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Effects of water stress on leaf growth and photosynthetic and transpiration rates of *Tectona grandis*

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Abstract

Plants of teak (*Tectona grandis* L.f.) growing after transplantation to fertile soil for 5 - 6 months were subjected to water stress by withholding watering continuously for 3 weeks. The growth rates of both plants in height and developing leaves in length were unaffected during the first week after withholding watering, but they were decreased by about 50 % during the second week and became negligible during the third week of water stress treatment. The rate of leaf production and internodal elongation were also decreased in plants experienced 2 weeks of water stress. However, after rewatering, these plants regained growth potential and exhibited high rates of leaf expansion and plant growth comparable to those of well-watered plants. Diurnal course of net photosynthetic rate (P_N) of plants subjected to water stress for 2 weeks was similar as that of well-watered plants. However, P_N of plants subjected to water stress for 3 weeks was reduced in the afternoon. Similarly, stomatal conductance (g_s) and transpiration rate (E) of plants experiencing 3-week water stress were decreased in the afternoon. Soon after rewatering, P_N, g_s and E reached similar values to those of well-watered plants.

Additional key words: environmental stress, internodal elongation, leaf expansion, leaf gas exchange, stomatal conductance, teak tree physiology.

Introduction

Teak (*Tectona grandis* L.f.) is economically important timber yielding forest tree. The most common environmental stresses which affect tree growth have been lack of adequate water supply, mineral deficiencies, unfavourable temperatures and atmospheric pollutants. Although attempts were made to study factors influencing the survival and performance of teak in their natural regions (Troup 1921, Hedegard 1973, Ravat *et al.* 1992, Rawat 1994), studies to assess growth and physiological potential of teak under unfavourable environments are limited. The present study has

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Abbreviations: E - transpiration rate; g_s - stomatal conductance; P_N - net photosynthetic rate.
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therefore been undertaken to assess the effects of water stress imposed by withholding watering on leaf growth and photosynthesis of field-grown teak.

Materials and methods

Plants and growth conditions: Three-months-old teak (*Tectona grandis* L.f.) seedlings were obtained from social forest nursery of Andhra Pradesh State Forest Department, Tirupati, India. The experimental site is located at 15 km in south-east direction from the university campus (latitude 13° 33′ N, longitude 70° 28′E). Seedlings were transplanted to red sandy loam soil with a spacing of 1.8 m between plants and rows and grown under natural environmental conditions. Plants were watered regularly once in two days and fertilised monthly. During the experimental period day temperatures ranged from 32 to 43 °C and night temperatures from 19 to 27 °C and air relative humidities from 45 to 60 % and 30 to 40 %, respectively. The maximum irradiance was about 1600 μmol(photon) m^{-2} s^{-1} on a clear sunny day around noon at the top of the canopy. All plants were grown under the same field conditions upto five months after which plants in two rows were subjected to water stress by withholding for three weeks. Control plants received regular watering to avoid water stress. At the time of imposing water stress treatment, plants had about 2 m height, 7 cm girth and 13 - 14 pairs of leaves.

Plant growth measurements: Plant growth rate was determined by measuring plant height from 0.25 m above the soil surface to shoot apex and the length of 2nd and 3rd internodes at weekly intervals. At the same time leaf length (including lamina and petiole) was measured. Initial observation on the growth of developing leaves in teak under well-watered conditions clearly indicated that it is typically sigmoidal. Therefore, growth rates of developing leaves measuring upto 10 cm and 10 - 40 cm was measured separately to represent initial and exponential phases of leaf growth.

Gas exchange measurement: Leaf gas exchange was measured at different times of the day (10.00, 12.00, 13.00 and 15.00) at weekly intervals. Earlier studies showed that net photosynthetic rates (P_N) for teak were low in immature leaves, increased basipetally on shoot and peaked in leaves (3rd and 4th from shoot apices) which had recently reached full expansion and thereafter declined in lower crown leaves (Rajendrudu aand Naidu 1997). In the present study, therefore, 3rd and 4th leaves on the stem from shoot apices were used to measure photosynthetic and transpiration rates.

