Combining Ability of Response to Photoperiod in Peanut

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ABSTRACT

Photoperiod insensitivity plays an important role in the adaptation of peanut (*Arachis hypogaea* L.) genotypes across environments. However, little is known of its genetic control. The objective of this study was to determine the combining ability of response to photoperiod in peanut. The F_1 progenies from a six-parent diallel cross excluding reciprocals were studied together with their parents for response to photoperiod under short and long day conditions in the field for three seasons. The experiment was conducted in a split plot design with photoperiod as main plots and genotype as subplots. The response to photoperiod (D_{SL}) was computed as the difference in harvest index (adjusted pod weight/adjusted biomass) between short and long day treatments. The mean square for response to photoperiod was highly significant for parents and their crosses. Season by cross interaction was the only significant interaction effect. The response to photoperiod was mainly associated with general combining ability variance. ICG 2405 and ICGV 86031 were good general combiners for insensitivity to photoperiod. All crosses of sensitive × sensitive and sensitive × insensitive parents were sensitive to photoperiod. However, in several cases, this response was not consistent across seasons and resulted in a significant season × cross interaction. The F_1 between insensitive parents was insensitive to photoperiod in the three seasons tested. A comparison of F_1 response with parents and midparent value of crosses between photoperiod sensitive and insensitive parents suggested additive gene action in some crosses and partial dominance to dominance in others.

Crop improvement programs in International Agricultural Research Centers distribute their improved germplasm worldwide. Very often, this germplasm is selected in relatively few test environments. How this material will perform outside of those environments remains a dilemma to breeders until the materials are actually tested. Among other factors, insensitivity to photoperiod plays a significant role in ensuring wide adaptability of these genotypes.

Photoperiod has little influence on time to flowering in peanut but affects its reproductive development in many ways by influencing the processes that occur mainly after flowering. Plants grown under short days (SD), in spite of fewer flowers per plant than under long days (LD), produce more pods (Wynne et al., 1973; Wynne and Emery, 1974; Ketring, 1979) due to increased reproductive efficiency and rate of development (Emery et al., 1981; Emery, 1983). Traits affected by photoperiod include number of pegs, peg growth, number of pods, pod weight, and seed weight. These traits and their rates of development are altered by greater partitioning and/or increased duration of effective pod filling phase under SD (Ketring, 1979; Witzenberger et al., 1988; Nigam et al., 1994). Temperature has a significant influence on this photoperiodic response (Bell et al., 1991; Nigam et al., 1994).

Although genotypic variation in response to photoperiod exists in peanut (Wynne and Emery, 1974; Emery, 1983; Witzenberger et al., 1985, 1988; Bagnall and King, 1991a,b; Bell et al., 1991; Nigam et al., 1994), little is known of its genetic control. In a study on photoperiod response of three peanut lines representing Valencia, Virginia, and Spanish types and their three F_1 hybrids with reciprocals, Wynne and Emery (1974) observed that lines and hybrids produced more and heavier fruits under SD (9 h of light period) than under LD (9 h of light period plus a 3-h interruption of dark period). All hybrids, in general, showed greater heterotic response for fruit number and fruit weight under SD than under LD. In another study, Emery (1983) observed greater reduction in reproductive efficiency in a Spanish (C_2, PI 262000) and relatively less in a Virginia (NC 4) genotype in 12-h (LD) than in 9-h (SD) light treatment. His study also revealed that F_1 plants from the cross C_2 × NC 4 had approximately the same plant weights as NC 4 but significantly greater reproductive efficiency than NC 4 when grown in SD conditions.

In field screening of peanut genotypes at International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Asia Center (IAC), Patancheru, India, the response to photoperiod is determined by the change in harvest index (HI) of a genotype grown under both SD and LD conditions (ICRISAT, 1989, p. 115–116). The genotypes that show a statistically significant decrease in HI from SD to LD condition are considered sensitive to photoperiod. Following this criterion, several germplasm lines have been characterized for their response to photoperiod. The objective of this study was to determine the combining ability of response to photoperiod in F_1 progenies from a six-parent diallel cross (excluding reciprocals) grown under SD and LD conditions for three seasons.

