Leaf gas exchange capacity in relation to leaf position on the stem in field grown teak (*Tectona grandis* L.f.)

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Abstract

Leaf gas exchange patterns in relation to leaf positions on stems were studied in field grown forest tree, teak (*Tectona grandis* L.f.) during first year growth under intensive culture plantation. Net photosynthetic rates (P_N) were low in immature leaves (1-2 from shoot apices), increased basipetally on shoot, peaked in leaves (3rd or 4th leaves from shoot apices) which had recently reached full expansion, and thereafter declined in lower crown leaves. High P_N found in fully expanded young leaves was associated with increased dark respiration rate (R_D) and high radiation saturation as well as compensating irradiance for P_N when compared to those of aged leaves. Intercellular CO_2 concentrations (C_i) determined at ambient CO_2 concentration and saturating irradiance were apparently low for leaves exhibiting high P_N when compared to those of aged leaves. Differences in stomatal conductance (g_s) and the rate of transpiration (E) were not apparent between leaves after full expansion. The relationship of P_N with C_i recorded for leaves at different positions on stems and under natural ambient CO_2 concentrations showed a linear decrease in P_N with marked increasing C_i and suggested that increase in mesophyll limitations could cause decline in P_N during aging of teak leaves after full expansion. Highly significant positive linear correlation was found between P_N and C_i determined at below ambient CO_2 concentrations and saturating irradiance for both fully expanded young and aged leaves. The estimate of linear relationship between P_N and C_i, often considered as carboxylation efficiency, was higher for fully expanded young leaves characterised by high P_N than for aged leaves exhibiting low P_N. Hence, the increase in mesophyll limitations or decrease in carboxylation efficiency could explain gradual reduction in photosynthetic potential with leaf age after maturation in teak.

Introduction

Growing world demand for energy, wood and wood products and also the ever increasing environmental risks such as air pollution caused by increasing CO_2 concentration in the atmosphere (Baes *et al.* 1977) suggest the need for expansion and improving tree growth both in and outside the natural forests. Further, the concern about future source of energy stimulates a renewed interest in improving tree growth because trees are more efficient sources than annual crops in terms of the energy harvested per unit energy invested (Smith and Johnson 1977). Therefore, protection of tree growth in their natural environment and new plantations of fast growing and/or economically important tree species would become potential and are of great importance for our future life. Due to growing demand, some of the economically important forest tree species have been planted and grown extensively outside their natural regions both in agricultural and marginal lands. The success of such attempts greatly depends on the productivity of selected tree species which in turn is determined by the magnitude of their annual growth. This might require consideration of potential types of trees for tree improvement programmes.

With the ever increasing demand for its timber, there is a need to expand teak plantations even in regions outside its natural occurrence. Thus, teak is being planted and grown extensively in southern parts of India by farmers and corporate bodies both in agricultural and marginal lands. The success of such teak cultivation depends on its productivity which is in turn determined by the interaction of its physiological processes with environmental factors. Physiological factors that determine productivity of trees include photosynthesis and respiration, partitioning of photosynthates within tree, duration of active growth, and seasonal pattern of CO_2 assimilation (Ledig 1969, Dickmann 1979). The P_N was one of the first selection criteria considered for tree improvement research, however, P_N was often not correlated with yield (Ledig 1969, Gifford and Evans 1981, McDonald 1984). Reasons for these poor correlations include mostly environmental variability, inadequate or differing nitrogen supply, differences in endogenous and diurnal as well as seasonal cycles (Ledig 1969, McDonald 1984), or measurement of P_N under suboptimal conditions and at varying age of leaves (Nelson 1984).

Although several attempts were made to study factors influencing the survival and performance of teak trees in their natural habitat (Troup 1921, Hedegard 1973, Rawat *et al.* 1992, Rawat 1994), studies to understand physiological basis of teak growth and productivity are limited. The present study therefore determined photosynthetic CO_2 exchange characteristics of teak growing outside its natural regions as well as their variations with the position of leaves on the stem to establish base physiological values for teak improvement and to provide a foundation for more efficient teak cultivation outside its natural regions. Furthermore, we determined the relationship between P_N and both C_i and irradiance (I) of two selected attached leaves at different positions (3rd and 6th from shoot apices) on stems which exhibited high and low P_N, respectively, in order to assess their photosynthetic potential.

