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VARIATION IN PHOTOSYNTHESIS, TRANSPIRATION AND INSTANTANEOUS WATER USE EFFICIENCY IN THE CLONES OF SANDALWOOD (*SANTALUM ALBUM* L.)

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SUMMARY

Variability in single leaf photosynthesis and related gas exchange parameters were studied on 37 clones of sandalwood (*Santalum album* L.). One-year-old grafts of each clone were grown under controlled conditions and gas exchange measurements were recorded using portable photosynthesis system under saturated light intensities and ambient CO_2 concentrations. Significant variations in single leaf photosynthesis (Pn), stomatal conductance (gs), intercellular CO_2 concentration (Ci), transpiration rate (Tr) has been observed among the clones studied. Instantaneous water use efficiency (WUE) calculated as Pn/gs and carboxylation efficiency (CE) estimated by Pn/Ci also showed significant variation. Biochemical parameters such as total chlorophyll and buffer soluble protein differed significantly. Correlation studies showed linear positive relationship between Pn and gs (r=0.80) suggesting that photosynthesis is controlled more by stomatal factors. Cluster analysis revealed that the clones did not cluster on the basis of their geographic locations.

Key words: **Net photosynthetic rate, *Santalum album*, transpiration, variability, water use efficiency**

INTRODUCTION

Sandalwood (*Santalum album* L.) a member of Santalaceae is popularly known for its scented heartwood and oil. The oil obtained from the heartwood is commercially known as “East Indian sandalwood oil” is one of the oldest known perfumery materials. Sandalwood occupies a pre-eminent position among all the other tree species in India and is called as ‘royal tree’. Due to over exploitation sandalwood has been categorized as ‘vulnerable’ in the Red Data List (IUCN 2009). Sandalwood tree is a small evergreen tree attaining a height of 12 to15 metres and a girth of 1 to 2.4 metres with slender drooping as well as erect branching. It grows well in early stages under partial shade but at the middle and late stages shows intolerance to heavy overhead shade. It flourishes well where there is moderate rainfall of 600 to 1600 mm (Srinivasan *et al*. 1992).

Various studies have shown that morphological variability exists in sandalwood tree with reference to crown shape, bark colour, leaf shape, flowering period and seed germination (Srimathi *et al*. 1977, Kulkarni and Srimathi 1982, Veerendra and Bagchi 1985). To utilize this variability, tree improvement studies in sandal was initiated in early 1980s. Plus trees were identified on the basis of heartwood and oil content in the four predominantly sandalwood growing southern states of India namely, Andhra Pradesh, Karnataka, Kerala and Tamil Nadu. A clonal germplasm bank was established at Gottipura, Hoskote, near Bangalore, India.

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Use of physiological measurements to assist in the determination of superior genotypes for tree improvement is gaining importance (Kramer 1986, Koehn 1987). To evaluate the yield/biomass production or water use efficiency (WUE) of any perennial species like sandalwood requires experiments of long duration. To overcome this problem, one can look into the behaviour of certain physiological parameters which can effectively be used to assess the clonal performances under given environmental conditions. Net photosynthetic rate (Pn), transpiration rate (Tr) and total leaf area per plant are the important factors that determine the biomass production and WUE of a species. Variation in Pn, has been reported as determinants of plant productivity (Nataraja and Jacob 1999). Significant differences in Pn and stomatal conductance (gs) have been reported to exist in different tree species (Zipperlen and Press 1996), *Eucalyptus camaldulensis* (Farrell *et al*. 1996), *Populus* (Kalina and Ceulemans 1997), *Azadirachta indica* (Kundu and Tigerstedt 1998) and *Hevea brasiliensis* (Nataraja and Jacob 1999). 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 (Ceulemans *et al*. 1988). The present study was carried out to characterize and identify the sandalwood clones by estimating the magnitude of variation existing among various clones with reference to gas exchange parameters and related biochemical traits. The information obtained would therefore facilitate in designing further tree improvement and breeding strategies.

