Combining ability of biomass and harvest index under short- and long-day conditions in groundnut

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Summary

Photoperiod insensitivity plays a significant role in ensuring wide adaptability of genotypes across environments. The effect of photoperiod in groundnut (*Arachis hypogaea* L.) is manifested in post-flowering development including partitioning. The partitioning of assimilates, as measured by harvest index (HI), has the greatest effect on pod yield. The F_1 progenies (excluding reciprocals) and their parents from a six-parent diallel cross were studied to estimate combining ability for biomass and HI under short (SD)- and long (LD)-day conditions, and to identify good combiners with high biomass and HI for use in breeding programmes. The experiment was conducted for three seasons in a split plot design with two photoperiods as main plots and 21 genotypes as subplots. The two photoperiod treatments were SD defined as normal-day light period and LD defined as normal-day light period extended by 4 h using incandescent lamps. The multi-environment analogue of Griffing's Method 2 – Model 1 was modified to analyse data for combining ability. While biomass was controlled by both GCA and SCA effects, HI was predominantly controlled by GCA effects. GCA and SCA effects for biomass and HI interacted with environments (six factorial combinations of photoperiods and seasons). SCA effects remained insensitive to variation in photoperiod both for biomass and HI. However, GCA effects for HI were sensitive to photoperiod. V6 (ICG 2405) was a good general combiner for both biomass and HI across environments. None of the crosses showed positive and significant SCA effects for both biomass and HI. Photoperiod influenced the sensitivity of GCA effects of V2 (ICGV 86694) and V6 for HI. However, the difference between SCA effects of V2 × V6 was not significant. The results of this study emphasise the need for future experiments with random genotypes over a range of photoperiods.

Introduction

Simultaneous selection for a superior rate of biomass accumulation and high harvest index (HI), and a length of time to harvest maturity that is neither shorter nor longer than the duration of the growing season has been suggested for increasing yield in self pollinated crops (Wallace *et al.*, 1993). The partitioning of assimilates, as measured by HI, has the greatest effect on pod yield in groundnut (*Arachis hypogaea* L.) (Duncan, McCloud, McGraw & Boote, 1978). Newly released groundnut cultivars have higher reproductive efficiency (RE), and produce more flowers, mature pod, mature seed and total plant dry weight than older cultivars (Coffelt, Seaton & Van Scoyoc, 1989; Thein & Kywe, 1991; Seaton, Coffelt & Van Scoyoc, 1992). Future increases in groundnut yield might best be accomplished by developing cultivars with combinations of high RE, HI, and total flower count (Coffelt *et al.*, 1989).

A low to moderate variation in HI (Dhopte & Zade, 1981; Murty, Reddy, Reddy & Sankara, 1983; Velu & Gopalakrishnan, 1985; Sharma & Varshney, 1995) and a large variation for total dry matter (Wright, Rao & Farquhar, 1994; ICRISAT unpublished data) have been reported in groundnut.

Photoperiod has no effect on flower initiation or flower intensity in groundnut. However, its effect is manifested in post-flowering reproductive development and phenology (e.g. Wynne, Emery & Downs, 1973; Wynne & Emery, 1974; Ketring, 1979; Emmery, Sherman & Wickers, 1981; Witzenberger, Williams & Lenz, 1988; Flohr, Williams & Lenz., 1990). Long days increase crop growth rate and decrease partitioning and the duration of effective pod filling phase (Wynne *et al.*, 1973; Wynne & Emery, 1974; Ketring, 1979; Witzenberger *et al.*, 1988). Photoperiod and temperature interactions are also reported. While photoperiod under short days has no significant influence on partitioning at low temperature, it does significantly affect it at higher temperature (Bell, Bagnall & Harch, 1991; Nigam *et al.*, 1994).

Biomass, in general, has extremely low heritability. Comparatively, HI and days to maturity have very high heritability (Wallace *et al.*, 1993). Little is known about the genetics of biomass in groundnut. HI is reported to be controlled predominantly by non-additive genetic variance (Makne, 1992).

The present experiment was conducted to study the combining ability of biomass and HI under short- and long-day conditions, and to identify good combiners with high biomass and HI for use in applied groundnut breeding.

