERATURE VARIES)				
24/28 27/28 33/28 36/28 (Expt. 2)	Increased with increased temperature up to 33/28 & decreased at 36/28	As DMP	Increased with increased temperature	Tends to parallel DMP pattern

	PREDICTED EFFECT	INTERPRETATION	COMMENT
Net photosynthesis	Increase with day temperature up to 31°C, not known at higher levels	NAR will increase with increased temperature probably up to 33/28 Not clear at 36/28	NAR pattern shows slight decrease at 36/28°C
Respiration	No effect - all high temperatures are the same		
No. of leaves	More at higher temperature	LA will increase with temperature	Not totally correct LA peaks at 33/28
Cell No.	more at higher temperature	LAR may increase with temperature depending on overall photosynthate production & allocation to different plant parts	LAR does increase with temperature
Cell size	Larger at higher temperature		

OVERALL INTERPRETATION

(1) The pattern of NAR suggests optimum temperature for photosynthate production in this provenance is about 33°C

(2) If so, the reduced production at 36/28 is offset to some extent by the increase in LAR at this temperature

Table 12.4 Interpretation of the results of the studies detailed in Parts I and II using the results of photosynthesis, respiration and leaf characteristics outlined in Part III.
DMP = Dry matter production; LA = Leaf area

CHAPTER 3	DMP	LA	LAR	NAR
KERALA PROVENANCE UNDER WINTER CONDITIONS - BT CABINET (NIGHT TEMPERATURE VARIES)				
33/19 33/25 33/28 33/31°C (Expts.1,3)	Increase with increased temperature	As DMP	As DMP	Low at 33/19. No difference within 33/25-33/31°C

PREDICTED EFFECT		INTERPRETATION	COMMENT
Net photosynthesis	no difference - day temperatures all the same	NAR will decrease with temperature	Incorrect, NAR does not change over 33/25-33/31°C
Respiration	increase with night temperature		
No. of leaves	More at higher temperature	LA will increase with temperature	Confirmed by LA pattern
Cell number	More at " "	LAR may increase with temperature depending on overall photosynthate production & allocation to plant parts	LAR does increase with temperature
Cell size	Larger at " "		

OVERALL INTERPRETATION

(1) The increased production at high temperature results primarily from increased LAR and not from photosynthesis (NAR)

(2) Anticipated decline in NAR did not occur - no certain explanation is available for this.

Table 12.5 Interpretation of the results of the studies detailed in Parts I and II using the results of photosynthesis, respiration and leaf characteristics outlined in Part III.
DMP = Dry matter production; LA = Leaf area

CHAPTER 3	DMP	LA	LAR	NAR
KERALA PROVENANCE UNDER WINTER CONDITIONS - OPEN GLASSHOUSE (DAY TEMPERATURE VARIES)				
24/28 27/28 33/28 36/28 (Expt. 2)	Increase with increased temperature	As DMP	As DMP	Increase with temperature but no difference between 33/28 and 36/28

	PREDICTED EFFECT	INTERPRETATION	COMMENT
Net photosynthesis	Increase with day temperature up to 33, not clear at 36°C	NAR will increase with increased temperature up to 33/28	NAR does increase with temperature & there is no difference between 33/28 and 36/28
Respiration	No effect - all night temperatures are the same		
No. of leaves	More at higher temperature	LA will increase with temperature	Confirmed by LA pattern
Cell number	More at " "	LAR may increase with temperature depending on overall photosynthate production & allocation to different parts of the plant	LAR does increase with temperature
Cell size	Larger at " "		

OVERALL INTERPRETATION

(1) The increased DMP with temperature from 24/28 to 33/28 is due both to the increased NAR and LAR over this temperature range

(2) The increased DMP at 36/28 is due to the increased LAR at this temperature

(3) The maintenance of NAR at 36/28 compared with 33/28 indicates no substantial difference in photosynthesis between these two day temperatures.