A portable open gas exchange measuring system (*Model LCA-3, ADC,* Hoddesdon, England) was used for CO_2 and water vapour exchange in attached leaves of teak under field conditions. Photosynthetic leaf chamber (*Model PLC-3(B), ADC*) was clipped onto the selected attached leaf which had been exposed to full natural solar irradiance (1100 - 1300 μmol m^{-2} s^{-1}). Atmospheric air containing normal concentrations of CO_2 (345 cm^3 m^{-3}) and O_2 (21 %) was allowed to pass through photosynthetic chamber at rate 5 cm^3 s^{-1} without changing its relative humidity. Steady-state was reached within 2 min. Measurements were repeated at

least on three different plants for each treatment. The apparent decrease in growth of developing leaves and stomatal conductance of 3rd/4th leaves from shoot apices were considered as indicators of the development of water stress.

Results and discussion

The rate of plant growth in height during 5 - 6 months growth period after transplantation under well-watered conditions was about 20 cm per week and it also remained nearly same during first week after withholding water supply (Table 1). But the growth rate of plants during second week after withholding water supply was decreased by 50 % compared to well watered plants and it became negligible during 3rd week of water stress treatment (Table 1). However, plants regained growth potential after rewatering and exhibited growth rates comparable to those of well-watered plants. The average length of 2nd and 3rd internodes from shoot apices was also decreased to a large extent (40 %) in plants subjected to 2-week water stress (data not presented).

Table 1. Effect of water stress on the rate of teak plant growth (height). Means ± S.D., n = 3 - 5.

Period of measurement	Growth rate [cm week^{-1}]	
	control	water stress
Before withholding watering	20.3 ± 0.98	18.5 ± 0.91
1st week after withholding watering	19.6 ± 1.33	18.3 ± 2.03
2nd week after withholding watering	18.1 ± 2.10	9.8 ± 1.05
3rd week after withholding watering	18.9 ± 1.75	2.1 ± 0.84
After rewatering	19.6 ± 2.03	17.5 ± 1.33

Length of developing leaves exhibited sigmoidal growth pattern (Fig. 1) as in many plants and plant organs. The maximum growth rate was about 4 cm per day and was unaffected during first week after withholding water supply to plants (Table 2). Leaves which appeared on plants after subjecting them to water stress treatment exhibited marked decrease in their growth after 1 week of withholding watering and it became negligible during the third week of plant water stress treatment (Fig. 1, Table 2). However, upon rewatering leaves which already initiated developing during water stress period as well as other leaves which appeared on plants after rewatering showed normal growth rates similar to those of well-watered plants (Table 2). Further it is evident that the affect of water stress was more pronounced during exponential phase than in initial lag phase. Under well watered conditions it was observed that new leaves at the shoot apices appeared at regular interval of 6 d but it took about 10 d gap for two successively developing leaves (*i.e.* 17th leaf and 18th leaf in Fig. 1) to make their appearance and grow to a measurable size on plants experiencing 2 - 3 weeks of water stress (Fig. 1). The decrease in leaf production and expansion and overall growth of teak subjected to water stress caused by withholding

watering is found to be those reported by others (*e.g.* Boyer 1988, Hinckley *et al.* 1991).

Table 2. Effect of water stress on the rate of teak leaf growth in length during initial and exponential phases. Means ± S.D.; $n = 3 - 5$ plants.

Period of measurement	Leaf growth rate [cm d^{-1}]			
	control		water stress	
	initial	exponential	initial	exponential
Before withholding watering	1.1 ± 0.17	3.9 ± 0.61	1.4 ± 0.12	4.0 ± 0.22
1st week after withholding watering	1.1 ± 0.25	3.7 ± 0.44	1.5 ± 0.10	3.8 ± 0.36
2nd week after withholding watering	1.2 ± 0.10	3.6 ± 0.25	0.7 ± 0.06	1.3 ± 0.30
3rd week after withholding watering	1.1 ± 0.21	3.6 ± 0.15	-	-
After rewatering	0.9 ± 0.12	4.2 ± 0.31	1.2 ± 0.36	4.7 ± 0.45

