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Inheritance of two components of early maturity in groundnut (*Arachis hypogaea* L.) *

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Summary

Knowledge of inheritance of early maturity or its components is important to groundnut breeders in developing short-duration cultivars. This study was conducted to determine the inheritance of two components of early maturity: days to first flower from sowing, and days to accumulation of 25 flowers from the appearance of first flower, using three groundnut genotypes. Two early-maturing (Chico and Gangapuri) and one late-maturing (M 13) genotypes were crossed in all possible combinations, including reciprocals. The parents, F_1, F_2, F_3, and backcross populations were evaluated for days to first flower from sowing, and for days to accumulation of 25 flowers. The data suggest that days to first flower in the crosses studied is governed by a single gene with additive gene action. Chico and Gangapuri possess the same allele for this component of earliness. Three independent genes with complete dominance at each locus appear to control the days to accumulation of 25 flowers. In crosses between late (M 13) and early (Chico or Gangapuri) parents, a segregation pattern suggesting dominant-recessive epistasis (13 late:3 early) was observed for this component. Segregation in the F_2 generation (1 late:15 early) of both early parents (Chico × Gangapuri) indicated that the genes for early accumulation of flowers in these two parents are at different loci.

Introduction

Breeding early-maturing cultivars is an important objective in most groundnut improvement programs. However, the subterranean nature of fruiting in the crop makes it difficult to assess maturity without uprooting the plants. A positive association between days to flower and crop duration (Seshadri, 1962; Yadava et al., 1981; Yadava et al., 1984) helps to some extent overcome this problem. Bailey & Bear (1973) demonstrated that the early onset of flowering and early accumulation of a given number of flowers (10 to 30) are important components of early maturity in groundnut. They further reported that a high proportion of the first 25 flowers developed into mature pods (Bear & Bailey, 1973). These two characters are potentially useful in formulating an effective breeding strategy for developing early-maturing cultivars.

Cultivated groundnut is a segmental allotetraploid (2n = 40, x = 10) with two genomes, A and B. But it behaves effectively as a diploidized tetraploid (Smartt & Stalker, 1982). There have been few studies on the quantitative inheritance of days to flowering (Gibori et al., 1978; Parker et al., 1970; Nigam et al., 1988; Wynne et al., 1970). Some of these studies have drawn contradictory conclusions. There is no published report on the inheritance of days taken to accumulate a certain number of flowers from the appearance of first flower.

In the present investigation the inheritance of these two components of early maturity was studied in crosses involving three diverse genotypes belonging to Spanish (Chico), Valencia (Gangapuri), and Virginia (M 13) botanical types.

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Materials and methods

Three groundnut (*Arachis hypogaea* L.) genotypes, Chico (subsp. *fastigiata* var. *vulgaris*), Gangapuri (subsp. *fastigiata* var. *fastigiata*), and M 13 (subsp. *hypogaea* var. *hypogaea*) were selected for the study which was carried out at ICRISAT Asia Center, Patancheru, India. Chico, a germplasm line, and Gangapuri, a local Indian cultivar, are early, and M 13, a large-seeded Indian cultivar, is late in maturity.

Chico, Gangapuri, and M 13 were crossed in all possible combinations including reciprocals in the glasshouse. Each of the six resultant F_1 hybrids was crossed to both parents to generate 12 backcross populations, and selfed to produce 6 F_2 populations. The parents, F_1, F_2, and backcross populations were sown in the 1991 rainy season on 60-cm ridges with a plant-to-plant distance of 15 cm. Care was taken to ensure uniform depth of sowing to avoid variation in days to emergence due to sowing depth. All seeds were treated with ethrel before sowing to overcome the possible effect of postharvest dormancy of cultivar M 13 in its cross populations. All the plants in the F_1 and backcross populations, except those on the border, were selected to record observations. Sixty plants in each parent, and 375 competitive plants in each F_2 population were selected randomly for this purpose. The date of appearance of first flower on each plant was recorded and days to flower after sowing were computed. The number of flowers opening each day on each selected plant were recorded, and days to accumulation of 25 flowers were computed. The experiment was affected by *Sclerotium rolfsii*. Plant mortality was negligible in the beginning, but increased as the plants grew old. Because of this situation, no attempt was made in this experiment to correlate days to first flower or days to 25 flowers with days to maturity or proportion of mature pods at harvest.