Table 12.6 Interpretation of the results of the studies detailed in Parts I and II using the results of photosynthesis, respiration and leaf characteristics outlined in Part III.
DMP = Dry matter production; LA = Leaf area

CHAPTER 5	DMP	LA	LAR	NAR
(i) TOTAL RADIATION 200 cal $cm^{-2}day^{-1}$ (KERALA PROVENANCE - LB CABINET)				
33/25 33/28 (Photoperiod 16 hr)	Greater at higher temperature	As DMP	As DMP	As DMP

	PREDICTED EFFECT	INTERPRETATION	COMMENT
Net photosynthesis	No effect during day temperature; increase with night temperature due to light level being maintained (see Fig. 9.1B, Chapter 9)	NAR will increase with temperature provided respiration losses are not too high	Confirmed by NAR pattern
Respiration	Increase with night temperature		
No. of leaves	More at higher temperature	LA will increase with temperature LAR may increase with temperature depending on overall photosynthetic production and allocation to plant	Confirmed by LA pattern LAR does increase with temperature
Cell number	" " "		
Cell size	Larger " "		

Table 12.7 Interpretation of the results of the studies detailed in Parts I and II using the results of photosynthesis, respiration and leaf characteristics outlined in Part III.
DMP = Dry matter production; LA = Leaf area

CHAPTER 5	DMP	LA	LAR	NAR
(ii) TOTAL RADIATION 100 cal $cm^{-2}day^{-1}$ (KERALA PROVENANCE - LB CABINET)				
33/25 33/28 (photoperiod 16 hr)	No difference	Slightly greater at higher temperature	No difference, but slightly greater at higher temperature	No difference

	PREDICTED EFFECT	INTERPRETATION	COMMENT
Net photosynthesis	No effect - day temperatures are the same No photosynthesis during period of night temperature (see Fig. 9.1A)	NAR will decrease with temperature	Incorrect, NAR does not change
Respiration	Increase with night temperature		
No. of leaves	More at higher temperature	LA will increase with temperature	Confirmed by LA pattern
Cell number	" " "	LAR may increase with temperature depending on overall photosynthate production & its allocation to plant parts	LAR is slightly greater at higher temperature
Cell size	Larger at higher temperature		

OVERALL INTERPRETATION Anticipated decline in NAR did not occur - no obvious explanation is available for this.

Table 12.8 Interpretation of the results of the studies detailed in Parts I and II using the results of photosynthesis, respiration and leaf characteristics outlined in Part III.
DMP = Dry matter production; LA - Leaf area

CHAPTER 5	DMP	LA	LAR	NAR
(iii) KERALA PROVENANCE - LB CABINET				
100 200 cal cm^{-2}day^{-1} (photoperiod 16 hr)	Greater at higher radiation	As DMP	Lower at higher radiation	As DMP

	PREDICTED EFFECT	INTERPRETATION	COMMENT
Net photosynthesis	Greater at high radiation solely from period 2 (see Fig. 9.1A-B, Chapter 9)	NAR will be greater at higher radiation level	Confirmed by NAR pattern
Respiration	Greater losses at lower radiation due to longer period for respiration		
No. of leaves	More at higher radiation	LA will be greater at higher radiation (cell No. is a more important determinant of leaf size than cell size)	Confirmed by LA pattern
Cell number	" " "		
Cell size	Smaller at higher radiation	LAR may increase with radiation depending on overall photosynthate production & allocation to plant parts	LAR is smaller at higher radiation

OVERALL INTERPRETATION The smaller LAR at the higher radiation level could be due to the heavier and thicker leaves under these conditions (Section 5.4.3, Chapter 5).

Table 12.9 Interpretation of the results of the studies detailed in Parts I and II using the results of photosynthesis, respiration and leaf characteristics outlined in Part III.
DMP = Dry matter production; LA = Leaf area

CHAPTER 6	DMP	LA	LAR	NAR
(i) TOTAL RADIATION 50 cal $cm^{-2}day^{-1}$ (KERALA PROVENANCE - LB CABINET)				
8 12 16 hrs 30/25°C	No difference	No difference	Greater at short day	Greater at long day

	PREDICTED EFFECT	INTERPRETATION	COMMENT
Net photosynthesis	Higher at the high light intensity at shorter day but this is counteracted at longer day by the increased period of photosynthesis	Not clear	NAR is greater at long day
Respiration	Greater losses at short day due to longer period for respiration		
No. of leaves	Slightly fewer at 8 hr	Not clear, LA affected both by increased No. of leaves & decreased cell size at long days	LA does not differ
Cell number	No effect		
Cell size	Larger at short day	LAR unclear	LAR is greater at short day

OVERALL INTERPRETATION

(1) NAR and LAR appear to compensate for each other thereby maintaining RGR at a uniform level and accordingly DMP remains unchanged

(2) The smaller LAR at long day is probably explained by the small leaf cell size and hence denser leaves at this photoperiod.