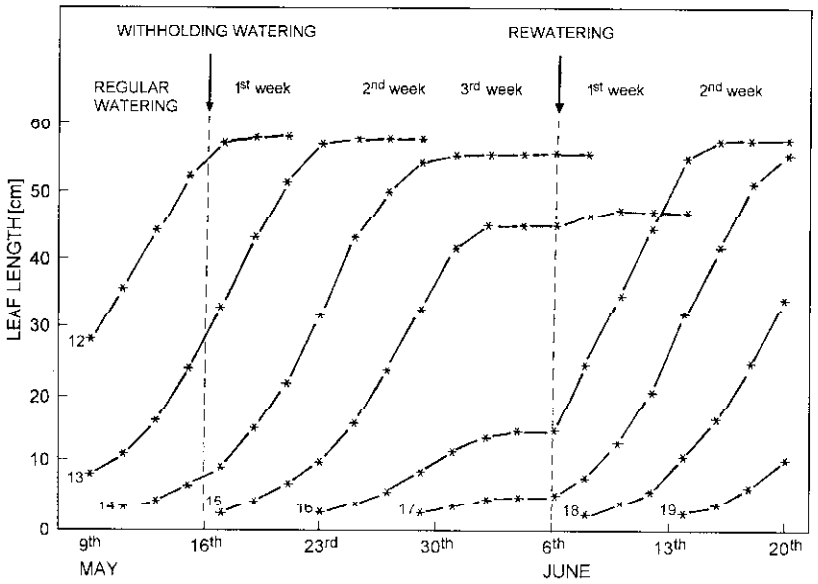

Fig. 1. Pattern of leaf growth before and after withholding watering and also after rewatering. Lengths including lamina and petioles of successive leaves 12 - 19 numbered in order of their appearance.

Maximum net photosynthetic rate (P_N) under well watered conditions was about 18 μmol(CO_2) m^{-2} s^{-1} and was found higher than values reported for most woody plants (Slatyer and Morrow 1977, Körner *et al.* 1979, Attivill and Clayton-Greene 1984, Pontailler *et al.* 1984, Pereira *et al.* 1986). During the day, P_N remained nearly the same under well-watered conditions and did not exhibit midday depression which was reported for many woody plants during summer season (Schulze *et al.* 1974,

Pereira and Kozlowski 1976, 1978, Benecke *et al.* 1981, Tenhunen *et al.* 1985, Pereira *et al.* 1986). But plants subjected to 3-week water stress exhibited large decrease in P_N during the afternoon (Fig. 2*A*). Similar to P_N, stomatal conductance (g_s) and transpiration rate (E) were also decreased significantly in the afternoon in plants experiencing water stress (Figs. 2*B,C*).

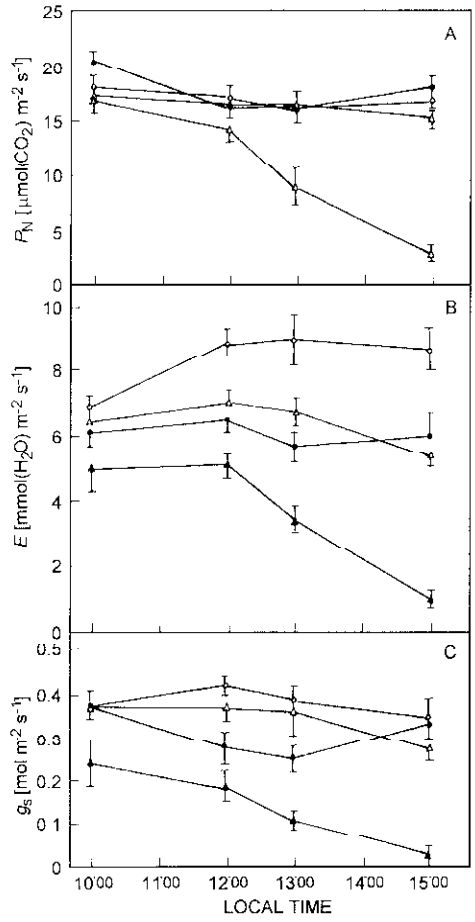

Fig. 2. Diurnal variation in net photosynthetic rate (*A*), transpiration rate (*B*), and stomatal conductance (*C*) of field grown teak plants before (*open circles*) stress and after one (*open triangles*) and two (*closed triangles*) weeks of water stress treatment as well as after rewatering (*closed circles*). Measurements were made on $3^{rd}/4^{th}$ leaves from shoot apices under saturating irradiance and normal CO_2 and O_2 concentrations. Each point represents mean ± S.D. of at least three measurements made on different plants.

After rewatering P_N was recovered along with concomitant increase in g_s as well as E and they were similar to those of well-watered plants (Fig. 2). These results suggest that large decrease in P_N of teak plants subjected to water stress could be

primarily due to stomatal closure. Based on these results it is evident that teak grown in field outside its natural regions is highly sensitive to soil water deficits.

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