Genetic variations in photosynthetic rate, pod yield and yield components in Spanish groundnut cultivars during three cropping seasons

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ABSTRACT

Thirty Spanish groundnut (*Arachis hypogaea* L.) cultivars were grown for three cropping seasons, i.e., for two consecutive rainy and summer, and one post-rainy, and evaluated for physiological, morphological and anatomical traits and yield components. Photosynthetic rate (P_N) was measured at full pod (R4) during rainy and post-rainy while at different reproductive growth stages during summer seasons. Response of cultivars to physiological traits differed significantly and cultivars belonging to high P_N expressed higher g_s and lower difference between leaf and air temperatures (ΔT) indicating that groundnut productivity could be increased by increasing g_s. Among the reproductive growth stages, P_N was higher during full pod (R4) and beginning seed (R5) in addition ΔT was least during this period. This indicated that Spanish groundnut is more close to the determinate type of growth habit and exhibited reproductive sink driven P_N. Associations between morphological and physiological traits and yield components were established and potential trade-offs between various traits were identified. For example, associations between P_N and total sink size ($r = 0.43^{**}$), weight of mature pods ($r = 0.45^{**}$) and harvest index (HI) ($r = 0.48^{**}$) were positive while association between P_N and ΔT ($r = -0.60^{**}$), leaf temperature ($r = -0.47^{**}$), petiole length ($r = -0.50^{**}$), both leaflet length and width ($r = -66^{**}$) were negative. Among the sources of variation, environment was found most detrimental to influence the traits and among the physiological traits influence of environment was more on g_s than the P_N and ΔT. Similarly, environment has influenced pod yield more than reproductive sink size. Among all the traits studied, P_N, g_s, pod yield and HI contributed maximum to the observed variation. In conclusion, knowledge on physiological understanding in relation to P_N and productivity and wide genetic variability among various traits, as reported in this study, could be utilized in developing new potential germplasm and designing ideotype for making the cultivars more adaptive for different water availability areas in semi-arid tropics worldwide.

1. Introduction

Groundnut (*Arachis hypogaea* L.) is an important food and oil crop, predominantly cultivated in the tropical and sub-tropical regions between 40°N and 40°S latitudes. It is the third major oilseed of the world, mainly grown by the resource poor farmers in Asia and Africa (FAO, 2000). Its seed is rich in oil (48–50%), protein (23–26%), carbohydrates (15–18%), vitamins and minerals, and haulms are used as quality fodder. Most of the groundnut varieties belong to Virginia and Spanish market types while Spanish type possesses relatively shorter crop duration than the Virginia.

Thus, Spanish type can be grown conveniently during different cropping seasons in tropical, sub-tropical and warm temperature regions, under both irrigated and rain-dependent conditions. In India, groundnut is cultivated during three different cropping seasons, i.e., summer (January–May), rainy (June–October) and post-rainy (October–March) and average productivity level ranges between 500 and 1500 kg ha^{-1}, however productivity is highest under irrigated condition during summer (DES, 2011). Groundnut being relatively indeterminate in growth habit, both vegetative and reproductive sinks operates concurrently, though Virginia is more indeterminate than Spanish types. Under such situation partitioning of photosynthates into developing pods has been reported to be the most important physiological trait in yield determination, besides number of pods and length of pod filling phase (Nigam et al., 1998; Nautiyal et al., 2002a). Therefore, single leaf photosynthesis may not truly reflect the potential of a genotype to determine productivity but such observations could be of immense value to access and identify the potential genotype, if P_N is measured over the seasons and during different crop growth stages and cultivar

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response is recorded meticulously. In groundnut, single leaf P_N has been studied for several genotypes and genetic variation was reported (Bhagsari and Brown, 1976; Nautiyal et al., 1995; Collino et al., 2001). Since, the process of photosynthesis seems to be fundamental in both biomass accumulation and productivity, it could be best utilized in identifying the efficient cultivars and to understand the physiological traits associated with productivity both under normal irrigation and rain-dependent conditions (Nautiyal et al., 1999a,b). The higher and lower P_N genotypes have also been identified in several crop species (Mauney et al., 1978; Reynolds et al., 2000; Takai et al., 2010) but there is no evidence of any indirect selection for increased photosynthetic efficiency per unit leaf area and its utilization to greater biomass accumulation and productivity. It is, however, clear that net photosynthetic capacity is a function of several interacting physiological phenomena, including supply, photosynthesis *per se* and sink-strength together with factors that determine the efficiency of these, and environmental influence. Thus in most of the crop species including groundnut, it seems that in the absence of genetic enhancement in photosynthesis and growth, past improvement in yield potential has been derived largely from increase in HI (see review by Zhu et al., 2010). Hence there is need to increase productivity by increasing both total biomass and harvest index and utilizing the genetic variability in physiological traits, especially in groundnut.

In addition, significant variability in P_N among groundnut cultivars also suggests the need to analyse the genetic potential (Nautiyal et al., 2002b). Thus information on physiological processes such as interaction between photosynthesis and sink potential and buffering of these processes to environmental fluxes could be of immense value in utilizing the genetic potential (Ferreyra et al., 2000; Niinemetes, 2007). Moreover, the fact that CO_2 enrichment of the atmosphere will enhance growth and yield of C_3 crops (Leakey et al., 2009) and indicates that growth is photosynthetically limited in some environments, where genetic factor may play an important role. In groundnut, under present circumstances a large pool of variability remains unutilized due to incomplete knowledge of available genetic resources and relationships among various yield and physiological traits and the technique to identify superior genotype.

The objectives were to test whether groundnut cultivars differ in responses of photosynthetic rate, dry matter production and pod yield, and whether associations can be detected between various morphological, anatomical and physiological traits, and yield components to elucidate the variability for higher productivity under different cropping environments. It may also be of interest that information gained on the subject would be of value to farmers when choosing cultivars and to breeders when developing new cultivars for different cropping seasons.

2. Materials and methods

2.1. Field trials and plant materials

A completely randomized block design (RBD) with three replicates was followed to conduct field trials during three different cropping seasons, i.e., two summers (January–June), two rainy (June–October) and one post-rainy (October–March) with 30 Spanish groundnut cultivars. Spanish cultivars possess relatively shorter crop duration having maturity periods between 110 and 120 days in summer (irrigated), 100 and 115 days in rainy (rain-dependent) and 135 and 150 days in post-rainy (irrigated) seasons. The trials were conducted at the farm site of the Directorate of Groundnut Research, Junagadh (lat 21°31′N, long 70°36′E). The soil of the experimental site is Vertic Ustochrept (pH 8.5) with low organic matter (1.64–1.91%), available nitrogen (N, 0.02%) and phosphorus

(P, 74–112 ppm). The plot size was $4 \times 3 \, m^2$ and a spacing of 45 cm between rows and 10 cm between plants was adopted. Nitrogen (N) and phosphorous (P) fertilizers were applied before sowing as basal doses such as N in the form of urea, i.e., 25 kg N ha^{-1} under irrigated and 12.5 kg N ha^{-1} under rain-dependent and P in the form of single super phosphate, i.e., 40 kg P_2O_5 ha^{-1} under irrigated and 20 kg P_2O_5 under rain-dependent conditions. The difference in the amount of fertilizer dozes is mainly due to differential uptake and utilization pattern under irrigated and rain-dependent conditions (Ghosh et al., 2001). After sowing, two irrigations were given for ensuring good emergence in summer and post-rainy seasons. Thereafter, the crop was irrigated to replenish 100% cpe at weekly intervals, while during rainy season crop was completely rain-dependent right from the sowing until the final harvest. Recommended plant protection measures were followed to maintain healthy crop stand.