Table 12.10 Interpretation of the results of the studies detailed in Parts I and II using the results of photosynthesis, respiration and leaf characteristics outlined in Part III.
DMP = Dry matter production; LA = Leaf area

CHAPTER 6	DMP	LA	LAR	NAR
(ii) TOTAL RADIATION 100 cal $cm^{-2} day^{-1}$ (KERALA PROVENANCE - LB CABINET)				
8 12 16 hr 30/25°C	Poor at 8 hr; no difference between 12 and 16 hr	As DMP	Decrease with increased daylength	Increase with increased daylength

	PREDICTED EFFECT	INTERPRETATION	COMMENT
Net photosynthesis	Higher at the high light intensity at shorter day but then is counteracted at longer day by increased period of photosynthesis	Not clear	NAR is greater at long day
Respiration	Greater losses at short day (due to longer period of respiration)		
No. of leaves	Slightly fewer at 8 hr	LA will be smaller at 8 hr and no difference between 12 & 16 hr	Confirmed by LA pattern
Cell No.	Slightly fewer at 8 hr, no difference between 12 & 16 hr	LAR not clear	LAR is greater at short day
Cell size	Larger at shorter day		

OVERALL INTERPRETATION

(1) In general NAR and LAR compensate each other and maintain growth rate. However the decreased NAR at 8 hr is not matched by the increased LAR resulting in poor growth at this daylength

(2) The smaller LAR at longer days is partially explained by the denser leaves due to the smaller leaf cell size.

Table 12.11 Interpretation of the results of the studies detailed in Parts I and II using the results of photosynthesis, respiration and leaf characteristics outlined in Part III.
DMP = Dry matter production; LA = Leaf area

CHAPTER 6	DMP	LA	LAR	NAR
(iii) KERALA PROVENANCE - LB CABINET				
50 100 cal $cm^{-2}day^{-1}$ 30/25°C	Greater at higher radiation	As DMP	Greater at lower radiation	As DMP

	PREDICTED EFFECT	INTERPRETATION	COMMENT
Net photosynthesis	Greater at higher radiation	NAR will be greater at higher radiation	Confirmed by NAR pattern
Respiration	No effect, same conditions at both radiation levels		
No. of leaves	More at higher radiation	LA will be greater at higher radiation (cell number is a more important determinant of leaf size than cell size)	Confirmed by LA pattern
Cell number	" " "		
Cell size	Smaller at higher radiation	LAR may increase with radiation depending on overall photosynthate production & allocation to plant parts	LAR is greater at lower radiation

OVERALL INTERPRETATION

(1) The greater DMP at higher radiation level is largely due to the greater NAR under this condition

(2) The smaller LAR at higher radiation level could be due to the heavier and thicker leaves at this radiation level

The patterns of photosynthesis, respiration and leaf area production determined in Part III were based on the material of Kerala provenance. The response of the material from Mysore provenance could be different.

12.2 CONCLUSION OF THE INTERPRETATION

The summaries detailed in Tables 12.1-12.11 indicate many results can be interpreted as simple responses to different temperature and radiation conditions. These conditions control seedling development by direct control of photosynthesis, respiration and leaf development.

The degree of photosynthesis which takes place during the period of night temperature in the phytotron is now seen to be a major factor confusing the interpretation of temperature effects. This probably accounts for many of the anomalies detailed in the studies of temperature effects on teak seedlings reported in this thesis and by previous workers (Section 1.6, Chapter 1).

However when due allowance is made for interactive effects of different regimes it is possible to make deductions about teak seedling performance in the experiments reported in this thesis.

