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Efficient Partitioning of Assimilates in Stress-Tolerant Groundnut Genotypes under High-Temperature Stress

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Abstract: Groundnut (*Arachis hypogaea* L.) genotypes were assessed for pod yield and physiological parameters under heat-stress and non-stress environments. The air temperatures under heat-stress environments were 35 °C and above during flowering, and below 35 °C in non-stress environments. Variability was significant for pod yield and physiological parameters among the genotypes under heat stress. A pod yield reduction of 1.5% to 43.2% was observed under heat-stress environments. However, in heat-tolerant genotypes, either stable or increased pod yield was recorded under high-temperature stress. GJG 31, ICGV 87846, ICGV 03057, ICGV 07038 and GG 20 showed an increase in pod yield by 9.0% to 47.0% at high temperatures, with a 0.65% to 3.6% increase in pod growth rate, while ICGV 06420, ICGV 87128, ICGV 97182, TCGS 1043 and ICGV 03042 are stable for pod yield and recorded a 0.25% to 3.1% increase in pod growth rate. Pod yield, hundred-seed weight, and pod growth rate under heat stress can be used as criteria for selection of heat stress tolerant-genotypes. Based on stress tolerance indices and pod yield performance, ICGVs 07246, 07012, 06039, 06040, 03042, 07038 and 06424 were identified as heat-tolerant genotypes.

Keywords: groundnut; heat stress; pod yield; high temperature; partitioning of assimilates; tolerance indices; heritability

1. Introduction

Groundnut or peanut (*Arachis hypogaea* L.), an annual legume, is an important oil and food crop. Global groundnut production has almost doubled, from 23.08 m tons in 1990 to 45.22 m tons in 2013, with an increase in cultivation area to 25.44 m ha from 19.75 m ha in the same period [1]. Future demand projections indicate an increase in global demand for groundnut and its products. To meet the growing demand, groundnut is increasingly grown outside its traditional area of adaptation and beyond its natural growing seasons. Expansion of groundnut cultivation to non-traditional areas and/or seasons happens in regions of high profitability. This is evident in a non-traditional Northern part of India, where spring cultivation of groundnut is popular owing to economic returns. Groundnut is grown in about 5.0 m ha in India, of which 20% is cultivated in post-rainy season with an average yield of 1.8 t ha^{-1} more than the rainy season yield of 0.8 t ha^{-1} [2]. High-temperature adaptation of groundnut varieties is needed for cultivation in non-traditional areas and/or seasons.

Drought and high-temperature stress, and their combination, are important abiotic constraints of groundnut production in Asia and Africa. Yield loss to an extent of 1.7% in maize in Africa [3] to 16% for soybean in the USA [4] is expected with each degree rise in temperature beyond 30 °C. In the case of groundnut, an increase in mean air temperature of 2–3 °C is predicted to reduce groundnut yields in India by 23–36% [5]. Vara Prasad et al. [6] reported that heat stress during critical stages will affect the pod yield. Further, heat stress aggravates moisture stress, contributing to pod yield losses.

High-temperature stress affects several crops, including groundnut, but is not well understood [7]. It is one of the major uncontrollable stresses affecting plant growth, development, and productivity [8,9]. Understanding of trait responses under stress and non-stress environments is important to design a breeding program and develop improved cultivars suitable for stress environments. A few studies were carried out to elucidate heat-tolerance mechanisms in groundnut [10], mungbean [11], wheat [12] and chickpea [13]. Stress indices, mostly yield-based, are found to be reliable for screening genotypes for heat tolerance. Stress tolerance index (STI) is responsive to evaluate genotypes in stress and non-stress environments, and *STI* has identified stress-tolerant genotypes in maize (*Zea mays*; [14]), mung bean (*Vigna radiata*; [15]), and common bean (*Phaseolus vulgaris*; [16]).

Plant response to high-temperature stress is genotype-specific and varies with phenological stage of crop [17], some specific physiological stages are more responsive to stress than others. Therefore, field tolerance of a genotype to heat stress is measured at several growth stages. Studies have shown that groundnut genotypes differ in sensitivity to temperature during both vegetative and pod growth [18–20], and reproductive stages are more sensitive to stresses [21]. Limited studies are available for screening of groundnut genotypes for high-temperature stress under controlled [10,22,23] and field conditions [13,21,24]. Screening of genotypes and understanding responses under field conditions is important to identify heat-tolerant genotypes. In the current study, variability for pod yield, yield parameters and physiological growth parameters are studied among groundnut genotypes under heat stress in field conditions, and heat-tolerant groundnut genotypes are identified.

2. Results

The three test environments are represented as E1, E2 and E3. In E1, the flowering was spread over a period of 25 days with maximum temperature reaching up to 34 °C, except for three days (45, 52 and 53 days after planting (DAP)) when the temperature was 35 °C or above (Figure 1a). In E2, on all the days of the flowering period, except five days (27, 28, 29, 30 and 43 DAP) the temperature was 35 °C or above for ca. 3–8 h in a day (Figure 1b). The temperature in E1 varied from 28 °C to 36 °C, from 29 °C to 38 °C in E2, and 33 °C to 39 °C in E3. In E3, on all the days except two (32 and 33 DAP), the day temperature was 35 °C or above for ca. 5–8 h in a day (Figure 1c). Duration of heat stress in E3 was 110 total hours, and 75 h in E2.

Individual ANOVA of three environments showed significant differences among the genotypes in heat-stress and non-stress environments for all traits, with an exception of crop growth rate (CGR) in E2, and sound mature kernel percentage (SMK) in E3 (Table 1). Combined ANOVA over three environments showed significant differences for yield and physiological traits among groundnut genotypes, and among environments. However, genotype and environment interactions were significant for days to 75% flowering and days to maturity (Table 2).