Materials and methods

Plants: Three-month-old teak (*Tectona grandis* L.f.) seedlings grown from stumps and established in polyethylene bags containing three parts field soil plus one part farm-yard manure mixture were obtained from the forest nursery of the Biotechnology Centre for Tree Improvement, Tirupati (India). Fifty seedlings were transplanted in a plot of 25×15 m fertile agricultural land characterised by red sandy loam soil (pH 8.1) and with a spacing of 2.5 m between plants and rows. Seedlings were planted in pits measuring 0.4×0.4×0.4 m and filled with three parts top soil plus one part farm-yard manure mixture, and grown under natural environment. Plants were watered periodically (once in three days) and fertilised bimonthly with 50 g per plant of 17:17:17 N-P-K water soluble commercial fertilizer. Weeds were removed manually to avoid competition for water and nutrients available in the soil.

The experimental planting site was located at 15 km in south-east direction from the University campus (latitude 13°33'N, longitude 79°28'E). During the experimental period, day temperatures ranged from 27 to 39 °C and night temperatures from 19 to 25 °C, the average air temperature, however, during much of this period was 34/23 °C day/night. Daily maximum and minimum atmospheric relative humidities during the experimental period ranged from 63 to 76 % and 31 to 42 %, respectively. Plants received full natural solar irradiance throughout the experimental period and the maximum I was about 1800 μmol(quantum) m^{-2} s^{-1} on a clear sunny day around noon at the top of the canopy. During the experimental period, plants had average height of approximately 0.8 m with 3-4 pairs of leaves at 2 months, 2.0 m with 9-10 pairs of leaves at 5 months, and 3.5 m with 15-17 pairs of leaves at 8 months after transplantation.

Values on gas exchange were recorded for attached leaves at different positions (nodes) on the stem and numbered from shoot apices. The leaf just unfolding at the shoot apex was considered as the first leaf. The concept of leaf plastochron index (LPI), which is an integral count of the number of emerged leaves plus a decimal fraction, represents the progress of an emerging leaf towards full emergence but can not be applied to plants grown under natural conditions (Silk 1980). This is because the traits underlying leaf emergence are often inconsistent during the course of plant growth under natural conditions (Ram *et al.* 1994). In the present study, therefore, gas exchange characteristics of teak leaves were studied and followed with respect to their position on stems from shoot apices.

Gas exchange measurements: A portable open gas exchange measuring system (model *LCA-3, ADC,* England) was used for rapid simultaneous determination of CO_2 and water vapour exchange in attached leaves of teak under field conditions. The portable measuring system used was equipped for recording basic data and instantaneous computation as well as storage of leaf gas exchange characteristics, namely P_N, g_s, C_i, and E. All leaf gas exchange measurements were made between 10:00 and 11:30 h (IST) on sunny and generally cloud-free days throughout the experimental period. For measuring P_N and E in light, photosynthetic leaf chamber (model *PLC-3 (B), ADC,* England) was clipped onto the selected attached leaf which

had been exposed to natural sunlight. The chamber was held at such an angle that the enclosed leaf surface directly faced the Sun to avoid the shading inside the cuvette. The I at the upper surface of leaf chamber was measured by a calibrated sensor (filtered silicon photocell, ADC, England) mounted on the same surface of leaf chamber; it was 1200-1300 μmol(quantum) m^{-2} s^{-1} during most of the photosynthetic gas exchange measurements. Atmospheric air drawn from 3 m height through a telescopic most was flown through the leaf chamber in order to avoid fluctuations in CO_2 concentration of the ambient air which could otherwise arise due to the addition of respired CO_2 by the researcher(s) at the time of the measurements. Atmospheric air containing ambient concentrations of CO_2 (345 cm^3 m^{-3}) and O_2 (21 %) was allowed to pass through the photosynthetic chamber at 5 cm^3 s^{-1} without changing its relative humidity. The P_N and g_s became stable within two min after clipping the chamber on to the selected attached leaf experiencing saturating solar irradiance and the values of photosynthetic gas exchange were then recorded. Measurements were repeated at least on five different plants for each selected leaf position on the stem.