MATERIAL AND METHODS

The study was carried out on 37 clones of sandalwood (Table 1). Scion materials were taken from the clonal plants established at clonal germplasm bank Gottipura, Hoskote (14º 18'N – 77º12'E). The scion materials from 37 clones were then cleft grafted over one and half year old seedlings (stock) grown in earthen pots. These grafted plants were initially kept in shade house till new shoots emerged and then shifted to open conditions (PAR of 1800 µmol m^{-2} s^{-1}, 60 - 65% RH and temperature 29 ± 2ºC) at four-leaf stage. These grafts were managed with normal agronomical practices (Srinivasan *et al.* 1992) and one year old grafts were used for this study.

Gas exchange traits such as net photosynthetic rate (Pn), stomatal conductance (gs), intercellular CO_2 concentration (Ci) and transpiration rate (Tr) were measured using portable photosynthesis system CIRAS-1 (PP Systems, UK) for three ramets per accession. Fully expanded leaf from the apex was clamped to the leaf chamber and the observations were recorded when Pn, gs, and Ci reached a stable value under growth conditions. All gas exchange parameters were recorded between 9 AM and 12 noon on bright sunny days. One fully expanded terminal leaf (also used for measuring photosynthesis) was detached from each ramet and leaf chlorophyll (a, b, and total) was estimated. For estimation of chlorophyll, healthy leaf material (100 mg) was taken and cut into small bits and incubated in a mixture of Dimethly sulfoxide : 80 per cent acetone (1:1, 10 ml) overnight at room temperature under dark conditions. The absorbance was recorded at 645, and 663 nm using a spectrophotometer (Shimadzu UV – 240) and the chlorophyll contents were calculated (Arnon 1949).

For the estimation of total soluble protein, leaf material (1 g) was homogenized in cold extraction buffer (100 mM phosphate buffer pH 7.8, 5mM $MgCl_2$, 5mM DTT, 0.1mM EDTA, 1.5% (w/v) PVPP and 1mM PMSF) and centrifuged at 15,000 rpm for 10 minutes at 4°C. Protein content in the supernatant was estimated by dye binding method (Bradford 1976).

The data collected was subjected for statistical analysis and estimates of mean, variance and standard error were determined (Panse and Sukhatme 1961). Standard 'F' table of Snedecor (1961) was referred to carry out the significance test. The variance analysis (Panse and Sukhatme 1961) was worked out for each character separately and was established by analysis of variance (ANOVA). Pearson's product moment correlations were performed to assess the relationship between the gas exchange parameters. The relationship among various clones with reference to geographic

