

ORIGINAL ARTICLE

**Gas Exchange Characteristics in *Tectona grandis* L.
Clones under Varying Concentrations of CO₂ Levels**

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The Institute of Forest Genetics and Tree Breeding, Coimbatore, India functioning under the Indian Council of Forestry Research and Education, Dehara Dun, has a long term systematic tree improvement program for *Tectona grandis* aimed to enhancing productivity and screening of clones for site specific. In the process, twenty clones of *T. grandis* L. were studied for the physiological parameters and water use efficiency with reference to the elevated CO₂ levels. CO₂ enrichment studies in special chambers help in understanding the changes at individual level, and also at physiological, biochemical and genetic level. It also provides valuable information for establishing plantations at different geographic locations. Considerable variations were observed when the selected 20 clones of *T. grandis* were subjected to physiological studies under elevated CO₂ conditions (600 and 900 mol mol⁻¹). Eight clones exhibited superior growth coupled with favorable physiological characteristics including high photosynthetic rate, carboxylation and water use efficiency under elevated CO₂ levels. Clones with minimal variation in physiological characteristics under elevated levels of CO₂ suggest their ability to overcome physiological stresses and adapt to varying climatic conditions.

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Plantation forestry programmes operating on a large scale are mostly with several species and in the species *T. grandis* also and a number of clones are being deployed to increase the productivity of this species particularly in the South-East Asian countries

like Vietnam, Thailand, Indonesia, Laos, Myanmar and in India also. Teak timber is particularly valued for its durability and water resistance, and is used for boat building, exterior construction, veneer, furniture, carving, turnings, and other small wood projects.

Approximately 3 million cubic metres of Teak is harvested globally per annum from both native forests and plantations. Teak being the most prized high value timber worldwide with an increasing international demand already fivefold greater than the resources currently available. In India, teak plantations are being maintained particularly in central and Southern parts.

Because of its repeated planting, teak plantations are facing low productivity and its right time to think for teak clonal plantations to meet the demand in local as well as international. There exists tremendous variation with reference to yield, tree form and physiological characteristics in teak clones. It is well understood that the cumulative growth of a tree is the result of genotypic and environmental effects and their interaction (Cornillon *et al.*, 2002). Use of physiological parameters to assist in the determination of superior genotypes for tree improvement has been in practice (Kramer, 1986).

Evaluation of the behaviour of certain physiological parameters can effectively be used to assess the clonal performances under given environmental conditions. Net photosynthesis rate (Pn), transpiration rate (Tr) and total leaf area per plant are the important factors that determine the biomass production and Water Use Efficiency of a species. Variation in Pn, has been reported as determinant of plant productivity in rubber. Significant differences in Pn and stomatal conductance (gs) have been reported to exist in different tree species (Zipperlen and Press, 1996), *viz.*, *Eucalyptus camaldulensis* (Farrel *et al.*, 1996) *Populus* (Kalina and Ceulemans, 1997), *Azadirachta*

indica (Kundu and Tigerstedt, 1998) and *Hevea brasiliensis* (Nataraja and Jacob, 1999).

As tree growth is the end result of the interactions of physiological processes that influences the availability of essential internal resources at meristematic sites, it is necessary to understand how these processes are affected by the environment to appreciate why trees grow differently under various environmental regimes (Kozlowski and Pallardy, 1997). Understanding the impacts of atmospheric CO₂ and its response to changes in temperature is critical to improve predictions of plant carbon-exchange with atmosphere (Crous *et al.*, 2011). Variations have been observed under tropical conditions in the responses of tree seedlings to elevated CO₂ levels (Varadharajan *et al.*, 2010).

Screening for genetic differences in ecophysiological traits such as net photosynthesis rates, respiration rates and nutritional attributes becomes imperative in a country with varied agro climatic and soil conditions, as the maximum performance potential of a tree species can be assessed only when data on these aspects are available (Warrier, 2010). Carbon enrichment studies in special chambers help in understanding the changes at individual level, and also at physiological, biochemical and genetic level. Reports on variations in responses of *Eucalyptus* species to carbon enrichment have been reported by Lima *et al.* (2003). Considerable variation has been reported in clones of *Eucalyptus camaldulensis* Dehnh for important physiological characteristics including high photosynthesis, carboxylation efficiency and water

use efficiency (Warrier, 2010). The objective of the present study was to analyse differences with respect to leaf photosynthetic characteristics in teak clones subjected to varying levels of CO₂. The information obtained would support designing further tree improvement and breeding strategies, to mitigate effects of climate change and teak clonal forestry programme.