12.2.1 Provenance Difference in Optimum Temperatures for Photosynthesis

It is possible to hypothesize a difference between the Kerala and Mysore provenances in the optimum temperature level of net photosynthesis.

In the Kerala provenance the rate of net photosynthesis is known to increase with an increase in temperature within the range 25 -31°C (Chapter 9). However, in Experiment 2, Chapter 3 (Table 12.5) the rate of net photosynthesis of this provenance, as reflected by the NAR pattern, increased up to 36°C. Since the NAR at 36°C was not significantly different from that at 33°C, the optimum temperature for NAR and for photosynthesis may be at about 36°C.

In the Mysore provenance, the optimum temperature for photosynthesis appears lower, at about 33°C. In Experiment 2, Chapter 3 (Table 12.3) NAR increased with temperature up to 33°C and was lower at 36°C.

12.2.2 Control of Leaf Development

The degree of control exerted by temperature and light on the leaf development of material from Kerala provenance is known (Part III). Similar control appears effective in determining leaf development of Mysore provenance material. Wherever direct comparison of leaf development in the two provenances was possible (Table 12.1) the response under different regimes was similar. In all cases the interpretation of leaf development of Mysore seedlings as if they were Kerala material proved satisfactory.

12.2.3 Allocation of Photosynthate

The allocation of photosynthate within the plant may differ at different temperatures and light intensities.

12.2.3.1 Temperature effect

At high temperatures, the teak seedlings distributed proportionately more photosynthate to leaf production. The effect of this was to give high LAR values at the high temperatures.

The increase in LAR occurred despite an associated decrease in NAR due presumably to constant rate of photosynthesis (Kerala provenance, Table 12.4) or declining rate of photosynthesis (Mysore provenance, Tables 12.2 and 12.3) and increased respiration losses at these temperatures. The increased LAR was often able to maintain or even increase dry matter production at the high temperatures despite the decline in NAR. The increased leaf production thus provided a mechanism for maintaining production at high temperatures.

12.2.3.2 Light intensity effect

At high light intensities there was a decline in LAR (Tables 12.8, 12.11). This indicated the greater photosynthate production at high light levels (Part III) must have been utilized to construct parts of plants other than the leaves.

Under conditions encouraging rates of high photosynthate production the parts of the plant which benefit are not necessarily the photosynthetic areas. The situation is not quite as clear as the LAR values indicate because the leaves themselves became denser and thus heavier under high light intensities (Chapter 5). Nevertheless it does indicate that stem and root growth will benefit under the more active photosynthesizing conditions.

12.2.4 Absence of a Decline in NAR at High Temperatures

A predicted decline in NAR at high temperatures did not occur in two experiments, both in cabinets and with light period strictly controlled (Tables 12.4, 12.7). There is no obvious explanation for this. The consistency of the occurrence in two experiments suggests some other factors apart from photosynthesis, respiration and leaf characteristics might have been involved. This needs more detailed study.

12.3 GENERAL DISCUSSION

12.3.1 Use of Phytotron Facilities

Studies of teak seedling growth and development using phytotron facilities must consider carefully the light and temperature regimes and their inter-relation. Under open glasshouse conditions there will be an effect of photosynthesis during the period of night temperature due to sufficient light for photosynthesis being maintained into this period. This effect will be particularly pronounced under summer conditions when plants at the higher night temperatures will be at an advantage. Under winter conditions the effect may still be present but of lesser importance because the natural photoperiod is much shorter. Thus night photosynthesis and seasonal variations in photoperiod can cause erroneous interpretation of temperature effects.

The seasonal effect of photoperiod has proved important in the studies reported in Chapter 3 (Tables 12.1-12.3) in which the material from Mysore provenance showed different responses to temperature between experiments. The Mysore material showed steady increase in growth with temperature up to 36/31°C under summer conditions (Table 12.1), and showed a decline in growth at this temperature level under winter conditions (Tables 12.2-12.3).

Furthermore the anomalous results observed between the studies of Ko Ko Gyi (1972) and Kanchanaburangura (1976) (Section 1.6, Chapter 1) could have been due to seasonal effects. It is possible that the study of Ko Ko Gyi was carried out in summer (i.e. growth increased with temperature up to 36/31°C) and that of Kanchanaburangura was carried out in winter (i.e. growth declined at 36/31°C).

