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Reproductive Efficiency of Cultivated Peanuts. V. Response of Parental and Virginia (NC 4) x Spanish (C2) Hybrid Families to Changes in Photoperiod[1]

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ABSTRACT

Spanish-type C2 and virginia-type NC 4 peanut plants were compared in 9H (9 hours light phase and 15 hours dark phase) and 9H + 3 (9 hours light phase with 15 hours dark phase interrupted with 3 hours of low intensity light) photoperiods. C2 tended to produce greater plant weights and increased numbers of flowers in long-day treatments when compared to short-day treatments but peg growth, fruit per flowers, fruits per plant, and seed weights were drastically reduced in 9H + 3 photoperiods. NC 4, on the contrary, had only slight reductions in reproductive efficiency when exposed to long days. C2 plants produce more early flowers, less pegs per flower, but more fruit per peg than NC 4 plants in 9H photoperiods. F_1 plants from crosses between C2 and NC 4 had approximately the same plant weights as the NC 4 parent, but significantly greater reproductive efficiency than the virginia-type parent when grown in 9H light treatments. Neither the position of the peg on the plant nor the light treatment of the maternal parent appeared to influence peg growth on F_1 plants. Significant differences in the growth of pegs bearing F_1 embryos from reciprocal crosses were noted, however. F_2 plants were selected from 9H, 9H + 3, and 15H light treatments which produced more virginia-type fruits and more pegs per early flower than the NC 4 (virginia-type) parent.

Key Words: Groundnuts, *Arachis hypogaea* L, flowering, fruiting, pegging, photoperiod, hybridization.

Plant breeders refer to genotypes which perform well in crossing programs as "good combiners". Historically, many of the "good combiners" were identified by trial and error and recognized only in retrospect. Carver, as quoted by Norden (6) after 30 years of peanut (*Arachis hypogaea* L.) breeding at the University of Florida, described White Spanish and Virginia Jumbo Runner as good parents in a crossing program. Similarly, 'NC 2' (4), 'Florigiant' (1), and 'Florunner' (7) --the three dominant virginia-type cultivars of the past two decades--all had common ancestry in breeding lines Spanish 18-38 and Basse (a runner type from Gambia, West Africa). 'NC 7' (13) also may be traced to the same heritage.

Acknowledging the inefficient and often inaccurate methods used in the past to choose parents for long term and costly hybridization programs, a series of investigations on combining ability were initiated in 1968 (8). These experiments utilized a diallel analysis crossing scheme to assess the combining ability of three botanical types (spanish, valencia, and virginia) representing three geographic regions of origin in South America. F_1 (12), F_2 (5, 14) and later generation (9) comparisons were made.

One of the parental genotypes, originally described by Parker *et al.* (8) and referred to as C2 (8) or I_1 (5), was found to have high positive general combining ability (GCA) effects for fruit yield, seed yield, and meat content in both the F_4 (5, 14) and F_5 bulk analyses (9). Significant correlations were noted between parental means and parental performance in hybrid combinations for seed yield

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and meat content (5).

Since C2 is a logical choice to transmit meat content and yield to its hybrid progenies, and since the C2 mean performance for these traits is correlated with its performance in cross combinations (5), it seemed important to assess the specific reproductive features which may be useful in selection. Wynne et al. (11) first reported C2's rather dramatic response to changes in photoperiod. The growth rate of all reproductive traits was increased when C2 was exposed to short-day treatments of 9 hours but radically curtailed by long-day treatments effected with 3-hour, low-intensity light interruptions of the dark period. More recently, Emery et al. (3) identified the specific portion of C2's growth period which is most responsive to changes in photoperiod and noted that changes in the sequences of light treatments during growth not only increased seed weight per plant but accelerated the rate of peg growth.

Wynne and Emery (10) found that F_1 hybrids involving C2 and an unadapted virginia type (B2) exceeded the mid-parent values for flower, peg and fruit production. The branching pattern of the F_1 tended to influence the response, however. Differences in F_1 yeild were also noted between reciprocal crosses of C2 x B2 and B2 x C2. C2, used as the maternal parent, produced the superior progeny.