MATERIALS AND METHODS

The selected clones were grown inside the open top chambers (OTCs) of 3 m diameter and 10 m height lined with transparent PVC sheets (0.125 mm thickness) with a CO₂ levels of 600 mol mol⁻¹. Pure CO₂ gas was used for the enrichment. Similarly OTCs were maintained at elevated temperatures (Ambient +4°C) under ambient CO₂ (380 mol mol⁻¹). Controls were maintained in open field outside OTCs, with ambient CO₂ (380 mol mol⁻¹). CO₂ was provided throughout the day and night (24 h period). The experiments were laid in a Complete Randomized Design. The period of CO₂ enrichment was 180 days. A software facility called Supervisory Control and Data Acquisition (SCADA) was used to continuously control, record and display the actual and desired CO₂ level, relative humidity and temperature in each OTC by feedback control loop passing through Programmable Logical Controllers (PLC) (Buvanewaran *et al.*, 2010).

The set that was maintained in the open served as the control under ambient conditions while the set maintained inside the chamber under ambient CO₂ conditions was used to eliminate the effects of the chamber on the response of the clones.

Measurements of photosynthesis and related parameters: Net photosynthesis rate (Pn), stomatal conductance (gs), intercellular CO₂ concentration (Ci) and transpiration rate (E) were measured using a Portable Photosynthesis System, LiCor-6400 (LiCor Instruments, USA). The measurements were taken between 9.30 am and 11.30 am under cloud free conditions at the end of six months. Observations were recorded from ten ramets per clone for all the physiological parameters.

Water use Efficiency (WUE) was also estimated for the clones. Intrinsic water use efficiency was estimated as the ratio of net photosynthesis rate to stomatal conductance (Pn/gs) whereas instantaneous water use efficiency was estimated as the ratio of net photosynthesis rate to transpiration (Pn/E). Intrinsic carboxylation efficiency was derived as the ratio of net photosynthetic rate to intercellular CO₂ concentration (Pn/Ci). Intrinsic mesophyll efficiency was estimated as the ratio of intercellular CO₂ concentration to stomatal conductance (Ci/gs).

Statistical Analysis: The data were subjected to analysis of variance for completely randomised design with five replications. A full-factorial multivariate general linear model (GLM) analysis was conducted using SPSS to determine whether there was significant variation in the different gas exchange characteristics between different CO₂ conditions within the clones. Post hoc range tests using Waller Duncan t-test was performed to group the significantly different clones.

RESULTS

The effects of elevated temperature and CO₂ on

the gas exchange characteristics in Teak clones in Table-1. In the Table-2 and Table-3, the information on the inter-clonal variation existing in net photosynthetic rate, stomatal conductance, intercellular CO₂ concentration, transpiration rate and the derived parameters namely intrinsic and instantaneous water use efficiency, intrinsic carboxylation efficiency and intrinsic mesophyll efficiency are given.

Arora and Gupta (1996) reported that photosynthetic rate varies among the plants belonging to different taxa and also among the varieties within the same species. Among the various parameters studied with reference to the physiological parameters, the primary physiological parameters were significantly higher for the clones maintained under control conditions, the clones subjected to elevated CO₂ showed higher values for the derived parameters and elevated conditions of temperature and CO₂ indicating the efficiency of the clones to divert water and nutrients for photosynthesis than transpiration. The overall variation in various gas exchange characteristics in clones of Teak subjected to conditions of elevated CO₂ suggests the species inherent ability to assimilate more of CO₂ and efficiency of photosynthesis under varying environmental conditions.

Teak have been shown to precisely regulate transpiration rate via stomatal movements (Bolhar-Nordenkanpf, 1987) allowing this species to take advantage of favourable conditions through enhanced CO₂ uptake (Fordyce *et al.*, 1995), especially when exposed to significant seasonal fluctuations

(Greenwood *et al.*, 2003).

