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Variation in Net Carbon Assimilation and Related Parameters in Coconut (*Cocos nucifera* L.) Under Field Conditions*

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Net carbon assimilation (P_N), stomatal conductance (gs) and transpiration rate (Tr) were measured in coconut genotypes during non-stress and stress periods under field conditions. The parameters showed significant differences only between the two periods. Intrinsic (P_N/gs) as well as instantaneous water use efficiency (P_N/Tr), intrinsic carboxylation efficiency (P_N/Ci) as well as mesophyll efficiency (Ci/gs) showed significant differences between non-stress and stress periods. Relation between the gas exchange parameters was understood by working out correlations. The results indicated the involvement of both stomatal and nonstomatal limitation in net carbon assimilation in coconut during stress periods.

Keywords: Coconut, carbon assimilation, conductance, stress, transpiration rate, water use efficiency.

INTRODUCTION

Coconut (*Cocos nucifera* L.) is a perennial plantation tree crop which grows well under warm humid weather conditions of the tropics. Since coconut is mainly grown under rainfed condition, both agrometeorological variables as well as soil water-deficit affect the growth and productivity of this crop during summer months (Ramadasan *et al.*, 1991). Impact of meteorological variables on the water relation of this crop has been reported by Kasturi Bai *et al.* (1988). The genotype which can maintain the water balance effectively by regulating the transpirational water loss during drought situation has been catogorized as drought-tolerant by Rajagopal *et al.* (1990). Since stomata play an important role in controlling the balance between photosynthetic CO_2 assimilation and transpiration (Cowan and Farquhar, 1977), the efficient stomatal closure can limit CO_2 diffusion into the leaf, thus reducing the CO_2 assimilation rate. The impact of agrometeorological variables on gas exchange characteristic of perennial plantation tree crops like rubber (Samsuddin and Impens, 1979), coffee (Nunes, 1988), cashew (Balasimha, 1991) and cocoa (Joly and Hahn, 1989; Balasimha *et al.*, 1991) has been well established, but not in coconut. Hence the present work was undertaken to assess the variation in net carbon assimilation rate and related parameters, viz. stomatal conductance, transpiration rate, etc. in the adult coconut palms growing under rainfed condition during non-stress and stress periods under field conditions.

MATERIALS AND METHODS

Coconut palms (18 to 22-year-old) growing in red sandy loam soil under rainfed condition at the Central Plantation Crops Research Institute, Kasaragod, under similar cultural and management practices were the material for the observations. The experimental material included one local tall variety (WCT), three dwarf varieties, viz. Chowghat Orange Dwarf (COD), Malayan Yellow Dwarf (MYD) Gangabondam (GB) and five hybrids, viz. WCT × WCT, WCT × COD, COD × WCT, Laccadive Ordinary (LO) × GB and LO × COD. The observations were carried out from six palms per genotype for three to four consecutive days twice in a year, i.e. just after the rains (September, non-stress) and during the summer months (April, stress) for two consecutive years. Photosynthetic parameters were measured

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between 10 and 11.30 hrs, in detached leaflets as described by Rajagopal *et al.* (1987) for water relation components.

Net carbon assimilation (P_N), stomatal conductance (gs) and transpiration rate (Tr) were measured using the portable photosynthesis system (Li-6200, Li Cor Inc, USA). The measurements were carried out with one litre chamber enclosing up to 15.5 cm^2 leaf area and equilibrated for one to two min. Two observations were made for each leaflet and the measurement was made on four leaflets from the opposite side of the leaf and the mean values of these four sets of readings were taken as one observation. The same instrument simultaneously measure other parameters, viz. ambient CO_2 concentration (Ca), radiation, vapour pressure deficit (VPD) and temperature. The internal CO_2 concentration (Ci) was computed in the instrument using the initial values of PN, Tr, Ca and leaf resistance. The ratios of P_N/Tr, P_N/gs, P_N/Ci and Ci/gs were calculated from the data of the gas exchange characteristics. Data on the daily pan evaporation rate was obtained from the climatological station established at the Institute and soil moisture content in the basins of the palms up to a depth of one meter was determined gravimetrically as per the standard procedures.