Variability among groundnut genotypes for yield and physiological parameters, and heritability estimates in a broad sense are summarized in Table 3. The pod yield over three environments varied from 1483 to 6767 kg ha^{-1}, and harvest index from 24.6% to 65.2%. Days to 75% flowering (DF) of the genotypes varied from 35 to 50 days in the non-stress environment (E1), while in the heat-stress environment it varied from 31 to 39 days in E2, and 29 to 37 days in E3. Hundred kernel weight in heat-stress environment varied from 17 to 52 g, while it is higher, 27 to 59 g, in non-stress environment (E1). The oil content of the genotypes in heat-stress environment varied between 48.1% and 61.4% and in non-stress environment it was 48.6% to 58.8%. The crop growth rate (CGR) varied from 8.4 to 15.7 g m^{-2} day^{-1} in E2, and from 7.4 to 15.9 g m^{-2} day^{-1} in E3, compared to 5.7–14.6 g m^{-2} day^{-1} in E1. However, pod growth rate (PGR) was low in heat-stress environments, varying from 5.7 to 12.8 g m^{-2} day^{-1} in E2, and from 3.1 to 13.2 g m^{-2} day^{-1} in E3, compared to 4.9–13.4 g m^{-2} day^{-1} in E1.

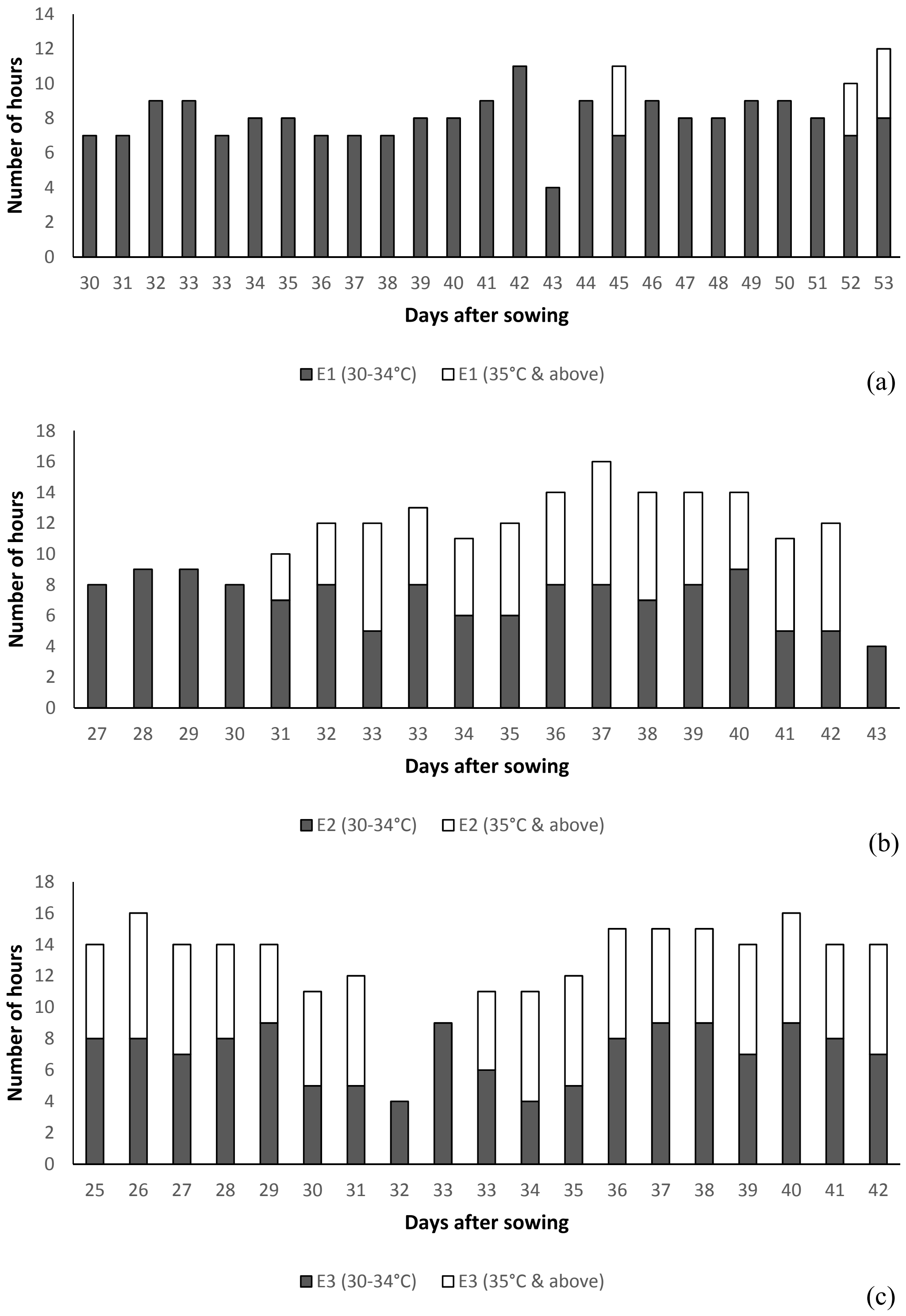

Figure 1. Graphical representation of temperature variation in the three environments during flowering period of groundnut genotypes (**a**) Non-stressed (E1); (**b**) Stressed (E2); (**c**) Stressed (E3).

The coefficient of variation (CV) for pod yield in heat-stress and non-stress environments varied from 1.1% to 27.5%. The genotypes are categorized based on CV and presented in Table 4. Stress tolerance index of groundnut genotypes under heat-stress environments and genotypes is categorized based on STI (Table 5).

Table 1. ANOVA for yield and associated traits of groundnut genotypes evaluated in three environments at ICRISAT-Patancheru during 2013/14 post-rainy season.