Similar reasoning can also be applied to the anomalous results between experiments observed by Hamzah (1975) for seedlings of *Eucalyptus decaisneana* and by Awang (1977) for seedlings of *Eucalyptus pilularis*. Both Hamzah and Awang found different results between summer and winter conditions using phytotron open glasshouse facilities.

Thus the open glasshouses in the phytotron appear to be suitable only for general studies of temperature effects. Cabinets provide precise control of light and temperature periods and are better suited for studies of these parameters than open glasshouses. However in using cabinets there must be consideration of light intensity levels which can be attained.

Naturally lit cabinets have an advantage over artificially lit cabinets because the natural daylight is of much higher intensity than artificial light. The light saturation level for photosynthesis in teak is about 900 $\mu Em^{-2}sec^{-1}$ (4000 f.c.) (Part III). It is difficult to provide light at this level of intensity for long periods in artificially lit cabinets of the phytotron type. To attain this level in such cabinets there must be none of the dulling of the reflective interior surfaces which takes place with usage of such cabinets and to maintain the level the fluorescent tubes have to be replaced frequently.

In contrast naturally lit cabinets suitably sited provide light intensities above the saturation level.

12.3.2 Provenance Difference

There was evidence (Chapter 3) of provenance difference in many growth characteristics despite the anomalous results between the experiments. These differences were found in height growth, diameter growth, dry matter production, leaf area production and growth analysis parameters. In general, material from Kerala provenance proved to be superior to that from Mysore provenance. Thus the results confirm those reported by Ko Ko Gyi (1972) and Kanchanaburangura (1976) that provenance variation in growth characters of teak occurs at seedling stage.

Delineation of temperature responses for a particular provenance has not been possible because of the photoperiodic effects. Nevertheless these studies have shown provenance differences in temperature response can be detected given suitable safeguards and conditions. Detailed study of teak provenance performance under different temperature regimes is now possible.

12.3.3 Allocation of Photosynthate Production

There appears to be a delicate control of photosynthate distribution within teak seedlings. Under conditions of high photosynthate production plant parts other than the leaves will benefit from this production. On the other hand, under conditions of declining photosynthesis the allocation of more photosynthate to the leaves takes place giving a larger area of photosynthetic material.

Re-allocation of photosynthate was also evident in the studies reported by Ko Ko Gyi (1972) and Kanchanaburangura (1976). Both used phytotron naturally lit cabinets and found LAR values increased and NAR values decreased with increasing night temperatures. This mechanism thus enables the seedling to maintain dry matter production levels at high temperatures.

CHAPTER 13

CONCLUSION

The studies reported in this thesis initially attempted to define the temperature control of teak seedlings of two different provenances using controlled environments. The absence of clear conclusions confirmed previous anomalous results and led to consideration of possible factors involved. There was evidence that a light radiation x temperature interaction could have been involved. This was examined in subsequent studies.

The results demonstrated the existence of a light radiation x temperature interaction and showed very important effects of light, particularly total daily radiation under phytotron conditions. Furthermore, growth analysis studies indicated net assimilation rate and leaf area ratio were both affected by both light radiation and temperature. This suggested photosynthesis, respiration and leaf development might be important determinants of teak seedling performance.

Subsequent studies therefore examined how light radiation and temperature affected teak seedling photosynthesis, respiration and leaf structure. The results indicated many of the results of earlier studies could be interpreted as simple responses of photosynthesis, respiration and leaf development to different temperature and radiation conditions. The anomalies in results recorded earlier were due simply to differing effects of light radiation at different times of the year.

The following conclusions are drawn from the studies in this thesis.

(1) There is a need to be very careful in planning phytotron experiments. All factors have to be considered. Seasonal variation in total light

radiation has proved particularly important as a control of seedlings in phytotron open glasshouse conditions. Ignoring this control can lead to erroneous interpretation of temperature effects. In particular under some conditions seedlings will maintain photosynthesis into period of 'night' temperature. Under these conditions the plants growing at the higher night temperature are at an advantage.

