Growth and Photosynthetic Responses of Groundnut Genotypes to High Temperature

H. S. Talwar,* H. Takeda, S. Yashima, and T. Senboku

ABSTRACT

Among abiotic factors, high temperature is one of the major constraints to adaptation of groundnut (*Arachis hypogaea* L.) in tropical and subtropical areas. The aims of this study were (i) to evaluate three genotypes (ICG 1236, ICGS 44, and Chico) of groundnut for their heat acclimation potential (HAP), and (ii) to examine whether the growth, yield, and photosynthetic responses of these genotypes to temperature related to the HAP. We defined HAP as the change in leaf heat tolerance based on plasmalemma thermostability at 40 to 60°C measured by electrolyte leakage after acclimation at 35/30°C day/night temperature. Initially, plants were raised in a glasshouse maintained at 25/25°C day/night temperature. One half of the plants were shifted to another glasshouse maintained at 35/30°C after the appearance of the third leaf. Heat killing time (HKT), defined as the time required to cause 50% relative injury, indicated that the three genotypes acclimated to high temperature stress, with significant variations in HAP. All genotypes maintained greater vegetative growth and higher photosynthetic rates when grown under the higher temperature regime and genetic differences in photosynthetic rate were related to HKT. The higher temperature regime affected the reproductive growth adversely by increasing flower abortion and decreasing seed size, however. Differences in chlorophyll fluorescence and membrane thermostability between growth temperature were found only after incubating the leaf tissue at temperatures of 50°C or higher. Genetic differences in HAP were small and unrelated to growth differences.

LEGUMES are the primary source of dietary protein and fat in many developing countries, including those in the semi-arid tropics. Groundnut is one of the major grain legumes in the semi-arid tropics with the average yield of around 0.8 Mg ha^{-1}, which is far below its potential yield of 7 Mg ha^{-1} (ICRISAT, 1993). The yield of groundnut is reduced by many abiotic and biotic factors such as high temperature in tropical and subtropical areas (ICRISAT, 1992). Therefore, improvement in heat tolerance is considered vital for yield improvement in many regions and cropping systems. Further, heat tolerance will be necessary if the frequency of hot weather increases in the future because of global climatic change (Schneider, 1989). This change, coupled with an increase in CO_2 concentration, may substantially increase the need for heat tolerant genotypes throughout the world (Hall, 1992).

High temperature stress affects many physiological processes such as photosynthesis, respiration, translocation, and membrane permeability (Björkman et al., 1980). Among these processes, photosynthesis is the most sensitive (Björkman et al., 1980; Nash et al., 1985). A wide range of photosynthetic responses has been reported in response to a concomitant increase in temperature and CO_2 (Campbell et al., 1990; Coleman and Bazzaz, 1992). Oxygen evolution and chlorophyll fluorescence are greatly altered by high temperature and widely used as indicators of heat injury to the photosynthetic apparatus (Björkman et al., 1980; Nash et al., 1985; Bar-Tsur et al., 1985). At temperatures of 40°C or greater, membrane disruption may occur. Likewise, heat tolerance coincides with thermal stability of primary photochemical reactions occurring in the thylakoid membrane system which determine photosynthetic efficiency (Weis and Berry, 1988).

A conductivity test based on the thermostability of the plasmalemma has been used to estimate heat tolerance in bean (*Phaseolus vulgaris* L.) and other crops (Chen et al., 1982; Chaisompongpan et al., 1990) and improvement in heat tolerance after acclimation at moderately high temperature has been reported in bean (Chaisompongpan et al., 1990). This improvement in heat tolerance after acclimating to moderately high temperature is hereafter defined as heat acclimation potential (HAP). The potential of a genotype or species to acclimate to moderately high temperature, thereby reducing heat injury (Alexandrov, 1964), is an important factor in determining plant performance in high temperature environments. The influence of temperature on groundnut growth is complex and disparity exists in the literature on groundnut response to temperature (Ketring, 1984; Sanders et al., 1985). Optimum temperature for vegetative growth of groundnut plants under controlled environment varies from 25 to 31°C (Fortanier, 1957; Wood, 1968; Cox, 1979; Bagnall and King, 1991). Similarly variable temperature optima are reported by others (Cox, 1979; Ketring, 1984) for different reproductive growth phases (flowering, pegging, pod formation, and kernel growth). Although the genotypic variations for heat tolerance have been reported in groundnut (Ketring, 1984), the physiological causes for acclimation to high temperature have yet to be elucidated. The objectives of the present experiments are (i) to evaluate selected genotypes of groundnut for their HAP and (ii) to examine whether the growth and photosynthetic responses of these genotypes under high temperature is related to HAP.

