Indian J. Hort. 64(2), June 2007: 181-189

Genetic analysis of drought responsive physiological characters in coconut

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ABSTRACT

Coconut (*Cocos nucifera* L.) is mainly grown as a rainfed crop and experiences drought during summer months. Earlier studies identified the physiological traits responsible for drought tolerance in coconut. For the first time an attempt is made to understand the genetics of these characters. Coconut cultivars (two Dwarfs- CGD and MYD; four Talls- ECT, PHOT, LCT and FMST) with desirable characters were selected and crossed in a 2 x 4 line x tester mating design to study the combining ability and gene action with respect to drought responsive physiological traits. Physiological parameters like leaf water potential, transpiration rate, net photosynthetic rate (*Pn*) and lipid peroxidation were recorded in seedlings under non-stress, water stress and recovery conditions. Analysis of variance for combining ability revealed significant differences among parents and hybrids for all characters. Seedling transpiration rates and leaf water potentials showed higher specific combining ability (SCA) effects than general combining ability (GCA) effects due to predominance of non-additive gene action indicating heterosis for this character. The *Pn* under stress was additive with good combining ability, while the *Pn* during non-stress and recovery were governed by non-additive gene action that can be exploited for heterosis. In case of lipid peroxidation, gene action was unpredictable in non-stress with additive gene action being nil with low dominance. Whereas, during stress and recovery, non-additive gene action was observed. These results indicate the possibility of exploiting the nature of gene action governing drought sensitive traits in breeding for tolerant coconuts.

Key words: *Cocos nucifera* L., genetic analysis, leaf water potential, lipid peroxidation, photosynthesis, water stress.

INTRODUCTION

Coconut, one of the economically important plantations of tropics, provides livelihood and employment to resource poor farmers in India. Since it is mainly grown as a rainfed crop, the palms experience summer dry periods and frequent drought years. These situations cause not only considerable yield loss but also make the plantation non-profitable in long run. Any deviation from the optimum weather conditions for growth and nut yield of coconut (Child, 4; Murray 15) will cause the palm to be under stress. The environmental stresses affected coconut yield in India (Rajagopal and Naresh Kumar, 23, 24) in intermediate and dry zones of Sri Lanka (Peiris *et al.,* 17; Peiris and Thattil, 18) and in Zanzibar (Juma and Fordham, 11). Bonneau and Subagio (2) earmarked the drought prone zones in coconut growing areas of Indonesia. All these highlight drought as the major constraint for coconut productivity and emphasize the need for identification and development of drought tolerant cultivars and hybrids. There were genotypic variations for drought index and drought tolerance (Pomier and de Taffin, 19; Rajagopal *et al.,* 22; Jayasekara *et al.*, 10; Repellin *et al.,* 26). Thus, it is important to identify the drought tolerant varieties and also to understand the genetics of the traits important for drought tolerance in coconut

Extensive research work carried out on coconut led to the development of screening methods for identification of drought tolerant genotypes (Rajagopal *et al.,* 22). Based on the physiological characters and nut yield (Rajagopal *et al.*, 20), biochemical characters (Chempakam *et al.*, 5., Kasturi Bai *et al.*, 12) and anatomical features and their integration with physiological responses to drought tolerance (Naresh Kumar *et al.,* 16), the drought tolerant coconut cultivars were identified in India and also other countries like Sri Lanka (Jayasekara *et al.,* 10) and Ivory Coast (Repellin *et al.,* 26). Selection of genotypes with desirable traits helped in breeding coconuts for drought tolerance. Screening of seedlings of parental lines and hybrids at the nursery stage indicated variations in stress responsive physiological characters like leaf water potential, lipid peroxidation, net photosynthetic and transpiration rates. Using these data genetic analysis was carried out to understand the gene action governing these traits. This paper discusses the combining ability and heterosis in coconut in relation to water stress and recovery.

MATERIALS AND METHODS

The experiment was conducted during summer months (March-April) for four years with fresh set of

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Table 1. Physiological response of different cross combinations and parents of coconut seedlings during water stress and recovery conditions (mean values).