One hundred and twenty F_3 progenies of Chico × M 13 and Gangapuri × M 13 crosses were grown along with their parents in the 1992 rainy season to further study the segregation pattern of these two traits in the F_3 generation. Fifty F_3 progenies of the cross Chico × Gangapuri were also evaluated for segregation pattern of days to accumulation of 25 flowers.

The means of F_1 and its reciprocal combination for the two traits under study were compared using the 't' test to determine the role of maternal factors in the inheritance of these traits. Using the mean ($\overline{X}$), standard deviation (SD), and distribution of parents and their F_1 generation, the plants in respective backcross, F_2, and F_3 generations were grouped as parental (early or late) or F_1 types for these two traits. The decision to use 1 or 2 SDs to classify plants into different categories in segregating generations was based on the matching of means of parents and F_1s with the dips in distribution of plants in segregating generations. Some of the plants in the F_2 and backcross generations did not fall into these groups. The behaviour of their progenies was used to predict the appropriate flowering category of such plants in the previous generations, i.e., F_2 and backcross generations. In some cases, where plants died before harvest without producing any progenies, the flowering category classification was based on the closeness of plant performance with the mean of the different flowering categories. This could have caused some wrong classification, but it would be expected to occur in both directions, thus cancelling or minimizing the effect of some possible wrong classification.

The chi-square test was applied to test the goodness of fit of the expected ratios in these populations. In instances where a segregating F_3 progeny could be classified into more than one ratio, the goodness of fit (probability) of ratios was compared, and the ratio which had a higher probability of fit was accepted as the most probable ratio to which a particular progeny belonged.

Results and discussion

Days to first flower. Chico and Gangapuri flowered early. Chico took 26.9 ± 0.16 (mean ± standard error of mean) days and Gangapuri 25.5 ± 0.12 days to flower from sowing. M 13 flowered late and took 37.4 ± 0.39 days.

The difference between the Chico × M 13 F_1 hybrid and its reciprocal (M 13 × Chico) for days to first flower was nonsignificant, indicating the absence of maternal effects in the control of this character. The mean number of days to first flower taken by the F_1 hybrid involving Chico and M 13 (31.8 ± 0.59) was similar to the midparental value, indicating additivity of the gene effects. The mean of backcrosses Chico × (Chico × M 13) and Chico × (M 13 × Chico) lay between the means of Chico and F_1 hybrid. The mean of M 13 × (Chico × M 13) and M 13 × (M 13 × Chico) was between the means of F_1 hybrid and M 13. The means of F_2 of Chico × M 13 (31.4 ± 0.20 days) and M 13 × Chico (31.4 ± 0.19 days) were similar to that of the F_1 hybrid mean.