Significance between the parameters was worked out by using analysis of variance as applied to completely randomized block design and correlation coefficient by standard method.

RESULTS AND DISCUSSION

Agrometeorological variables during non-stress and stress periods

The microclimate at the time of taking the observations indicated clear cut differences between non-stress and stress periods (Table 1). The non-stress period was characterized by irradiance of 1067 μmol m^{-2} s^{-1}, mean ambient temperature of 33.3°C and a VPD of 2.2 KPa, whereas the stress period, by an increase in radiation (1444 μmol m^{-2} s^{-1}), air temperature (36°C) and VPD (3.3 KPa). This coupled with a high pan evaporation rate (5.3 mm) as compared to the non-stress period (3.6 mm) indicated high evaporative demand of the atmosphere, leading to atmospheric drought. The soil moisture content,

Table 1. Agrometeorological variables during non-stress and stress periods (mean and range)

Variable	Non-stress	Stress
PAR (μmol $m^2 s^{-1}$)	1067 (1000–1070)	1444 (1350–1470)
Air temperature (°C)	33.3 (31.4–34.1)	36.1 (34.7–37.3)
VPD (KPa)	2.2 (1.9–2.8)	3.3 (3.1–3.6)
Pan evaporation (mm day^{-1})	3.6 (3.3–3.8)	5.3 (5.2–5.5)

5.6% during stress period as compared to 8.7% during non-stress period which accounted for 36% reduction during stress period indicated the soil water deficit during the period.

Gas exchange characteristics

The observation on gas exchange characteristics during non-stress and stress periods is given in Tables 2 and 3 and the correlation between these parameters during stress period is given in Table 4. P_N, gs and Tr showed significant differences between the two periods. However genotypic differences were not significant (Table 2). P_N rate ranged between 6.7 and 9.0 μmol^{-2} s^{-1} during non-stress period while it ranged between 4.0 and 5.3 μmol m^{-2} s^{-1} during stress period, thus showing 42% reduction during stress period as compared with the non-stress period. Similarly gs showed 64% reduction during stress period as compared with the non-stress period. This shows that gs is affected more than the P_N rate. This variation in P_N and gs has been widely reported in annual as well as perennial crops (Farquhar and Sharkey, 1982; Balasimha *et al.*, 1991). The relation between P_N and gs has been found to be significant during stress period (r^2 = 46**, P = 1%), thus indicating that high P_N is associated with higher gs and reduction can be attributed to the stress-induced stomatal closure. Farquhar and Sharkey (1982) reported that gs impart more limitation to P_N rate during abiotic stress. Parallel with the reduction in P_N, Tr rate also showed 37% reduction during stress period.

The functional significance of stomatal closure in intrinsic (P_N/gs) and instantaneous water use efficiency (P_N/Tr) has been discussed by Comstock and

Table 2. Genotypic variation in P_N, gs and Tr in coconut. (mean of non-stress (no-str) and stress (str) periods, n = 6)

	P_N (µmol m^{-2} s^{-1})		gs (mol m^{-2} s^{-1})		Tr (mmol m^{-2} s^{-1})	
Genotype	no-str	str	no-str	str	no-str	str
WCT	6.88	3.98	0.45	0.14	8.30	5.00
COD	7.72	5.00	0.31	0.16	7.27	5.87
MYD	6.67	5.01	0.50	0.16	8.10	6.23
GB	7.68	5.34	0.43	0.15	8.77	6.60
WCT × WCT	7.86	4.14	0.51	0.15	8.90	4.87
WCT × COD	8.68	4.48	0.39	0.14	7.63	4.47
COD × WCT	8.85	4.00	0.37	0.14	7.80	4.43
LO × GB	8.41	5.32	0.35	0.15	7.07	4.53
LO × COD	9.01	4.67	0.35	0.12	8.80	3.80
CD (P = 0.05)	NS	NS	NS	NS	NS	NS

NS: Not-significant.