Source of Variation	df	HSW	PYH	SHP	HI	CGR	DF	DH	KYH	OC	PGR	SMK
Environment 1												
Genotype	61	108.4 *	2,384,353 *	54.4 *	91.5 *	58.0 *	18.3 *	64.5 *	1,067,839 *	12.8 *	81.1 *	24.2 *
Error	61	24.4	597,880	31.9	21.7	13.2	1.6	4.5	398,066	2.0	27.9	13.8
Environment 2												
Genotype	61	61.4 *	2,378,533 *	60.7 *	106.6 *	44.2 ^{NS}	4.5 *	231.1 *	903,795 *	12.9 *	57.1 *	61.8 *
Error	61	8.7	512,739	17.8	28.9	25.4	0.5	20.4	229,684	2.3	19.9	26.3
Environment 3												
Genotype	61	99.6 *	2,380,653 *	84.5 *	120.0 *	60.2 *	3.9 *	268.1 *	992,383 *	15.2 *	88.1 *	43.1 ^{NS}
Error	61	18.1	608,927	28.2	25.1	20.6	0.9	47.3	301,551	2.8	19.3	24.3

* Significant at 5%; ^{NS} non-significant; df, degree of freedom; HSW, 100-kernel weight (g); PYH, pod yield (kg ha^{-1}); SHP, shelling percentage (%); HI, harvest index (%); CGR, crop growth rate (g m^{-2} day^{-1}); DF, days to 75% flowering; DH, days to harvest; KYH, kernel yield (kg ha^{-1}); OC, oil content (%); PGR, pod growth rate (g m^{-2} day^{-1}); SMK, sound mature kernel (%).

Table 2. Combined ANOVA for pod yield and associated traits of groundnut genotypes evaluated in three environments at ICRISAT-Patancheru during 2013/14 post-rainy season.

Source of Variation	df	HSW	PYH	SHP	HI	CGR	DF	DH	KYH	OC	PGR	SMK
Genotype	61	229.9 *	6,182,834 *	136.5 *	262.4 *	114.3 *	21.4 *	473.6 *	2,426,473 *	36.4 *	172.4 *	53.7 *
Environment	2	1253.2 *	11,292,308 *	1215.5 *	1025.6 *	249.1 *	2564.2 *	3071.1 *	9,160,152 *	14.2 ^{NS}	464.4 *	230.3 *
Genotype × Environment	122	21.4 ^{NS}	495,882 ^{NS}	31.7 ^{NS}	28.8 ^{NS}	24.9 ^{NS}	4.3 *	44.5 *	270,253 ^{NS}	2.3 ^{NS}	26.7 ^{NS}	36.3 ^{NS}

* Significant at 5%; ^{NS} non-significant; df, degree of freedom; HSW, 100-kernel weight (g); PYH, pod yield (kg ha^{-1}); SHP, shelling percentage (%); HI, harvest index (%); CGR, crop growth rate (g m^{-2} day^{-1}); DF, days to 75% flowering; DH, days to harvest; KYH, kernel yield (kg ha^{-1}); OC, oil content (%); PGR, pod growth rate (g m^{-2} day^{-1}); SMK, sound mature kernel (%).

Table 3. Variability and heritability for yield and associated traits among groundnut genotypes evaluated in three environments at ICRISAT-Patancheru.

Trait	Environment 1 (E1)		Environment 2 (E2)		Environment 3 (E3)	
	Range	H (%)	Range	H (%)	Range	H (%)
Days to 75% flowering (days)	35–50	92.5	31–39	89.9	29–37	80.5
Days to maturity (days)	123–139	92.9	105–139	91	101–139	95.6
Pod Yield (kg ha^{-1})	2205–6761	77.6	2034–6767	80	1483–6180	76.5
Hundred Kernel Weight (g)	27–59	79.8	21–44	85.1	17–52	84.5
Oil Content (%)	48.6–58.8	84.4	48.1–58.4	81.6	48.2–61.4	84.3
Harvest Index (%)	33.2–65.2	76	31.7–62.6	71.9	24.6–64.6	80.2
Crop Growth Rate (g m^{-2} day^{-1})	5.7–14.6	85.3	8.4–15.7	51.1	7.4–15.9	61.6
Pod Growth Rate (g m^{-2} day^{-1})	4.9–13.4	69.7	5.7–12.8	67.9	3.1–13.2	75.8

E1, non-stress environment; E2 and E3, heat-stress environments; H, heritability in broad sense.

Table 4. Co-efficient of variation (CV) for pod yield of groundnut genotypes across heat-stress and non-stress environments evaluated at ICRISAT-Patancheru.

Genotypes	CV (%)
ICGV 07356, ICGV 97183, GG 20, Abhaya, K 6, J 11, TPG 41, ICGV 06175, ICGV 06424, ICGV 99001, GPBD 4	20–27.5
Chico, GJG 31, ICGV 03109, ICGV 05155, ICGV 86325, ICGV 91114, ICGV 02271, ICGV 00308, ICGV 96346, ICGV 93468, ICGV 92035, ICGV 01232, ICGV 07148, VRI 6, ICGS 11, ICGV 07268, ICGV 87846 , ICGV 07012, ICGV 95390, ICGV 07246, ICGV 07038, ICGV 06099, ICGV 05200, ICGV 03057, JL 24, ICGV 07273, ICGV 07217, ICGV 06040	10–19.9
ICGV 92195, ICGV 07456, ICGV 07213, ICGV 07211, ICGV 98294, ICGV 00350, ICGV 00351, ICGV 07013, ICGV 06039, ICGV 05032, TG 37, ICGV 89280, ICGV 02266, TMV 2, ICGV 00298, TAG 24, ICGV 03042	5–9.9
TCGS 1043, ICGV 97182, ICGV 87141, ICGV 87128, ICGV 06420	<5

Table 5. Estimates stress tolerance index of groundnut genotypes under heat-stress environments.

Genotypes	Stress Tolerance Index (E2)	Stress Tolerance Index (E3)
ICGV 99001, ICGV 86325, TMV 2, JL 24, ICGV 02271, GG 20, ICGV 07456, ICGV 91114, GPBD 4, K 6, ICGV 00298, ICGV 87141, ICGV 92195, Chico, GJG 31, J 11, ICGV 00308, ICGV 07211, ICGV 87128, ICGV 98294, VRI 6, ICGV 06175, ICGV 07356, ICGV 87846, ICGV 93468, ICGV 95390, ICGV 96346, TCGS 1043, Abhaya, ICGS 11, ICGV 07217, TPG 41	0.2–0.9	0.2–0.8
ICGV 92035, ICGV 97183, ICGV 05200	1.0–1.1	0.7–0.9
ICGV 97182, TG 37, ICGV 01232, ICGV 07013, ICGV 07213, ICGV 89280, TAG 24, ICGV 00350, ICGV 03057, ICGV 06420, ICGV 02266, ICGV 03109, ICGV 06099, ICGV 07273, ICGV 00351, ICGV 07268, ICGV 06039, ICGV 07148, ICGV 03042, ICGV 05032, ICGV 07038, ICGV 05155, ICGV 06040, ICGV 07012, ICGV 06424, ICGV 07246	1.1–2.1	1.0–1.7

3. Discussion

Flowering stage in groundnut is highly sensitive to high air temperatures of 35 °C and above, and results in pod yield reduction [25]. The greatest sensitivity to hot days occurs from six days before to 15 days after flowering [6,26]. Exposure to hot day temperatures of 35 °C and above continuously for six days relative to 28 °C reduced flower production by about 50% [26]. Day temperature above 35 °C during reproductive phase reduces fruit set and, consequently, the number of pods and ultimately seed yield [26,27]. In the present study, groundnut genotypes were exposed to different temperature regimes during flowering period, with increasing temperatures from E1 to E3 (Figure 1).