Teak clone TC-7 ranked highest with reference to the net photosynthetic rate followed by TC-13. Clones TC-5, 2, 3 and 6 recorded the lowest net photosynthetic rate. The net photosynthetic rate ranged from 6.23 to 12.68 $\mu\text{molm}^{-2}\text{s}^{-1}$ with the mean value of 8.0, 6.34 and 5.35 $\mu\text{molm}^{-2}\text{s}^{-1}$ under the ambient conditions, elevated temperature and elevated CO₂ conditions, respectively. Palanisamy (1999) reported that, increase in net photosynthetic rates in Eucalyptus seedlings after eight months of differential CO₂ exposure at 800 ppm CO₂. In the present study also, similar line of observations were recorded in the clonal responses to physiological stresses in Teak. Teak clones of TC-4, 6 and 11 showed increased rates in chamber conditions under ambient CO₂ levels. Remaining clones are exhibited the decreasing trend under the elevated CO₂ level and temperature compared to the control (ambient). Teak clones TC-2, 3, 5, 16, 14, 6 and 19 exhibited poor photosynthetic rates under the different conditions also.

With reference to the stomatal conductance recorded in different teak clones, it varied from 0.021 to 0.266 $\text{mol}^{-2}\text{s}^{-1}$ with the mean of 0.094, 0.055 and 0.038 $\text{mol}^{-2}\text{s}^{-1}$ recorded under the ambient, elevated temperature and CO₂, respectively in different teak clones. It was observed that there was a reduction in the stomatal conductance in eucalyptus when subjected to elevated CO₂ conditions. Among the teak clones, TC-17, 13, 14 and 15 recorded maximum and clones of TC-11, 2, 4, 3 and 20 were recorded the minimum stomatal conductance. All the teak clones

are recorded lower stomatal conductance values in the elevated temperature and CO₂ compared to the control (ambient).

In the case of transpiration rate among the teak clones with respect to elevated temperature and CO₂, there is no systematic increase or decrease rate was noticed in the ambient, elevated temperature and CO₂ treatments. Higher the transpiration rate of 3.58 mmol m⁻² s⁻¹ was recorded under the elevated temperature treatment in TC-14 clone and lowest transpiration rate of 0.67 mmol m⁻² s⁻¹ was recorded in the TC-6 clone under ambient condition with the mean of 2.03, 2.0 and 1.79 mmol m⁻² s⁻¹ under the ambient, elevated temperature and CO₂, respectively.

Higher the intercellular CO₂ concentration was observed in teak clones of TC-16, 14, 13 and 8 and lower intercellular CO₂ concentration was noticed in TC- 6, 4, 11 and 19 with the mean of 275.36, 294.14 and 230.79 µl l⁻¹ under the ambient, elevated temperature and CO₂, respectively.

Carbondioxide is an essential substrate in the photosynthetic process and is incorporated in the light-independent reaction of photosynthesis to produce simple sugars (Kramer *et al.*, 2004). For photosynthesis to occur stomata must open to obtain CO₂ which produces an unavoidable trade-off: as CO₂ moves into the leaf, water from within the leaf is lost through the open stomata via transpiration (Gutschick, 1999). In order to optimize photosynthetic returns the plant must balance CO₂ uptake with transpirational losses, thereby trying to maximize carbon gain while minimizing water loss (Givnish, 1978).

The water molecules lost per molecule of carbon fixed by the plant during photosynthesis, is referred to as water use efficiency (Ellsworth, 1999). Intrinsic water use efficiency (Pn/gs) implies the inherent ability of the plant to assimilate CO₂ (Ares and Fownes, 1999). A higher value indicates better ability of the plant for carbon assimilation. The intrinsic water use efficiency value ranged from 5.35 to 407.86 µmol mol⁻¹ in TC-6 and TC-2 in elevated CO₂ with the mean of 148.03, 136.82 and 185.78 µmol mol⁻¹ respectively in the ambient, elevated temperature and CO₂.

In the case of intrinsic water use efficiency, about 15 clones registered higher the value and only 5 clones recorded the lowest value (Table-3). Li (2000) reported that measurement of WUE may be a useful trait for selecting genotypes with improved drought adaptation and biomass productivity under different environmental conditions. Net photosynthesis and related gas exchange parameters have been suggested as early selection criteria to improve the efficiency of tree breeding. The values ranged from 5.8-330 under varying levels of CO₂. It was observed that water stressed *Pinus radiata* trees had higher WUE (Thompson and Wheeler 1992).