Table 1. List of sandalwood (*Santalum album*) clones and their origin

Sl. No.	Clonal code	Origin
1	AP4	Nehru Zoological park, Hyderabad, Andhra Pradesh
2	K1	Anekad, Kushal Nagar, Madikeri, Karnataka
3	K2	Thindlu, Hoskote, Bangalore, Karnataka
4	K3	Hulihatti, Ranibennur, Gadag, Karnataka
5	K4	PWD guest house, Vanivilas Sagar, Chitradurga, Karnataka
6	K5	IWST, Bangalore, Karnataka
7	K6	IWST, Bangalore, Karnataka
8	K9	IWST, Bangalore, Karnataka
9	K10	IWST, Bangalore, Karnataka
10	K11	Hardanhalli, Chamarajnagar, Karnataka
11	K13	Hardanhalli, Chamarajnagar, Karnataka
12	K23	Honehatti MF, Bhadravathi, Karnataka
13	K27	Chandrakala, SF, Shikaripura, Sagar, Karnataka
14	K31	Tangali sandal reserve, Kadur, Chickmagalur, Karnataka
15	K35	Sandal Koti, Kushalangar, Madikeri, Karnataka
16	K37	Silva Experiment Station, Mudigere, Bangalore, Karnataka
17	T1	Sholavaram Research Garden, RR Pudukottai, Tanjavur, Tamil Nadu
18	T3	Forest Guest House, Anchety, Hosur, Tamil Nadu
19	T4	Komateri, Polur, Vellore, Tamil Nadu
20	T5	Inner Javadhis RF, Alangayam, Thirupathur, Tamil Nadu
21	T6	Veerapannur RF, Polur, Vellore (1968 plantation), Tamil Nadu
22	T7	Veerapannur RF, Polur, Vellore (1970 plantation), Tamil Nadu
23	T8	Pavanamials Farm, Patta land, Shirkali, Tanjavur, Tamil Nadu
24	T9	FRC, Kurumbapatty, Shevroys, South Salem, Tamil Nadu
25	T11	FRC, Kurumbapatty, Shevroys, South Salem, Tamil Nadu
26	T12	FRC, Kurumbapatty, Shevroys, South Salem, Tamil Nadu
27	T13	FRC, Kurumbapatty, Shevroys, South Salem, Tamil Nadu
28	T14	FRC, Kurumbapatty, Shevroys, South Salem, Tamil Nadu
29	T19	Mundanthorai, Tirunelveli (1966 plantation), Tamil Nadu
30	T21	Mundanthorai, Tirunelveli (1966 plantation), Tamil Nadu
31	T22	Nachikotai, Harur, Chitteri Dharmpuri, Tamil Nadu
32	T23	Perieri Village, Pudur East, Chitteri, Harur, Dharmpuri, Tamil Nadu
33	T24	Thombakal, RF, Shanimadu, Harur, Chitteri, Dharmpuri, Tamil Nadu
34	T26	Thombakal, RF, Tholthuki Tending Plot, Harur, Chitteri, Dharmpuri, Tamil Nadu
35	T27	Parigam, Dharmpuri (1974 plantation), Tamil Nadu
36	T28	Jirgehalli, Hanur, Tamil Nadu
37	T29	Cattle Farm, Padak – 3 Hosur, Tamil Nadu

locations was examined on the basis of cluster analysis by applying Euclidean distance and single linkage method using STATISTICA (Stat Soft, Inc, USA) software package.

RESULTS AND DISCUSSION

Sandalwood is one of the most economically important trees heavily exploited for its heartwood and oil. While developing any tree improvement strategies, information pertaining to variability for morphological, genetical and physiological traits is necessary. However, in case of sandalwood variability in some basic physiological parameters such as Pn, gs, Tr, WUE etc., have not been examined and such an analysis is essential for selection of promising clones for further tree improvement programme. Significant clonal variation in Pn, gs, Ci, Tr, instantaneous WUE and *in vivo* carboxylation efficiency indicate the possibilities of choosing the best clones for a breeding programme. Similar attempt has been made to select high yielding hybrid aspen clones by using gas exchange and related parameters (Yu 2001). The parameter, Pn can be effectively used in trees for selecting the elite clones. It has been observed that Pn is under strong genetic control in *Populus* clones (Nelson and Ehlers 1984)

Variation in gas exchange traits and biochemical parameters among clones: Significant difference between sandalwood clones in Pn has been noticed. Among the clones examined, K37 showed the highest Pn, while T9 showed the lowest when measurements were made under saturated light intensities. Similarly, significant differences in gs, Ci and Tr were observed between the sandalwood clones (Table 2). Some of the clones such as T6, K37 and T21, which recorded high Pn also showed relatively higher gs. Instantaneous water use efficiency (WUE) calculated as Pn/gs differed significantly among the clones. The clone T14 had significantly higher WUE while K11 had the lowest. *In vivo* carboxylation efficiency as calculated by Pn/Ci showed significant variation among the clones. Clones such as K37 and T6, which maintained high Pn, also showed high carboxylation efficiency. Significant differences in chlorophyll a, chlorophyll b and total chlorophyll were recorded between clones (Table 3). The total chlorophyll values ranged from 0.512 mg g^{-1} in K1 to 1.483 mg g^{-1} in T14. Buffer soluble proteins extracted from healthy leaves of different clones exhibited significant differences. The protein value varied from 10.09 mg g^{-1} in clone K37 to 19.29 mg g^{-1} in clone T13. The clones (T13 and T14) that showed relatively higher chlorophyll content also showed higher protein values.