2.2. Measurement of photosynthetic rate

Photosynthetic rate (P_N) was measured during three different cropping seasons, i.e., during rainy and post-rainy seasons at full pod (R4), and during summer season at beginning peg (R2), beginning pod (R3), full pod (R4), beginning seed (R5), full seed (R6), and harvest maturity (R8). These reproductive growth stages were followed as defined by Boote (1982). Single leaf P_N, stomatal conductance (g_s) and leaf temperature (T_{leaf}) and air temperature (T_{air}) were recorded on second or third fully expanded leaf from the top of the main axis, using a portable photosynthesis system (Model; LI-6200, LICOR, Lincoln, NE, USA) between 0900 and 1000 h local time and difference between T_{leaf} and T_{air} was computed as ΔT. Care was taken to measure P_N at the natural angles of the leaf facing sun in the canopy. The measurements were performed on three consecutive days and three observations on single leaflet were recorded on each day. Thus single replicate was calculated based on three observations recorded daily on single leaflet of each cultivar. After the measurements, the leaflets were excised and leaf area was determined with an area meter (Model; LI 3000, LICOR, Lincoln, NE, USA).

2.3. Measurement of plant morphological and anatomical parameters

Plant height was measured and number of branches was counted at the final harvest during summer season on five plants randomly selected from each cultivar and replicate. Leaf morphology, i.e., leaf width, petiole length, leaflet length and width of upper and lower pairs were measured at full pod stage (R4) on nine leaves (usually the second or third from the top of the main axis) from each cultivar. Thickness of epidermis, palisade and spongy parenchyma, size of water storage cells and number of xylem rows were measured/counted in the transverse section of the leaf under microscope. To measure specific leaf area (SLA) five leaves, 3 or 4 fully opened from the top of the main axis or branches from five plants were sampled between 0900 and 1000 h local time and leaf area was measured immediately in the laboratory. Plant samples were dried at 80 °C to constant weight. Specific leaf area was computed by dividing the area (cm^2) of leaf samples with the corresponding dry weight and expressed as $cm^2 \, g^{-1}$.

2.4. Measurement of pod yield and yield components

At final harvest, plants were sampled from 0.30 m^2 and observations on number of pegs, and immature and mature pods were recorded. After removing the pods, plant samples were dried at 80 °C to constant weight in hot air oven. Total number of pods in each sampled area was divided by the corresponding area to obtain

the number of pods per m². Weight per pod was determined by dividing total pod weight of the sampled area by the total number of pods. Pod yield was recorded after drying pods thoroughly in open sun in thin layers. Total biomass was calculated by adding the vegetative and pod dry weights. Pod weight was corrected for the oil energy conversion by multiplying it with 1.65 as suggested by Duncan et al. (1978). Harvest index (HI) was computed as the ratio of total energy converted pod weight to the total biomass at the final harvest, however during rainy season HI was calculated with the total vegetative dry weight recorded at full seed stage to avoid the reduction in leaf dry mass due to foliar diseases (Nautiyal et al., 2002b). Relative reproductive sink size was calculated by the following formula: (weight of mature pods + weight of immature pods)/(weight of mature pods − weight of immature pods) × total number of mature pods.

2.5. Statistical analysis

Data was analysed in RBD design for two summers, two rainy and one post-rainy seasons and used to analyse the variations in physiological traits and yield components due to cropping seasons. For each measured trait, a combined analysis of variance over all seasons was performed in a conventional manner, with genotype as fixed factor and a combination of season and year being random following Gomez and Gomez (1984). Analysis of variance was used to examine the genetic variations in parameters ($P = 0.05$). Variability among 30 cultivars was estimated using principle component analysis (PCA) following Davis (1986) and using a correlation matrix. The eigen value of PCs was used as a criterion to determine how many PCs should be utilized. The PCs with eigen value >1.0 were considered determining the agro-morphological variability in the cultivars (Kaiser, 1960). Number of significant PCs was identified based on "Screen plot" as suggested by Jackson (1993). For PCA analysis data was standardised with square root transformation and PC 1 and PC 2 scores were used to develop a scatter plot of traits.

3. Results

3.1. Photosynthetic rate during different cropping seasons

Based on average P_N over the cropping seasons, cultivars were divided into high (12.08–15.43 μmol m^{-2} s^{-1}), medium (11.05–11.95 μmol m^{-2} s^{-1}) and low (9.45–10.93 μmol m^{-2} s^{-1}) groups and influence of environment on P_N, g_s and ΔT was accessed (Fig. 1). In high P_N group, P_N was at par during summer and rainy whereas in medium group it was higher during summer followed by rainy and post-rainy, seasons. On the contrary, in low P_N group, it was higher during summer followed by post-rainy and rainy seasons (Fig. 1a). Stomatal conductance in cultivars belonging to high P_N group was almost at par during all the three seasons, but in medium and low groups it was higher during rainy followed by summer and post-rainy seasons (Fig. 1b). Thus average g_s over the seasons was higher during rainy (0.42 mol m^{-2} s^{-1}) and lower during summer (0.26 mol m^{-2} s^{-1}) and post-rainy (0.24 mol m^{-2} s^{-1}) seasons. Hence, P_N was higher at lower g_s during summer, while lower at higher g_s during rainy, seasons. Thus could be attributed to varying environmental conditions such as lower sunshine hours, lower VPD, and higher rainfall and rainy days during crop growth stages before P_N measurements, in rainy season (Table 1). Whereas, during post-rainy season, both P_N (10.53 μmol m^{-2} s^{-1}) and g_s (0.24 mol m^{-2} s^{-1}) were lower and this could be mainly due to lower day/night temperatures (Table 1). In addition, P_N and g_s were associated closely, however the association varied during different season, such as, it was relatively stronger during summer ($r = 0.80$**) and slightly weaker during
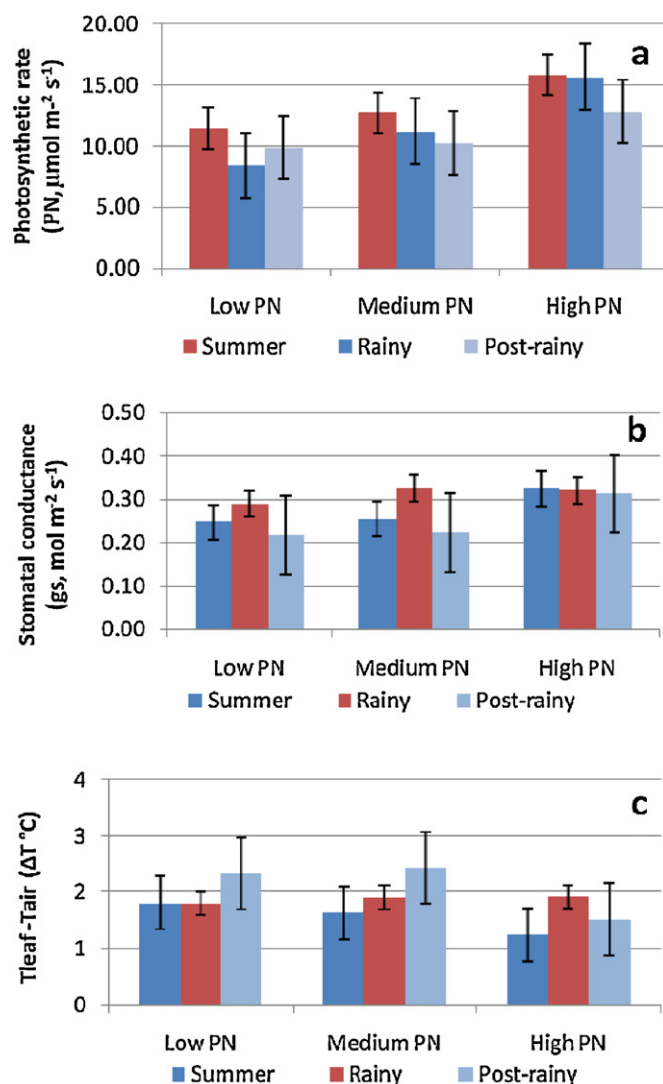