Higher intrinsic WUE was associated with productivity in *Prosopis glandulosa* and *Acacia smallii* (Polley *et al.*1996). It is reported that long-term structural and growth adjustments as well as changes in intrinsic WUE are important mechanisms of *Acacia koa* to withstand water limitation (Ares and Fownes 1999). Restricted stomatal opening will result in decreased stomatal conductance, lower transpiration rates and hence, increased plant water use efficiency

(Tricker *et al.*, 2005). As a result, the plant may reduce stomatal frequencies under elevated CO₂ concentration and maintain equal or increased carbon intake, so the relationship is of an inverse nature (Gregory, 1996; Fernandez *et al.*, 1998).

Combined with reduced stomatal opening, conductance and transpiration rates, elevated CO₂ concentration also depresses dark respiration rates also leading to increased water use efficiency (Wullschlegler *et al.*, 1992; Murray, 1995). Increase in water use efficiency has been found to increase drought tolerance in many plant species, which may allow increased plant distributions (Tyree and Alexander, 1993; Huxman *et al.*, 1998). Whether future increases in plant distribution are realized is dependent upon whether increased water use efficiency will be greater than enhanced transpiration, as a result of global warming (Houghton *et al.*, 1990 & 2001; Crowley, 2000).

Transpiration is one of the major gas exchange related traits associated with plant growth and productivity. In tree species stomatal transpiration

contributes more than 90% of total transpiration (Taiz and Zeiger 2002).

Instantaneous WUE is estimated as the ratio of net photosynthetic rate to transpiration (Petite *et al.* 2000). Higher the value, better the efficiency of the plant to divert water for photosynthesis than transpiration. Instantaneous water use efficiency, the ratio of amount of carbon fixed per unit amount of water lost through transpiration, differed significantly amongst the clones studied. Transpiration and photosynthesis are two major gas exchange parameters, which determine WUE of plants. With reference to the instantaneous water use efficiency, 3 clones (TC-1, 12 and 16) and 5 clones (TC-7, 8, 12, 13 and 20) sowed higher instantaneous water use efficiency value in elevated temperature and CO₂ respectively compared to the ambient. These clones could be the ideal clones for water limited conditions. Kannan Warriar *et al.* (2007) found considerable variation with respect to physiological parameters including water use efficiency in 33 clones of *Casuarina equisetifolia*.

Table 1. Gas exchange characteristics in Teak clones subjected to conditions of elevated temperature and CO₂ at the end of eight months.

Sl. No	Gas exchange characteristics	Treatments		
		Control	Elevated temperature	Elevated CO ₂
1.	Net Photosynthetic Rate (Pn) ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	8.0 ^a	6.34 ^b	5.35 ^c
2.	Stomatal Conductance (gs) ($\text{mol m}^{-2} \text{s}^{-1}$)	0.09 ^a	0.06 ^b	0.04 ^b
3.	Intercellular CO ₂ Concentration (Ci) ($\mu\text{l l}^{-1}$)	275.26 ^b	294.14 ^a	230.79 ^c
4.	Transpiration Rate (E) ($\text{mmol m}^{-2} \text{s}^{-1}$)	2.03 ^a	2.00 ^b	1.79 ^c
5.	Intrinsic Water Use Efficiency ($\mu\text{mol mol}^{-1}$)	148.03 ^b	122.76 ^c	185.78 ^a
6.	Instantaneous Water Use Efficiency ($\mu\text{mol mmol}^{-1}$)	4.84 ^c	3.04 ^a	3.71 ^b
7.	Intrinsic Carboxylation Efficiency ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.034 ^c	0.021 ^a	0.025 ^b
8.	Intrinsic Mesophyll Efficiency $\mu\text{l l}^{-1} (\text{mol m}^{-2} \text{s}^{-1})^{-1}$	4283.2 ^c	6175.35 ^b	7273.43 ^a

Table-2: Net photosynthetic rate, stomatal conductance, intercellular CO₂ concentration and transpiration rate in Teak clones subjected to elevated temperature and CO₂ at the age of 8 months.