Cabinets are better suited for studies of temperature and light effects because temperature and light periods are precisely controlled. However, naturally lit cabinets have an advantage over artificially lit cabinets because the light source, natural daylight, provides light intensity levels higher than artificial light. The intensity of artificial light is generally below the putative saturation level for teak (see below). This is generally not so in the naturally lit cabinet.

(2) Provenance differences in teak seedlings have been demonstrated under different temperature and light conditions. The material from Kerala provenance has proved to be superior to that from Mysore provenance, particularly at high temperature regimes (e.g. 33/31 and 26/28°C). However, clear delineation of the temperature control for particular provenances has not been possible. Further study on this aspect is needed.

(3) That teak is a light demanding species is confirmed by the putative light compensation point (55 $\mu Em^{-2} sec^{-1}$ or 200 f.c.) and the putative light saturation level (900 $\mu Em^{-2} sec^{-1}$ or 4000 f.c.). However the light curve of photosynthesis showed a rapid rise in the rate of photosynthesis at low light intensities suggesting that teak can survive and grow under some degree of shading.

(4) The rate of net photosynthesis and respiration is increased with an increase in temperature from 25 to 31°C. Optimum temperature for net

photosynthesis appeared to differ between provenances. The optimum level for the Kerala provenance was at 36°C and for the Mysore provenance at 33°C approximately.

(5) Leaf growth and development of teak seedlings are strongly controlled by temperature within the range studied (33/25 - 33/31°C). At higher temperatures teak seedlings produce more and larger leaves. These larger leaves are due to both more and larger epidermal cells.

(6) Leaf characteristics also differ at different levels of light radiation. There are more and larger leaves at light radiation levels of 100 cal $cm^{-2}day^{-1}$ than at 50 cal $cm^{-2}day^{-1}$. There are more but smaller cells in these larger leaves.

Leaves receiving light radiation of 200 cal $cm^{-2}day^{-1}$ have been shown to have more chlorophyll content than those receiving 100 cal $cm^{-2}day^{-1}$.

(7) Leaf development and net photosynthesis of teak seedlings are interrelated in allocation of photosynthate production. Under conditions of high photosynthate production plant parts other than leaves benefit from this production. Under conditions of reduced net photosynthesis at high temperatures there is an increase in the leaf area ratio. This is interpreted as an attempt by the plant to maintain dry matter production as conditions become adverse.

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APPENDIX I

COMPOSITION OF NUTRIENT SOLUTION

Nutrient solution is Hoagland (No. 2) solution (Hewitt, 1966) with some modification to the minor elements.

Composition		Elements	
$Ca(NO_3)_2.4H_2O$	950 mg/l	N	211.7 mg/l
$(NH_4)H_2PO_4$	120 "	P	32.2 "
KNO_3	610 "	K	235.9 "
$MgSO_4.7H_2O$	490 "	Ca	160.9 "
H_3BO_3	0.6 "	Mg	48.3 "
$MnCl_2.4H_2O$	0.4 "	Na	3.61 "
$ZnSO_4.7H_2O$	0.09 "	S	66.7 "
$CuSO_4.5H_2O$	0.05 "	Cl	0.143 "
H_2MoO_4	0.02 "	Fe	5.007 "
$Co(NO_3)_2.6H_2O$	0.025 "	B	0.105 "
$FeSO_4.7H_2O$ (chelated with EDTA)	24.9 "	Co	0.005 "
		Mn	0.111 "
NaOH	6.3 "	Cu	0.013 "
		Zn	0.02 "
		Mo	0.012 "

APPENDIX II

Summarized results of analysis of variance of the data in Appendix III.

*, ** and *** indicate significance at the 5,1 and 0.1% levels respectively

Source of variation	Degree of freedom	Mean squares	F ratio	Significance
Diameter				
Temperature	3	2.625	4.847	*
Error	8	.542		
Dry matter production				
Temperature	3	15.222	41.941	***
Error	8	.363		
Total leaf area				
Temperature	3	88.032	35.501	***
Error	8	2.480		
Height				
Temperature	3	378.316	328.967	***
Error	8	1.150		
RGR				
Temperature	3	.015	11.812	**
Error	8	.001		
NAR				
Temperature	3	.004	10.349	**
Error	8	.000		
LAR				
Temperature	3	.266	11.978	**
Error	8	.022		

APPENDIX III

Effect of four night temperature regimes on the growth of teak seedlings of the Mysore provenance. Within each parameter figures not connected with a vertical line are significantly different at the 5% level according to Duncan's multiple range test.