Fig. 1. Photosynthetic rate (P_N) (a), stomatal conductance (g_s) (b) and $T_{leaf} - T_{air}$ (ΔT) (c) during three different seasons in low medium and high P_N cultivars.

rainy ($r = 0.57$**) and post-rainy ($r = 0.48$**) seasons. Irrespective of the season, P_N (14.7 μmol m^{-2} s^{-1}) and g_s (0.31 mol m^{-2} s^{-1}) were higher and ΔT was lower (1.5 °C) in the cultivars belonging to high P_N group. Thus high P_N group was able to maintain least ΔT during all the three seasons, whereas in medium and low groups ΔT was higher during summer and lower during rainy and post-rainy, seasons (Fig. 1c). In addition, irrespective of the P_N groups, ΔT was lower (1.60 °C) during summer while higher both (2.14 °C) during rainy and post-rainy seasons. Also, a negative association between P_N and ΔT varied in significance level such as stronger during summer ($r = -0.60$**) than the post-rainy ($r = -0.33$*) and non significant during rainy ($r = -0.23$) seasons. These results clearly showed that lower ΔT during summer season might have contributed positively to increased P_N and productivity. From weather data, it is also clear that overall environmental conditions during summer were much favorable to express full genetic potential for photosynthesis and productivity as compared to the rainy and post-rainy seasons, at Junagadh location (Table 1). Thus seasonal response in P_N in different groups varied which has contributed for the variation in total biomass and pod yield.

Among cultivars, P_N ranged between 18.76 μmol m^{-2} s^{-1} in TAG 24 and 7.59 μmol m^{-2} s^{-1} in DH 3–30 during rainy season. Based on average P_N over the season, i.e., $\geq$12.0 μmol m^{-2} s^{-1} and potential

Table 1
Environmental parameters during three different cropping seasons at Junagadh, Gujarat, India.

| Parameters	Summer (February–May)	Rainy (June–September)	Post-rainy (October–January)
Daily minimum temperature (°C)	13.5	22.0	7.4
Average minimum temperature (°C)	21.0	24.3	16.3
Daily maximum temperature (°C)	42.8	39.0	37.0
Average daily maximum temperature (°C)	36.6	32.3	30.3
Average precipitation (mm)	0.0	14.9	0.0
Total precipitation during the crop growth period (mm)	12.5	1791.5	0.0
Total number of rainy days	1.0	51.0	0.0
Sunshine hours	9.4	3.1	8.8
Relative humidity (%)	45.2	77.9	50.1
Evaporation ($L m^{-2}$)	8.1	4.5	4.6
Seasonal VPD (kPa)	2.16	0.85	1.42
VPD (kPa) based on average T_{leaf}	3.83	2.03	3.05

cultivars were identified. A set of cultivars, i.e., ICGS 11, Girnar 1, ICGS 44 and ICG 45 for the use during all the seasons and another sets, i.e., TAG 24, GG 2, VRI 2, CGC 4018 and DH 8 for summer, and VRI 3 and Akola Selection for post-rainy seasons. In addition, during both summer and rainy seasons cvs. TAG 24 showed higher P_N and g_s, and lower ΔT, while Girnar 1 showed higher P_N and g_s during post rainy seasons (Table 2).

3.2. Photosynthetic rate during different reproductive growth stages

Photosynthetic rate and associated traits measured during different reproductive growth stages in summer season showed wide genetic variability in their response to meet the extra demand of photosynthates by the developing pods (Fig. 2). Among cultivars average P_N ranged between 11.09 in Jawan and 17.06 $\mu mol\, m^{-2}\, s^{-1}$ in TAG 24, however it was highest (30.3 $\mu mol\, m^{-2}\, s^{-1}$) in TAG 24 during R4 and least (6.2 $\mu mol\, m^{-2}\, s^{-1}$) in ICGS 11 during R8 stages. During different growth stages P_N was higher in TAG 24 being 13.9, 15.7, 19.2, 30.3, 10.1 and 9.9 $\mu mol\, m^{-2}\, s^{-1}$ during R2, R3, R4, R5, R6 and R8 stages, respectively (Fig. 2a). In addition, g_s was also higher (0.69 $mol\, m^{-2}\, s^{-1}$) in cvs. TAG 24 followed by DH 3–30 and TMV 2 during R4 stage (Fig. 2b). Cultivars VRI 3, S 206, DH 8 and Jawan during R4, and TMV 2, Jyoti, and TAG 24 during R5 stages showed negative value for ΔT (Fig. 2c). Thus cv. TAG 24 showed higher P_N during all the growth stages and maintained least ΔT (1.0 °C), this makes it most suitable for cultivation in summer season.

Among reproductive growth stages P_N was higher (17.91 $\mu mol\, m^{-2}\, s^{-1}$) during R4 and R5 (17.17 $\mu mol\, m^{-2}\, s^{-1}$) and lower during R6 (8.70 $\mu mol\, m^{-2}\, s^{-1}$) and R8 (8.32 $\mu mol\, m^{-2}\, s^{-1}$). This indicated a perfect source–sink relationship and regulation of P_N based on reproductive sink demand for extra photosynthates. The g_s also followed similar trend as shown by P_N. The ΔT during R2 (2.17 °C) and R3 (2.07 °C) was higher while it was lower during R4 (0.87 °C) and R5 (1.27 °C) stages. Thus cultivars belonging to high P_N group maintained higher P_N along with higher g_s and
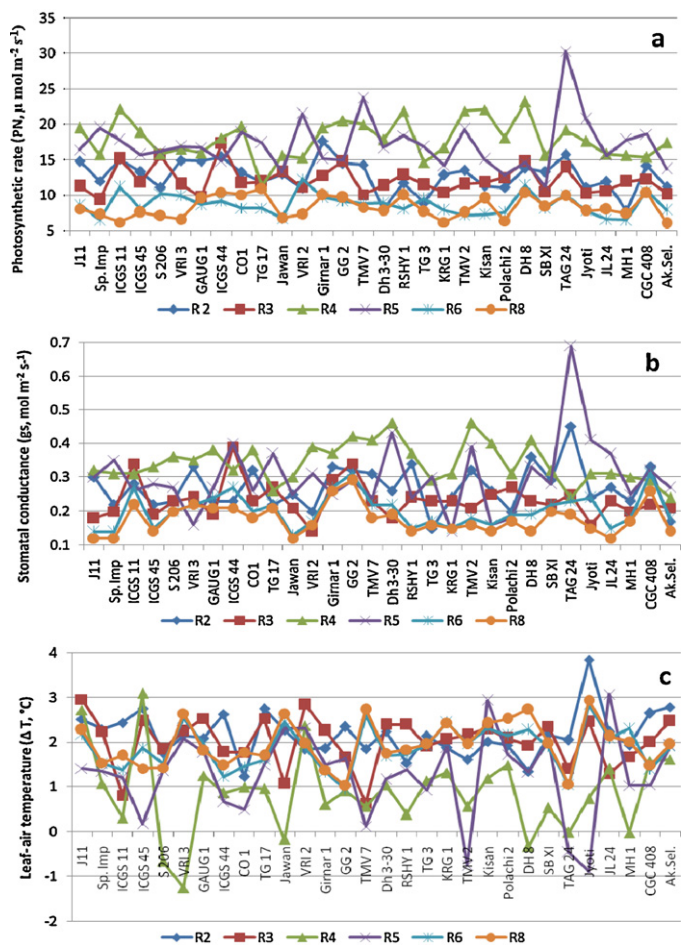
Fig. 2. Photosynthetic rate (a), stomatal conductance (b) and difference between leaf and air temperature in 30 Spanish groundnut cultivars during different reproductive stages, i.e., begnning peg (R2), begnning pod (R3), full pod (R4), begnning seed (R5), full seed (R6) and harvest maturity (R8) (the CD values (P = 0.05) for P_N, g_s and ΔT, at different developmental stages were: R2 = 2.89, 0.03 and 0.47, R3 = 2.54, 0.11 and 1.11, R4 = 3.92, 0.03 and 0.41, R5 = 4.36, 0.05 and 1.11, R6 = 1.96, 0.03 and 0.35, and R8 = 1.67, 0.07 and 0.39, respectively).