In stress environments, E2 and E3, the genotypes were exposed to more than 35 °C temperature during flowering. Even after ca. 15–30 days of flowering, the air temperatures in E2 and E3 were higher than in E1. E1 was considered a stress-free environment as the maximum temperature was below 35 °C except for about eleven hours except on three days (on 45, 52 and 53 DAP) during flowering period. In E2, the temperature was 35 °C or above for 3–8 h in a day with a total of 75 h, and in E3, temperatures were 35 °C or above for 5–8 h in a day totaling to 110 h. Thus, both E2 and E3 represented heat-stress environments and severity of stress being higher in E3, compared to E2 (Figure 1). Soil temperature is critical to pod formation and development, thus affecting pod filling and ultimately pod yield [28,29]. In the present study, variability was not significant in average minimum and maximum soil temperatures in stress and non-stress environments. It varied from 17 to 33 °C in non-stress environments, while it was 21.7 to 37.5 °C in stress environments.

Combined ANOVA showed non-significant G × E interactions for pod yield and other physiological parameters (Table 2), suggesting that genotypes responded in different ways in three different environments. The same was evident from the performance of the genotypes, wherein some genotypes showed a reduction in pod yield under heat stress, while others were either stable or recorded an increased pod yield. The observation suggests scope to identify groundnut genotypes that perform well in normal as well as heat-stress environments. Genotypic variation for pod yield [30–32] for harvest index [33] under high temperature among groundnut genotypes was associated with differences in botanical type. Our study involved two botanical types, var. *hypogaea* (Virginia market class) and var. *vulgaris* (Spanish market type) of *Arachis hypogaea* subsp. *fastigiata* but did show such an association.

High broad-sense heritability for pod yield, hundred kernel weight, oil content, harvest index, pod growth rate and crop growth rate in heat-stress and non-stress environments indicates the role of additive gene action in inheritance of these traits, and possible genetic gains through selection (Table 3). Heritability was also high for days to 75% flowering and maturity duration, suggesting genetic gains through selection for these traits that may be useful in breeding early maturing varieties. Earlier studies reported high heritability for pod yield, harvest index [34,35] and hundred kernel weight [36,37] and moderate heritability for oil content [38].

The influence of high temperature on flowering and maturity duration was profound among the groundnut genotypes. In non-stress environment, E1, the genotypes completed 75% of flowering in 35 to 50 days, while in heat-stress environments, they completed 75% flowering in 31 to 39 days in E2, and in 29 to 37 days in E3. Thus, under elevated temperature, groundnut genotypes complete flowering early, and matured early compared to non-stress environment. Similar to earlier observations [39], early maturing genotypes that took 123 days in non-stress environment matured early by at least 18 days under heat-stress environments.

Pod and kernel yield of ca. 50% of the genotypes was reduced in heat-stress environments (E2 and E3), among which many genotypes recorded a pod yield reduction of up to 20% in E2, and over 20% in E3 (data not shown). Studies have shown that the reduction in pod yield at higher air temperatures is a consequence of the decrease in fruit set resulting from fewer pegs and pods [10,40,41]. From controlled environment studies, Ketring [27] showed that the numbers of pegs and pods were reduced by 33% by an exposure to a day temperature of 35 °C compared with 30 °C. Ntare et al. [24], based on his field study, reported more than a 50% decline in pod yield when flowering and pod formation occurred at maximum temperature of 40 °C. Significant reduction in kernel mass due to heat stress to an extent of 45–46% was observed in heat-stress environments, E2 and E3 compared to non-stress environment, E1. It may be possible that kernel mass reduction, in part, may have contributed to pod yield reduction under heat stress, besides other factors.

The oil content of the genotypes in heat-stress and non-stress environment did not show variation. The oil accumulation in groundnut can be divided into three stages based on the phenotype, namely, the initial accumulation stage, the fast accumulation stage and the steady accumulation stage [42]. Maximum oil accumulation in groundnut happens during the fast accumulation stage, which occurs towards the later part of seed development [43]. In the present study, the maximum air temperature during late pod development stages is about 40 °C in all three environments and soil temperatures were also normal during entire pod developmental stages. Thus, to study the influence of heat stress on oil accumulation, it may be desirable to evaluate the genotypes by exposing them to varying temperatures of air and soil at late pod developmental stages. The reduction in duration of genotypes in the heat-stress environment did not show any effect on oil accumulation, suggesting the possibility of breeding early maturing varieties with high oil content.

The Crop Growth Rate (CGR) was high under heat-stress environments, E2 and E3, compared to non-stress environment, E1, indicating a greater accumulation of photosynthates at higher temperature. However, genotypic differences for CGR in the heat-stress environment indicate that the magnitude of response to heat stress is variable among genotypes. Pod Growth Rate (PGR) was low in heat-stress environments, E2 and E3, compared to non-stress environment, E1, indicating poor partitioning of accumulated photosynthates. Although groundnut accumulates higher photosynthates in response to high temperature, the partitioning of photosynthates is affected under high temperature, thus reducing the pod yield. However, the response of genotypes to CGR and PGR is variable under heat stress and did not follow a common trend. The heat-tolerant genotypes showed a marginal reduction in PGR under heat stress, suggesting the possible utility of PGR as a criterion to select high pod yielding genotypes for heat-stress environments. Earlier reports suggested that CGR and PGR may be useful to derive the partitioning factor (PF), which is the ratio of PGR to CGR, and PF was correlated with pod yield under heat-stress and water-deficit environments [30,44] and PF was found to be one of the best indicators to screen heat-tolerant genotypes in Sahel environments [24]. Harvest index of heat-tolerant genotypes did not vary much under heat-stress and non-stress environment, while in other genotypes, harvest index showed a reduction under heat stress. Under extreme heat stress, as in E3, there is a significant reduction in harvest index of heat sensitive genotypes from 33.2% to 24.6%.