Clone ID	Net Photosynthetic Rate (Pn) ($\mu\text{mol m}^{-2} \text{s}^{-1}$)			Stomatal Conductance (gs) ($\text{m}^2 \text{s}^{-1}$)			Intercellular CO ₂ Concentration (Ci)($\mu\text{l l}^{-1}$)			Transpiration Rate (E) ($\text{mmol m}^{-2} \text{s}^{-1}$)		
	Control	ET	EC	Control	ET	EC	Control	ET	EC	Control	ET	EC
TC-1	7.96 ^{eh}	5.64 ^{eh}	5.3 ^{eh}	0.04 ^{ci}	0.055 ^{ci}	0.076 ^{ci}	233.0 ^{di}	293.2 ^{di}	286.3 ^{di}	2.07 ^c	1.08 ^a	3.54 ^c
TC-2	6.62 ⁱ	4.3 ⁱ	3.96 ⁱ	0.023 ⁱ	0.017 ⁱ	0.018 ⁱ	214.0 ^{hi}	215.3 ^{hi}	216.5 ^{hi}	0.89 ^a	1.24 ^b	0.81 ^a
TC-3	6.63 ⁱ	4.32 ⁱ	3.98 ⁱ	0.024 ^{gh}	0.043 ^{g-i}	0.016 ^{gh}	224.3 ^{dg}	342.5 ^{dg}	220.4 ^{dg}	0.92 ^a	1.86 ^b	0.86 ^a
TC-4	8.36 ^{hi}	9.05 ^{hi}	5.7 ^{hi}	0.023 ^{hi}	0.045 ^{hi}	0.014 ^{hi}	117.8 ⁱ	342.8 ⁱ	117.6 ⁱ	1.21 ^b	1.68 ^b	0.95 ^a
TC-5	6.23 ^{bc}	3.92 ^{bc}	3.57 ^{bc}	0.163 ^{ac}	0.051 ^{ac}	0.050 ^{ac}	356.8 ^{be}	246.5 ^{be}	232.5 ^{be}	2.16 ^c	2.01 ^c	2.34 ^c
TC-6	7.01 ⁱ	8.69 ⁱ	4.35 ⁱ	0.027 ^{gh}	0.057 ^{gh}	0.015 ^{gh}	116.5 ⁱ	357.4 ⁱ	135.2 ⁱ	0.67 ^a	1.62 ^b	0.82 ^a
TC-7	12.68 ^a	10.37 ^a	10.03 ^a	0.142 ^{ab}	0.083 ^{ab}	0.039 ^{ab}	365.4 ^{dg}	242.6 ^{dg}	207.6 ^{dg}	3.27 ^c	3.05 ^c	1.35 ^b
TC-8	8.15 ^{dg}	5.84 ^{dg}	5.5 ^{dg}	0.158 ^{ab}	0.084 ^{ab}	0.015 ^{ab}	388.6 ^{ad}	351.3 ^{ad}	138.2 ^{ad}	2.57 ^c	2.42 ^c	0.84 ^a
TC-9	8.02 ^{bd}	5.7 ^{bd}	5.36 ^{bd}	0.082 ^{ac}	0.118 ^{ac}	0.060 ^{ac}	351.6 ^{ab}	314.6 ^{ab}	286.4 ^{ab}	2.19 ^c	1.98 ^c	2.43 ^c
TC-10	8.36 ^{gh}	6.05 ^{gh}	5.71 ^{gh}	0.052 ^{gh}	0.039 ^{gh}	0.053 ^{gh}	234.5 ^{cd}	351.7 ^{cd}	243.8 ^{cd}	1.59 ^b	1.42 ^c	3.12 ^c
TC-11	7.52 ^{hi}	8.21 ^{hi}	4.87 ^{hi}	0.021 ⁱ	0.035 ⁱ	0.017 ⁱ	131.5 ^{hi}	299.3 ⁱ	201.4 ^{hi}	0.92 ^a	1.28 ^b	0.96 ^a
TC-12	9.44 ^{eh}	7.12 ^{eh}	6.78 ^{eh}	0.081 ^{hi}	0.024 ^{fi}	0.025 ^{hi}	246.7 ^{hi}	196.4 ^{hi}	216.3 ^{hi}	2.24 ^c	1.62 ^b	1.24 ^b
TC-13	9.48 ^b	7.16 ^b	6.82 ^b	0.179 ^{ab}	0.046 ^{ab}	0.039 ^{ab}	394.6 ^{de}	168.6 ^{de}	251.4 ^{de}	3.27 ^c	2.55 ^c	1.82 ^b
TC-14	6.92 ^{ce}	4.61 ^{ce}	4.27 ^{ce}	0.172 ^{ab}	0.080 ^{ab}	0.048 ^{ab}	410.3 ^a	350.5 ^a	223.8 ^a	3.44 ^c	3.58 ^c	2.56 ^c
TC-15	8.49 ^{bd}	6.17 ^{bd}	5.83 ^{bd}	0.163 ^{ad}	0.078 ^{ad}	0.049 ^{ad}	382.7 ^a	274.6 ^a	324.6 ^a	2.67 ^c	2.18 ^c	2.46 ^c
TC-16	6.72 ^{ci}	4.41 ^{ci}	4.07 ^{ci}	0.102 ^{dh}	0.065 ^{dh}	0.061 ^{dh}	442.9 ^a	304.6 ^a	246.2 ^a	3.42 ^c	1.82 ^c	2.48 ^c
TC-17	9.28 ^{gh}	6.97 ^{gh}	6.63 ^{gh}	0.266 ^{ei}	0.037 ^{pi}	0.055 ^{pi}	232.1 ^{be}	307.3 ^{be}	319.5 ^{be}	2.47 ^c	2.68 ^c	2.15 ^c
TC-18	7.42 ^{gh}	5.11 ^{gh}	4.76 ^{gh}	0.064 ^{hi}	0.044 ^{hi}	0.050 ^{hi}	270.3 ^{dg}	246.8 ^{dg}	284.3 ^{dg}	1.62 ^c	2.38 ^c	1.86 ^c
TC-19	7.19 ⁱ	7.88 ⁱ	4.54 ⁱ	0.044 ^{hi}	0.051 ^{hi}	0.039 ^{hi}	148.4 ^{ei}	318.3 ^{pi}	288.3 ^{pi}	0.95 ^a	1.84 ^c	2.11 ^c
TC-20	7.6 ^{hi}	5.29 ^{hi}	4.95 ^{hi}	0.027 ^{be}	0.052 ^{be}	0.020 ^{be}	245.2 ^{dg}	358.4 ^{dg}	175.4 ^{dg}	2.08 ^c	1.62 ^c	1.08 ^b