Parameter	Parent/hybrid	Non-stress	Stress	Recovery
Leaf water potential	Dwarf (Line)	-5.91	-8.53	-6.57
(bars)	Tall (Tester)	-6.61	-9.31	-7.05
	Hybrid	-5.78	-8.44	-6.83
Transpiration rate	Dwarf (Line)	1.33	0.25	0.56
($mmol.m^{-2}.s^{-1}$)	Tall (Tester)	1.01	0.21	0.95
	Hybrid	0.54	0.30	0.68
Net photosynthetic rate	Dwarf (Line)	2.41	0.67	2.37
($mmol.m^{-2}.s^{-1}$)	Tall (Tester)	2.59	0.32	2.99
	Hybrid	1.55	0.92	1.89
Lipid peroxidation	Dwarf (Line)	0.62	0.82	0.76
(OD values)	Tall (Tester)	0.61	0.68	0.57
	Hybrid	0.58	0.85	0.58

Table 2. Analysis of variance for combining ability for physiological traits in coconut.

Parameter	Source	df	Mean sum of square		
			Non-stress	Stress	Recovery
Ψ_{leaf}	Year	3	0.749	1.763	0.264
	Lines	1	2.820*	3.511	0.000
	Testers	3	1.028	3.672*	2.139*
	L x T	3	2.280*	2.370	5.788**
	Error	21	0.409	0.980	0.548
E	Year	3	0.004	0.001	0.009
	Lines	1	0.022	0.451**	0.176
	Testers	3	0.239**	0.056**	0.179**
	L x T	3	0.244**	0.081**	0.022
	Error	21	0.019	0.005	0.021
Pn	Year	3	0.189	0.153	0.053
	Lines	1	0.000	4.836**	0.839**
	Testers	3	1.279**	0.252*	0.729**
	L x T	3	0.494*	0.375**	1.317**
	Error	21	0.133	0.055	0.099
LP	Year	3	0.001	0.020	0.003
	Lines	1	0.003	0.323**	0.122**
	Testers	3	0.037**	0.015	0.049**
	L x T	3	0.021**	0.079**	0.049**
	Error	21	0.004	0.007	0.008

seedlings every year. The experimental material comprised 2 lines (CGD, MYD) and four testers (WCT, PHOT, LCT, FMST). They were crossed in line x tester mating design. The parental lines and hybrids (CGD x WCT, CGD x PHOT, CGD x LCT, CGD x FMST, MYD x WCT, MYD x PHOT, MYD x LCT and MYD x FMST) were sown in the nursery beds under uniform shade in red loamy soils. Nursery beds were given sufficient irrigation to ensure proper germination and initial growth of seedling. The seedlings (18-month-old), maintained under recommended package of practices, were evaluated for tolerance to drought under field conditions. Moisture stress was imposed to the seedlings by withholding irrigation up to a period of 20 days to attain desirable level of moisture stress. The stress sensitive parameters *viz.,* leaf water potential

Table 3. General and specific combining ability effects for seedling physiological parameters under water stress and recovery conditions.