Height cm	Diameter mm	Dry matter prod.^{n} g	Total leaf area dm^2	RGR $gg^{-1}week^{-1}$	NAR $gdm^{-2}week^{-1}$	LAR $dm^2\ g^{-1}$
11.5(33/19)	5.3(33/19)	3.88(33/19)	6.10(33/19)	0.29(33/19)	0.17(33/31)	1.57(33/19)
25.8(33/25)	6.7(33/31)	6.48(33/31)	14.08(33/31)	0.35(33/31)	0.18(33/19)	1.99(33/25)
32.0(33/28)	6.8(33/28)	7.41(33/28)	16.52(33/28)	0.41(33/28)	0.19(33/28)	2.16(33/28)
37.6(33/31)	7.5(33/25)	9.29(33/25)	18.41(33/25)	0.46(33/25)	0.25(33/25)	2.20(33/31)

APPENDIX IV

THE EXTRACTION AND ESTIMATION OF CHLOROPHYLL CONTENT OF LEAVES OF TEAK SEEDLINGS

EXTRACTION OF CHLOROPHYLL

The procedure outlined below is adapted from the method described by Wood (1969).

(i) The fresh leaf discs were finely macerated with a mortar and pestle and, after washing with 80% acetone, the macerated material and solvent were transferred to a centrifuge tube.

(ii) Centrifuged at 4000 rpm for 30 minutes.

(iii) Decanted off the supernatant into a 10 ml volumetric flask.

(iv) Added 80% acetone to the volumetric flask to bring them to volume.

ESTIMATION OF CHLOROPHYLL CONTENT

The absorbance of the solvent was determined at 645 and 663 mμ with a Pye unicam SP 1800 Ultraviolet Spectrophotometer. The concentration of chlorophyll (chlorophyll a + b) was estimated using a nomogram for determination of chlorophyll from the absorbances as detailed in Kirk (1968).

APPENDIX V

Table V.1 Leaf area (Y) and leaf length and width product (X) of fifty leaves of teak seedlings

No.	Leaf area (cm^2) Y	Length x width X	No.	Leaf area (cm^2) Y	Length x width X
1	59.91	91.76	26	11.09	17.60
2	23.07	36.71	27	15.95	23.80
3	39.09	58.24	28	12.08	17.11
4	6.38	9.34	29	15.79	22.61
5	41.47	60.90	30	12.76	18.45
6	57.66	89.79	31	10.79	15.96
7	61.51	94.38	32	8.73	12.87
8	66.19	102.98	33	24.49	36.52
9	15.39	24.42	34	26.20	38.70
10	35.32	51.52	35	16.34	23.00
11	38.22	60.48	36	13.81	19.87
12	26.34	41.13	37	6.59	9.30
13	48.30	74.58	38	5.68	8.51
14	47.25	66.56	39	10.65	15.05
15	26.77	42.88	40	5.77	8.71
16	22.89	35.67	41	7.17	9.14
17	41.94	66.64	42	11.27	16.61
18	40.33	63.56	43	40.10	61.33
19	21.73	33.21	44	43.94	66.40
20	19.82	30.02	45	23.72	36.96
21	9.42	14.58	46	29.00	43.20
22	9.76	15.54	47	26.30	39.82
23	39.92	63.25	48	29.44	44.26
24	42.13	66.39	49	12.47	17.84
25	16.80	26.40	50	13.35	19.20

APPENDIX V (cont)

Correlation coefficient (r) = .998

Regression coefficient (b) = .6432

Y-intercept (a) = .5697

Regression equation: $Y = .5697 + .6432 X$.

Analysis of variance of the data in Table V.1 is shown in the table below.