lower ΔT during R4 and R5 stages. In general, both P_N and g_s were higher in high followed by medium and low groups. But different groups varied significantly in P_N, g_s and ΔT, for example, in high P_N group two distinct peaks during R4 and R5 were recorded. Similar peaks were recorded by medium and low P_N groups but they were always lower than the high P_N group (Fig. 3a). Whereas, g_s showed two distinct peaks in high P_N group during R4 and R5 and single peak during R4 in low and medium groups (Fig. 3b). On the other hand, ΔT showed two distinct depressions indicating lower leaf temperatures during R4 and R5 in high P_N and a single depression during R4 in medium which decreased gradually from R2 to R8 in low groups (Fig. 3c). Moreover, association between P_N and pod yield was higher during R4 ($r = 0.43^{**}$) than R3 ($r = 0.37^*$) stages. Thus to increase productivity P_N also need to be enhanced during R4 and R5 stages as shown by the cultivars belonging to high P_N group.

3.3. Associations among various traits and yield components

Associations among various leaf morphological and anatomical traits were established, for example, thickness of palisade layer was associated with leaflet width ($r = -0.40^{**}$) and length ($r = -42^{**}$), T_{leaf} ($r = -0.32^*$) and g_s ($r = 0.38^*$). Associations between P_N and thickness of palisade layer and number of xylem rows

Table 2
Photosynthetic rate (P_N), stomatal conductance (g_s) and difference between T_{leaf} and T_{air} ($\Delta T °C$) in 30 Spanish groundnut cultivars during summer, rainy and post rainy seasons.

Cultivars	P_N (μ.mol m^{-2} s^{-1})			g_s (mol m^{-2} s^{-1})			ΔT (°C)		
	Summer	Rainy	Post-rainy	Summer	Rainy	Post-rainy	Summer	Rainy	Post-rainy
J 11	12.98	10.86	11.90	0.24	0.41	0.27	2.04	2.38	2.94
Spanish imp.	12.29	7.96	10.43	0.24	0.38	0.24	1.63	1.93	2.79
ICGS 11	14.20	15.34	14.41	0.35	0.44	0.41	1.33	3.53	0.52
ICG 45	12.80	13.65	12.10	0.23	0.23	0.22	1.88	1.61	2.36
S 206	11.93	11.03	11.04	0.27	0.35	0.27	1.09	2.20	2.82
VRI 3	12.59	8.35	12.80	0.25	0.36	0.30	1.43	2.04	3.05
GAUG 1	12.96	12.75	10.81	0.30	0.76	0.30	1.88	1.10	2.56
ICGS 44	13.59	13.80	12.42	0.28	0.72	0.26	1.51	2.69	2.24
CO 1	13.69	10.90	7.32	0.29	0.33	0.20	1.18	3.49	1.97
TG 17	11.62	12.68	7.97	0.27	0.53	0.28	1.69	2.09	2.85
Jawan	11.06	8.80	8.50	0.20	0.23	0.15	1.77	1.59	2.68
VRI 2	13.97	12.45	10.51	0.27	0.49	0.23	2.05	0.73	2.72
Girnar 1	14.18	13.35	15.76	0.30	0.51	0.32	1.38	0.47	1.54
GG 2	13.15	17.02	11.06	0.32	0.67	0.37	1.39	1.22	1.78
TMV 7	15.10	6.99	10.31	0.31	0.37	0.22	1.53	1.08	1.92
Dh 3-30	11.33	7.59	10.47	0.31	0.18	0.27	1.63	1.56	1.82
RSHY 1	13.84	10.81	11.61	0.27	0.21	0.25	1.32	2.91	1.44
TG 3	11.48	10.20	11.11	0.20	0.21	0.23	1.58	1.48	1.32
KRG 1	11.41	11.08	11.40	0.18	0.32	0.26	1.95	1.40	2.07
TMV 2	13.93	9.72	10.38	0.29	0.20	0.21	1.04	2.26	1.93
Kisan	13.23	10.45	10.18	0.22	0.22	0.17	2.06	2.81	2.27
Polachi 2	11.11	12.95	9.49	0.21	0.49	0.19	1.90	0.96	2.23
DH 8	14.59	13.58	7.21	0.30	0.43	0.13	1.43	0.60	3.34
SBXI	11.40	12.73	8.16	0.26	0.66	0.14	1.71	1.08	1.88
TAG 24	17.10	18.76	10.43	0.37	1.20	0.30	0.64	1.70	1.52
Jyoti	13.21	10.07	9.96	0.25	0.30	0.19	1.69	2.13	2.00
JL 24	11.17	9.32	10.19	0.24	0.37	0.21	2.23	2.10	2.05
MH 1	11.96	12.71	8.50	0.23	0.35	0.18	1.51	1.22	2.08
CGC 4018	13.45	13.69	9.12	0.32	0.41	0.23	1.80	0.77	1.66
Akola selection	10.94	8.01	13.46	0.20	0.61	0.20	2.12	0.16	2.29
Mean	12.88	11.59	10.63	0.27	0.43	0.24	1.61	1.71	2.15
LSD 0.05	1.67	2.70	2.60	0.04	0.03	0.09	0.47	0.21	0.64

were direct, while thickness of epidermis was associated inversely with leaf width, and width of water storage cells, but statistically non-significant. In addition, association between SLA and P_N was inverse, however the strength of the associations varied during different cropping seasons such as strong ($r = -0.47^{**}$) during post-rainy and weak ($r = -0.27$) during summer and none during rainy.

Other associations indicative of the trade-off between various morphological and physiological traits, and yield components were also established. For example, number of branches during different growth stages was associated with pod yield, the most significant being at the vegetative ($r = 0.61^{**}$) and pegging ($r = 0.62^{**}$). While plant height was associated with leaflet length ($r = 0.55^{**}$) and width ($r = 0.51^{**}$), petiole length ($r = 0.41^{**}$), P_N ($r = -0.45^{**}$) and g_s ($r = -0.55^{**}$). Plant height was also associated with total sink number ($r = -0.40^{**}$) and T_{leaf} (0.44^{**}). Similarly, petiole length was associated with leaflet length ($r = 0.54^{**}$) and width ($r = 0.77^{**}$), P_N ($r = -0.44^{**}$) and g_s ($r = -0.33^{*}$). On the other hand, g_s was associated with leaflet length ($r = -0.53^{**}$) and width ($r = -0.68^{**}$). Associations between T_{leaf} and P_N ($r = -0.47^{**}$), g_s ($r = -0.54^{**}$) and leaflet width ($r = 0.30^{*}$) were also established. In addition, P_N was associated with important yield components, i.e., total sink number ($r = 0.43^{**}$), total sink dry weight ($r = 0.44^{**}$), weight of mature pod ($r = 0.45^{**}$) and HI ($r = 0.48^{**}$) however association between HI and g_s ($r = 0.51^{**}$) was positive.