Table 3. P_N rate and related parameters during non-stress and stress periods. (Mean values n = 54)

Parameter	Non-stress	Stress	CD (P = 0.05)
P_N (µmol m^{-2}s^{-1})	7.97	4.66	0.586
gs (mol m^{-2}s^{-1})	0.41	0.15	0.034
Tr (mmol m^{-2}s^{-1})	8.07	5.09	0.542
Ci (µl l^{-1})	283.4	261.8	5.552
P_N/gs (µmol mol^{-1})	20.51	32.78	3.118
P_N/Tr (µmol mmol^{-1})	1.00	0.91	0.08
P_N/Ci (µmol m^{-2} s^{-1} µl^{-1} l^{-1} × 10^{-2})	2.85	1.76	0.286
Ci/gs (µl l^{-1} mol^{-1} m^{-2} s^{-1})	0.74	1.87	0.154

Ehleringer (1993). The higher decrease in gs more than that of P_N rate lead to an increase in P_N/gs (60%) during stress period as compared with the non-stress period. As reported by Maroco *et al.* (1997) the higher P_N/gs implies an efficient stomatal regulatory capacity of coconut palms during stress period. The negative correlation observed between P_N/gs and gs ($r^{-2} = -0.60$**, P = 1%) corroborates with the report (Table 4). However, P_N/Tr showed significant reduction during stress period (P = 5%) as compared with the non-stress period. This can be attributed to the higher reduction in P_N than that of Tr rate during stress period. High correlation observed between gs and P_N ($r^2 = 0.46$*, P = 5%) as well as gs and Tr ($r^2 = 0.90$**, P = 1%) suggests a consequential close relationship between P_N and Tr (Table 4). The significant and positive relationship between P_N/gs and P_N/Tr supports the above observation (Table 4).

Ci showed 8% decrease during stress period as compared with the non-stress period. Decrease in Ci in water-stressed *Phaseolus* plants has been reported by Cornic and Briantais (1991). No correlation has been observed between P_N and Ci, thus indicating nonstomatal limitation of P_N (Anderson *et al.*, 1995). The ratio of P_N/Ci which measures the intrinsic carboxylation efficiency (Farquhar and Sharkey, 1982) showed 38% reduction during stress period and showed significant positive relationship with P_N ($r^2 = 0.73$**). Similarly Ci/gs which gives an indication of the mesophyll capacity (Sheshshayee *et al.*, 1996) showed an increase of 155% during stress period as compared with the non-stress period. The decreased P_N/Ci ratio as well as increased Ci/gs ratio indicate the reduced mesophyll capacity during stress period. Sheshshayee *et al.* (1996) also attributed the reduction in assimilation rate during water stress to the reduced mesophyll capacity. The negative correlation ($r^2 = -0.54$**) observed between P_N and Ci/gs ratio during stress period confirms this.

Thus the following inferences can be drawn from the above results: coconut palm adapt to short dry season of summer months by stomatal closure, thus regulating the transpiration rate. The positive correlation between P_N and gs as well as the negative correlation between P_N and Ci/gs clearly indicate that both stomatal and non-stomatal factors influence the net carbon assimilation rate in coconut during stress period.

Table 4. Correlation coefficient (r^2) for gas exchange characteristics during stress period in coconut ($n = 54$)

	Tr	gs	P_N/gs	P_N/Tr	P_N/Ci	Ci/gs
P_N	0.78**	0.46*	0.42*	0.46*	0.73**	−0.54**
Tr		0.90**	−0.91**	−0.79**	0.61**	–
gs			−0.60**	–	0.38*	−0.96**
P_N/gs				0.60**	–	0.51**
P_N/Tr					–	0.57**
P_N/Ci						−0.48**

*, **: Significant at 5% and 1% probability levels respectively; –, not significant.

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