3.1. Performance of Groundnut Genotypes under Heat Stress

Based on pod yield performance in heat-stress and non-stress environments, groundnut genotypes were categorized into three groups. The first group consisted of genotypes that were stable across heat-stress and non-stress environments, which implies that these genotypes are stable for pod yield under heat stress. The second group consisted of genotypes that showed an increase in pod yield in heat-stress environments, while the third are the heat-sensitive genotypes that recorded pod yield reduction under heat stress. Coefficient of variation (CV), one of the simplest parameters for determining stable genotypes [45,46], was used in the present study.

Genotypes with a very low CV for pod yield are stable across environments. ICGV 06420 was identified as a stable genotype (CV of 1.1%) and its pod yield varied from 5089 to 5198 kg ha^{-1} in heat-stress and non-stress environments (Table 4). The other stable genotypes, ICGV 87128, ICGV 87141, ICGV 97182, TCGS 1043 and ICGV 03042, recorded high pod yield varying from 3511 to 6192 kg ha^{-1}. The mean PGR of these genotypes in heat-stress environments, E2 and E3, varied from 0.25 to 3.1 g m^{-2} day^{-1} which was higher in comparison to non-stress environment, E1. Five genotypes, GJG 31, ICGV 87846, ICGV 03057, ICGV 07038 and GG 20, showed an increased pod yield by at least 9.0% under heat-stress environments as compared to non-stress environment. Pod yield increase of over 47% under heat stress was recorded by GG 20 and GJG 31. The mean PGR of these two genotypes in heat-stress environments, E2 and E3, is 0.65 to 3.6 g m^{-2} day^{-1} higher than in stress-free environment. Understanding the physiological mechanisms underlying increased accumulation of photosynthates and subsequent enhanced and/or efficient partitioning to the sink may be useful to develop promising groundnut genotypes for cultivation under heat-stress environments. The genotypes with an increase in yield under heat stress may have greater potential to be developed as heat-tolerant genotypes through breeding program. Ntare et al. [24] reported genotypes with increased pod yield and partitioning factor under high temperatures as a consequence of high radiation-use-efficiency of these genotypes. On the contrary, pod yield reduction of ca. 18–26% due to high air temperature was reported [6,26–29,47].

3.2. Heat-Tolerant and Superior Pod-Yielding Groundnut Genotypes

Stress tolerance index (STI) is associated with pod yield (r = 0.9) under heat-stress environments, thus *STI* is considered as a reliable parameter to identify heat-tolerant groundnut genotypes. Porch [16], in their evaluation of heat tolerance indices, reported *STI* and geometric mean as effective stress indices in common bean (*Phaseolus vulgaris*) for selection of genotypes with good yield potential under heat-stress and non-stress conditions.

From the study, twenty-six groundnut genotypes with high *STI* values ranging from 1.0–2.1 in E2 and E3 environments were identified as heat-tolerant genotypes. Heat stress-tolerant genotypes, ICGVs 97182, 01232, 07013, 07213, 89280, 00350, 03057, 06420, 02266, 03109, 06099, 07273, 00351, 07268, 06039, 07148, 03042, 05032, 07038, 05155, 06040, 07012, 06424, 07246, TG 37 and TAG 24, identified based on STI, also possess several other important traits. ICGV 00351 was released in India as a drought-tolerant variety [48], and ICGV 00350 and TAG 24 were released for post-rainy season cultivation in Zone 5 of India. ICGVs 06040 and 06099 were identified as high kernel Fe- and Zn-containing lines [49], and ICGVs 05155, 06420, 03057 and 03042 are high oil containing lines now in national level multi-location testing in India under the All India Coordinated Research Project on Groundnut.

Based on STI and superior pod yield performance, seven heat-tolerant genotypes, ICGV 07246 (5385–6761 kg ha^{-1}), ICGV 03042 (5662–6192 kg ha^{-1}), ICGV 06039 (5308–6041 kg ha^{-1}), ICGV 07012 (5237–6761 kg ha^{-1}), ICGV 06040 (5606–6767 kg ha^{-1}), ICGV 06424 (4496–6597 kg ha^{-1}) and ICGV 07038 (5206–6521 kg ha^{-1}) were identified for use as varieties and/or in breeding programs as parents. In heat-tolerant genotypes, hundred seed mass was not reduced under heat stress as a consequence of the biological processes in these genotypes that enable efficient partitioning of photosynthates to pods even under heat stress. Thus, seed mass can also be used as selection criteria to select for superior pod-yielding genotypes under heat stress.

4. Materials and Methods

4.1. Experimental Conditions and Environments

An evaluation trial with sixty-two groundnut genotypes comprised of advanced breeding lines, popular varieties and germplasm lines was conducted in Alfisols (Alfisol-Patancheru Soil Series; Udic Rhodustolf) fields at ICRISAT, Patancheru, India (at 17.53° N latitude and 78.27° E, 545 m) during post-rainy season, 2013/14. The experimental trial was conducted in three contrasting environments of stress and non-stress conditions. In the first environment, E1, sown on 25 January 2014, the genotypes did not experience heat stress during flowering. For the second and third environments, E2 and E3, sown on 18 February and 2 March 2014 respectively, the genotypes were exposed to heat stress during flowering period. The temperature and duration of stress were higher in E3 than in E2. The experiment in each of the environments was laid out in a randomized block design with two replications. The plot size consisted of four 2-m long rows, and a spacing of 30 cm between rows and 10 cm between plants of a row on a broad-bed-and-furrow system. Standard agronomic management practices were followed for each environment that included basal application of 60 kg phosphorus pent-oxide (P_2O_5), seed treatment with mancozeb (2 g kg^{-1} seed), pre-emergence application of pendimethalin (1 kg active ingredient ha^{-1}), irrigation soon after planting, and subsequently as and when needed, and gypsum (400 kg ha^{-1}) at peak flowering and protection against insect pests and diseases.