Means with atleast one letter common in a column to not differ significantly as per Duncan's Multiple Range Test (significant at 0.05% level).
ET - Elevated Temperature, EC - Elevated CO₂.

Table-3: Water use efficiency, carboxylation efficiency and mesophyll efficiency in Teak clones subjected to elevated temperature and CO₂ at the age of 8 months.

Clone ID	Intrinsic water use efficiency ($\mu\text{mol mol}^{-1}$)			Instantaneous water use efficiency ($\mu\text{mol mmol}^{-1}$)			Intrinsic Carboxylation Efficiency ($\mu\text{mol m}^{-2} \text{s}^{-2}$)			Intrinsic Mesophyll Efficiency ($\mu\text{l}^{-1} (\text{mol m}^{-2} \text{s}^{-1})^{-1}$)		
	Control	ET	EC	Control	ET	EC	Control	ET	EC	Control	ET	EC
TC-1	199.00 ^{bc}	102.55 ^b	69.74 ^a	3.85 ^a	5.22 ^c	1.50 ^a	0.034 ^b	0.019 ^a	0.019 ^a	5825 ^d	5331 ^d	3767 ^a
TC-2	287.83 ^{cd}	252.94 ^c	220.00 ^c	7.44 ^d	3.47 ^b	4.89 ^c	0.031 ^b	0.020 ^b	0.018 ^a	9304 ⁱ	12665 ⁱ	12028 ^b
TC-3	276.25 ^{cd}	100.47 ^b	248.75 ^c	7.21 ^d	2.32 ^a	4.63 ^c	0.030 ^b	0.013 ^a	0.018 ^a	9346 ⁱ	7965 ⁱ	13775 ^b
TC-4	363.48 ^d	201.11 ^c	407.86 ^d	6.91 ^c	5.39 ^c	6.01 ^d	0.071 ^e	0.026 ^b	0.049 ^d	5122 ^d	7618 ⁱ	8400 ^e
TC-5	38.22 ^a	76.86 ^a	71.40 ^a	2.88 ^a	1.95 ^a	1.53 ^a	0.017 ^a	0.016 ^a	0.015 ^a	2189 ^a	4833 ^c	4650 ^b
TC-6	114.92 ^b	152.46 ^b	290.00 ^c	10.46 ^e	5.36 ^c	5.30 ^c	0.060 ^d	0.024 ^b	0.032 ^c	1910 ^a	6270 ^e	9013 ⁱ
TC-7	89.30 ^a	124.94 ^b	257.18 ^c	3.88 ^a	3.40 ^b	7.43 ^d	0.035 ^b	0.043 ^d	0.048 ^d	2573 ^a	2923 ^a	5323 ^c
TC-8	51.58 ^a	69.52 ^a	366.67 ^d	3.17 ^a	2.41 ^a	6.55 ^d	0.021 ^a	0.017 ^a	0.040 ^d	2459 ^a	4182 ^c	9213 ⁱ
TC-9	97.80 ^a	48.31 ^a	89.33 ^a	3.66 ^a	2.88 ^a	2.21 ^a	0.023 ^a	0.018 ^a	0.019 ^a	4288 ^c	2666 ^c	4773 ^b
TC-10	160.77 ^b	155.13 ^b	107.74 ^b	5.26 ^c	4.26 ^b	1.83 ^a	0.036 ^b	0.017 ^a	0.023 ^b	4510 ^c	9018 ^b	4600 ^b
TC-11	358.10 ^c	234.57 ^c	286.47 ^c	8.17 ^d	6.41 ^d	5.07 ^c	0.057 ^d	0.027 ^b	0.024 ^b	6262 ^e	8551 ^g	11847 ^g
TC-12	116.54 ^b	296.67 ^c	271.20 ^c	4.21 ^b	4.40 ^c	5.47 ^c	0.038 ^b	0.036 ^c	0.031 ^c	3046 ^b	8183 ^g	8652 ^e