It is the purpose of the present research to investigate reproductive responses to changes in photoperiod when C2 is crossed to a long-time inbred but widely adapted virginia type, 'NC 4'.

Materials and Methods

The reproductive efficiency of the peanut lines C2, NC 4, and the F_1 and F_2 progeny of crosses involving the same lines was measured in the North Carolina State University Phytotron Unit. The dimensions of the chambers and growth media used were previously described (3). The growth chambers (2) use a combination of cool white fluorescent and incandescent lamps to provide a photosynthetic photon flux density of 670 to 735 μ E $m^{-2}s^{-1}$ between 700 and 800 nm. Measurements were made with a cosine-corrected, Lambda Instruments quantum/radiometer/photometer located 95 cm from the lamps.

Daylengths were kept effectively long by either interrupting the dark period from 11 PM to 2 AM with 12 W m^{-2} of photomorphic radiation (PR) from incandescent lamps (9H + 3) or by extending the daylength to 15 hours (15H) in the same manner.

Air temperatures were maintained at $\pm$ .25 C of the set point as measured with a #24 type "T" welded-bead thermocouple in a shielded, aspirated housing. Day/night temperatures were 30/26 C. This arrangement prevented direct comparisons of light effects between the 9H + 3 and 15H chambers due to the extension of 30 C temperature more nearly simulated field conditions for peanuts in midseason than would a daylight extension of 6 hours at 26 C.

Relative humidity was maintained at 70% at the temperatures used and CO_2 concentrations were controlled at 300 to 400 ppm by injection of commercial grade CO_2.

The plant arrangements in the chambers differed for the parental, F_1 and F_2 generations. The parents were grown in 9H and 9H + 3 light treatment chambers. Two entries of each parental line were replicated three times in a randomized complete block design. Each entry was a single plant grown in a 44.44-cm x 38.10-cm x 15-cm wooden box especially designed to promote pegging and fruiting. The 12 plants (two entries x 2 parents x 3 replicates) were grown in individual chambers representing 9H and 9H + 3 light treatments.

The F_1 generation was grown in a 9H light treatment only. Limited space necessitated the use of only one parental check, NC 4. It was chosen because the direction of selection in late generations would be toward virginia-type plants. Furthermore, branching patterns of F_1 hybrid plants from a cross involving virginia-type and spanish-type parents would be expected to be of the virginia type (10). The entries included NC 4, NC 4 x C2, and C2 x NC 4. Entries were arranged in a randomized complete block design with three replicates represented by a single plant grown in boxes of the type described for the parents.

The reproductive efficiency of the F_2 generation was evaluated in 9H, 9H + 3, and 15H photoperiods. Plants were arranged in a split split-plot design for each light treatment with main plots represented by three F_1 families, subplots (genotypes) by either parents or hybrids and sub-subplots by the lines (NC 4 or C2) within each parental or arbitrarily assigned F_2 plant subplot. The three F_1 families represented NC 4 x C2 (maternal parent in short-day treatment), C2 x NC 4 (maternal parent in long-day treatment) and NC 4 x C2 (maternal parent in long-day treatment). Since each sub-subplot was a single plant grown in a 25.4-cm pot and each truck held four plants, a main plot (two subplots x two sub-subplots) could be grown in each cart. The three main plots were replicated four times providing 12 main plots or 24 subplots or 48 sub-subplots per chamber.

The parental, F_1 and F_2 generations were grown for 109, 108, and 110 days, respectively, in their respective light treatments. Freshly opened flowers were counted daily as they appeared for 93 days in the parental generation, 106 days in the F_1 generation, and 63 days in the F_2 generation.

Peg measurements were made as described by Emery et al. (3) by identifying the peg at emergence and measuring its growth at 2-day intervals over a 6-day period. The total growth of the peg during that period is used in the analyses. The position of the peg on the reproductive or vegetative branches of the cotyledonary lateral and on branches higher on the main stem was recorded on F_1 plants. Pegs were measured when F_1 plants were 32 to 36 and 51 to 52 days of age.

The number of shellable fruit, seed weight and dry plant weight were recorded at harvest. These data were used to compare the reproductive efficiencies of the parental, F_1, and F_2 plants.