Studying the yield potential or complex traits like WUE of any perennial plants like sandalwood requires long gestation period experiments. To overcome this problem, Nataraja and Jacob (1999) suggested to look into the behaviour of growth related physiological parameters such as photosynthesis to evaluate the performance of clones. Positive correlation between photosynthesis and biomass has been reported in different species (Mythili and Nair 1996, Gerik *et al.* 1996, Hampson *et al.* 1996, Atkin *et al.* 1997, Thomas *et al*. 1997, Orlovic *et al.* 1998). It is likely that in case of sandalwood clones having high photosynthesis might have high growth rate and biomass production ability. We believe that clones T6 and K37, which showed significantly high Pn, can be used as high biomass types.

Net photosynthesis rate (Pn) and gs are often strongly related (Kundu and Tigerstedt 1998). Significant positive Pearson's coefficient correlation was observed between Pn and gs (r = 0.80), Pn and Tr (r = 0.63) and between gs and Tr (r = 0.80) (Table 4). In most of the species, photosynthesis rate increases when stomatal conductance increases (Heber *et al*. 1986, Bunce 1988). Significant variation among clones in gs and positive correlation (r = 0.80) between gs and Pn indicate that gs is one of the major factors regulating photosynthesis in sandalwood. Positive relationship was reported by Saraswathi and Paliwal (2008) in case of *Dalbergia sissoo*.

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). In the present study, we observed significant positive correlation between gs and total transpiration (r = 0.80) as reported in other studies and Tr was also positively associated with Pn (Table 4). Transpiration and photosynthesis are two major gas exchange parameters, which determine WUE of plants.

Table 2. Photosynthetic gas exchange parameters for various sandalwood clones*.

Clones	Net photosynthetic rate (Pn)(μmol $m^{-2}s^{-1}$)	Intercellular CO_2 concentration (Ci) (μlit lit^{-1})	Transpiration rate (Tr) (mol $m^{-2}s^{-1}$)	Stomatal conductance (gs) (m mol $m^{-2}s^{-1}$)	Water use efficiency (Pn/gs) (μmol milli mol^{-1})	Carboxylation efficiency (Pn/Ci) (μmol $m^{-2}s^{-1}$ μlit lit^{-1})
AP4	6.40	295.33	3.59	232.67	0.028	0.022
K1	6.37	310.00	4.10	224.33	0.033	0.024
K2	6.60	263.00	3.56	259.00	0.025	0.025
K3	6.77	314.00	3.75	268.33	0.025	0.022
K4	8.20	272.67	5.50	268.00	0.038	0.037
K5	6.77	278.33	4.63	220.67	0.036	0.028
K6	7.27	313.67	6.02	322.67	0.023	0.023
K9	9.37	294.67	5.20	326.00	0.029	0.032
K10	7.23	310.67	4.00	226.33	0.032	0.023
K11	10.10	296.67	6.12	469.33	0.017	0.027
K13	8.70	244.00	3.69	246.00	0.035	0.036
K23	8.03	269.33	3.86	269.67	0.030	0.030
K27	7.70	295.33	5.34	290.33	0.027	0.026
K31	9.60	295.33	6.02	362.00	0.027	0.033
K35	7.40	286.33	4.60	242.67	0.031	0.026
K37	12.40	285.67	5.56	386.00	0.032	0.043
T1	7.53	296.00	5.81	328.33	0.023	0.025
T3	6.47	285.00	3.69	230.33	0.032	0.026
T4	9.80	280.00	5.59	342.33	0.029	0.035
T5	8.10	290.67	6.16	346.67	0.023	0.028
T6	12.10	283.67	5.93	415.00	0.029	0.043
T7	8.10	290.00	4.88	346.00	0.023	0.028
T8	6.77	293.00	4.31	242.33	0.028	0.023
T9	6.33	268.33	3.65	232.67	0.027	0.024
T11	8.83	266.33	3.73	233.67	0.038	0.033
T12	6.87	296.67	5.30	285.67	0.024	0.023
T13	7.47	284.33	5.53	286.67	0.026	0.026
T14	6.93	269.00	4.51	220.67	0.040	0.033
T19	9.23	287.33	5.73	335.67	0.028	0.032
T21	10.60	280.33	5.57	348.33	0.030	0.038
T22	10.20	282.00	5.91	345.33	0.030	0.036
T23	6.37	292.33	4.14	240.67	0.026	0.022
T24	7.40	297.67	4.92	318.00	0.020	0.022
T26	6.70	287.33	4.38	222.00	0.030	0.023
T27	6.67	292.00	3.57	257.67	0.026	0.023
T28	6.57	286.33	3.51	237.67	0.032	0.026
T29	6.93	274.33	4.52	244.67	0.032	0.029
Mean	7.969	286.69	4.781	288.50	0.029	0.028
SEm(±)	0.224	6.011	0.103	9.663	0.001	0.001
CD	0.440	11.78	0.202	18.941	0.002	0.002