Materials and Methods

Four photoperiod sensitive [ICGVs 86364, 86694, and 86020, and ICG 1697 (NC Ac 17090, PI 433525)] and two photoperiod insensitive [ICGV 86031 (PI 561917) and ICG 2405 (NC Ac 2821, Holland Virginia Jumbo)] genotypes were selected for the study. These are designated as V1, V2, V3, V4, V5, and V6, respectively. V1, V2, and V6 belong to the subsp. *hypogaea* var *hypogaea*, V5 and V3 to the subsp *fastigiata* var *vulgaris*, and V4 to the subsp *fastigiata* var *peruviana*. V4 and V6 are germplasm lines, and the remaining are elite breeding lines developed at ICRISAT, Patancheru, India. The genotypes were crossed in a diallel mating design to produce 15 non-reciprocal F_1 hybrids. The six parents and 15 F_1's were evaluated in alfisol (clayey-skeletal, mixed, isohypertheric family of Udic Rhodustalfs) fields under short day (SD) and long day (LD) conditions at Patancheru (18°N, 78°E) for 3 seasons (E1 = rainy season 1990; E2 = postrainy season 1990/1991; E3 = rainy season 1991). The experiment was conducted in a 3-replicate split plot randomised complete block design with photoperiod as main plot and genotype as subplot factors. The plot size was one row of 4 m with an inter- and intra-row spacing of 60 cm and 15 cm, respectively.

The crop received 60 kg P_2O_5 ha^{-1} as a basal dose, and 400 kg gypsum ha^{-1} at peak flowering. In addition to 661 mm and 716 mm rainfall in E1 and E3 seasons, the crop received four supplemental irrigations in the former and five supplemental irrigations in the latter (50 mm each irrigation). In the E2, where the rainfall was only 88 mm, the crop received 16 irrigations (50 mm each irrigation). During the three 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 Kavach® (Tetrachloroisophthalonitrile) at the rate of 1.8 litre ha^{-1} and insect pests by applying dimethoate® [O, O-Dimethyl S-(N-methylcarbamoylmethyl) phosphorodithioate] and mono-crotophos® (dimethyl phosphate of 3-hydroxy-N-methyl-cis-crotonamide) alternately at the rate of 1 litre ha^{-1}. The number of fungicide and insecticide sprays were three and four in E1, one and six in E2, and four and five in E3.

The two photoperiod treatments were SD (13.2 h in rainy and 12.1 h in post-rainy season) and LD (17.2 in rainy and 16.1 h in post-rainy season). The normal day light period was considered as SD. The LD conditions were established by extending the normal day length by another 4 h in the evening soon after the natural light intensity fell to around 576 J m^{-2}. The daylength was extended using 100 W incandescent lamps, suspended 0.75 m above the crop in a 3 × 3 m grid pattern. In spite of spatial variation, light intensity was above the minimum required to induce photoperiod response in groundnut. No temperature differences due to lighting were detected at the crop canopy level between the SD and LD plots. A light gradient experiment had shown that LD effects were usually restricted up to a distance of about 6 m from the light source (V M Ramraj, 1988, unpublished data). In the present study, the SD and LD plots were separated by a distance of 12 m in all directions. The LD treatment started soon after seedling emergence.

Observations on vegetative (above ground parts) and pod weight were recorded at harvest for individual plants in each plot in each replication. 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. Pod weight was multiplied with 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. The total biomass and HI were determined as,

> Biomass = adjusted pod weight + vegetative weight
>
> HI= Adjusted pod weight/Biomass,

where adjusted pod weight = pod weight × 1.67

Pooled analysis of variance over three seasons (S) and two photoperiods (Ph), based on a mixed linear model with seasons as random and photoperiod and genotype (G) as fixed effects, was performed, on plot means, to separate season, photoperiod, genotype, and their interaction effects for biomass and HI. The statistical significance of S was tested against Blocks/Seasons, of Ph against S × Ph, of S × Ph against Pooled Error (a), of G against S × G, of S × G and S × Ph × G against Pooled Error (b), and that of Ph × G against S × Ph × G following the last column in Table 4 of McIntosh (1983).