MATERIALS AND METHODS

Plant Culture

Seeds of groundnut genotypes (ICG 1236, ICGS 44, and Chico) were procured from ICRISAT Asia Center, India.

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Abbreviations: DAS, days after sowing; HKT, heat killing time; HAP, heat acclimation potential; PSII, photosystem II; Fm, maximum fluorescence; Fo, initial fluorescence; Fv, variable fluorescence; AC, acclimated; NAC, non-acclimated.

Seeds were germinated in petri dishes lined with moist filter paper. After the emergence of the radical, germinated seeds were transferred to plastic pots containing 4 kg powdered kaolinitic hyperthermic Ultisol. The soil was prepared by mixing with lime ($CaCO_3$) at 5 g kg^{-1} to raise the pH to 5.5 and NPK fertilizer (14:14:14) at 0.5 g kg^{-1} soil. Plants (one plant per pot) were initially raised in a glasshouse maintained at 25/25 ± 1°C day/night temperature. After the appearance of the third leaf (approximately 12 d after sowing), one half of the plants were shifted to another glasshouse maintained at 12-h day/night temperature of 35/30 ± 1°C. Plants were maintained under natural day /night light conditions and watered (100 mL pot^{-1}) every day once in the morning and once in the evening (only in 35/30°C).

Growth

Selective vegetative parameters (plant height, number of leaves on the main stem, number of leaves on the whole plant, leaf area, oven dry weights of leaves, stem, root, and total biomass) and yield components (number of aerial pegs, number of pods; pod dry weight, kernel weight, etc.) were recorded at maturity. The measurements were made on five plants of each genotype. The samples were dried at 80°C for 48 h. Flowers were counted on five plants every day in the morning and data are presented as cumulative flowers per plant. Specific leaf area (SLA), weight per seed, harvest index, shelling percent, and setting percent were calculated as follows:

SLA = Leaf area/Leaf dry weight;
Weight per seed = Dry weight of seeds per plant/Number of seeds per plant;
Harvest Index = [Total pod (shell + seed) yield/Total Biomass];
Shelling percentage = (Seed weight/Pod weight) × 100;
Setting percentage = (Aerial pegs + Subterranean pegs + all pods)/(Total flowers up to 10 d before final harvest at maturity) × 100.

Percent change in Flower Abortion, Weight Per Seed, and Pod Yield Per Plant when grown at 35/30°C compared with 25/25°C were calculated as follows:

Percent change in flower abortion = (100 − Setting percentage at 35/30°C) − (100 − Setting percentage at 25/25°C) = Setting % at 25/25°C − Setting % at 35/30°C;

Percent change in Weight Per Seed = [(Weight Per Seed at 25/25°C − Weight Per Seed at 35/30°C)/Weight Per Seed at 25/25°C] × 100;

Percent change in Pod Yield Per Plant = [(pod yield at 25/25°C − pod yield at 35/30°C)/pod yield at 25/25°C] × 100.

Heat Acclimation Potential

Leaf tissue from plants growing at 25/25°C and 35/30°C were exposed to heat stress in temperature controlled water baths under dim light conditions and their heat tolerance was measured as HKT (time needed to cause 50% relative injury) by a cell membrane thermostability test (Hossain et al., 1995). The data were measured at 30 and 60 d after sowing (DAS) and presented as the average of the two stages. Four leaf discs (13-mm diam.) were cut from the leaflets of the second fully expanded leaf from the top of main axis of each genotype under each growth temperature. For each main unit and each replicate, four plants were used from each genotype × growth temperature combination and two sets of tubes (150 by 25 mm) were prepared. Each tube contained eight leaf discs (two from each of four plants). The leaf discs were washed thoroughly for about 10 min with three changes of distilled water to remove the electrolyte adhering to leaf surface and released from the cut edge. The tubes were transported to a laboratory and 10 mL of distilled water was added to each tube. The initial conductivity reading (I) of the solution was measured with an EC meter (Model CM-115, Kyoto Electronics Co. Ltd., Kyoto, Japan) after 1 h of incubation at room temperature. The tubes were capped and one set of tubes was placed in a 50°C water bath and other in 55°C. These two heat temperatures were chosen based on results of our preliminary experiment conducted to test these three groundnut genotypes under a range of water bath temperatures of 40, 45, 50, 55, and 60°C. Water bath temperatures of 50 and 55°C were found be most appropriate to distinguish genotype HKT within 6 to 7 h . After the initial reading, a series of electric conductivity readings (E) were taken at 30-min intervals for 7 h. Subsequently, the samples were autoclaved at 120°C for 15 min to disrupt the cell membranes completely. The samples were placed back in their respective water baths at 50 or 55°C for 30 min after which a final conductivity (F) was recorded. Injury induced during the time course was calculated as follows:

$$\text{Injury (\%)} = [(E - I)/F] \times 100.$$

Heat killing time was determined by regressing percentage injury vs. time. Heat acclimation potential (HAP) was determined as the difference between the heat killing times calculated for plants grown at 35/30°C and 25/25°C temperature.

Photosynthetic Response

Net Photosynthetic Rate. Leaf photosynthetic rate was measured at 30 and 60 DAS on four plants (two proximal leaflets per plant) of each genotype with a portable leaf chamber analyzer (Model LCA-2, ADC, Herts, UK). The measurement was made on the leaflets of a fully expanded second leaf, from the top of the main stem under natural day light conditions during 1000 to 1200 h local time. The PAR was 750 to 800 μmol m^{-2} s^{-1} and ambient CO_2 concentration was 360 to 370 μmol mol^{-1} during the measurements.

Chlorophyll Fluorescence. Chlorophyll fluorescence was measured at two growth stages, 30 and 60 DAS. The procedure used to measure chlorophyll fluorescence characteristics was similar to that of Smillie and Hetherington (1990). As stated before, for each main unit and replicate, four leaflets of the second fully expanded leaf from the top of main axis were detached and evenly distributed among four test tubes (150 by 25 mm) containing 2 mL of distilled water. Four more leaflets from each of three additional plants were detached and distributed among these four tubes, so that each tube had four leaflets, all from different plants. One tube was designated for each of four different heat treatments. The heat treatments were growth temperature (25°C for non-acclimated and 35°C for acclimated treatment), 45, 50, and 55°C. The tubes were capped and placed in water baths maintained at selected temperatures for 10 min. After the heat treatment, leaves were dark adapted for 45 min in petri dishes lined with moist filter paper and covered with tin foil, and enclosed in a box. Chlorophyll fluorescence was recorded with a Modulated Fluorescence Measurement System (Model MK II MFMS/2S, Hansa-

Table 1. Vegetative growth and total biomass of groundnut genotypes grown at 25/25°C or 35/30°C.

Genotype	Plant height		Leaf number main stem		Leaf number whole plant		Leaf area	
	25/25°C	35/30°C	25/25°C	35/30°C	25/25°C	35/30°C	25/25°C	35/30°C
	cm						cm^2 $plant^{-1}$	
ICG 1236	12.9	31.0	13	21	35	76	820	2292
ICGS 44	15.6	28.9	16	23	59	142	694	2269
CHICO	9.2	25.2	15	25	33	86	534	1921
LSD(0.05)†	3.6		2		15		140	
	Specific leaf area		Stem dry weight		Root dry weight		Biomass	
	25/25°C	35/30°C	25/25°C	35/30°C	25/25°C	35/30°C	25/25°C	35/30°C
	cm^2 g^{-1}		g $plant^{-1}$		g $plant^{-1}$		g $plant^{-1}$	
ICG 1236	254	232	2.3	8.7	2.1	6.6	12.9	27.1
ICGS 44	229	252	3.6	11.2	1.9	4.6	14.5	30.2
CHICO	289	293	1.2	6.4	0.9	4.6	9.4	21.8
LSD(0.05)†	15		0.7		1.1		1.6	

† LSD(0.05) between all genotypes and treatments combinations for each parameter.

tech Electronics Ltd., UK). Fiber optic cables connected to a Björkman lamp were used to send actinic light and saturating light pulses. The equipment detected fluorescence signal at 695 nm and the output was read on a computer. Initial (Fo) and maximum (Fm) fluorescence values were recorded. Variable fluorescence (Fv) was derived by subtracting Fo from Fm. Ratio of Fv to Fm was calculated to determine the degree of thermoinhibition (Havaux, 1993).

Experimental Design and Statistical Analysis

Because growth temperatures were not replicated, its effect was not testable. Therefore, the experimental design for each growth temperature was a split plot. The main unit treatment was genotype with three replications and subunit was either disc (for HKT) or leaflet (for Fo, Fv/Fm) temperature treatment. There were 135 plants per growth temperature arranged in three locations (replications) so that there were 15 plants per genotype per replicate.