Results and Discussion

The spanish-type peanut C2 is known to have high positive general combining ability (GCA) effects for fruit yield, seed yield, and meat content in F_4 (5, 14) and F_5 bulk analyses (9). It is also known to be markedly responsive to changes in photoperiod (3). The effect of photoperiod on the progenies of crosses between spanish type and virginia type is of particular interest to the breeder of virginia-type peanuts because the extended duration of flowering and pegging makes it particularly vulnerable to environmental stress. It is not uncommon for farmers in the North Carolina-Virginia peanut belt, for example, to rely on a late peg and fruit set to compensate for early season moisture stress. The breeder is interested in developing lines that have the ability to respond to the shorter daylengths (longer nights) of the fall without sacrificing the yield potential resulting from pegs set during the long days (short nights) of July and August.

Parental Plants

This investigation demonstrates that the reproductive responses of C2 (spanish type) and NC 4 (virginia type) peanut plants to changes in photoperiod are clearly different. Even though plant-to-plant variability was high and magnified with the small populations used in the growth chambers, C2 plants grown in 9H + 3 photoperiods had sharply increased flower production (Table 1), reduced peg growth (Table 3), and severely reduced fruit and peg/flower and seed weight/plant weight ratios (Table 1) when responses were compared to those in 9H photoperiods.

NC 4 plants, on the contrary, had only moderate increases in flower production (Table 1), slight reductions in peg growth (Table 3), no change in fruit and peg/flower ratios, and either moderate or no reduction in seed weight/plant weight ratios (Table 1) when grown in the same environments.

Table 1. Means for vegetative and reproductive traits of parent plants in two photoperiods.

Parents†	Plant wt (g)‡		Flowers/ plant§		Fruit/ plant		Fruit+peg/ flower ratio		Seed wt/ plant (g)		Seed wt/ plant wt	
	9H	9H+3	9H	9H+3	9H	9H+3	9H	9H+3	9H	9H+3	9H	9H+3
C2	214.3	464.3	828.7	1565.7	164.7	33.3	.645	.304	141.5	22.1	.660	.049
C2	187.5	484.7	--	--	168.3	68.0	--	--	143.3	39.7	.764	.082
NC 4	311.4	320.3	901.0	1163.0	81.3	79.3	.855	.867	67.6	72.7	.214	.228
NC 4	294.0	389.6	--	--	113.7	70.7	--	--	114.7	61.5	.391	.148
LSD .05	38.4	71.6	NS	110.4	45.5	NS	.121	.057	28.8	31.5	.091	.081

†Two independent representatives (each a mean of three plants) of each parent.

‡Plants harvested 109 days.

§Flowers in first 93 days, data recorded on one set of parent plants only.

Table 2. Means for vegetative and reproductive traits of NC 4 and F_1 hybrids in 9H photoperiods.

Parents	Plant wt (g)†	Flowers/ plant‡	Fruit/ plant	Fruit+peg/ flower ratio	Seed wt/ plant (g)	Seed wt/ plant wt
NC 4	188.0	373.7	35.3	.617	28.2	.151
NC 4 x C2	183.8	271.3	62.0	.700	68.6	.372
C2 x NC 4	186.1	248.4	62.9	.807	69.8	.382
LSD .05	NS	48.5	19.6	.107	25.3	.169

†Plants harvested 108 days.

‡Flowers in first 106 days.

Table 3. Effect of photoperiod, genotype and time of peg placement on growth of pegs bearing parental, F_1 and F_2 embryos.

Genotype	Mean peg growth (mm)							
	Parental and F1 embryos				Parental and F2 embryos			
	9H†	Avg plant age (days)	9H+3	Avg plant age (days)	9H‡	Avg plant age (days)	9H§	Avg plant age (days)
NC 4	53.4	27	41.5	28	50.4	36	35.7	51
C2	48.7	39	28.5	41	--	--	--	--
NC 4 x C2	68.7	51	66.7	51	55.7	32	77.0	52
C2 x NC 4	58.3	43	46.0	43	63.6	33	64.0	51
LSD .05	8.5		7.1		NS		15.3	

†Mean of 10 fastest growing pegs of those measured on parental, NC 4 virginia-type and C2 spanish-type plants. Analysis based on 10 replicates of single peg measurements.