The multi-environment analogue of Method 2-Model 1 of Griffing (1956), as proposed by Singh (1973), was modified to study the interaction of general combining ability (GCA) and specific combining ability (SCA) effects with photoperiod and seasons. This modified model can be written as

$$y_{ij(kl)} = m + g_i + g_j + s_{ij} + E_{(kl)} + (gE)_{i(kl)} + (sE)_{ij(kl)} + e_{ij(kl)} \quad i,j = 1, \ldots, 6 \ (kl) = 1, \ldots, 6 \quad (1)$$

where $y_{ij(kl)}$ is the observation on (i,j)-th F_1 in (kl)-th environment, g_i and g_j are GCA effects of parents i and j, s_{ij} is the SCA effect of (i,j)-th F_1, $E_{(kl)}$ is the effect of (kl)-th environment,

Table 1. *Pooled analysis of variance for biomass and harvest index in 6 × 6 diallel cross F_1 progenies (non-reciprocals) of groundnut grown under SD and LD conditions over three seasons*

		MS	
Sources	d.f.	Biomass	Harvest index
Seasons (S)	2	96505***	1.0129***
Residual	6	719	0.0151
Photoperiod (Ph)	1	1239	2.2073***
S × Ph	2	2760	0.0361
Pooled error (a)	6	654	0.0119
Genotype (G)	20	3996***	0.0658***
Parent (P)	5	1550***	0.1225***
Cross (C)	14	1762	0.0343**
P vs C	1	47502	0.2242*
S × G	40	1081***	0.0092***
S × P	10	184	0.0036
S × C	28	910***	0.0111***
S × P vs C	2	7966***	0.0036
Ph × G	20	334	0.0145**
Ph × P	5	73	0.0336***
Ph × C	14	451	0.0035
Ph × P vs C	1	5	0.0025
S × Ph × G	40	435***	0.0053***
S × Ph × P	10	43	0.0028
S × Ph × C	28	585***	0.0061***
S × Ph × P vs C	2	304	0.0070***
Pooled error (b)	240	259	0.0022

*$P<0.05$, **$P<0.01$, ***$P<0.001$.
SD = Short day (13.2 and 12.1 h during the rainy and post-rainy seasons, respectively).
LD = Long day (17.2 and 16.1 h during the rainy and post-rainy seasons, respectively).

$(gE)_{i(kl)}$ and $(sE)_{ij(kl)}$ represent interaction of GCA and SCA effects with environments, and $e_{ij(kl)}$ is the residual which is assumed to follow a normal distribution with mean zero and a constant variance. The environment effect $E_{(kl)}$, representing the six factorial combinations of three seasons and two photoperiods, was expanded to $E_{(kl)} = t_k + p_l + (tp)_{kl}$ with corresponding expansion of $(gE)_{i(kl)}$ and $(sE)_{ij(kl)}$ terms in order to study the interactions of GCA and SCA effects with seasons and photoperiods. In the expanded form of $E_{(kl)}$, t_k represents the effect of season k (k = 1, 2, 3), p_l the effect of photoperiod l (l = 1, 2), and $(tp)_{kl}$ the interaction of photoperiod with season. The least squares estimates of various main effects and interactions occurring in the expanded form of model (1) were computed using a GENSTAT program specifically developed for this purpose (A copy of the program can be obtained from Statistics Unit at ICRISAT). The statistical significance of various effects, this being a fully fixed effects model, was assessed against the pooled error mean square corresponding to the model error term $e_{ij(kl)}$. The components of mean squares (MS), κ_g^2 and κ_s^2, for GCA and SCA were estimated by equating their MS values to the expected values of the MS under Model 1. Following Baker (1978), the ratio $2\kappa_g^2/(2\kappa_g^2 + \kappa_s^2)$, termed here as Baker's ratio, was used to assess the relative importance of GCA and SCA estimates.

Separate analyses, based on Griffing's Method 2-Model 1 (Singh, 1973), were carried out to estimate GCA effects of parents and SCA effects of crosses under SD and LD conditions. When GCA effects of the parents differed significantly from zero under both SD and LD conditions, their equality was tested using a two-sample t-test.