MATERIALS AND METHODS

Four photoperiod sensitive [ICGVs 86364, 86020, and 86694 and ICG 1697 (NC Ac 17090, PI 433525)] and two photoperiod insensitive genotypes [ICGV 86031 (PI 561917) and ICG 2405 (NC Ac 2821, Holland Virginia Jumbo)] were selected for the combining ability study. ICGVs 86364, 86694, and ICG 2405 belong to the subsp. *hypogaea* var *hypogaea*, ICGVs 86031 and 86020 to the subsp *fastigiata* var *vulgaris*, and ICG 1697 to the subsp. *fastigiata* var *peruviana*. ICG 1697 and ICG 2405 are germplasm lines, and the remaining genotypes are elite breeding lines developed at IAC. The genotypes were crossed prior to each season in a half diallel mating design to produce

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Abbreviations: SD, short days; LD, long days; HI, harvest index; HI_S, harvest index under short day; HI_L, harvest index under long day; GCA, general combining ability.

15 nonreciprocal F_1 hybrids. Six parents and 15 F_1 were evaluated in the Alfisol (clayey-skeletal, mixed, isohypertheric family of Udic Rhodustalfs) fields under SD and LD conditions at IAC, Patancheru, India (18°N, 78°E) for three seasons (E 1 = rainy season 1990; E 2 = post-rainy season 1990–1991; E 3 = rainy season 1991).

The experiment was conducted in a three-replicate split plot randomized complete-block design with photoperiod as main plots and genotype as subplots. The plot size was one row 4 m long with inter- and intra-row spacing of 0.60 and 0.15 m, respectively. The crop received 60 kg ha^{-1} P_2O_5 as a basal dose, and 400 kg ha^{-1} gypsum at peak flowering. In addition to 661.0 and 716.0 mm rainfall in E 1 and E 3 seasons, the crop received four supplemental irrigations in the former and five supplemental irrigations in the latter (50 mm each irrigation). In the E 2, where the rainfall was only 87.5 mm, the crop received 16 irrigations (50 mm each irrigation). During E 1, E 2, and E 3 seasons, the crop was protected against rust (*Puccinia arachidis* Speg.), late leafspot (*Phaeoisariopsis personata* Berk. & Curtis), thrips (*Thrips palmi* Karny), jassids or leafhoppers (*Empoasca Kerry* Pruthi), and leafminer (*Aproaerema modicella* Deventer). The foliar diseases were controlled by applying chlorothalonil (tetrachloroisophthalonitrile) at the rate of 1.8 L ha^{-1} and the insect pests by applying dimethoate [*O*,*O*-dimethyl *S*-(*N*-methylcarbamoylmethyl) phosphorodithioate] and monocrotophos (dimethyl phosphate of 3-hydroxy-*N*-methyl-cis-crotonamide) alternately at the rate of 1 L ha^{-1}. The fungicide and insecticide sprayings in E 1 were 3 and 4, in E 2, 1 and 6, and in E 3, 4 and 5, respectively.

The two photoperiod treatments were SD (13.2 and 12.1 h during the rainy and post-rainy seasons, respectively) and LD (17.2 and 16.1 h during the rainy and post-rainy seasons, respectively). The normal daylight period was considered as SD. The LD conditions were established by extending the normal day length by 4 h in the evening soon after the natural light intensity fell to around 0.16 W m^{-2}. The day length was extended using 100 W incandescent lamps, suspended 0.75 m above the crop in a 3 by 3 m grid pattern. In spite of spatial variation, light intensity was above the minimum required to induce photoperiod response in peanut. No temperature differences due to lighting were detected at the crop canopy level between the SD and LD plots. A light gradient experiment at ICRISAT had shown that LD effects usually are restricted to a distance of ≈6 m from the light source (V.M. Ramraj, 1988, unpublished data). In this study, the SD and LD plots were separated by a distance of 12 m in all directions. The nonexperimental area between the plots was planted with peanut. The LD treatment was started soon after seedling emergence and continued until harvest.

Individual plants in each plot (except for suspected selfed plants in F_1) were hand harvested. All pods (including immatures) were detached from the plant and bulked together with pods recovered from the soil. Pods and the remaining plant were oven dried separately at 70°C until a constant weight was achieved for each. The dried pod and vegetative (remaining plant) weights (grams) were used in final calculations. Pod weight was multiplied by a correction factor of 1.67 (Duncan et al., 1978) to adjust for the differences in energy requirement for producing vegetative vs. pod dry matter. Harvest index (HI) was computed as

$$\mathrm{HI} = P/B$$

where P, adjusted pod weight, = 1.67 × pod weight, B, adjusted biomass weight, = P + vegetative weight.