4.2. Observations

During the crop growing period, hourly air temperatures were obtained from the meteorological station located close to the experimental field on ICRISAT campus. Soil temperatures were measured using Tinytag Radio Temperature Logger for Thermistor Probe (−40 to 125 °C). Maturity was recorded by randomly picking the border plant and examining the internal pod walls for characteristic blackening. At harvest, the entire four rows per plot were sampled. The plants were air dried for 2–3 days in the field, pods were separated from the haulms and cleaned of soil particles, and further dried under shade before recording dry weight of the pods.

Haulm weight and pod weight obtained per plot were converted into haulm yield (Hy) and pod yield (Py), expressed in g m^{-2} and used to determine the total biomass (Bt) given as: Bt = Hy + (Py × 1.65). The pod weight was multiplied by a correction factor of 1.65 to adjust for the differences in the energy requirement for producing pod dry matter compared with vegetative part [50]. Harvest index (HI) was determined as a ratio of adjusted pod weight to total biomass, given as: HI = (1.65 × Py)/Bt. For each plot, days to 75% flowering, days to maturity, pod yield (kg ha^{-1}), kernel yield (kg ha^{-1}), hundred kernel weight (g), sound mature kernel (%) and oil content (%) were recorded. Oil content was estimated with near infrared reflectance spectroscopy (NIRS) (model XDS RCA, FOSS Analytical AB, Sweden, Denmark) using whole kernels [51]. Two physiological parameters, crop growth rate (CGR) (g m^{-2} day^{-1}) and pod growth rate (PGR) (g m^{-2} day^{-1}) were estimated following a modified procedure given by Williams and Saxena [52]. Stress susceptible and tolerance indices were calculated to identify heat-tolerant genotypes using the following formula:

$$SSI = \frac{1 - \frac{Y_s}{Y_p}}{SI}$$

$$SI = 1 - \frac{\overline{Y_s}}{\overline{Y_p}},$$

$$STI = \frac{Y_s \times Y_p}{\left(\overline{Y_p}\right)^2}$$

SSI = Stress Susceptibility Index [53]; *SI* = Susceptibility Index; *STI* = Stress Tolerance Index [15]; Y_s and Y_p = Yields of genotypes evaluated under stress and non-stress conditions, and $\overline{Ys}$ and $\overline{Yp}$ = Mean yield over all genotypes evaluated under stress and non-stress conditions.

4.3. Statistical Analysis

The data obtained were subjected to analysis of variance (ANOVA) to test the significance of genotypes in each environment using F-test. Further, to study the performance of genotypes across different environments, combined ANOVA was done to assess variation attributed to different sources for which mixed model procedure was used to model individual environment error variance. Estimates of heritability were calculated as per the formula given by Allard [54]. All statistical analysis was performed using GenStat 15th edition for windows [55]. Co-efficient of variation (CV) was used for determining stable genotypes.

5. Conclusions

Pod yield, hundred seed weight, and pod growth rate under heat stress can be used as selection criteria to identify heat-tolerant groundnut genotypes. Partitioning of the photosynthates to the pods is one of the key processes affected by high-temperature stress in groundnut, consequently heat-susceptible genotypes recorded reduced pod yield under high-temperature stress. Groundnut genotypes accumulated higher photosynthates under high temperatures; however, only heat-tolerant genotypes have coping mechanisms to partition the photosynthates to pods. As a consequence, the pod yield in heat-tolerant genotypes is either increased or stable under heat stress. Variability among genotypes observed for coping processes involved in partitioning of photosynthates to pods under heat stress will be useful for improving groundnut genotypes with heat-tolerance. Groundnut genotypes, ICGVs 07246, 03042, 06039, 07012, 06040, 06424 and 07038 were identified as heat-tolerant lines based on stress tolerance index and pod yield performance.

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References

1. FAOSTAT. 2014. Available online: http://faostat3.fao.org/ (accessed on 25 June 2016).
2. Anonymous. *All India Coordinated Research Project on Groundnut (Annual Report)*; ICAR-DGR: Sagdividi, India, 2014.
3. Lobell, D.B.; Banziger, M.; Magorokosho, C.; Vivek, B. Nonlinear effects on African maize as evidenced by historical yield trials. *Nat. Clim. Chang.* **2011**, *1*, 42–45. [CrossRef]
4. Kucharik, C.J.; Serbin, S.P. Impacts of recent climate change on Wisconsin corn and soybean yield trends. *Environ. Res. Lett.* **2008**, *3*, 034003. [CrossRef]
5. Hundal, S.S.; Kaur, P. Climate change and its impact on crop productivity in Punjab, India. In *Climate Variability and Agriculture*; Abrol, Y.P., Gadgil, S., Pant, G.B., Eds.; Narosa Publishing House: New Delhi, India, 1996; pp. 377–393.
6. Vara Prasad, P.V.; Craufurd, P.Q.; Summerfield, R.J. Fruit number in relation to pollen production and viability in groundnut exposed to short episodes of heat stress. *Ann. Bot.* **1999**, *84*, 381–386. [CrossRef]
7. Paulsen, G.M. High temperature responses of crop plants. In *Physiology and Determination of Crop Yield*; Boote, K.J., Bennett, J.M., Sinclair, T.R., Paulsen, G.M., Eds.; American Society of Agronomy: Madison, WI, USA, 1994; pp. 365–389.
8. Marshall, H.G. Breeding for tolerance to heat and cold. In *Breeding Plants for Less Favourable Environments*; Christiansen, M.N., Lewis, C.F., Eds.; John Wiley & Sons: New York, NY, USA, 1982; pp. 47–70.
9. Ong, C.K. Agroclimatological factors affecting phenology of peanut. In *Agrometeorology of Groundnut, Proceedings of An International Symposium, Niamey, Niger, 21–26 August 1985*; International Crops Research Institute for the Semi-Arid Tropics: Patancheru, India, 1986; pp. 115–125.
10. Craufurd, P.Q.; Prasad, P.V.; Kakani, G.V.; Wheeler, T.R.; Nigam, S.N. Heat tolerance in groundnut. *Field Crop. Res.* **2003**, *80*, 63–77. [CrossRef]
11. Khattak, G.S.S.; Saeed, I.; Muhammad, T. Breeding for heat tolerance in mungbean (*Vigna radiata* (L.) Wilczek). *Pak. J. Bot.* **2006**, *38*, 1539–1550.
12. Rehman, A.; Habib, I.; Ahmad, N.; Hussain, N.; Arif Khan, M.; Farooq, J.; Amjad, M. Screening wheat germplasm for heat tolerance at terminal growth stage. *Plant Omics J.* **2009**, *2*, 9–19.
13. Devasirvatham, V.; Tan, D.K.Y.; Gaur, P.M.; Raju, T.N.; Trethowan, R.M. High temperature tolerance in chickpea and its implications for plant development. *Crop Pasture Sci.* **2012**, *63*, 419–428. [CrossRef]
14. Moghaddam, A.; Hadizadeh, M.H. Study use of compression stress in drought stress tolerance varieties selection in maize (*Zea mays* L.). *J. Crop Sci.* **2000**, *2*, 25–38.
15. Fernandez, G.J. Effective selection criteria for assessing plant stress tolerance. In Proceedings of the International Symposium on Adaptation of Vegetables and other Food Crops in Temperature and Water Stress, Shanhua, Taiwan, 13–16 August 1992; pp. 257–270.
16. Porch, T.G. Application of Stress Indices for Heat Tolerance Screening of Common Bean. *J. Agron. Crop Sci.* **2006**, *192*, 390–394. [CrossRef]
17. Wahid, A.; Gelani, S.; Ashraf, M.; Foolad, M.R. Heat tolerance in plants: An overview. *Environ. Exp. Bot.* **2007**, *61*, 199–223. [CrossRef]