‡Mean of 30 fastest growing pegs of those measured on NC 4 virginia-type and F1 plants. Analysis based on three plants/genotype with 10 early peg measurements/plant.

§Mean of 15 fastest growing pegs of those measured on NC 4 virginia-type and F1 plants. Analysis based on three plants/genotype with five late peg measurements/plant.

F_1 Plants

Based on parental responses in the 9H treatment (Table 1) and assuming additive gene action with no maternal effects, one would predict that F_1 hybrids between C2 and NC 4 grown in 9H photoperiods would have somewhat less total flower production, less fruit and peg/flower ratios, more fruit/plant, more seed weight/plant, and higher seed weight/plant ratio than NC 4. In general, these predictions were fulfilled (Table 2). One of the F_1 hybrids (C2 x NC 4) had significantly higher proportions of fruit and pegs/flower than NC 4 or the reciprocal cross NC 4 x C2.

The reciprocal crosses were not statistically different for flowers/plant, fruit/plant, seed weight/plant, seed weight/plant weight, and plant weight. Wynne and Emery (10) reported differences in reciprocal crosses of C2 and B2, an unselected and unadapted line from Bolivia (8), but fruit production was limited in that investigation. Secondly, assuming that maternal effects on crop yield can be substantial, NC 4 would more closely approximate the yield of C2 than would B2.

Peg Growth, Parents and F_1 Plants

Emery et al. (3) reported a strong influence of photoperiod on rates of peg growth. The peg growth rate of C2 and NC 4 could not be differentiated in the 9H treatment but NC 4 had significantly greater peg growth rates than C2 in the 9H + 3 treatments (Table 3). Also, long-day treatments did not appear to decrease peg growth rates of NC 4 as sharply as those of C2 (3). Pegs bearing certain F_1 embryos, *i.e.*, resulting from cross-pollination, had faster growth rates than NC 4 in both 9H and 9H + 3 photoperiods. Reciprocal differences were noted with NC 4 x C2 pegs having faster growth rates than C2 x NC 4 pegs (Table 3). These differences must be attributed to the direct effect of cross-pollination because the response occurred in both light treatments. Growth rates of pegs bearing C2 x NC 4 and NC 4 x C2 F_2 embryos could not be distinguished (Table 3), but both crosses had significantly higher late peg growth rates than the NC 4 parent.

To improve selection schemes involving peg growth measurements, attempts were made to determine the effect of peg position, time of peg emergence, genotype, and light treatment of the maternal parent on growth rates of pegs on the F_1 plants, *i.e.*, bearing F_2 embryos. Contingency tables comparing rates of peg growth with the four characters mentioned above were used to calculate chi-squares. Light treatment of the maternal parent and position of the peg appeared to have little, if any, effect on F_1 peg growth rates (Table 4). Late peg emergence reduced the peg growth rates of NC 4, however, to the point where they could be differentiated from the peg growth rates of the F_1 plants (Table 4). Late set pegs gen-

Table 4. Chi-square contingency tables: Effect of peg position, time of peg set, genotype and light treatment of parent on peg growth on F_1 plants.

Peg growth categories (mm)	Plant position of peg			Time of peg set		Genotype			Light treatment (maternal parent)	
	Vegetative branch	Reproductive branch	Main stem branch	Flowers 5/15-5/25	Flowers 6/14-6/18	NC 4	C2 x NC 4	NC 4 x C2	NC 4 x C2 (9H+3)	NC 4 x C2 (9H)
25-40	4	3	3	4	13	7	0	3	3	1
41-55	31	20	7	32	19	18	7	18	18	14
56+	26	25	10	33	25	9	18	14	14	20
Total	57	48	20	69	57	34	25	35	35	35
χ^2		3.52NS		8.10*		15.34**			2.54NS	

*Probability of less than 5% that such differences occurred by chance.

**Probability of less than 1% that such differences occurred by chance.

erally tended to grow slower than early pegs set on the same plant (Table 4).