In addition, seasonal variation in pod yield, number of pods (m^{-2}), HI and shelling outturn were quite substantial and associations between number of pods and pod yield ($r = 0.76^{**}$), HI and pod yield ($r = 0.79^{**}$), HI and total biomass ($r = -0.53^{**}$), pod yield and shelling outturn ($r = 0.47^{**}$), HI and 100-seed mass ($r = 0.50^{**}$) were established. Whereas, associations between days to maturity and biomass was weak but positive ($r = 0.14$) while days to maturity and HI was negative ($r = -0.37^{*}$). The association between pod yield

and number of pods (m^{-2}) however varied during three different cropping seasons, such as, stronger in rainy ($r = 0.58^{**}$) than in summer ($r = 0.54^{**}$) and non-significant in post-rainy ($r = 0.23$) seasons. Among the yield and yield components, based on three major associations, three yield determinants were identified. First, the linear relationship between pod yield and number of pods (m^{-2}) varied due to different cropping seasons and accounted for 58, 54 and 23% of their respective total variations in rainy, summer and post-rainy, respectively (data not presented). Second, the association between pod yield and HI was linear and accounted for 62, 45 and 34% of their respective total variation in rainy, summer and post-rainy seasons, respectively. Third, the relationship between pod yield and shelling outturn accounted for 54, 51 and 23% for rainy, summer and post-rainy seasons. Further, these results could be explained on the basis of environmental influence on P_N and sink size, such as, during summer season genetic variations in pod yield and P_N were low as compared to the two other seasons, suggesting that there could be less environmental restriction on supply of photosynthates to the pods that were formed. Hence, it is presumed that groundnut productivity could be enhanced by increasing reproductive sink-size *vis-à-vis* increasing number of pods (m^{-2}), total biomass productivity and efficient partitioning of biomass to increase HI and shelling outturn.

### 3.4. Genotype by environment analysis of the traits

The results of ANOVA presented an overall picture of the relative magnitudes of the G (genotype), E (environment) and G × E interactions on each morphological and physiological traits and yield components, though the level of significance varied (Table 3). From the analysis it was clear that all the source of variation influenced g_s significantly whereas limited number of sources, i.e., G × E and

Table 3
Pooled analysis of variance for different morphological and physiological traits and yield components and genotype by environment interaction (G × E) in 30 Spanish groundnut cultivars.

Source	d.f.	Mean sum of square											
		P_N	g_s	ΔT	Plant height	SLA	Number of immature pods	Number of mature pods	Total sink number	Total sink dry weight	TBM	HI	PY
Genotype	29	6.10**	0.001**	0.317	24.97**	750.2**	1.73	6.28	24.35	18.06	85975.12*	0.010**	1845.78**
Environment	60	4.90**	0.027**	0.523	27.30**	490.8**	1.27	5.89	16.86	53.81**	46039.75**	0.012**	10244.50**
G × E	2	39.25**	0.025**	2.432**	577.78**	4334.7**	5.18**	41.23**	128.06**	1104.22**	104311**	0.238**	269120.91**
Environment + (G × E)	58	3.72**	0.330**	0.457**	8.32**	358.3**	1.14	4.67	13.03	17.59	44030.37	0.005*	1317.72
Environment (linear)	1	78.50**	0.014**	4.865**	1155.56**	8669.4**	10.37**	82.46**	256.12**	2208.45**	208623.71**	0.475**	53241.82**
G × E (linear)	29	2.35**	0.660**	0.292	16.55**	582.5**	0.90	3.52	8.25	19.62	43722.32	0.007**	1910.80*
Pooled deviation	30	4.92**	0.026**	0.601**	0.07	129.5**	1.33**	5.63**	17.22**	15.04**	4860.48	0.002**	700.50
Pooled error	174	0.31	0.002	0.012	0.56	6.3**	0.23	0.15	0.57	0.70	168.43	0.001**	10.31

* Significant at 5% levels.
** Significant at 1% levels.
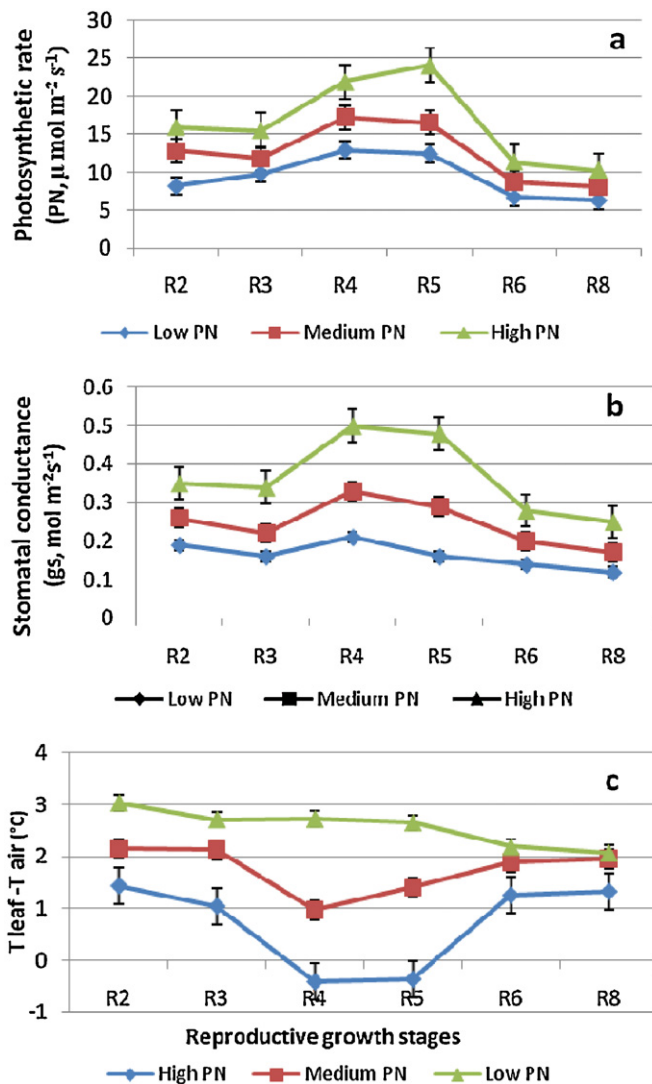

Fig. 3. Photosynthesis (P_N), conductance (g_s) and difference between leaf and air temperature ($T_{leaf} - T_{air}$, ΔT) during different reproductive growth stages in low, medium and high P_N cultivars (values are average of the six growth stages).

environment (linear) influenced P_N and ΔT. Morphological traits such as plant height and SLA influenced significantly due to all sources of variation (Table 3). Among the yield components total sink number including the number of immature and mature pods influenced due to G × E, environment (linear) whereas total sink dry weight influenced due to environment, G × E and environment (linear), and total biomass due to G, E and G × E. Harvest index and pod yield however influenced due to all source of variations (Table 3). This indicated that influence of sources of variation was more on g_s than P_N and ΔT and similarly on total biomass than total reproductive sink dry weight. Thus for all the traits environment was always remain the most important source of variation.