Table 2. *Mean squares (MS) and components of MS of general combining ability (GCA) and specific combining ability (SCA) for biomass and harvest index in 6 × 6 diallel cross F_1 progenies (nonreciprocal) of groundnut grown over six environments (three seasons and two photoperiod)*

Sources	d.f.	MS	
		Biomass	Harvest index
GCA	5	1437***	0.046***
SCA	15	1297***	0.014***
Environments (E)	5	13318***	0.287***
Photoperiod (Ph)	1	413*	0.736***
Season (S)	2	32168***	0.338***
Ph × S	2	920***	0.012***
GCA × E	25	231***	0.006***
GCA × Ph	5	125	0.016***
GCA × S	10	380***	0.006***
GCA × Ph × S	10	135	0.002*
SCA × E	75	222***	0.002***
SCA × Ph	15	107	0.001
SCA × S	30	354***	0.002**
SCA × Ph × S	30	148*	0.002**
Residual	240	86	0.001
		Components of MS and their ratio	
κ^2_{gca}		168.87	0.006
κ^2_{sca}		201.83	0.002
$2\kappa^2_{gca}/(2\kappa^2_{gca} + \kappa^2_{sca})$		0.63	0.84

$*P<0.05$, $**P<0.01$, $***P<0.001$.

Results and Discussion

Pooled analysis of variance (Table 1) revealed that biomass differed ($P < 0.001$) among S and G. The influence of Ph on biomass was not evident. S was the major source of variation for this trait. The variation for biomass among G arose mainly from parents (P). S × G ($P < 0.001$) and S × Ph × G ($P < 0.01$) interactions were significant for biomass. Crosses (C) interacted with S and Ph more than parents. HI differed ($P < 0.001$) among S, Ph, and G. Unlike in the case of biomass, the Ph was the main source of variation in HI. Seasons' influence on HI could result from the difference in photoperiod (about 1 h for both SD and LD) between the rainy and post-rainy seasons. Previous studies have also reported a significant influence of photoperiod on the partitioning of dry matter to pods in groundnut (Ketring, 1979; Witzenberger *et al.*, 1988; Flohr *et al.*, 1990; Bell *et al.*, 1991; Nigam *et al.*, 1994). Although all the three components of G, P ($P < 0.001$), C ($P < 0.01$), and P *vs* C ($P < 0.05$) contributed towards variation in G, the variation caused by P was most evident. Interactions S × G ($P < 0.001$), Ph × G ($P < 0.01$), and S × Ph × G ($P < 0.001$) were significant for HI. C were more sensitive to variation in S, but they did not interact with Ph. The reverse was true for P. The significance of S × Ph × G revealed that the performance of a cross *vis-a-vis* its parents, was not consistent across seasons and photoperiods.

In the pooled analysis of combining ability over six environments (E) (three seasons and two photoperiods), both GCA and SCA were equally important for biomass but there was predominance of GCA for HI (Table 2). These observations were further confirmed from the values of Baker's ratio reported in Table 2. However, in an earlier study, which was conducted only for one season, HI in groundnut was reported to be controlled by non-additive

Table 3. *Mean performance and general combining ability (GCA) effects of the parents for biomass and harvest index in 6 × 6 diallel cross F_1 progenies (non-reciprocals) of groundnut grown under SD and LD conditions over three seasons*

Parent	GCA effects over 6 environments				GCA effects under SD and LD over 3 environments							
	Biomass		Harvest index		Biomass				Harvest index			
	Mean	GCA	Mean	GCA	Mean		GCA		Mean		GCA	
					SD	LD	SD	LD	SD	LD	SD	LD
V1	74.4	−5.87***	0.387	0.013***	72.1	76.6	−8.03***	−3.72*	0.500	0.274	0.030***	−0.004
V2	94.1	9.22***	0.318	−0.043***	94.7	93.5	9.10***	9.34***	0.412	0.224	−0.034***	−0.052***
V3	76.4	−2.99**	0.400	0.008*	76.6	76.2	−2.21	−3.77*	0.490	0.310	−0.022***	−0.007
V4	68.5	−3.66**	0.321	−0.031***	64.3	72.6	−5.32***	−2.01	0.422	0.221	−0.027***	−0.036***
V5	69.4	0.56	0.473	0.014***	67.2	71.7	2.27	−1.15	0.481	0.464	−0.011	0.040***
V6	78.0	2.74*	0.525	0.039***	74.0	82.0	4.18*	1.30	0.553	0.498	0.019***	0.059***
SE mean	±3.79		±0.0219		±5.32	±5.40			±0.0178	±0.0134		
SE gi		±1.224		±0.0036			±1.708	±1.753			±0.0057	±0.0043
SE (gi-gi)		±1.896		±0.0056			±2.646	±2.715			±0.0089	±0.0067

*$P<0.05$, **$P<0.01$, ***$P<0.001$.