$\alpha = 0.05$

*Measurements at saturated PPFD and ambient CO_2 concentration.

Table 3. Biochemical parameters for various sandalwood clones

Clones	Chlorophyll a (mg/g fw)	Chlorophyll b (mg/g fw)	Total chlorophyll (mg/g fw)	Total soluble leaf protein (mg/g fw)
AP4	0.299	0.325	0.624	14.61
K1	0.360	0.152	0.512	12.94
K2	0.398	0.315	0.713	13.26
K3	0.387	0.148	0.535	13.15
K4	0.420	0.341	0.761	11.84
K5	0.461	0.298	0.758	12.15
K6	0.562	0.291	0.853	11.85
K9	0.330	0.254	0.584	11.03
K10	0.326	0.104	0.530	12.24
K11	0.641	0.353	0.993	17.56
K13	0.568	0.286	0.854	13.19
K23	0.448	0.147	0.595	15.71
K27	0.291	0.229	0.519	11.63
K31	0.640	0.386	1.026	16.58
K35	0.636	0.222	0.858	10.82
K37	0.439	0.184	0.624	10.09
T1	0.884	0.304	1.189	13.55
T3	0.652	0.190	0.842	11.36
T4	0.695	0.252	0.947	12.18
T5	0.813	0.351	1.164	16.35
T6	0.624	0.315	0.940	13.56
T7	0.595	0.292	0.887	16.76
T8	0.427	0.314	0.742	14.23
T9	0.370	0.254	0.624	11.54
T11	0.544	0.378	0.922	11.81
T12	0.627	0.261	0.887	18.75
T13	1.020	0.463	1.483	19.29
T14	1.054	0.409	1.463	17.46
T19	0.390	0.384	0.774	16.06
T21	0.947	0.400	1.347	16.70
T22	0.865	0.513	1.378	15.90
T23	0.889	0.394	1.283	12.41
T24	0.916	0.507	1.422	14.05
T26	0.566	0.232	0.799	14.90
T27	0.530	0.222	0.752	13.76
T28	0.817	0.212	1.029	12.47
T29	0.354	0.172	0.526	14.54
Mean	0.589	0.293	0.885	13.95
SEm(±)	0.393	0.730	0.005	0.019
CD	0.073	0.143	0.011	0.037