### 3.4.1. Genotype by trait biplots and trait relationship analysis

The genotype-by-trait (GT-biplot) for each of the three different seasons explained, 51.0 (rainy)–58.7% (summer) of the total variation (Fig. 4). The relatively low proportion of variation reflects the complexity of the relationships among the traits (Fig. 4). In the GT-biplot, a vector is drawn from the origin to each of the traits to facilitate the visualization of the relationship between and among traits. Coefficient of correlation (r) between any two traits is approximated by the cosine of the angle between their vectors. The
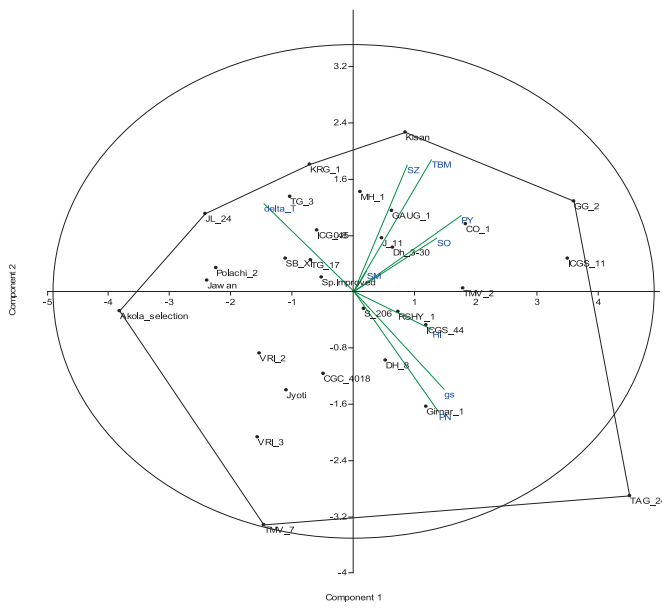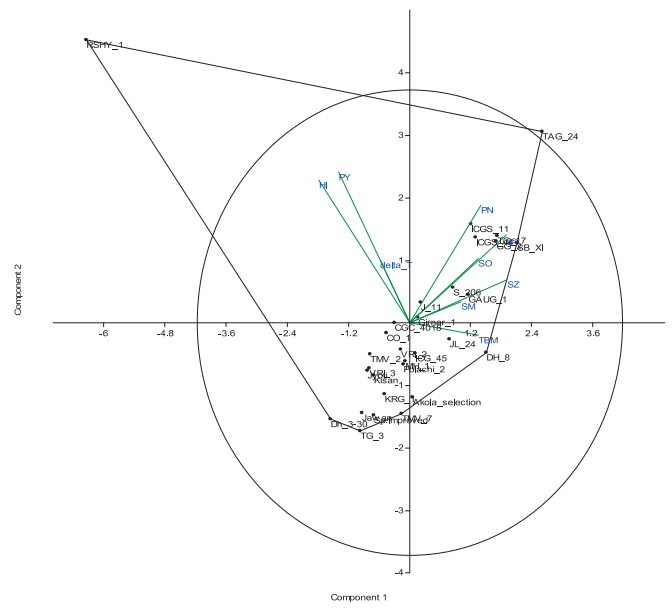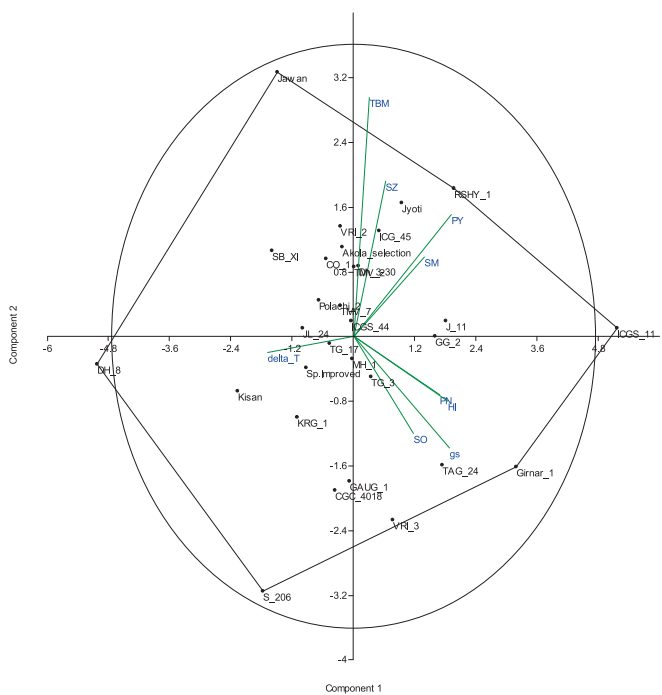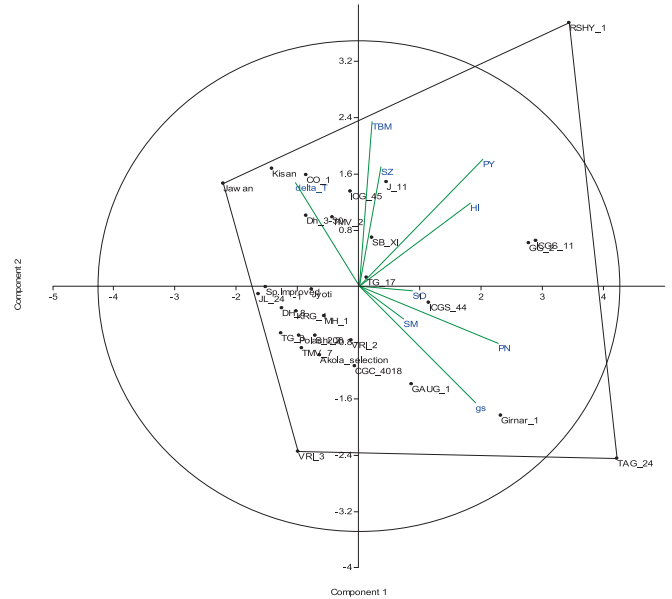
Fig. 4. Vector view of genotype × trait biplot summarising the interrelationship among the traits studied during summer (a), rainy (b), post rainy seasons (c) and over the seasons (d). P_N = photosynthetic rate, g_s = stomatal conductance, ΔT = difference between the leaf and air temperature, SZ = reproductive sink size, TBM = total biomass, PY = pod yield, HI = harvest index, SO = shelling outturn and SM = 100-seed mass.

GT-biplot was used to compare cultivars on the basis of multiple traits and to identify cultivar that possesses desirable traits. Traits with longer vectors explain the larger proportion of the observed variation whereas traits with shorter vectors explain limited variation. Thus GT-biplot was used to study relationship among multiple traits and to identify cultivars that were desirable for a specific season or all the three seasons.

3.4.2. Summer season

The PC 1 and PC 2 scores were used to draw GT-biplot and the proportion of total variation explained by the first three PC axes was 71% (Fig. 4a). PCA loadings revealed the contribution of most of the traits except ΔT and SM (100-seed mass) in explaining the variation. A positive association of pod yield (PY) with reproductive sink size (SZ), total biomass (TBM) and shelling outturn (SO)

has been indicated by an acute angle. In addition, an acute angle between vectors of PY and SO with HI indicated positive association among these traits. Whereas, a right angle between vectors of PY and SO with g_s and P_N indicated a weak association. Further, an obtuse angle between vectors of TBM and SZ with g_s and P_N indicated a negative association between these traits.

The GT-biplot also can be used to discriminate cultivars based on each trait. Thus the best cultivars based on PY and SO were GG 2, Co 1 and ICGS 11, while based on TBM and SZ were Kisan and GUAG 1, and based on P_N and g_s, were Girnar 1 and TAG 24. Contribution of each trait was accessed by its correlation with different seasons and during summer highest contribution was shown by PY (0.83) followed by g_s (0.73) and ΔT (−0.70) (data not presented). This indicated that if g_s is increased, it may help in maintaining the leaf temperature which may result in higher P_N and PY. Contribution of 100-seed mass (SM) trait seems to be negligible in increasing groundnut productivity due to very high environmental influence.