Parent/Hybrid	Non-stress				Stress				Recovery			
	Ψ_{leaf}	E	*Pn*	LP	Ψ_{leaf}	*E*	*Pn*	LP	Ψ_{leaf}	*E*	*Pn*	LP
Lines												
CGD	-0.30**	-0.03	0.00	-0.01	0.33*	-0.12**	-0.39**	-0.10**	0.00	-0.07**	0.16**	-0.06**
MYD	0.30**	0.03	0.00	0.01	-0.33*	0.12**	0.39**	0.10**	0.00	0.07**	0.16**	0.06**
SE (GCA)	0.09	0.02	0.05	0.01	0.27	0.02	0.06	0.02	0.10	0.02	0.08	0.02
Testers												
WCT	-0.33	0.03	0.10	0.09**	-0.44	0.11**	0.25**	0.02	-0.12	-0.01	0.17*	0.01
PHOT	-0.23	0.13**	0.37**	-0.07**	0.69**	-0.07**	0.00	0.03	-0.68	0.07*	0.19*	0.04
LCT	0.45*	0.1**	0.10	0.02	0.36	0.03	-0.16**	-0.06**	0.44	0.14**	0.08	-0.11**
FMST	0.12	-0.25**	-0.57**	-0.03**	0.76**	-0.07**	-0.08	0.02	0.36	-0.20**	-0.45**	0.06**
SE (GCA)	0.16	0.06	0.08	0.01	0.23	0.04	0.10	0.04	0.17	0.03	0.07	0.04
Hybrids												
CGD x WCT	0.02	0.2**	0.24**	0.00	-0.41	0.09**	-0.29**	-0.07**	-0.46	0.07*	0.07	-0.06**
CGD x PHOT	0.72**	0.09**	0.03	0.07**	0.49*	0.07**	0.23**	-0.09**	-0.42	0.00	-0.27**	0.00
CGD x LCT	-0.54**	-0.15**	0.08	-0.02	0.44	-0.12**	0.05	0.13**	1.28	-0.04	0.54**	0.11**
CGD x FMST	-0.20	-0.14**	-0.35**	-0.05**	-0.53*	-0.04	0.00	0.03	-0.39	-0.03	-0.35**	-0.05*
MYD x WCT	-0.02	-0.20**	-0.24**	0.00	0.41	-0.09**	0.29**	0.07**	0.46	-0.07*	-0.07	0.06**
MYD x PHOT	-0.72**	-0.09**	-0.03	-0.07**	-0.49*	-0.07**	-0.23**	0.09**	0.43	0.00	0.27**	0.00**
MYD x LCT	0.54**	0.15**	-0.08	0.02	-0.44	0.12**	-0.05	-0.13**	-1.27	0.04	-0.54**	-0.11**
MYD x FMST	0.20	0.14**	0.35**	0.05**	0.53*	0.04	0.00	-0.03	0.39	0.03	0.35**	0.05*
SE (SCA)	0.16	0.03	0.08	0.01	0.23	0.04	0.10	0.04	0.17	0.03	0.07	0.04
Gene effects												
$\sigma2A$	-0.12	-0.04	0.05	0.00	0.41	0.06	0.72	0.03	-1.57	0.05	-0.18	0.01
$\sigma2D$	1.81	0.22	0.36	0.02	1.39	0.08	0.32	0.07	5.24	0.00	1.22	0.04
$\sigma2GCA$	0.03	0.01	0.01	0.00	0.10	0.02	0.18	0.01	-0.40	0.02	-0.05	0.05
$\sigma2SCA$	0.45	0.06	0.09	0.00	0.35	0.02	0.08	0.02	1.31	0.00	0.30	0.01

(Scholander's Pressure Chamber - Plant Water Console - 3000, Soil moisture Co. USA) transpiration rate, net photosynthetic rate (Portable IRGA-ADC LCA-4, UK) and peroxidation rate of cell wall lipids (Heath and Packer, 8) were determined for the evaluation of the seedlings. The details of the methods employed are the same as reported earlier for coconut seedlings and juvenile palms (Rajagopal *et al.*, 25). Parameters were recorded on the seedlings during fully irrigated (non-stress), stress (20 days after withholding the irrigation) and recovery periods. Recovery potential of these seedlings was determined after re-watering the seedlings continuously for seven days. At least 24 readings were taken for each parameter. The data thus obtained were subjected to line x tester analysis as per the procedure of Kempthorne (14).

RESULTS AND DISCUSSION

The physiological parameters like leaf water potential (Ψ_{leaf}), transpiration rate (*E*), net photosynthetic rate (*Pn*) and lipid peroxidation (*LP*) indicated the relative tolerance of certain parental lines and cross combinations (Table 1). Leaf water potential (Ψ_{leaf}) which indicates the water balance of a plant, differed among dwarfs, talls and hybrids during non-stress, stress and recovery conditions. When exposed to stress the Ψ_{leaf} was reduced in all the seedlings and the reduction from non-stress period was minimum in FMST and the maximum in CGD x LCT. Among the hybrids, MYD x LCT could maintain Ψ_{Leaf} with only 13.3% reduction as compared to other hybrids. The revival capacity in Ψ_{Leaf} was higher in CGD x PHOT, PHOT and CGD among the three groups (Fig.1). When the seedlings were normally watered (non-stress) the mean transpiration rate (*E*) of Dwarfs (lines) was high as compared that in Talls (testers) and hybrids. Imposition of moisture stress resulted in lowering the transpiration rate in all seedlings to different degrees. When the stress was relieved by re-watering, high degree of recovery (> 600% over stress values) was

Table 4. Percentage heterosis (over better parent) for different parameters.