$\alpha = 0.05$

Water use efficiency, the ratio of amount of carbon fixed per unit amount of water lost through transpiration, differed significantly amongst the clones studied (Table 2). The clones such as T14 and T11, which showed higher instantaneous WUE could be the ideal clones for water limited conditions. Kannan Warrier *et al*. (2007) found considerable variation with respect to physiological parameters including water use efficiency in 33 clones of *Casuarina equisetifolia*. We calculated Pn/Ci as carboxylation efficiency (CE). The CE differed significantly among the clones and the clones such as K37, T6, T21 and K4, which had high CE also showed relatively higher WUE. These clones might have greater dependency of photosynthesis on mesophyll characters than stomatal characters as reported in *Hevea brasiliensis* (Nataraja and Jacob 1999), suggesting that these clones may be potential parents for tree improvement for WUE.

Cluster analysis: Cluster analysis based on physiological and biochemical parameters revealed that 37 clones studied clustered into two major clusters subdivided into five sub clusters with AP4 and K13 spanning the extremes (Fig. 1). The clustering pattern revealed that the tendency of genotypes from diverse geographic region to group together in one cluster might be due to the similarity of the nature of selection pressure operating under the respective domestic conditions.

Conclusion: Variability in sandalwood with reference to morphological traits has been well documented. However, evaluation through basic physiological parameters such as photosynthetic gas exchange parameters has not been attempted so far. In the present study, significant variation has been observed for all the gas exchange traits studied on 37 clones of sandalwood. Variation among clones for gs and positive correlation (r = 0.80) between gs and Pn indicate the importance of gs in regulating photosynthesis. Clones T14 and T11 showed higher instantaneous WUE and clones K37, T6, T21 and K4 which had high CE also showed relatively higher WUE. The clones were clustered into five sub clusters, however, none of them clustered on the basis of geographic origin. Further studies should be aimed at field evaluation of those clones showing initial superiority with reference to various photosynthetic gas exchange traits.

Table 4. Pearson's product moment correlation coefficients (r) among photosynthetic gas exchange parameters (measurements made on 111 ramets representing 37 accessions)

Trait	Pn	gs	Ci	Tr	Pn/gs	Pn/Ci
Pn	1.00					
gs	0.80***	1.00				
Ci	-0.14	0.19	1.00			
Tr	0.63***	0.80***	0.24*	1.00		
Pn/gs	0.004	-0.54***	-0.52***	-0.35***	1.00	
Pn/Ci	0.86***	0.47***	-0.48***	0.43***	0.45***	1.00

* = significant at p<0.05 ; *** = significant at p<0.001

Abbreviations: Pn = net photosynthetic rate; gs = stomatal conductance; Ci = intercellular CO_2 concentration; Tr = transpiration rate, Pn/gs = instantaneous water use efficiency, Pn/ci = *in vivo* carboxylation efficiency

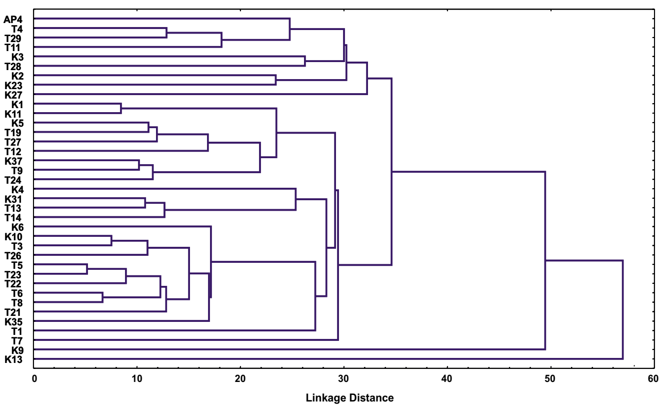

Fig. 1. Similarity (identity) dendrogram for 37 clones based on photosynthetic gas exchange and biochemical traits

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