For growth and photosynthesis, the design was two growth temperatures and three genotypes. For HAP, the design was two growth temperatures, three genotypes (main plot) and two heat stress temperatures (subplot; 50 or 55°C). For chlorophyll fluorescence, the design was two growth temperatures, three genotypes (main plot) and 4 heat stress temperature (growth temperature, 45, 50, 55°C).

Data were subjected to standard analysis of variance with IRRISTAT version 3/1992 software (IRRI, 1992). Where appropriate, Duncan's multiple range test at 0.05 probability level was used to separate the treatment means. The results presented are from one main experiment, although several preliminary experiments were performed.

RESULTS

Growth

Vegetative

The plants of three genotypes grew taller and produced significantly more leaves on the main stem as well as on whole plant under 35/30°C than at 25/25°C day/night temperatures (Table 1). ICGS 44 bore more leaves than the other two genotypes. All vegetative growth parameters except specific leaf area (SLA), increased significantly in all the genotypes under higher temperature. The percent increase over 25/25°C in growth was maximum in Chico followed by ICGS 44 and ICG 1236. SLA of ICG 1236 was less than ICGS 44 and Chico when grown at 35/30°C.

Reproductive

Time to first flower was shortened by 5 to 6 d under the higher temperature regime for all three genotypes (Table 2). All three genotypes produced more flowers at higher temperature regimes. The increases in cumulative flowers per plant at final harvest were 55, 195, and 156 in ICG 1236, ICGS 44, and Chico, respectively,

Table 2. Reproductive growth of groundnut genotypes grown at 25/25°C or 35/30°C.

Genotype	Days to first flower		Flower number per plant		Aerial pegs per plant		Pod number per plant		Pod weight	
	25/25°C	35/30°C	25/25°C	35/30°C	25/25°C	35/30°C	25/25°C	35/30°C	25/25°C	35/30°C
	d								g $plant^{-1}$	
ICG 1236	37	31	47	104	3	10	13	9	5.2	4.7
ICGS 44	38	33	76	271	3	35	22	14	7.0	5.5
CHICO	33	27	42	198	4	27	17	13	5.4	3.7
LSD(0.05)†	1		8		7		3		0.8	
	Seed yield		Setting percentage		Weight per seed		Harvest index		Shelling percentage	
	25/25°C	35/30°C	25/25°C	35/30°C	25/25°C	35/30°C	25/25°C	35/30°C	25/25°C	35/30°C
	g $plant^{-1}$		%		mg		g pod/g plant		g seed/g pod × 100	
ICG 1236	3.2	2.35	44	30	194	140	0.41	0.15	62	50
ICGS 44	4.2	2.25	43	21	248	158	0.48	0.18	60	41
CHICO	4.1	2.29	63	23	186	116	0.58	0.17	76	62
LSD(0.05)†	0.6		6		52		0.05		7	

† LSD(0.05) for all genotypes and treatments combination for each parameters.

Table 3. Analysis variance of heat killing time (HKT) and chlorophyll fluorescence ratio (Fv/Fm) as influenced by growth temperature, disc (for HKT) or leaflet (for Fv/Fm) incubation temperature and genotype. Data were transformed to logarithmic scale, log(χ) for HKT, and log(χ + 1) for Fv/Fm.

	HKT		Fv/Fm	
Source of Variation	df†	MS‡	df†	MS‡
Growth temperature (T)	1	not testable	1	not testable
Rep. (growth temperature)	4	0.0031	4	0.000011
Genotypes (G)	2	0.0112**	2	0.004087**
G × T	2	0.0199**	2	0.000677**
Error b	8	0.0004	8	0.000043
Disc or leaflet temperature (D)	1	2.9459**	3	0.192948**
T × D	1	0.00020	3	0.003201**
G × D	2	0.00015	9	0.001171**
T × G × D	2	0.00152	9	0.000538**
Error c	12	0.00100	30	0.000028

*,** Significant at the 0.05 and 0.01 probability level, respectively.
† Degrees of freedom.
‡ Mean square.

grown under high temperature. There was a positive linear relationship between number of leaves and number of flowers per plant (data not shown). The relationship between setting percentage and number of leaves was negative and was equally strong under both temperature regimes despite a large increase in the number of leaves and flowers under higher temperature (data not shown).