Parameter	Seedling leaf water potential			Seedling transpiration rate			Net photosynthesis rate			Seedling lipid peroxidation		
	Non-stress	Stress	Recovery	Non-stress	Stress	Recovery	Non-stress	Stress	Recovery	Non-stress	Stress	Recovery
CGD x WCT	-16.19**	-10.45**	0.81**	-36.52**	208.00**	39.27**	-23.08**	10.17**	-27.30**	3.43**	-10.86**	-31.71**
CGD x PO	-3.24**	-6.79**	-7.66**	-37.79**	316.67**	42.93**	-58.90**	74.01**	-68.77**	-10.36**	-7.00**	-11.84**
CGD x LO	-12.55**	11.99**	44.92**	-20.35**	-46.27**	174.76**	-29.42**	-5.65**	-13.33**	12.72**	42.69**	29.33**
CGD x FMS	-12.55**	5.88**	9.63**	-85.03**	-60.00**	-21.99**	-74.36**	1.69**	-65.53**	-15.04**	28.04**	4.48**
MYD x WCT	1.33**	2.87	3.24**	-70.2**4	248.00**	3.09**	-40.67**	105.29**	-14.20**	12.12**	33.43**	-2.58**
MYD x PO	-9.29**	-11.78**	-1.13**	-52.83**	527.78**	27.41**	-60.01**	20.33**	-52.61**	-26.14**	43.69**	9.02**
MYD x LO	25.22**	2.23	1.69**	-41.58**	240.30**	266.02**	-34.04**	21.73**	-20.77**	22.99**	33.80**	4.15**
MYD x FMS	13.27**	19.75**	3.06**	-45.51**	32.23**	-9.65**	-44.15**	35.93**	-14.89**	6.44**	49.80**	49.65**
$CD_{0.05}$	1.02	1.41	1.35	0.21	0.08	0.37	0.69	0.33	0.69	0.1	0.17	0.15

noticed in WCT, CGD x LCT and PHOT, as these were the ones which suffered more due to moisture stress. MYD x FMST, which was least affected also had a low recovery (45%) (Fig. 1).

Net photosynthetic rate (*Pn*) also was affected significantly during stress period. The reduction in *Pn* rate was less in the hybrids as compared to Talls and Dwarfs. When re-watered the increase in *Pn* rate was more in PHOT and lowest increase was observed in MYD x WCT. Among the hybrids CGD x LCT and CGD x WCT had high recovery and high *Pn* rates. Between the three groups higher increase in *Pn* rate was observed in Talls than the Dwarfs and hybrids (Fig.2). Peroxidation of membrane lipids (*LP*), which gives an indication of the cell membrane stability, also showed significant differences during stress and recovery periods. During stress period peroxidation of lipids increased in all the genotypes compared to that in non-stress period. This increase was least in CGD x WCT. In general, LP increase in hybrids was higher than in Talls and Dwarfs. Consequently, recovery percentage was higher in hybrids than Dwarfs and Talls. The MYD hybrids had high LP levels compared to others. The LP levels were low in LCT and FMST among the testers and CGD among the lines. MYD x LCT exhibited higher recovery and CGD x PHOT the lower than other combinations (Fig. 3).

Analysis of variance detected significant differences among parents and hybrids for all characters, except Ψ_{leaf} during non-stress in the parents and *E* on recovery, in hybrids. The hybrid versus parent comparisons were significant for most traits, the exceptions were Ψ_{leaf} on recovery and cell membrane LP during non-stress and recovery indicating the expression of heterosis effects for the rest of the parameters. Analysis of variances for combining ability (Table 2) revealed that variances due to male parents and female parents were significant for most parameters. The interactions between the parents were also significant for most traits, except *E* on recovery and Ψ_{leaf} under stress. The exceptions were *E* and LP during non-stress periods.

The GCA and SCA effects for Ψ_{leaf} (Table 3) under non-stress were highly significant among the lines and the hybrids CGD x PHOT, CGD x LCT, MYD x PHOT and MYD x LCT. Under stress condition, combining ability effects were highly significant for lines, PHOT and FMST hybrids. Under recovery, significant SCA effects were observed for all hybrids and testers (except WCT). The combining ability effects for *E* were highly significant for hybrids in non-stress and stress periods (Table 3). In case of parents, GCA and SCA effects were non-significant for lines and among the testers, for WCT under non-stress and LCT under stress