3.4.3. Rainy season

The GT-biplot of first four PCs with eigen values more than one explained 78.5% variation observed (Fig. 4b). Among the traits, SZ and g_s explained maximum variation in cultivars followed by P_N, SO and TBM. An obtuse angle between the vectors of traits such as PY, HI and ΔT with TBM indicated negative association among them. This further indicates that by decreasing the ΔT, total biomass production could be increased. An acute angle observed between PY and HI, and between P_N, g_s, SO, SZ and SM indicated positive associations among these traits. The cvs. ICGS 11, ICGS 44, GG 2, TG 17, SB X1 and TAG 24 were found superior for P_N, g_s, SZ, SM and SO. However none of the traits were found superior for pod yield and harvest index during rainy season. Thus, selecting groundnut cultivars for a rain dependent system based on pod yield and HI should be time tested.

3.4.4. Post-rainy season

The first three PCs explained 67.2% of the variation among the cultivars (Fig. 4c). The PCA loading for PC 1 indicated that traits such as g_s, PY, HI, P_N, SM and SO explained maximum variation. Based on GT-biplot, it was observed that the traits SZ, TBM, SO had positive association with PY as indicated by acute angle between them. Vectors of the traits, PY and SM were perpendicular to those of P_N, HI, SO and g_s which indicated very weak associations among them. The trait ΔT showed an obtuse angle with all the remaining traits thus indicating a negative association. The cultivars Jyoti and RSHY 1 were superior for PY, SM and SZ while TAG 24 and Girnar1 for P_N, SO, g_s and HI and DH 8 for ΔT.

3.4.5. Over the seasons

The first three PCs explained 67.4% variation in cultivars while more than 30% variation could not be explained by the traits studied (Fig. 4d). The PCA loadings for PC 1 indicated that the traits such as P_N, g_s, PY and HI explained maximum variation in cultivars as also indicated by the length of vectors in GT-biplot. The GT-biplot of first two PCs explained 58.6% variation. A positive association between traits PY, HI and TBM and between P_N, g_s, SO and SM were also evident from the biplot. The cultivars Girnar 1and TAG 24 were found superior for P_N, GAUG 1 for SO and SM, and Jawan, Kisan and Spanish improved for ΔT.

4. Discussion

In this communication, we have demonstrated the trade-offs between P_N and several morphological, anatomical and physiological traits, and yield components in 30 Spanish groundnut cultivars grown under three different environments. After analyzing the cultivars for genotype by environment and genotype by trait interactions, potential cultivars were identified and suggested for the use in improving groundnut productivity. Thus large pool of variability and understanding developed on potential trade-offs between various traits could be of immense value in developing new germplasm and designing ideotype for making the cultivars more adaptive for a crop specific season or over the seasons. Understanding the genetics of these traits, using agronomically relevant germplasm, will further provide new opportunity for sustainable and productive groundnut production.

Further, response of physiological traits indicated variation in genetic potential in P_N, g_s and ΔT and cultivars were divided into low, medium and high P_N groups. This exercise finally leads us to conclude that photosynthetic efficiency could be enhanced through enhanced g_s and this was corroborated by the following facts. Such as, the varying level of significance of associations between P_N and ΔT during different cropping seasons indicated that crop yield is usually limited due to lower photosynthetic efficiency. Existence of strong association between P_N and ΔT in cultivars belonging to higher P_N during pod fill (R4) and beginning seed (R5) stages further strengthens this hypothesis. In addition, a negative association between ΔT and yield even in the absence of water deficit stress suggests that if ΔT is maintained by increased g_s, this may lead to higher P_N. It is presumed that ΔT may derive from change in the balance between leaf g_s and photosynthetic capacity, assuming that if the intrinsic photosynthetic capacity of leaves is increased, ΔT could decrease and water use efficiency could increase, without compromising yield potential. It is also suggested that the donor parent for higher photosynthetic efficiency, identified in this study, could be valuable materials for the use in breeding programmes aimed at improving groundnut. Selection for higher P_N in segregating population and advanced breeding materials however could be performed by measuring the ΔT. Moreover, associations of ΔT with P_N and total sink size provide a strong base for selection for higher photosynthetic efficiency. Since, groundnut is cultivated under different climatic conditions such as irrigated and rain-dependent, it is imperative to identify the desirable traits for each cropping situation. One opportunity seems to alter SLA in the fashion that exploiting lower SLA for its drought tolerant characteristics and higher SLA for pre-anthesis biomass production. There are several reports that groundnut genotypes differ significantly in their ability to withstand drought, and lower SLA is considered an important trait to increase water use efficiency or drought tolerance (Nautiyal et al., 2002b; Nautiyal, 2009). Also in this study, leaf thickness was positively associated with thickness of palisade layer and P_N. In addition, direct association between ΔT and SLA ($r = 0.46^{**}$) indicates that lower SLA genotype may possess higher photosynthetic efficiency and thus maintain lower ΔT. On the other hand, higher SLA could be exploited for their characteristics to provide higher preanthesis leaf area index and biomass production. Because in short duration crop leaf area (or leaf area index) determining canopy size during vegetative state has a major role in productivity. In this study, cultivars JL 24 expressed higher SLA while ICGS 11 and ICGS 44 lower, thus JL 24 may serve a donor parent to provide higher pre-anthesis leaf area index and total biomass under irrigated, while ICGS 11 and ICGS 44 could be better source for increasing drought tolerance under rain-dependent conditions (data not shown). An ideotype plant having the capacity to maintain higher pre-anthesis SLA and thus higher biomass production, and at the same time having the capacity to maintain lower post-anthesis SLA may be designed for the use under both irrigated and rain-dependent conditions. In addition, efforts are needed to develop potential cultivars for post rainy season by induction of cold tolerance during pod development phase. This study clearly showed that groundnut photosynthesis and reproductive processes are susceptible for lower temperature. Susceptibility of groundnut seed germination and field emergence under lower temperature was

reported by Joshi et al. (1996). Also, in the literature narrow genetic differences for cold tolerance are reported, except that in case of wild *Arachis* species (Nautiyal et al., 2008). Under this investigation also, only Girnar 1 showed slightly higher tolerance for cold as compared to other cultivars.

Results of this study further suggests that strategy need to develop new promising germplasm and designing ideotype based on the requirements of target environment. Based on the trade-offs between various traits as recorded in this study promising options could be overall reduction in plant height, petiole length, leaflets length and widths and specific leaf area, and increase in the number of branches and reproductive sink size. This might lead to compact crop canopy architecture and may alter the photosynthetic potential. Moreover, this alteration will make plant suitable for cultivation under water scarcity environment. Alteration in leaf functional anatomy, i.e., increasing the leaf hydraulic conductance by increasing the size of water storage cells, the most salient feature of groundnut leaf, and number of xylem rows and size of xylem cells seems to be used in enhancing groundnut productivity. Such alterations were considered beneficial to improve productivity of crop species and to get more production from less water (Boote et al., 2001; Zhu et al., 2010). In most of the crops including groundnut increase in yield, so far, is mainly because of increased HI and further increase in HI without improving total biomass production could be a nonviable option. This also warrants increasing productivity through increased photosynthetic efficiency and total biomass production. Genotype by environment and genotype by trait interaction suggests that influence of environment on each trait is the most important source of variation. Thus potential donor source identified, in this study, provide new opportunity for increasing production. Such as cultivars TAG 24 showed highest adaptability under irrigated conditions during summer, ICGS 11 during rain-dependent and Girnar 1during post-rainy seasons. Similarly, potential cultivars with desirable traits were also identified, i.e., cultivars Kisan with higher reproductive sink size and total biomass production, TAG 24 and ICGS 44 with higher HI and GG 2 with higher pod yield (a local cultivar), RSHY 1 with higher pod yield and HI, DH 8 and JL 24 with higher total biomass, and ICGS 11 and ICGS 44 with higher P_N and g_s. In addition, TAG 24 possesses many desirable traits including higher photosynthetic efficiency and HI but needs to be improved for total biomass production leading to a sustainable increase in pod yield.