High temperature increased shoot and root growth but reduced final reproductive biomass (Tables 1 and 2). However, there was a significant increase in the number of aerial pegs at higher temperature compared with lower temperature in all three genotypes. The increase in aerial pegs under higher temperature was greatest in ICGS 44, followed by Chico and ICG 1236. The decrease in the number of pods per plant under higher temperature was greatest in ICGS 44 (36%), followed by ICG 1236 (30%) and Chico (23%). The decrease in weight per seed at higher temperature was greatest in ICGS 44 followed by Chico and ICG 1236. The setting percentage at higher temperature decreased most in Chico followed by ICGS 44 and ICG 1236. Similar type of trends were noticed in shelling percentage, harvest index, pod, and seed yield per plant.

These results indicated that increased flower abortion and decreased pod filling (i.e., smaller seed) were the two major components that decreased yield under higher temperature. The increase in flower abortion and decrease in weight per seed under higher temperature was least in ICG 1236 compared with other genotypes.

Heat Acclimation Potential

The analysis of variance for HKT indicates that there is a significant interaction between growth temperature and genotype (Table 3). No significant genotypic variations were noticed when non-acclimated (NAC) plants of three genotypes were heat treated to 50 or 55°C (Table 4). HKT of leaf tissue of the acclimated (AC) plants was longer than that of NAC plants in all genotypes at both 50 and 55°C incubations, but the difference was not statistically testable. For both 50 and 55°C, HKT of ICG 1236 of AC plants and HAP was greater than that of ICGS 44 and Chico.

Table 4. Heat killing time (HKT) and heat acclimation potential (HAP) among the selected genotypes of groundnut grown at 25/25°C (NAC) or 35/30°C (AC). Data were transformed to logarithmic scale, log(x).

		Leaf HKT†		
Genotype	Heat treatment	NAC	AC	Leaf HAP‡
		log (min)		
ICG 1236	50°C	2.37	2.57	2.14
ICGS 44	50°C	2.39	2.48	1.76
Chico	50°C	2.36	2.46	1.77
ICG 1236	55°C	1.79	2.02	1.64
ICGS 44	55°C	1.83	1.87	0.84
Chico	55°C	1.81	1.89	1.15
LSD(0.05)	50 vs 55°C	0.05	0.05	0.13
LSD(0.05)	Genotypes	0.03	0.03	0.32

† Leaf HKT is the time in minutes needed to result in 50% relative injury.
‡ Leaf HAP, the change in leaf HKT following the growing of plants at 35/30°C.

Photosynthesis

The net photosynthetic rate of the second leaf from the apex at 30 DAS and at 25/25°C was similar among genotypes (Table 5). At 35/30°C, the highest photosynthetic rate was recorded in ICG 1236 and lowest in ICGS 44. At 60 DAS, photosynthetic rate was 62% higher in ICG 1236 and 38% higher in ICGS 44 at 35/30°C compared to 25/25°C. Within each growth temperature, HKT (heat tolerance) was positively related to photosynthetic rate at both 30 and 60 DAS (data not shown).

Chlorophyll Fluorescence

A significant interaction between heat treatments, growth temperatures, and genotypes was found for the Fv/Fm ratio (Table 3). The Fv/Fm ratio decreased as the level of leaflet heat treatment rose from 45 to 55°C in both NAC and AC plants of three genotypes (Fig. 1). The decrease of Fv/Fm was greater in NAC than in AC plants. Significant genotypic variations in Fv/Fm ratio were observed when leaf tissue from NAC and AC plants was exposed to 50 or 55°C. The leaves from NAC plants, when exposed to the highest level of heat stress (55°C), suffered complete thermoinhibition in two genotypes, while AC plants maintained some photochemical activity in all the three genotypes. The Fv/Fm ratio of ICG 1236 was highest among the AC plants of three genotypes when their leaves were exposed to 50 or 55°C. The percent change in Fo and Fv/Fm with

Table 5. Leaf photosynthetic rates at two growth stages in selected genotypes of groundnut grown at 25/25°C (NAC) or 35/30°C (AC).

	30 DAS‡		60 DAS	
Genotype	NAC	AC	NAC	AC
	μmol m^{-2} s^{-1}			
ICG 1236	16.5a†	28.7a	17.2a	27.7a
ICGS 44	18.9a	18.7b	13.8a	19.1b
Chico	14.8a	22.5b	15.4a	11.9c

† The values in columns followed by same letters are not different significantly by Duncan multiple range test at $P \leq 0.05$.
‡ DAS, Days after saving; NAC, Non-acclimated; AC, Acclimated.