F_2 Plants

The reproductive traits of F_1 families tracing to reciprocal crosses and to different maternal plant light environments could not be distinguished in the F_2 generation (Tables 5 and 7). Significant differences between genotypes (parents *vs* hybrids) were observed for early flower production in long-day, 9H + 3, and 15H treatments. Significant differences between lines (particularly between the two parents) and for genotype x line interaction (probably caused by the significant difference between parents and the similar responses of the F_2 plants) were also noted in each of the 9H, 9H + 3, and 15H photoperiods (Table 5). NC 4 (line 2 in the parental genotype) had significantly less early flowers produced than either C2 or F_2 segregates in all light treatments (Table 6). NC 4 also had smaller proportions of early flowers (flowers in 18 days compared to flowers in 45 days) than did C2 or F_2 segregates in the 9H or 15H photoperiods (Table 6).

Table 5. Analyses of variance, four reproductive traits, three photoperiods.†

Source	df	9H	9H+3	15H	9H	9H+3	15H
		Plant weight (g)			Early flowers		
Blocks	3	3989.5	4199.8	4792.0	1131.6	854.2	3591.4
Families (F)	2	90.7	4070.7	741.7	394.8	656.7	2070.3
Error a	6	1143.9	2462.4	2730.3	689.7	2484.9	1091.4
Genotypes (G)	1	721.5	2000.8	960.3	1220.1	5208.3*	1646.5*
F x G	2	1732.4	914.6	4735.9	740.4	174.2	3906.1
Error b	9	1030.9	4137.1	4260.1	565.3	725.3	1766.9
Lines (L)	1	12762.9*	13672.1	38845.6*	42840.8**	55624.1**	23629.7**
F x L	2	3386.8	1722.1	812.9	113.4	565.4	961.8
G x L	1	5489.1	12278.4	6535.7	10325.3**	43681.3**	20131.0**
F x G x L	2	2511.1	2667.2	5320.7	468.2	186.5	905.1
Error c	18	2313.7	3537.8	4870.4	796.0	732.5	1060.7
		Early flowers/late flowers, %			Pegs/early flowers, %		
Blocks	3	.008	.016	.040	293.4	159.0	133.4
Families (F)	2	.018	.014	.004	107.7	9.2	67.4
Error a	6	.008	.021	.026	126.1	84.3	207.3
Genotypes (G)	1	.011	.058	.028	182.9	28.7	296.0
F x G	2	.001	.007	.016	13.9	104.3	135.8
Error b	9	.013	.025	.049	116.4	107.5	198.6
Lines (L)	1	.363**	.003	.204**	1650.9**	311.6*	142.8
F x L	2	.002	.009	.008	189.8	74.2	63.3
G x L	1	.344**	.062	.355**	263.7	115.0	28.8
F x G x L	2	.023	.015	.037	133.3	215.5*	4.5
Error c	18	.013	.026	.020	189.0	50.5	203.6

†Figures represent mean squares from split-split plot design where F = F_1 families, G = parents, hybrids and L = lines within parents and hybrids.

*Significance at 5% level.

**Significance at 1% level.

Table 6. Effect of photoperiod on reproductive efficiency of parents and F_2 progeny.†

Trait	Genotype	9H Line 1	9H Line 2	9H+3 Line 1	9H+3 Line 2	15H Line 1	15H Line 2
Plant wt (g)	Parents	406.2	460.2	489.4	423.7	422.0	502.2
	F_2 plants	419.6	431.0	470.4	468.6	454.2	487.8
	(A) LSD .05‡		50.5		NS		73.4
	(B) LSD .05§		NS		NS		NS
Early flowers (27 days)	Parents	184.9	95.1	184.3	55.9	169.8	84.8
	F_2 plants	145.5	115.1	103.2	95.3	91.9	88.4
	(A) LSD .05		29.7		28.5		34.2
	(B) LSD .05		23.0		24.0		33.9
Flowers (18 days)/ flowers (45 days)	Parents	57.3	23.3	44.6	36.0	56.5	26.3
	F_2 plants	43.3	43.0	30.3	36.7	34.5	38.7
	(A) LSD .05		11.9		NS		14.8
	(B) LSD .05		10.2		NS		16.8
Pegs/early flowers	Parents	26.9	43.4	6.5	14.6	7.7	12.7
	F_2 plants	35.5	42.6	11.1	13.1	14.2	16.1
	(A) LSD .05		14.4		7.5		NS
	(B) LSD .05		NS		NS		NS

†Parent line 1 = mean of 12 spanish (C2) plants, parent line 2 = mean of 12 virginia-type (NC 4) plants. Each F_2 mean represents 12 F_2 plants randomly assigned to sub-subplots in association with either line 1 or line 2 parent plants.