Response to photoperiod, D_{SL}, for each genotype in each replicate in each season was derived as

Table 1. Analysis of variance for response to photoperiod (D_{SL}) of 6 × 6 diallel cross nonreciprocal F_1 progenies and their parents in peanut.

Source	d.f.†	Mean square
Season (S)	2	0.072
Residual (Rep/season)	6	0.024
Parent (P)	5	0.067**
Cross (C)	14	0.017**
P vs. C	1	0.005
S × P	10	0.006
S × C	28	0.012**
S × (P vs. C)	2	0.014
Error	120	0.005

** F value is significant at $P \leq 0.01$.
† d.f. = degrees of freedom.

$$D_{SL} = \mathrm{HI}_S - \mathrm{HI}_L \qquad [1]$$

where HI_S = average of HI values under SD treatment, HI_L = average of HI values under LD treatment.

The observed D_{SL} values, representing response to photoperiod, were used to evaluate the combining ability of response to photoperiod. The D_{SL} values were analyzed in randomized complete-block design separately for each season. Bartlett's test indicated that error variances across seasons were homogeneous. An unweighted pooled analysis of variance of D_{SL} data across seasons was performed to assess the statistical significance of differences in response arising from seasons, parents, crosses, parents vs. crosses, and their interactions. Combining ability analysis of diallel crosses for D_{SL} data across seasons was conducted as per Method 2 Model 1 of Singh (1973). Season effects were assumed to be random and the genotypic effects to be fixed.

RESULTS AND DISCUSSION

Variation in D_{SL} due to parents and crosses and the season × cross interaction effect was highly significant (Table 1). The season and general combining ability (GCA) effects were also highly significant (Table 2). In pooled analysis, GCA × season interaction was significant but its mean square value was low (Table 2). When data were analyzed separately for each season, GCA effects were highly significant in E 1 and E 2 and nonsignificant in E 3. Response to photoperiod in this study was mainly controlled by variance associated with GCA. The inheritance of photoperiod sensitivity in peanut is not reported in detail in the literature. Emery (1983), based on the results of F_1 hybrids between C_2 and NC 4 genotypes under SD, suggested additive gene action with no maternal effects for photoperiod response in peanut. However, in other crops, which have different mechanisms of reaction to photoperiod, both quantita-

Table 2. Analysis of variance of general combining ability (GCA) and specific combining ability (SCA) for response to photoperiod (D_{SL}) of 6 × 6 diallel cross nonreciprocal F_1 progenies in peanut.

Source	d.f.†	Mean square
GCA	5	0.031**
SCA	15	0.002
Season	2	0.024**
GCA × Season	10	0.004*
SCA × Season	30	0.003
Error	120	0.002

*,** F value is significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.
† d.f. = degrees of freedom.

Table 3. Mean performance and general combining ability (GCA) effect for response to photoperiod (D_{SL}) of parents of a 6 × 6 diallel cross nonreciprocal F_1 progenies in peanut.

Parent	Mean†			
	HI_S	HI_L	Mean D_{SL}	GCA effect
ICGV 86364	0.499	0.274	0.226*	0.034**
ICGV 86694	0.412	0.224	0.188*	0.018*
ICGV 86031	0.481	0.464	0.017	−0.051**
ICGV 86020	0.490	0.309	0.181*	0.029**
ICG 2405	0.553	0.498	0.055	−0.039**
ICG 1697	0.422	0.221	0.201*	0.009
Mean	0.476	0.332	–	–
SEm			0.024	–
SE (g_i)		–		0.008
SE (g_i−g_j)		–		0.012

*,** Significant at $P \leq 0.05$ and ≤ 0.01, respectively.