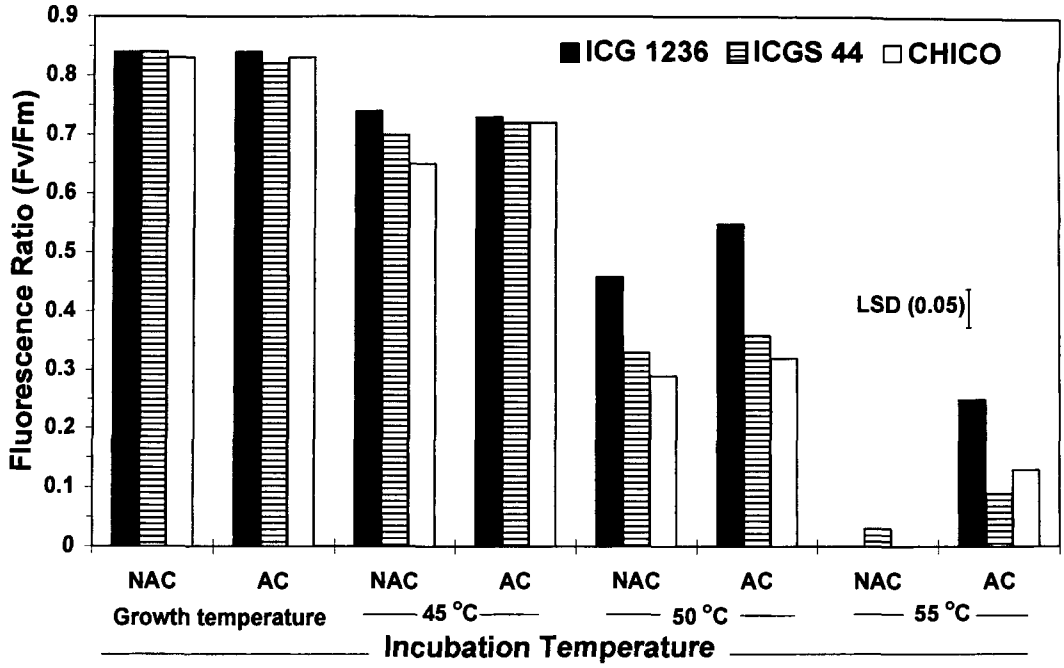

Fig. 1. Chlorophyll fluorescence ratio (Fv/Fm) in leaves of three groundnut genotypes grown at 25/25°C (NAC) or 35/30°C (AC) and whose leaflets were exposed to growth temperature (25 or 35°C), 45, 50, or 55°C for 10 min. Fluorescence was measured after the heat treatment and dark adaptation of 45 min. Vertical bar indicates LSD(0.05) between all genotypes and leaflet temperature treatment combinations.

increasing level of heat stress over their respective control (growth temperatures, 25/25 or 35/30°C) indicate that Fo increased and Fv/Fm (ratio of variable to maximum fluorescence) decreased with increasing level of heat stress in both NAC and AC plants of three genotypes (Fig. 2). The AC plants maintained lower Fo and higher Fv/Fm values than NAC plants. The genotypic variations in NAC and AC plants for percent change in Fo with increasing stress level relative to the controls were evident when leaves were exposed to temperature higher than 45°C. The increase in Fo with increasing stress was least in both NAC and AC plants of ICG 1236 among the three genotypes. The percent decreases in Fv/Fm ratio was greater in NAC than in AC plants of all the three genotypes. The genotypic variations for percent decrease in Fv/Fm ratio with increasing level of heat stress over their respective controls were evident among NAC and AC plants of three genotypes. The decrease in Fv/Fm ratio with increasing stress level was least in the AC plants of ICG 1236 while it was greatest in NAC plants.

DISCUSSION

The impact of high temperature on plant development depends upon the species, growth stage, and growth conditions. Previous studies (Fortanier, 1957; Wood, 1968; Ketring, 1984) indicated that optimum temperature for growth of most groundnut genotypes was between 25 and 30°C. Vegetative and reproductive growth were affected adversely if exposed continuously to higher temperatures. In our study, the growth parameters of groundnut which were enhanced under high temperature were leaf area, plant height, number of leaves on main stem, and number of leaves per plant. Because of an increase in number of leaves, number of flowering nodes increased, which resulted in a sharp rise in the number of flowers produced per plant. In most of previous studies on groundnut where vegetative growth was affected adversely by temperature above 30°C, the fluctuation between the day and night temperature was more than 10°C. Fortanier (1957) suggested that day and night temperature would not adversely affect growth and development of groundnut unless the difference exceeded 10°C. In the present study, the fluctuation between day and night temperature was 5°C.