Since, all the cultivars used in this study belong to Spanish type, which possess relatively shorter crop duration and seems to be closer to the determinate type of crop plants. Response of cultivars in physiological traits and source sink relationship also indicated their proximity to the determinate type of crop such as wheat (Morgan et al., 1993; Reynolds et al., 2001). Thus implication of these findings could be restricted to the Spanish type, only. On the other hand, Virginia type which possesses longer crop duration and lesser canopy height than the Spanish type, need to be investigated and combining the desirable traits from the Spanish and Virginia types may lead to widen the genetic base. In such a manner that the benefits of shorter and longer crop duration and crop canopy architecture may be utilized to its fullest potential based on the need of a cropping situation. Moreover, enhancement in groundnut productivity in future will rely much on enhancing photosynthetic efficiency by developing new productive germplasm and combining the desirable traits in a pyramid fashion using the broad genetic base. This will make the understanding of physiology relevant to the crop improvement. Nevertheless, there are still major gaps in our understanding of how crops adapt to the varying environmental conditions and still need further research on understanding groundnut physiology for the effective application of new techniques in breeding such as genetic transformation, functional genomics, and marker assisted selection.

References

Bhagsari, A.S., Brown, R.H., 1976. Photosynthesis in peanut genotypes. Peanut Sci. 3, 1–5.

Boote, K.J., 1982. Growth stages of peanut. Peanut Sci. 9, 35–40.

Boote, K.J., Kropff, M.J., Bindraban, P.S., 2001. Physiology and modeling of traits in crop plants: implications for genetic improvement. Agri. Syst. 70, 395–420.

Collino, D.J., Dardanelli, J.L., Sereno, R., Racca, R.W., 2001. Physiological response of argentine peanut varieties to water stress. Light interception, radiation use efficiency and partitioning of assimilate. Field Crops Res. 70, 177–184.

Davis, J.C., 1986. Statistics and data analysis in geology. John Wiley and Sons.

Duncan, W.G., Mc-Cloud, R.L., MCGrow, Boote, K.J., 1978. Physiological Aspects of Peanut Yield and Technology. American Peanut Res. Edu. Soc., Yaokum, TX, USA.

DES, 2011. Directorate of Economics and Statistics. Department of Agriculture and Cooperation, Govt. Ind., http://dacnet.nic.in.

FAO, 2000. www//http: fao.org/Agri/statistic.

Ferreyra, R.A., Pachepsky, L.P., Collino, D., Acock, B., 2000. Modelling peanut leaf gas exchange for the calibration of crop models for different cultivars. Ecolgil. Modell. 131, 285–298.

Ghosh, P.K., Bandyopadhyay, A., Nautiyal, P.C., Mathur, R.K., 2001. Technologies for rabi and summer groundnut cultivation. Technol. Bull. Published by NRCG, Junagadh (ICAR), 1–30.

Gomez, K.A., Gomez, A.A., 1984. Statistical Procedures for Agriculture Research. Wiley, New York.

Jackson, D.A., 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology 74, 2204–2214.

Joshi, Y.C., Nautiyal, P.C., Ravindra, V., 1996. Screening for cold tolerance and osmo-conditioning to enhance germination of groundnut in suboptimal temperatures. Trop. Sci. 36, 224–228.

Kaiser, H.F., 1960. The application of electronic computers to factor analysis. Educ. Psychol. Meas. 20, 141–151.

Leakey, A.D.B., Elizabeth, A.A., Bernacchi, C.J., Rogers, A., Long, S.P., Donald, R.O., 2009. Elevated CO_2 effects on plant carbon, nitrogen, and water relations: six important lesions from FACE. J. Expt. Bot. 60, 2859–2876.

Mauney, J.R., Fry, K.E., Guinn, G., 1978. Relationship of photosynthetic rate to growth and fruiting of cotton, soyabean, sorghum and sunflower. Crop Sci. 18, 259–263.

Morgan, J.A., Le Cain, D.R., McCaig, T.N., Quick, J.S., 1993. Gas exchange, carbon isotope discrimination and productivity in winter wheat. Crop Sci. 33, 178–186.

Nautiyal, P.C., Ravindra, V., Joshi, Y.C., 1995. Gas exchange and leaf water relations in two peanut cultivars of different drought tolerance. Biol. Plant. 7, 371–374.

Nautiyal, P.C., Ravindra, V., Joshi, Y.C., 1999a. Net photosynthetic rate in peanut (*Arachis hypogaea* L.): influence of leaf position, time of day, and reproductive sink. Photosynthetica 36, 129–138.

Nautiyal, P.C., Ravindra, V., Zala, P.V., Joshi, Y.C., 1999b. Enhancement of yield in groundnut following the imposition of transient soil-moisture-deficit stress during the vegetative phase. Expt. Agri. 35, 371–385.

Nautiyal, P.C., Ravindra, V., Joshi, Y.C., 2002a. Dry matter partitioning and water use efficiency under water-deficit during various growth stages in groundnut. Ind. J. Plant Physiol. 7, 135–139.

Nautiyal, P.C., Rachaputi, Nageswara Rao, Joshi, Y.C., 2002b. Mosisture-deficit-induced changes in leaf-water content, leaf carbon exchange rate and biomass production in groundnut cultivars differing in specific leaf area. Field Crops Res. 74, 67–79.

Nautiyal, P.C., Rajgopal, K., Zala, P.V., Dipti, S. Pujari, Basu, Manojit, Dhadhal, Bhuwaneshwariba, Bharat, M. Nandre, 2008. Evaluation of Wild *Arachis* species for abiotic stress tolerance: I. Thermal stress and leaf water relations. Euphytica 159, 43–57.

Nautiyal, P.C., 2009. Seed and seedling vigour traits in groundnut (*Arachis hypogaea* L.). Seed Sci. Technol. 37, 721–735.

Nigam, S.N., Nageswara Rao, R.C., Wynne, J.C., 1998. Effect of temperature and photoperiod on vegetative and reproductive growth of groundnut (*Arachis hypogaea* L.). J. Agro. Crop Sci. 181, 117–124.

Niinemets, U., 2007. Photosynthesis and source distribution through plant canopies. Plant Cell Environ. 30, 1052–1071.

Reynolds, M.P., Delgado, B.M.I., Gutierrez-Rodrguez, M., Larque-Saavedra, A., 2000. Photosynthesis of wheat in a warm, irrigated environment: genetic diversity and crop productivity. Field Crop Res. 66, 37–50.

Reynolds, M.P., Ortiz-Monasterio, J.I., McNab, A., 2001. Application of Physiology in Wheat Breeding. CIMMYT, Maxico, DF.

Takai, T., Yano, M., Yamamoto, T., 2010. Canopy temperature on clear and cloudy day could be used to estimate varietal differences in stomatal conductance in rice. Field Crop Res. 115, 165–170.

Zhu, Xin-Guang, Long Stephen, P., Ort Donald, R., 2010. Improving photosynthetic efficiency for greater yield. Ann. Rev. Plant Biol. 61, 235–261.