† HI_S and HI_L = harvest index under short and long day conditions, respectively.

tive inheritance, as in maize (*Zea mays* L.; Russell and Stuber, 1983) and barley (*Hordeum vulgare* L.; Barham and Rasmusson, 1981), and qualitative inheritance, as in soybean [*Glycine max* (L.) Merr.; Saindon et al., 1989], mungbean [*Vigna radiata* (L.) Wilczek; Swindell and Poehlman, 1978], Andean and Mesoamerican common bean (*Phaseolus vulgaris* L.; Kornegay et al., 1993), rice (*Oryza sativa* L.; Li, 1970), and wheat (*Triticum aestivum* L. emend. Thell.; Keim et al., 1973) were reported.

The mean photoperiodic response and breeding potential of the parents were compared by D_{SL} means per se and GCA effects (Table 3). Parents with nonsignificant D_{SL} and significant negative GCA effects were considered good general combiners for photoperiod insensitivity. As might be expected, both photoperiod insensitive parents, ICGV 86031 and ICG 2405, were found to be good general combiners for photoperiod insensitivity. However, ICGV 86031 should also make a good parental choice for a spanish type in a breeding program because of its multiple resistance and/or tolerance to insect pests such as thrips, jassids, leafminer, and tobacco caterpillar (*Spodoptera litura* Fabricius), peanut bud necrosis virus, and iron chlorosis (Dwivedi et al., 1993). Of the four photoperiod sensitive parents, ICGV 86364 is resistant to thrips and jassids and the other three, ICGVs 86694, and 86020, and ICG 1697, are resistant to rust and late leafspot. Other pest- and foliar-disease-resistant genotypes screened have likewise shown, in general, greater sensitivity to photoperiod (ICRISAT, 1989, p. 115–116). This has significant bearing on pest–disease resistance breeding where wide adaptability of genotypes is also sought.

Table 4. Photoperiod response (D_{SL}) of the parents and their nonreciprocal F_1 in peanut.

Parent/Cross	D_{SL}†			
	E 1	E 2	E 3	Pooled
Parent				
ICGV 86364	0.178*	0.278*	0.221*	0.226*
ICGV 86694	0.193*	0.229*	0.144*	0.188*
ICGV 86031	−0.026	0.038	0.038	0.017
ICGV 86020	0.181*	0.209*	0.152*	0.181*
ICG 2405	0.062	0.069	0.035	0.055
ICG 1697	0.090	0.253	0.260*	0.201*
Sensitive × sensitive				
ICGV 86364/ICGV 86694	0.197*	0.292*	0.170*	0.220*
ICGV 86364/ICGV 86020	0.160*	0.303*	0.183*	0.215*
ICGV 86364/ICG 1697	0.186*	0.235*	0.016	0.146*
ICGV 86694/ICGV 86020	0.223*	0.282*	0.167*	0.224*
ICGV 86694/ICG 1697	0.123*	0.254*	0.072	0.150*
ICGV 86020/ICG 1697	0.212*	0.194*	0.101	0.169*
Sensitive × insensitive				
ICGV 86364/ICGV 86031	0.105	0.198*	0.162*	0.155*
ICGV 86364/ICG 2405	0.194*	0.243*	0.028	0.155*
ICGV 86694/ICGV 86031	0.100	0.137*	0.065	0.101*
ICGV 86694/ICG 2405	0.069	0.233*	0.130	0.144*
ICGV 86020/ICGV 86031	0.139*	0.160*	0.200*	0.166*
ICGV 86020/ICG 2405	0.140*	0.178*	0.177*	0.165*
ICG 1697/ICGV 86031	0.210*	0.126*	0.116	0.151*
ICG 1697/ICG 2405	0.175*	0.143*	0.058	0.125**
Insensitive × insensitive				
ICGV 86031/ICG 2405	0.093	0.052	0.130	0.057
SE	0.042	0.034	0.046	0.024

* Significant at $P \leq 0.05$.

† E 1, E 2, E 3 = 1990 rainy season, 1990–1991 post-rainy season, and 1991 rainy season, respectively.

The photoperiod sensitive and insensitive parents selected for this study (based on earlier screening) maintained their respective photoperiod responses in this study as well (Table 4). Mean D_{SL} values of 14 F_1 be-

Table 5. Average photoperiod response (D_{SL}) of the parents, F_1, midparental values (MP), and deviation of F_1 mean from P_1, P_2, and MP values in peanut.