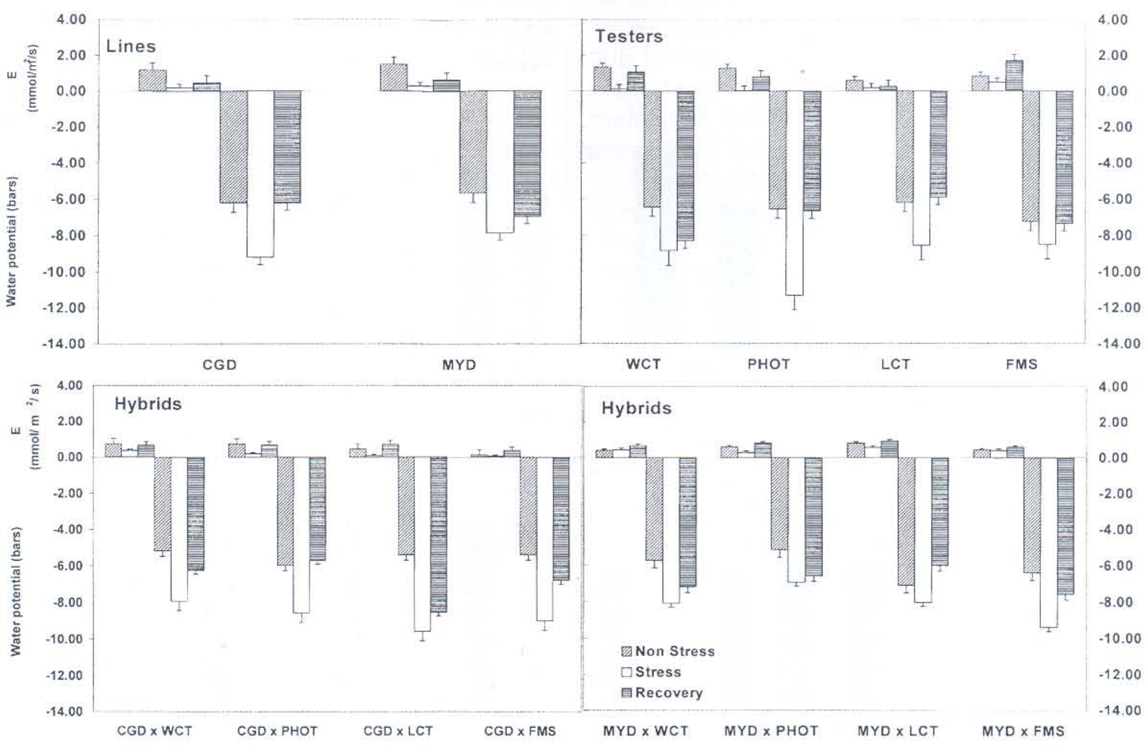

Fig. 1. Leaflet water potential and transpiration rates (E) in coconut seedlings of different cross combinations and their parents under non-stress, water stress and recovery conditions.