TC-13	52.96 ^a	155.65 ^b	174.87 ^b	2.90 ^a	2.81 ^a	3.75 ^b	0.024 ^a	0.042 ^d	0.027 ^b	2204 ^a	3665 ^b	6446 ^d
TC-14	40.23 ^a	57.63 ^a	88.96 ^a	2.01 ^a	1.29 ^a	1.67 ^a	0.017 ^a	0.013 ^a	0.019 ^a	2385 ^a	4381 ^c	4663 ^b
TC-15	52.09 ^a	79.10 ^a	118.98 ^b	3.18 ^a	2.83 ^a	2.37 ^a	0.022 ^a	0.022 ^b	0.018 ^a	2348 ^a	3521 ^b	6624 ^d
TC-16	65.88 ^a	67.85 ^a	66.72 ^a	1.96 ^a	2.42 ^a	1.64 ^a	0.015 ^a	0.014 ^a	0.017 ^a	4342 ^c	4686 ^c	4036 ^b
TC-17	34.89 ^a	188.38 ^b	120.55 ^b	3.76 ^a	2.60 ^a	3.08 ^b	0.040 ^c	0.023 ^b	0.021 ^b	873 ^a	8305 ^g	5809 ^c
TC-18	115.94 ^b	116.14 ^b	95.20 ^a	4.58 ^b	2.15 ^a	2.56 ^a	0.027 ^a	0.021 ^b	0.017 ^a	4223 ^c	5609 ^d	5686 ^c
TC-19	163.41 ^b	154.51 ^b	116.41 ^b	7.57 ^d	4.28 ^b	2.15 ^a	0.048 ^c	0.025 ^b	0.016 ^a	3373 ^b	6241 ^e	7392 ^e
TC-20	281.48 ^{cd}	101.73 ^b	247.50 ^c	3.65 ^a	3.27 ^b	4.58 ^c	0.031 ^b	0.015 ^a	0.028 ^b	9081 ⁱ	6892 ^e	8770 ^e

Means with atleast one letter common in a column to not differ significantly as per Duncan's Multiple Range Test (significant at 0.05% level).
ET- Elevated Temperature, EC - Elevated CO₂.

The Pn/Ci ratio explained as the intrinsic among the clones and the same clones which showed carboxylation efficiency also differed significantly relatively higher WUE had high CE also. These clones

might have greater dependency of photosynthesis on mesophyll characters than stomatal characters. This was evident from the comparatively higher intrinsic mesophyll efficiency values for these clones over those exhibiting higher WUE and carboxylation efficiency. Similar observations have been made in rubber (*Hevea brasiliensis*) (Nataraja and Jacob, 1999) and sandal wood (Arunkumar *et al.*, 2009).

Net photosynthesis and related physiological parameters have been suggested as early selection criteria to improve the efficiency of tree breeding (Balasubramanian and Gurumurthi, 2001). The selections made in the study could be potential candidates' for different agroclimatic zones due to their ability to adapt to varied climatic conditions and also for the development of site specific seed orchards.

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