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F-ratio
regression	1	13156.4	13156.4	14734.4***
error	48	42.8594	.8929	
total	49	13199.3		

*** Indicates significance at the 0.1% level

APPENDIX V (cont)

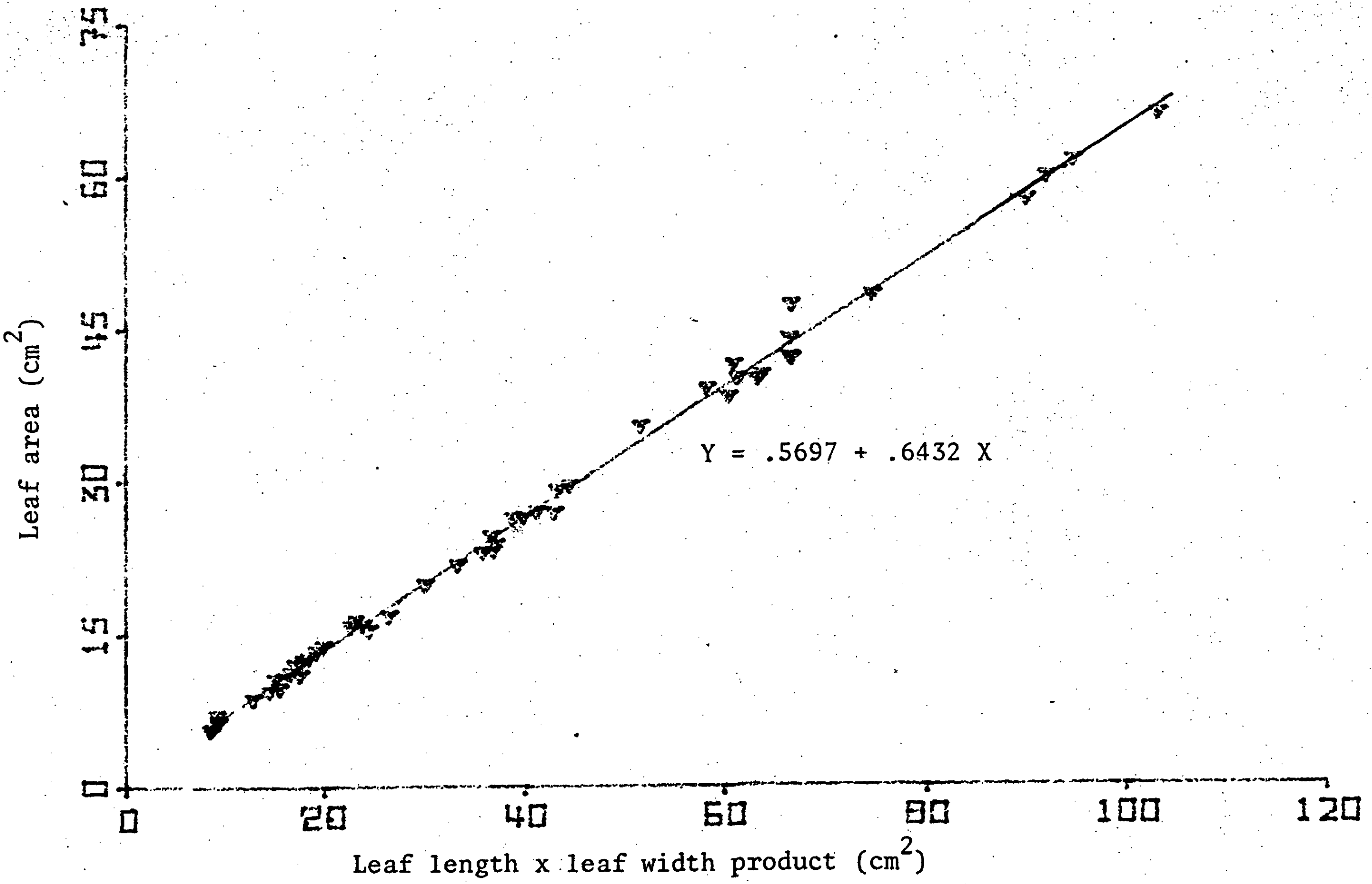

Figure V.1 Relationship between leaf area (Y) and leaf length x leaf width product (X) of teak seedlings