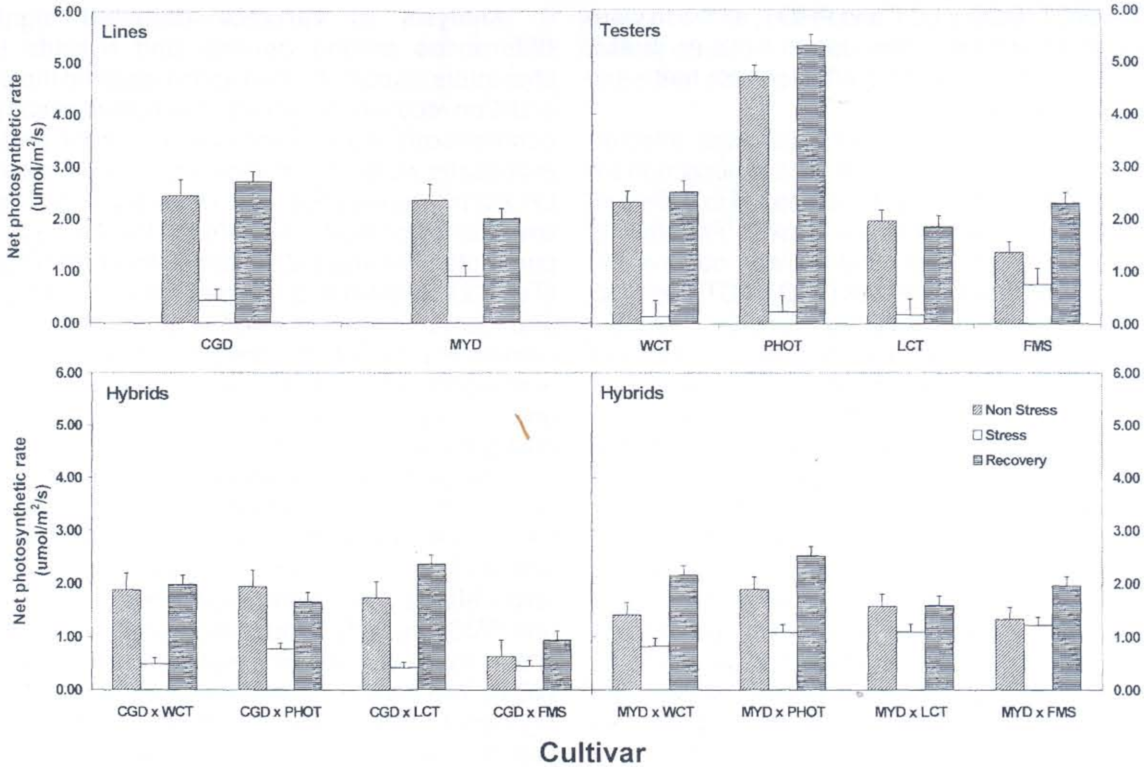

Fig. 2. Net photosynthetic rates in coconut seedlings of different cross combinations and their parents under non-stress, water stress and recovery conditions.