The P_N response to sub-atmospheric CO_2 levels was also determined for two selected leaves (3rd and 6th from shoot apices) exhibiting variations in P_N in order to assess their *in vivo* carboxylation efficiency. Using the LCA-3 leaf gas exchange measuring system, it was made easy and possible to vary CO_2 concentration of the air entering leaf chamber by regulating the air flow passing through a soda-lime (8-14 mesh) column. The P_N response to CO_2 was determined for each selected leaf by lowering CO_2 concentration of the air entering leaf chamber in steps from the atmospheric concentration (345 cm^3 m^{-3}). At each selected CO_2 concentration, values of CO_2 exchange were recorded after the g_s and P_N became stable. All CO_2 dependent photosynthetic CO_2 exchange measurements for all selected leaves were made at about the same saturating I [$ca.$ 1200-1300 μmol(quantum) m^{-2} s^{-1}]. The irradiation dependent CO_2 uptake of selected leaves was also determined particularly at solar irradiances lower than the naturally available irradiance. Lowering of natural solar irradiance in steps was achieved by using and varying the number of cloth filters at the upper surface of leaf chamber. At each step of I, CO_2 exchange values were recorded after they had become stable. The P_N response to I was linear at very low I for each selected leaf. The slope of linear relationship between P_N and I was estimated by least squares linear regression analysis and expressed as radiation use efficiency (RUE).

Leaf dark respiration rates (R_D) were measured on leaves kept continuously in dark for at least 30 min which was achieved by covering leaves with aluminium foil. Generally, about 15-20 min was required for establishment of steady states that were maintained for at least 2 h. The R_D values of leaves reported are steady state rates reached after equilibration period. At the time of measuring R_D, the leaf chamber was clipped on to dark equilibrated leaf and the chamber was darkened by using aluminium foil. Atmospheric air containing ambient CO_2 (345 cm^3 m^{-3}) and O_2 (21 %) concentrations was allowed to flow through the leaf chamber at 5 cm^3 s^{-1}. Dark CO_2 exchange by leaves became stable at about 3 min after enclosing dark equilibrated leaf in the chamber and the values were then recorded. The R_D

measurements were repeated for each selected leaf position on at least five different plants.

Analysis of results: The relationship of P_N with C_i recorded for leaves at different positions on stems of different plants and under natural environmental conditions was analyzed by least square linear regression analysis to establish the relationship, if any, between them. Similarly, least square linear regression analysis was also applied to study the relationship of P_N with C_i recorded at different CO_2 concentrations lower than that of ambient air for two selected leaves (3rd and 6th from shoot apices) exhibiting high and low P_N. The P_N response to C_i for each selected leaf with respect to its position was linear and highly significant and the estimate of such linear relationship between P_N and C_i was expressed as *in vivo* carboxylation efficiency (Farquhar and Sharkey 1982) of the respective leaf samples.

Table 1 Net photosynthetic CO_2 exchange (P_N) [μmol(CO_2) m^{-2} s^{-1}] in relation to leaf position on stems in field grown teak during its eight months growth after transplantation. The P_N measurements were made at ambient CO_2 concentration and under natural environmental conditions [33 $\pm$ 1 °C, 50-55 % RH, 1250$\pm$50 μmol(quantum) m^{-2} s^{-1}]. Values were recorded at three months interval starting two months after transplantation. Values are means $\pm$ SD of at least five replicated measurements made on different plants. - = values not recorded due to lack of healthy leaves.