The previous studies on groundnut under controlled environment (Cox, 1979; Ketring, 1984) reported a reduction in various reproductive growth parameters when either the day or night temperature approached 35°C. Our results, indicate that alternative sinks develop under high temperature regimes as indicated by the increase in stem, root, and leaf weights but not pods or kernels. Our results on the relationship between number of leaves and flowers confirm the view of Bagnall and King (1991) that increasing temperature can increase flower numbers, and that this increase is correlated with increases in leaf number and plant dry weight. The decrease in setting percentage combined with the increase in flower number and leaf number suggested that an increase in flower abortion under higher temperature resulted in the development of alternate sinks (i.e., vegetative parts).

The justification for temperatures of 45°C or above being used for assessing acclimation to heat stress is based on previous studies which suggested heat stress of 50°C in cabbage (*Brassica oleracea* L.) (Hossain et al., 1995) and 54°C in groundnut (Srinivasan et al., 1996) are most appropriate to distinguish genotypes within each crop on the basis of relative injury in the leaf tissue. Our results showed that groundnut can acclimate to high temperature, as indicated by the increase in heat

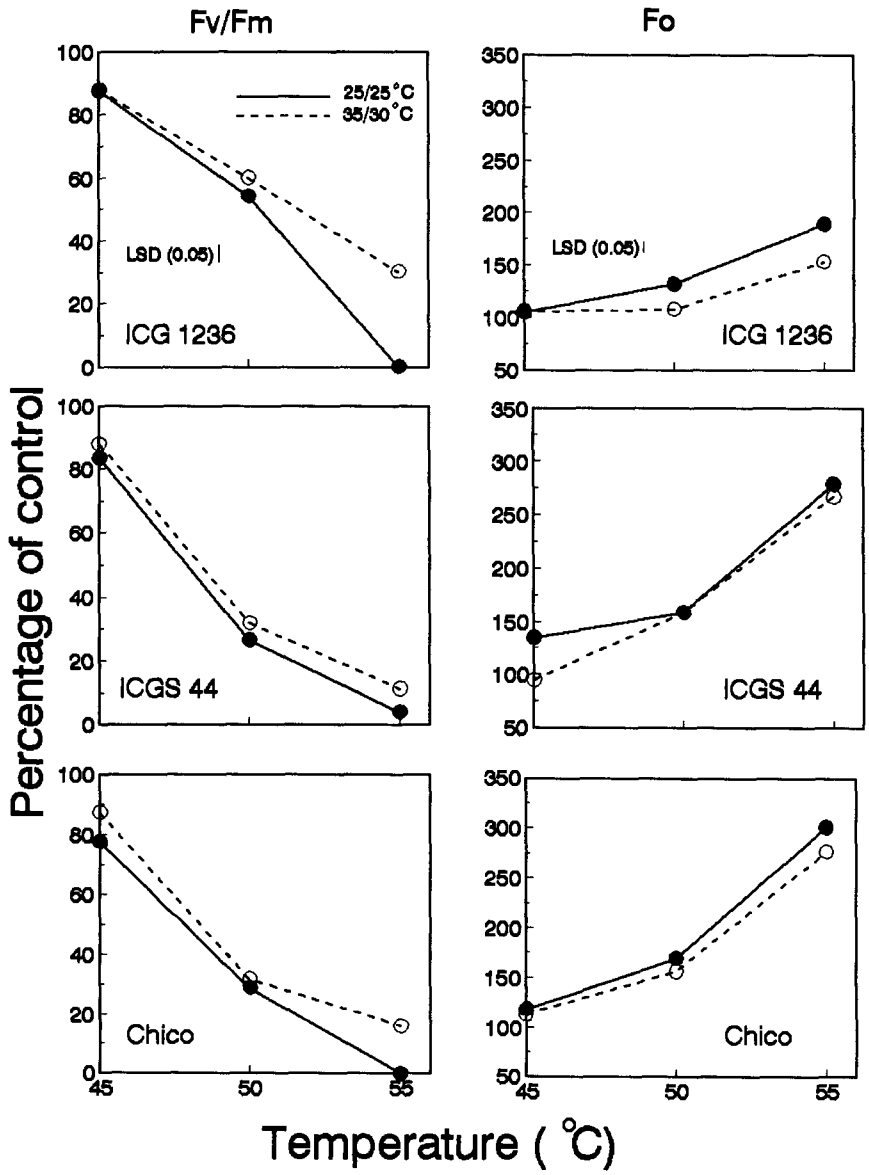

Fig. 2. Chlorophyll fluorescence characteristics of leaves of three groundnut genotypes grown at 25/25°C (closed symbols) or 35/30°C (open symbols) and whose leaflets were exposed to growth temperature (25 or 35°C), 45, 50, and 55°C for 10 min. Fluorescence was measured after the heat treatment and dark adaptation of 45 min. All values are expressed as a percent of control (growth temperature, 25/25 or 35/30°C). Fv/Fm (Fluorescence ratio) represents photoinhibition. Increase in Fo (initial fluorescence) represents the physical damage to the PS II. Vertical bars indicate the LSD(0.05) between all genotypes and leaflet temperature treatment combinations.

killing time and decrease in thermoinhibition when plants were grown at 35/30°C. The photosynthetic rate increased under high temperature in all the three genotypes of groundnut. Genotypic differences in the photosynthetic response to higher growth temperature also were evident. The increase in photosynthetic rate in ICGS 44 was significant at 60 DAS, but not at 30 DAS. The converse was true for Chico, which is matures earlier than ICG 1236 (medium) and ICGS 44 (late). This result suggests that growth at higher temperature resulted in the acclimation of photosynthetic apparatus and improvement of photosynthetic rate (Chen et al., 1982). The acclimation seems to be associated with considerable reorganization of thylakoid membrane (Berry and Björkman, 1980, Quinn and Williams, 1985, Yordanov et al., 1986). The increase in photosynthetic rate was greater in ICG 1236 than in other two genotypes. We found a positive relationship between photosynthetic rate and HKT. This relationship weakened with plant age because of the decrease in photosynthetic rate in Chico, the early maturing cultivar. In C_3 plants, global temperature and CO_2 increases are predicted to increase the photosynthesis and growth in a synergistic manner (Long, 1991)