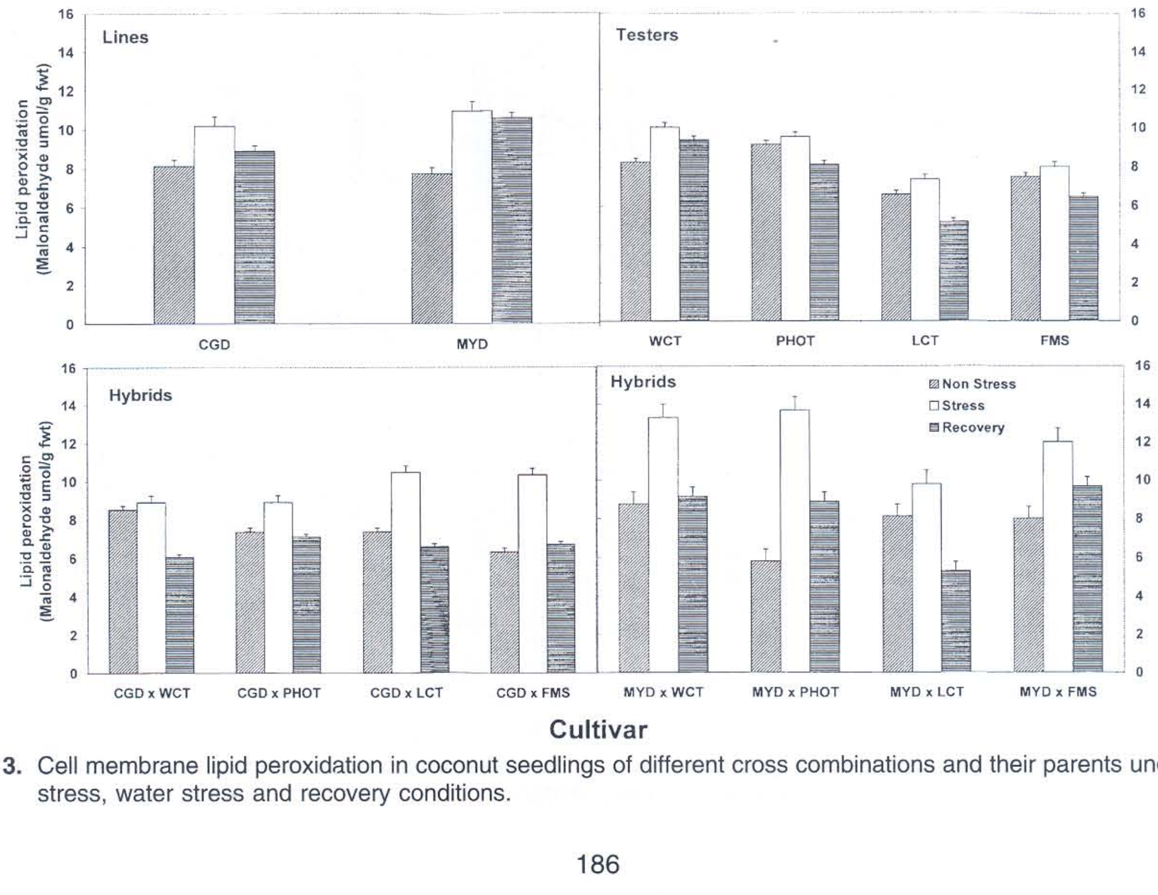

Fig. 3. Cell membrane lipid peroxidation in coconut seedlings of different cross combinations and their parents under non-stress, water stress and recovery conditions.

conditions. In recovery condition, SCA effect of hybrids was significant for CGD x WCT and MYD x WCT. The *Pn* showed highly significant GCA effects for both lines during stress periods (Table 3). SCA effects were highly significant for WCT and LCT among testers and the hybrids CGD x WCT, CGD x PHOT, MYD x WCT, MYD x PHOT. The SCA effects during non-stress were highly significant for the testers (PHOT and FMST) and the hybrids involving WCT and FMST. However, under recovery condition, significant GCA and SCA effects were observed for most genotypes, except LCT among the testers and hybrids involving WCT. Combining ability effects for cell wall LP (Table 3) under non-stress were highly significant among testers (WCT and PHOT) and for the hybrids involving PHOT and FMST as male parents. The lines showed highly significant GCA effects under stress and on recovery. Among testers, LCT recorded highly significant GCA effects under stress and on recovery and FMST on recovery. Among hybrids SCA effects were significant for most hybrids, except those involving FMST under stress and PHOT under recovery.

The percentage heterosis over better parent was computed for the parameters studied. The Ψ_{leaf} (Table 4) under non-stress expressed as negative heterosis for many of the crosses. While CGD x LCT, MYD x FMST showed positive heterosis over the better parent during stress and recovery conditions, whereas MYD x LCT showed positive heterosis only under non-stress. Further, among these combinations CGD x LCT indicated higher heterosis under recovery condition. Negative heterosis over the parents, under all three conditions, was observed in CGD x PHOT and MYD x PHOT. The *E* (Table 4) indicated highly significant negative heterosis for all hybrids, except MYD x LCT, under non-stress condition and a few hybrids under stress and recovery condition. In general, the hybrids were showing lower values than the parents, indicative of negative heterobelteosis during non-stress periods, while under stress and recovery some hybrids were better than the parents. Under stress, CGD x LCT and CGD x FMST showed negative heterosis while MYD x PHOT and CGD x PHOT showed very high positive heterosis. On recovery CGD x FMST and MYD x FMST had negative heterosis over the parents, while CGD x LCT and MYD x LCT showed positive heterosis. Among the hybrids, only CGD x LCT recorded negative heterosis under stress and non-stress condition followed by high and positive heterosis under recovery condition. Heterosis over better parent for the *Pn* (Table 4) in all crosses has been negative under non-stress and recovery condition, indicating non-allelic interactions. The *Pn* in MYD x WCT and CGD x PHOT showed high heterobelteosis in stress period. The MYD crosses and CGD x WCT also showed positive heterosis under stress conditions, while only CGD x LCT showed negative heterosis. The leaf cell membrane LP (Table 4) exhibited high negative heterosis in CGD x PHOT and high positive heterosis in MYD x LCT, MYD x FMST and CGD x LCT under all conditions. However, MYD x WCT showed positive heterosis during non-stress and stress conditions and negative heterosis on recovery, whereas CGD x WCT exhibited negative heterosis during stress and recovery and positive heterosis during non-stress. In case of CGD x FMST and MYD x PHOT, high negative heterosis was observed only for non-stress condition.

The physiological parameters varied among the cultivars during non-stress and stress periods, indicating variations among cultivars in their response to water stress. The recovery potential of these cultivars with respect to these parameters also varied. Coconut cultivars are reported to vary in their tolerance to drought (Rajagopal *et al.,* 22; Jayasekara *et al.*, 10; Repellin *et al.*, 26). The Dwarfs, Talls and hybrids vary for their leaf anatomical features in imparting physiological efficiency for drought tolerance in coconut cultivars (Naresh Kumar *et al.,* 16).