Time [month after transplantation]	Leaf position on stem from shoot apex								
	1	2	3	4	5	6	7	8	9
2	12.3±1.2	17.8±1.3	16.5±0.9	15.9±1.1	-	-	-	-	-
5	11.3±1.5	16.6±1.2	16.9±0.8	15.2±0.7	14.2±0.6	13.4±1.0	-	-	-
8	10.6±2.1	14.2±1.8	17.3±1.7	16.2±1.9	15.2±1.1	13.5±1.8	12.6±1.4	10.5±1.7	9.1±1.2

Results and discussion

A clear understanding of the photosynthetic potential of leaves at different positions on the stem is fundamental in assessing the contribution of an individual leaf to plant growth and carbon economy of whole plant. There is abundant literature concerning the changes in P_N during leaf ontogeny (Šesták 1985, Čatský and Šesták 1997), but little information is available with respect to tropical tree species, particularly in teak. We estimated P_N for different leaves with respect to their position on stems at three times during 8 months growth of teak after transplantation (Table 1). The P_N was low for youngest leaves (1st from shoot apices) at all times of growth/measurements, it increased in 2nd leaves on 2 months old plants, exhibited gradual increase upto 3rd leaves on 5 and 8 months old plants, and then it declined gradually with leaf age after maturation. A similar decline in P_N with leaf aging and towards senescence was also reported for other tree species (Nelson 1985, Lange 1988).

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Changes in P_N with leaf age and position on the plant are related with anatomical and morphological alterations. Increased P_N observed with gradual increase in leaf age upto maturity during the course of leaf expansion is related to development of internal leaf structure, synthesis of chlorophyll, decrease in diffusion resistance, increase in photosynthetic phosphorylation, increase in protein synthesis and RuBP carboxylase activity, and decrease in mitochondrial respiration. The gradual decrease in P_N after leaves had become fully expanded may be mainly due to decrease in photophosphorylation and RuBP carboxylase activities as well as to a significant decrease in protein and RNA turnover. Furthermore, marked decrease in mitochondrial respiration and relative increase in photorespiration which could occur after leaf expansion are also cited for decreased P_N with leaf aging and towards senescence (Dickmann et al. 1975).
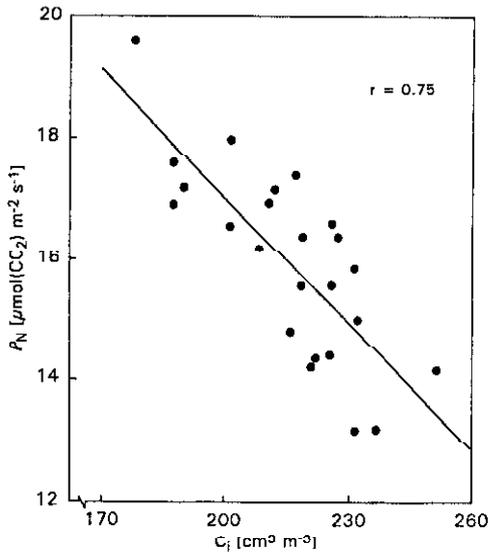

Fig. 1. The relation between net photosynthetic rate (P_N) and intercellular CO_2 concentration (C_i) in field grown teak. The P_N measurements were made on leaves at different positions on the stem and with normal atmospheric CO_2 concentration (345 cm^3 m^{-3}) entering the leaf chamber and under natural environmental conditions [50-55 % RH, 33±1 °C and 1250±50 μmol(quantum) m^{-2} s^{-1}]. Points are results pooled from measurements made on different plants and at different times during 8 months growth of plants after transplantation. Solid line through points represent first order regression, Y = 30.76 - 0.0686 X, r = 0.75.

The P_N was related with C_i in leaves at different positions on stems, of different individual plants, and under natural environmental conditions (Fig. 1). Thus the decrease in P_N of aged leaves was commensurate with marked increase in their C_i values. Although marked differences were found in P_N and C_i of leaves with respect to their positions on stems, g_s of these leaves did not vary significantly at all times of measurements (results not presented). A decline in P_N with a marked increase in C_i and without apparent change in g_s found under natural environmental conditions