18. Bell, M.J.; Bagnall, D.J.; Harch, G. Effect of photoperiod on reproductive development of peanut (*Arachis hypogaea* L.) in a cool subtropical environment. II. Temperature interactions. *Aust. J. Agric. Res.* **1991**, *42*, 1151–1161. [CrossRef]
19. Bell, M.J.; Wright, G.C.; Harch, G. Environmental and agronomic effects on the growth of four peanut cultivars in a sub-tropical environment. II. Dry matter partitioning. *Exp. Agric.* **1993**, *29*, 491–501. [CrossRef]
20. Nigam, S.N.; Nageswara Rao, R.C.; Wynne, J.C.; Williams, J.H.; Eitzner, M.; Nagabhushanam, G.V.S. Effect and interaction of temperature and photoperiod on growth and partitioning in three groundnut (*Arachis hypogaea* L.) genotypes. *Ann. Appl. Biol.* **1994**, *125*, 541–552. [CrossRef]
21. Hamidou, F.; Halilou, O.; Vadez, V. Assessment of groundnut under Combined Heat and Drought Stress. *J. Agron. Crop Sci.* **2013**, *199*, 1–11. [CrossRef]
22. Gangappa, E.; Ravi, N.; Veerakumar, G.N. Evaluation of groundnut (*Arachis hypogaea* L.) genotypes for temperature tolerance based on Temperature Induction Response (TIR) technique. *Indian J. Genet. Plant Breed.* **2006**, *66*, 127–130.
23. Selvaraj, M.; Burow, G.B.; Burke, J.J.; Belamkar, V.; Puppala, N.; Burow, M. Heat stress screening of peanut seedlings for acquired thermotolerance. *J. Plant Growth Regul.* **2011**, *65*, 83–91. [CrossRef]
24. Ntare, B.R.; Williams, J.H.; Dougbedji, J. Evaluation of groundnut genotypes for heat tolerance under field conditions in a Sahelian environment using a simple physiological model for yield. *J. Agric. Sci.* **2001**, *136*, 81–88. [CrossRef]
25. Vara Prasad, P.V.; Craufurd, P.Q.; Summerfield, R.J.; Wheeler, T.R. Effect of short episodes of heat stress on flower production and fruit-set of groundnut (*Arachis hypogaea* L.). *J. Exp. Bot.* **2000a**, *51*, 777–784.
26. Vara Prasad, P.V.; Craufurd, P.Q.; Summerfield, R.J. Sensitivity of peanut to timing of heat stress during reproductive development. *Crop Sci.* **1999**, *39*, 1352–1357. [CrossRef]
27. Ketring, D.L. Temperature effects on vegetative and reproductive development of peanut. *Crop Sci.* **1984**, *24*, 877–882. [CrossRef]
28. Golombek, S.D.; Johansen, C. Effect of soil temperature on vegetative and reproductive growth and development in three Spanish genotypes of peanut (*Arachis hypogaea* L.). *Peanut Sci.* **1997**, *24*, 67–72. [CrossRef]
29. Ono, Y.; Nakayama, K.; Kubota, M. Effects of soil temperature and soil moisture in podding zone on pod development of peanut plants. *Crop Sci. Soc. Jpn.* **1974**, *43*, 247–251. [CrossRef]
30. Greenberg, D.C.; Williams, J.H.; Ndunguru, B.J. Differences in yield determining processes of peanut (*Arachis hypogaea*) genotypes in varied drought environments. *Ann. Appl. Biol.* **1992**, *120*, 557–566. [CrossRef]
31. Wheeler, T.R.; Chatzialioglou, A.; Craufurd, P.Q.; Ellis, R.H.; Summerfield, R.J. Dry matter partitioning in groundnut exposed to high temperature stress. *Crop Sci.* **1997**, *37*, 1507–1513. [CrossRef]
32. Shinde, P.P.; Khanpara, M.D.; Vachhani, J.H.; Jivani, L.L.; Kachhadia, V.H. Genetic variability in virginia bunch groundnut (*Arachis hypogaea* L.). *Plant Arch.* **2010**, *10*, 703–706.
33. Injeti, S.K.; Venkataravana, P.; Rao, M.R.G. Evaluation of new germplasm and advanced breeding lines of groundnut (*Arachis hypogaea* L.) under late kharif situation. *Legum. Res.* **2008**, *31*, 254–258.
34. John, K.; Vasanthi, R.P.; Venkateswarlu, O. Variability and correlation studies for pod yield and its attributes in F_2 generation of six Virginia × Spanish crosses of groundnut (*Arachis hypogaea* L.). *Legume Res.* **2007**, *30*, 292–296.
35. Khote, A.C.; Bendle, V.W.; Bhave, S.G.; Patil, P.P. Genetic variability, heritability and genetic advance in some exotic genotype of groundnut (*Arachis hypogaea* L.). *Crop Res.* **2009**, *37*, 186–191.
36. Mahalakshmi, P.; Manivannan, N.; Muralidharan, V. Variability and correlation studies in groundnut (*Arachis hypogaea* L.). *Legume Res.* **2005**, *28*, 194–197.
37. Thirumalarao, V.; Venkanna, V.; Bhadru, D.; Bharathi, D. Studies on Variability, Character Association and Path Analysis on Groundnut (*Arachis hypogaea* L.). *Int. J. Pure Appl. Bioscience* **2014**, *2*, 194–197.
38. Noubissie, T.J.B.; Njintang, N.Y.; Dolinassou, S. Heritability studies of Protein and oil contents in groundnut (*Arachis hypogaea* L.) genotypes. *Int. J. Innovations Biol. Chem. Sci.* **2012**, *2*, 162–171.
39. Thakur, S.B.; Ghimire, S.K.; Chaudhary, N.K.; Shrestha, S.M.; Mishra, B. Genic variability, heritability and genic advance of pod-yield component traits of groundnut (*Arachis hypogaea* L.). *J. Instant Agric. Anim. Sci.* **2011**, *32*, 133–141.
40. Craufurd, P.Q.; Wheeler, T.R.; Ellis, R.H.; Summerfield, J.; Vara Prasad, J.V. Escape and tolerance to high temperature at flowering in groundnut (*Arachis hypogaea* L.). *J. Agric. Sci.* **2000**, *135*, 371–378. [CrossRef]