V1 = ICGV 86364, V2 = ICGV 86694, V3 = ICGV 86020, V4 = ICG 1697, V5 = ICGV 86031, V6 = ICG 2405.

SD = Short day (13.2 and 12.1 h during the rainy and post-rainy seasons, respectively).

LD = Long day (17.2 and 16.1 h during the rainy and post-rainy seasons, respectively).

genetic variance (Makne, 1992). GCA × E and SCA × E interactions for biomass were significant and of similar magnitude. Both GCA and SCA for biomass were highly sensitive to variation in seasons. They did not interact with photoperiod. These main interactions were also significant for HI, but the magnitude of GCA × E was three times more than that of SCA × E, indicating a greater sensitivity of GCA to environments. Photoperiod interacted more strongly than season with GCA for HI. The reverse was true for SCA.

Estimates of GCA effects of the parents and their mean performance over six environments and under SD and LD conditions over three seasons are presented in Table 3. Across seasons and photoperiods, V2 was a good general combiner for biomass but it was a poor combiner for HI. The reverse was true for V1. V4 was a poor combiner for both the traits. V5 and V6 were good combiners for HI. V6 was also a good combiner for biomass. The differences between GCA effects of the parents for HI under SD and LD conditions were significant for V2 ($P < 0.05$) and V6 ($P < 0.001$) indicating the sensitivity of their GCA to photoperiod. GCA of the parents for biomass was not influenced by photoperiod.

Pooled analysis of SCA effects (data not presented) of the crosses over six environments revealed that six crosses showed positive SCA effects ($P < 0.01$) for biomass and negative SCA effects ($P < 0.01$) for HI. Three other crosses showed positive SCA effects ($P < 0.05$–0.01) for HI only. However, when the SCA effects were estimated separately for SD and LD (data not presented), a different picture emerged. Seven crosses under SD and four crosses under LD showed significant positive SCA effects ($P < 0.05$–0.001) for biomass. Two crosses, V2 × V4 and V4 × V6, were common under both the photoperiods. For HI, seven crosses under SD and 11 under LD showed significant SCA effects ($P < 0.05$–0.001). Six of these effects under SD and eight under LD were negative. Five crosses with negative SCA effects and one cross with positive SCA effect were common under both the photoperiods. The common cross with the positive SCA effect was V1 × V2. When the difference between SCA effects under SD and LD for each cross was tested, only one cross each for biomass and HI had significant difference ($P < 0.05$). These crosses were V1 × V6 for biomass and V1 × V4 for HI.

The difference in HI between SD and LD was used to characterise the photoperiod response of the genotypes included in this study (Nigam *et al.*, 1994). Of the six crosses, which had significant SCA effects for HI under both the photoperiods, four had photoperiod sensitive (PS) × photoperiod insensitive (PI) combination, and one each PS × PS and PI × PI combination. The HI values of crosses involving PS × PI parents were similar to those of PS parents, which had HI values lower than PI parents. The genes for HI in PS parents were dominant over those present in PI parents. In the PS × PS crosses, parent ICGV 86364 showed dominance over ICGV 86694 for HI. Interestingly, the PI × PI cross showed a HI value lower than both the parents indicating a interlocus interaction.

Groundnut is a self pollinated crop, currently having a little scope for exploitation of non-additive genetic variance except for additive × additive type of interactions. In none of the crosses, a desirable combination of SCA effects (positive and significant) for biomass and HI was obtained. However, these traits could be improved individually in some crosses.

Since genotypes and photoperiod treatments in this study were fixed effects, the applicability of these results is limited. The study needs to be carried out with random sample of genotypes. As GCA for biomass is influenced by seasons and that for HI by photoperiod, the evaluation of genotypes should be carried out over seasons in a range of photoperiods to identify genotypes with stable performance of GCA for these traits. Genotypes with high and stable GCA for biomass and HI should be intercrossed to select recombinants with simultaneous improvement in these traits for increased productivity across environments.

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