during the course of aging of teak leaves pointed out that increase in mesophyll limitations could cause decline in P_N during aging of leaves.
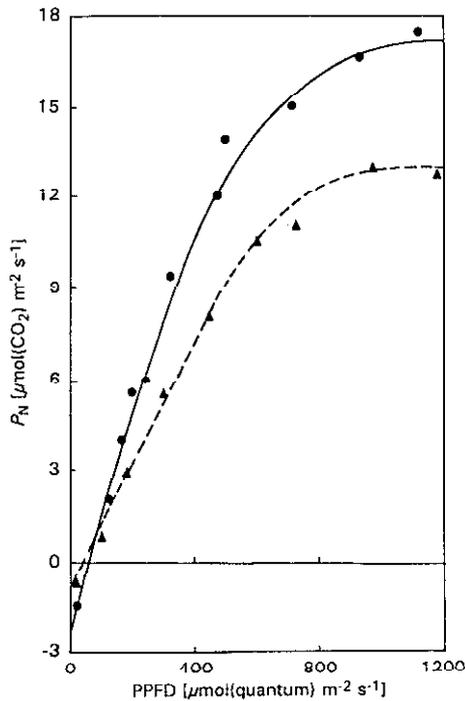

Fig. 2. The P_N response to irradiance (*PPFD*) in 3rd (●) and 6th (▲) leaves from shoot apices in teak. Measurements were made under conditions similar to those specified in Fig. 1 except of varying *I*. The values are means of 3-5 measurements made on different plants and on different days.

The P_N of both fully expanded young (3rd from shoot apex) and aged (6th from shoot apex) leaves increased with *I* (Fig. 2). Yet young and fully expanded leaves showed much higher saturation radiation for P_N than the aged leaves. Compensating *I*s for P_N of the 3rd and 6th leaves were about 70 and 55 µmol(quantum) m^{-2} s^{-1}, respectively (Table 2). Furthermore, the initial slope of P_N response to *I* was greater for fully expanded young leaves than for aged leaves. A similar relationship between P_N and *I* was also reported for other tree species (Sharkey and Ogawa 1987, Tenhunen *et al.* 1987, Michael *et al.* 1990, Masarovičová 1992). These results indicate that radiant energy is apparently one of the principal factors governing the photosynthetic potential of fully expanded leaves in teak.

The P_N response to C_i recorded at CO_2 concentrations lower than the ambient air CO_2 concentration for two selected leaves on the stem (3rd and 6th leaves from shoot apices) characterised by high and low P_N (Fig. 3) was linear and highly significant ($r = 0.98$). However, the P_N response to C_i was apparently higher for the fully expanded young (3rd) leaves than for the aged (6th) leaves. The estimate of linear relationship between P_N and C_i determined at extremely low ambient CO_2

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concentrations is often considered as *in vivo* carboxylation efficiency or mesophyll conductance (Farquhar and Sharkey 1982). Differences in P_N response to C_i found between leaves exhibiting high and low P_N apparently reflect physiological characteristics of the CO_2 exchange properties of these two leaf types. The decrease

Table 2. Leaf gas exchange characteristics of two selected leaves which were characterised by high and low net photosynthetic rate (P_N) and located at two different positions on the stem. The P_N and transpiration rate (E) measurements were made on field grown plants at ambient CO_2 concentrations and under natural environmental conditions [33±1 °C, 50-55 % RH, 1250±50 µmol(quantum) m^{-2} s^{-1}]. Dark respiration rate (R_D) measurements were also made under the same conditions except irradiance. Values are means ± SD of 5 replicated measurements made on different plants.

Gas exchange characteristic	Leaf position on the stem from shoot apices	
	3rd	6th
P_N [µmol(CO_2) m^{-2} s^{-1}]	18.50 ± 0.99	14.00 ± 1.91
Intercellular CO_2 concentration, C_i [cm^3 m^{-3}]	185 ± 9	227 ± 7
E [mmol(H_2O) m^{-2} s^{-1}]	9.30 ± 1.41	9.80 ± 1.47
Stomatal conductance, g_s [mol m^{-2} s^{-1}]	0.79 ± 0.16	0.85 ± 0.21
R_D [µmol(CO_2) m^{-2} s^{-1}]	2.30 ± 0.35	1.50 ± 0.32
Saturating irradiance[a] [µmol(quantum) m^{-2} s^{-1}]	1050	900
Compensating irradiance[a] [µmol(quantum) m^{-2} s^{-1}]	70	55
Carboxylation efficiency[b], CE [µmol(CO_2) s^{-1} cm^{-3} m^{-1}]	0.127	0.109
Water use efficiency[c], WUE [mmol(CO_2) mol^{-1}(H_2O)]	1.989	1.429
Radiation use efficiency[d], RUE [mmol(CO_2) mol^{-1}(quantum)]	22.8	15.6