Exposure to heat stress of 45 to 55°C caused a depression of quantum efficiency as indicated by a reduction in Fv/Fm. Many studies have demonstrated abrupt decrease in PS II photochemistry above a threshold temperature (Terzaghi et al,. 1989; Havaux et al., 1996). Results from our study confirm that the photosynthetic apparatus in groundnut is more sensitive than plasmalemma integrity to high temperature stress (Chaisompongpan et al., 1990). Heat stress of 50°C for 10 min was sufficient to cause 50% thermoinhibition as

indicated by the decrease in Fv/Fm ratio. On the other hand, heat stress of 50°C damaged the plasmalemma of NAC plants within 231 to 244 min. Similar treatment took 290 to 325 min to damage the plasmalemma of AC plants to the same extent.

Our results indicate that the three genotypes of groundnut used in this study acclimate to high temperature and as shown by improved tolerance to higher intensity of heat stress. The heat acclimation involves the increase in photosynthetic rate by maintaining PSII activity. The positive relationship between HKT and photosynthetic rate suggest that the thermal adaptation of PS II is a key factor for the acclimation of groundnut to high temperature. Havaux (1993) confirmed the thermal plasticity of PS II in vivo by demonstrating that the brief exposure of potato (*Solanum tuberosum* L.) leaves to moderately elevated temperature induced noticeable increase in the heat tolerance of PS II. Previously, Weis (1981) reported that the thylakoid membrane is a primary temperature sensor which starts the process of temperature adaptation in plants. Havaux et al. (1996) suggested that thermal adaptation to mild heat stress involves the stabilization of permeability properties of the thylakoid membrane which is protected by de-epoxidization of xanthophyll in potato leaves. This acclimation in thylakoid membrane and PS II to mild heat stress resulted in the production of greater biomass under higher temperature in groundnut. Despite higher biomass production under higher temperature, there was a significant reduction in yield components. This reduction in yield seems to be due to increased flower abortion under higher temperature which resulted in the reduction of reproductive sinks and formation of alternate sinks in vegetative parts. Genotype ICG 1236, which showed the greatest leaf HAP, performed best among the three genotypes in terms of pod setting percentage, pod filling (decrease in weight per seed), and seed yield under higher temperature. Although genotypic variation for HAP was evident, more genotypes of groundnut need to be evaluated. Moreover, heat acclimation during vegetative growth is not reflected in reproductive efficiency. Further studies are in progress to understand the heat tolerance mechanism during reproductive growth of groundnut.

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