‡LSD = least significant difference between lines within the same genotype.

§LSD = least significant difference between lines for different genotypes or between genotypes for the same line.

Table 7. Analyses of variance, three reproductive traits, 9H photoperiods.†

Source	df	Fruit/pegs + fruit	Seed wt, g	Seed wt/ plant wt, %
Blocks	3	.003	65.4	.0001
Families (F)	2	.005	134.5	.0007
Error a	6	.012	309.6	.0015
Genotypes (G)	1	.010	1189.3	.0068*
F x G	2	.000	568.3	.0029
Error b	9	.006	170.8	.0008
Lines (L)	1	.250**	3768.3**	.0256**
F x L	2	.000	281.1	.0011
G x L	1	.180**	7094.0**	.0406**
F x G x L	2	.000	376.3	.0020
Error c	18	.006	138.2	.0007

†Figures represent mean squares from split-split plot design where F = F_1 families, G = parents, hybrids and L = lines within parents and hybrids.

*Significance at 5% level.

**Significance at 1% level.

While NC 4 produced fewer early flowers than C2, more of the early flowers resulted in pegs than did those of C2 when plants were grown in 9H or 9H + 3 photoperiods (Tables 5 and 6) but proportionally less fruit/peg than either C2 or F_2 segregates in the 9H photoperiod (Tables 7 and 8).

Table 8. Reproductive efficiency of parents and F_2 progeny, 9H photoperiod.†

Trait	Genotype	Line 1	Line 2
Fruit/pegs + fruit (%)	Parents	30.0	4.0
	F_2 plants	15.0	12.0
(A) LSD .05‡		8.0	
(B) LSD .05§		7.0	
Seed wt (g)	Parents	49.5	7.4
	F_2 plants	15.1	21.7
(A) LSD .05		12.4	
(B) LSD .05		11.1	
Seed wt/plant wt (%)	Parents	11.9	1.5
	F_2 plants	3.6	4.8
(A) LSD .05		2.8	
(B) LSD .05		2.4	

†Parent line 1 = mean of 12 spanish (C2) plants, parent line 2 = mean of 12 virginia-type (NC 4) plants. Each F_2 mean represents 12 F_2 plants randomly assigned to sub-subplots in association with either line 1 or line 2 parent plants.

‡LSD = least significant difference between lines within the same genotype.

§LSD = least significant difference between lines for different genotypes or between genotypes for the same line.

C2 produced greater seed weight and greater seed weight/plant weight than either NC 4 or the hybrid genotypes when plants were grown in the 9H treatment (Tables 7 and 8). Unfortunately, fruit and seed production in the 9H + 3 and 15H photoperiods were not adequate for statistical analyses. Individual F_2 plants were selected from each light treatment, however, bearing virginia-type fruits and having more early flowers, more early flowers with pegs, and larger numbers of fruit than the mean of the NC 4 parents (Table 9). The F_2 families are now in advanced generation.

Table 9. Comparison of reproductive traits for F_2 selections bearing virginia-type fruit with parental means in the same light treatment.

Treatment	Early flowers (27 days)	Pegs/early flowers (%)	Fruit no.	No. F_3 plants selected
9H				
NC 4 mean	95.8	43.4	9.0	-
C2 mean	184.9	27.0	54.8	-
F_2 1	109.0	52.3	19.0	9
F_2 2	116.0	50.9	26.0	2
F_2 3	117.0	31.6	39.0	3
9H+3				
NC 4 mean	55.8	16.7	0.42	-
C2 mean	184.3	6.4	2.0	-
F_2 1	79.0	32.9	22.0	4
15H				
NC 4 mean	84.4	12.7	0.25	-
C2 mean	169.8	7.7	0.92	-
F_2 1	101.0	27.1	21.0	3
F_2 2	39.0	53.8	20.0	14
F_2 3	68.0	48.5	9.0	2

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