[a] Estimated from P_N/I curves. [b] Estimated from initial slope of P_N/ C_i curves. [c] Calculated from mean values. [d] Estimated from initial slope of P_N/I curves.

in P_N response to C_i from the 3rd to the 6th leaves represented a change in mesophyll conductance or carboxylation efficiency. Since leaves at 6th node of stems (from shoot apices) had grown and over-matured, anatomical and physiological alterations associated with aging of leaves could have decreased mesophyll conductance or carboxylation efficiency of these leaves. In addition, since the I saturated P_N was reduced in aged leaves (Table 2, Fig. 2), the carboxylation might have been reduced to balance the effects of reduced electron flow capacity (Sharkey 1985, Wullschleger 1993). A marked decrease in P_N of aged leaves without an apparent change in E (Table 2) found in comparison with that of fully expanded young leaves clearly indicated that low P_N of aged leaves was related to increase in mesophyll limitations rather than to stomatal limitations. Values on CO_2 and water vapour exchange characteristics of two selected leaf types with respect to their age and position on stems (Table 2) showed that P_N, R_D and radiation saturation as well as compensating irradiance for P_N were consistantly higher for fully expanded young leaves than for aged leaves. The increased R_D found in fully expanded young leaves is thought to be due to their increasing demand for metabolic energy and may be mediated by high amounts of saccharides generated by increased P_N in these leaves (Hrubec *et al.*

1985, Rajendrudu *et al.* 1987, 1996). On the other hand, C_i determined at ambient CO_2 concentration and saturating I was apparently low for young and fully expanded leaves compared to those of aged leaves. However, the differences in E and g_s were not apparent between the two selected leaf types in the present study. The CE determined based on P_N response to C_i at low ambient CO_2 levels, the WUE
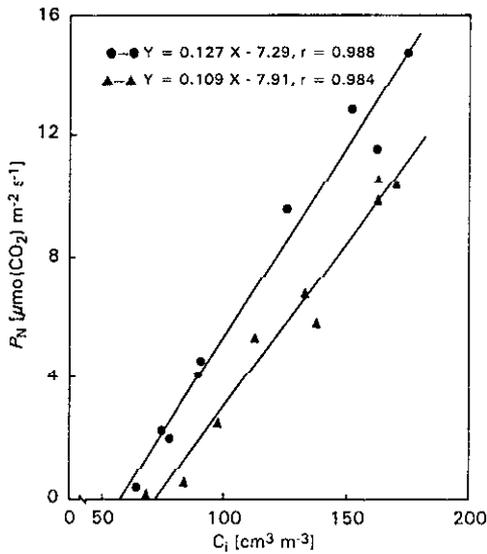

Fig. 3. Intercellular CO_2 concentration (C_i) response of net photosynthetic rate (P_N) in 3rd (●) and 6th (▲) leaves (from shoot apices) on the stem in teak. The P_N measurements were made with air containing various CO_2 concentrations below to that of normal air and under natural environmental conditions [33±1 °C, 50-55 % RH, 1250±50 μmol(quantum) m⁻² s⁻¹]. Values are means of at least three measurements made on different plants. Solid lines through data points represent first order regressions: ●, Y = 0.127X - 7.29; r = 0.988. ▲, Y = 0.109X - 7.91; r = 0.984.

calculated as the ratio of E/P_N, and the RUE estimated based on initial slopes of P_N response to I were also higher for fully expanded young leaves than for aged leaves. These results indicated that fully expanded young leaves usually located at 3rd node (from shoot apices) on stems had high photosynthetic potential, and these could be selected and used for studies related to teak improvement. Because of complex interactions among factors governing the productivity of tree species, it is doubtful whether any single gas exchange or morphological variable can be a useful and reliable indicator of productivity of tree species. However, we believe that our approach of determining high photosynthetic potential characteristic to a fixed leaf position on the stem shows promise for use as a criterion in clonal selection and for explaining inherent growth differences among clones or between plants growing under the same or different environment.

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