41. Vara Prasad, P.V.; Craufurd, P.Q.; Summerfield, R.J. Effect of high air and soil temperature on dry matter production, pod yield and yield components of groundnut. *Plant Soil* **2000b**, *222*, 231–239. [CrossRef]
42. Chen, S.L.; Li, Y.R.; Xu, G.Z.; Cheng, Z.S. Simulation on Oil Accumulation characteristics in Different High-Oil Peanut Varieties. *Acta Agron. Sin.* **2008**, *34*, 142–149. [CrossRef]
43. Chi, X.; Hu, R.; Zhang, H.; Chen, M.; Chen, N.; Pan, L.; Wang, T.; Wang, M.; Wang, Z.; Wang, Q.; et al. Cloning and functional analysis of three diacylglycerol acyltransferase genes from peanut (*Arachis hypogaea* L.). *PLoS ONE* **2014**, *9*, e105834. [CrossRef] [PubMed]
44. Ndunguru, B.J.; Ntare, B.R.; Williams, J.H.; Greenberg, D.C. Assessment of groundnut cultivars for end-of-season drought tolerance in a Sahelian environment. *J. Agric. Sci.* **1995**, *125*, 79–85. [CrossRef]
45. Rahmatollah, K.; Mohtasham, M.; Naser, S.; Mohammad, K.S. Using different aspects of stability concepts for interpreting genotype by environment interaction of some lentil genotypes. *Aust. J. Crop Sci.* **2012**, *6*, 1017–1023.
46. Finlay, K.W.; Wilkinson, G.N. The analysis of adaptation in a plant breeding programme. *Aust. J. Agric. Res.* **1963**, *14*, 742–754. [CrossRef]
47. Wood, I.M.W. The effect of temperature at early flowering on the growth and development of peanuts (*Arachis hypogaea*). *Aust. J. Agric. Res.* **1968**, *19*, 241–251. [CrossRef]
48. Vindhiyavarman, P.; Nigam, S.N.; Janila, P.; Vaidhyalingan, M.; Manivannan, N.; Saravanan, S.; Meenakumari, B.; Gopalakrishnan, C.; Kennedy, J.S. A new high yielding Spanish bunch groundnut variety CO 7 (ICGV 00351) for the drought prone areas of Tamil Nadu. *Electron. J. Plant Breed.* **2014**, *5*, 192–196.
49. Janila, P.; Nigam, S.N.; Abhishek, R.; Kumar, V.A.; Manohar, S.S.; Venuprasad, R. Iron and zinc concentrations in peanut (*Arachis hypogaea* L.) seeds and their relationship with other nutritional and yield parameters. *J. Agric. Sci.* **2014**, *153*, 975–994. [CrossRef]
50. Duncan, W.G.; Mccloud, D.E.; Mcgraw, R.L.; Boote, K.J. Physiological aspects of peanut yield improvement. *Crop Sci.* **1978**, *18*, 1015–1020. [CrossRef]
51. Sundaram, J.; Kandala, C.V.; Holser, R.A.; Butts, C.L.; Windham, W.R. Determination of in-shell peanut oil and fatty acid composition using near infrared reflectance spectroscopy. *J. Am. Oil Chem. Soc.* **2010**, *87*, 1103–1114. [CrossRef]
52. Williams, J.H.; Saxena, N.P. The use of non-destructive measurement and physiological models of yield determination to investigate factors affecting differences in seed yield between genotypes of 'desi' chickpeas (*Cicer arietum*). *Ann. Appl. Biol.* **1991**, *119*, 105–112. [CrossRef]
53. Fischer, R.A.; Maurer, R. Drought resistance in spring wheat (*Triticum aestivum* L.) cultivars. I Grain yield responses. *Aust. J. Agric. Res.* **1978**, *29*, 897–912. [CrossRef]
54. Allard, R.W. *Principles of Plant Breeding*; John Wiley & Sons Inc.: New York, NY, USA, 1960; pp. 1–485.
55. VSN International. *GenStat*, 15th ed.; VSN International: Indore, India, 2012.