The hybrid versus parent comparisons were significant for most traits, the exceptions were Ψ_{leaf} on recovery and cell membrane LP during non-stress and recovery indicating the expression of heterosis effects for the rest of the parameters. Analysis of variances for combining ability (Table 2) revealed that variances due to male and female parents were significant for most parameters. This indicates diversity among the male and female parents used in the study. The interactions between the parents were also significant for most traits, except *E* on recovery and Ψ_{leaf} under stress. Both additive and non-additive gene actions were at work for the expression of all traits. For *E*, dominance variance was higher than that due to additive variance, indicating the predominance of non-additive effects that can be exploited through heterosis breeding. Ψ_{Leaf} and LP followed a similar trend. For *Pn,* gene action is additive with good general combing ability during stress period, while during non-stress and recovery periods *Pn* is governed by non-additive gene action and could be exploited for heterosis. No information is available on such gene action studies in palms. However, limited information is available on annual crops and which is in agreement with our findings (Blum *et al.,* 1; Chen *et al.,* 3).

The percentage heterosis over better parent was computed for the parameters studied. The Ψ_{leaf} under non-stress expressed as negative heterosis for many of the crosses. The variations negative heterosis for *E* indicated during non-stress, stress and recovery condition may be attributed to the non-allelic interaction, which can either increase or decrease the expression of heterosis. It may also be due to presence of dominant loci in different direction resulting in cancellation of effects. In general, the hybrids were showing lower values than the parents, indicative of negative heterobelteosis during non-stress periods, while under stress and recovery some hybrids were better than the parents. No work on tree crops is available to draw a conclusion. However, similar results have been reported in many annual crops (Blum *et al.,* 1; Chen *et al.,* 3).

Heterosis analysis regarding *Pn* in coconut seedlings indicated non-allelic interactions. Heterosis for photosynthetic rate has been observed in case of some annuals (Erina, 7; Tagmaz, 28; Staner *et al.*, 27). This implies that yield could be increased by breeding for improved photosynthesis rate per unit leaf area in conjunction with high leaf area as also was suggested by Heichel and Musgrave (9). Further, results indicated that the expression of heterosis for *Pn* is governed by environmental stresses as well. Studies on heterosis and morphological and physiological components like transpiration, water potential, water use efficiency and photosynthesis of maize in two moisture conditions indicated female lines showed a reduction in the agronomic parameters according to the inbreeding degree (Gomez *et al.,* 6).

This is the first report on the gene action and combining ability for some of the drought tolerant traits *viz.,* leaf water potential, net photosynthetic rate, transpiration rate and peroxidation rate of cell wall lipids. Analysis of variance detected significant differences among the parents and hybrids for all the parameters. Analysis of variance for combining ability revealed diversity among the lines and testers used in the study. Both additive and non-additive gene actions were at work for the expressions of above traits. GCA and SCA effects of the traits were also significant for lines, testers and hybrids under a given condition. The percentage heterosis over better parent for different traits varied with hybrids. Variations due to general and specific combining abilities were significant for most of the traits.

The studies clearly showed differential response drought sensitive traits of seedlings of various cross combinations to water stress conditions. Analysis of variance of the parameters indicated that the stress sensitive traits i.e., transpiration rates, lipid peroxidation, photosynthetic rates and water potentials are governed by genetic control. The transpiration rate had higher SCA indicating heterosis for this character. *Pn* rates are governed by the non-additive gene action, and can be exploited for heterosis. The nature of gene action governing some of these drought sensitive traits can be exploited in selective breeding for drought tolerance.

ACKNOWLEDGEMENTS

Authors are thankful to Director, CPCRI for providing facilities and encouragement for the study.

ABBREVIATIONS

CGD- Choughat Green Dwarf, E - Transpiration Rate, FMST- Federated Malay States Tall, GCA- General Combining Ability, LCT - Laccadive Tall, LP - Lipid Peroxidation, MYD- Malayan Yellow Dwarf, PHOT - Philippines Ordinary Tall, *Pn* - Net Photosynthetic rate, SCA - Specific Combining Ability, WCT- West Coast Tall, Ψ_{leaf} - Leaf Water Potential.

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(Received: October, 2006; Revised: February, 2007; Accepted: April, 2007)