Cross	F_1	P_1	F_1 vs. P_1	P_2	F_1 vs. P_2	MP	F_1 vs. MP	Apparent gene action
Sensitive × sensitive								
ICGV 86364/ICGV 86694	0.220*	0.226	ns	0.188	ns	0.207	ns	
ICGV 86364/ICGV 86020	0.215*	0.226	ns	0.181	ns	0.204	ns	
ICGV 86364/ICG 1697	0.146*	0.226	*	0.201	ns	0.214	*	
ICGV 86694/ICGV 86020	0.224*	0.188	ns	0.181	ns	0.185	ns	
ICGV 86694/ICG 1697	0.150*	0.188	ns	0.201	ns	0.195	ns	
ICGV 86020/ICG 1697	0.169*	0.181	ns	0.201	ns	0.191	ns	
Sensitive × insensitive								
ICGV 86364/ICGV 86031	0.155*	0.226	*	0.017	**	0.122	ns	Additive
ICGV 86364/ICG 2405	0.155*	0.226	*	0.055	**	0.141	ns	Additive
ICGV 86694/ICGV 86031	0.101*	0.188	*	0.017	*	0.103	ns	Additive
ICGV 86694/ICG 2405	0.144*	0.188	ns	0.055	*	0.122	ns	Partial dominant
ICGV 86020/ICGV 86031	0.166*	0.181	ns	0.017	**	0.099	*	Dominant
ICGV 86020/ICG 2405	0.165*	0.181	ns	0.055	**	0.118	ns	Partial dominant
ICG 1697/ICGV 86031	0.151*	0.201	ns	0.017	**	0.109	ns	Partial dominant
ICG 1697/ICG 2405	0.125*	0.201	*	0.055	*	0.128	ns	Additive
Insensitive × insensitive								
ICGV 86031/ICG 2405	0.057	0.017	ns	0.055	ns	0.036	ns	
SE of comparison with F_1		0.024		0.024		0.029		

*,** Values are significant at $P \leq 0.05$ and $P \leq 0.01$ levels, respectively.

tween sensitive × sensitive and sensitive × insensitive parents were significantly greater than zero across seasons. These F_1 were, therefore, sensitive to photoperiod. However, they responded differentially to changes in daylength among seasons. While all 14 F_1 in E 2 (post-rainy season, 12.1 h SD and 16.1 h LD) were sensitive, only 11 in E 1 and 6 in E 3 (both rainy season, 13.2 h SD and 17.2 h LD) were sensitive to photoperiod. The seasons not only differed for photoperiod but also for temperature. Temperature can influence the photoperiodic response in peanut (Bell et al., 1991; Nigam et al., 1994). In the rainy seasons (E 1 and E 3) during the crop growth period, the minimum and maximum temperature ranged from 19.7 to 32.4°C and in the post-rainy season from 14.8 to 37.8°C. The rainy season starts with a high temperature and ends with a low temperature. The reverse is true for the post-rainy season. A temperature of 35°C during the light period (dark period temperature of 22°C held constant) is reported to have an inhibitory effect on peanut development even when plants are grown under well-watered conditions. It reduces the total leaf area, stem elongation, number of subterranean pegs, and mature seed weight (Ketring, 1984).

All F_1 from crosses among the photoperiod-sensitive parents were sensitive. However, in the cross ICGV 86364 / ICG 1697, the F_1 was significantly less sensitive than the more sensitive parent and also the midparent (Table 5). In all crosses of photoperiod sensitive with insensitive parents, the difference between parents was significant, and all F_1 were sensitive based on the test of D_{SL} (Table 5). In each such cross, the F_1 was significantly more sensitive than the insensitive parent, but in four out of eight crosses, it was also less sensitive than the sensitive parent and not significantly different from the midparent. In these crosses, there appears to be additive gene action or cancelling effects of genes exhibiting dominance. In three of the crosses, the F_1 was significantly different from the insensitive parent but not from the sensitive parent or the midparent, suggesting that there is incomplete dominance for photoperiodic response in those crosses. In one cross, the F_1 was significantly more sensitive than either the insensitive parent or the midparent and not significantly different from the sensitive parent, indicating partial to complete dominance in that cross.

In general, parents maintained their photoperiod response across seasons. Because of the practical difficulty in evaluating segregating populations for photoperiod insensitivity, it is suggested that selection for this trait be delayed to later generations when phenotypically uniform homozygous progenies could be evaluated under both short and long day in field conditions.

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