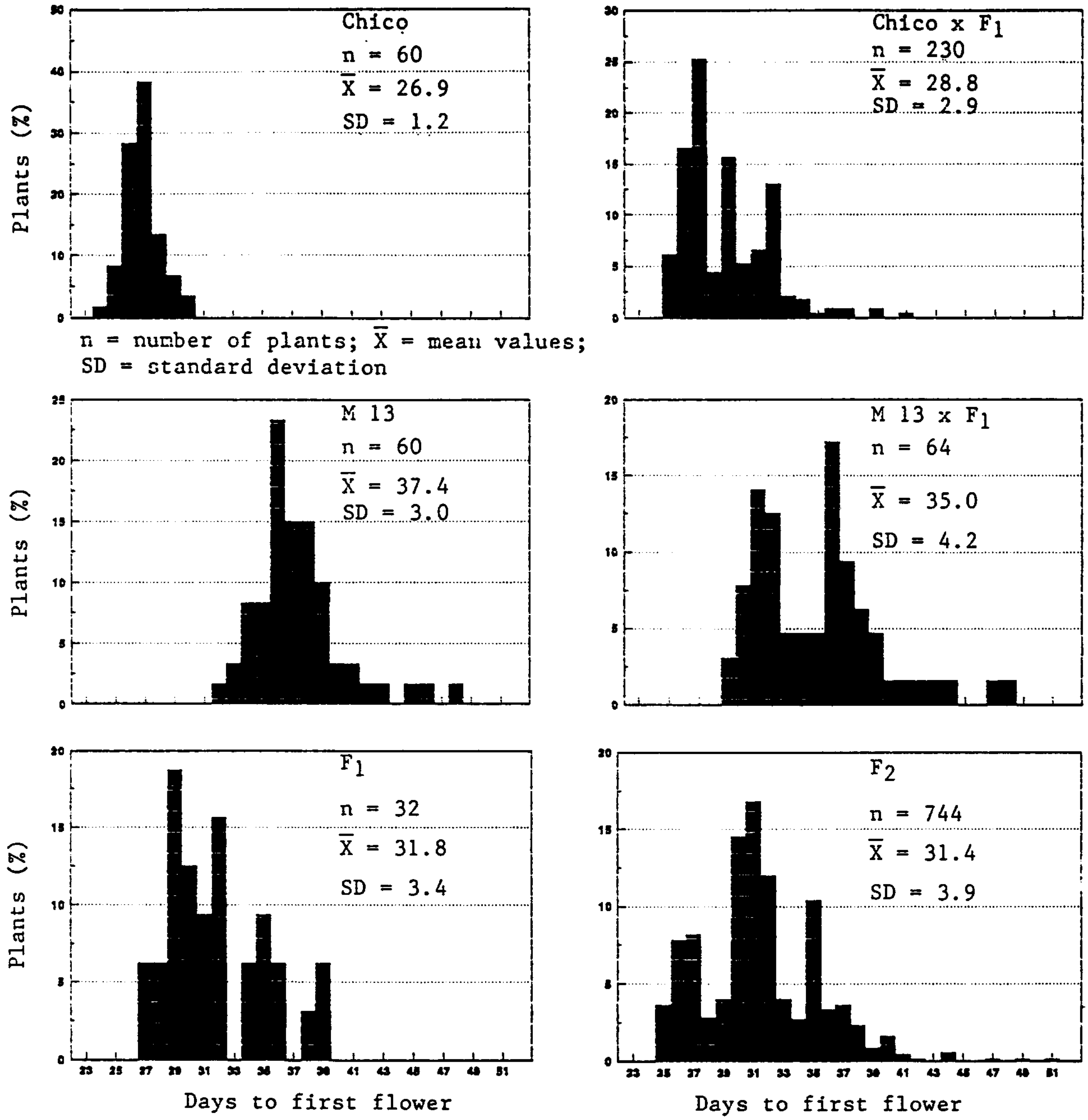

Fig. 1. Distribution of plants (%) for number of days from sowing to first flower in groundnut genotypes Chico and M 13, and their F_1, F_2, and backcross generations.

The plants in the backcross, F_2, and F_3 generations did not segregate into discrete groups of early, intermediate, and late types. Nevertheless, the distribution of parents Chico and M 13 did not overlap (Fig. 1), and the three peaks in the F_2 distribution at around 27, 32, and 36 days after sowing (DAS) coincided with those of Chico, F_1 hybrid, and M 13, and the dips at 28 and 34 DAS indicated the points of separation of these three groups. Similarly, the dip at 28 DAS in the backcross with Chico separated early and intermedi-

Table 1. The chi-square values and probabilities for goodness of fit for a ratio of 1 early:2 intermediate:1 late flowering plants in the F_2 generation of crosses of M 13 with Chico and Gangapuri

Cross	Number of plants			χ^2	P
	Early	Inter-mediate	Late		
Chico × M 13	81	199	92	2.468	0.250–0.500
M 13 × Chico	86	203	83	3.156	0.100–0.250
Gangapuri × M 13	94	198	77	3.542	0.100–0.250
M 13 × Gangapuri	78	187	102	3.272	0.100–0.250
Total	339	787	354	6.274	0.025–0.050
Heterogeneity				6.164	0.250–0.500

Table 2. The chi-square values and probabilities for goodness of fit for the expected ratios for days to flower in the backcross generations of crosses of M 13 with Chico and Gangapuri

Cross	Number of plants			Expected ratios			
	Early	Inter-mediate	Late	(1 Early:1 Inter-mediate)		(1 Inter-mediate:1 late)	
				χ^2	P	χ^2	P
Chico × (Chico × M 13)	31	29		0.067	0.750–0.900		
Chico × (M 13 × Chico)	89	81		0.376	0.500–0.750		
Gangapuri × (Gangapuri × M 13)	38	30		0.941	0.250–0.500		
Gangapuri × (M 13 × Gangapuri)	23	15		1.684	0.100–0.250		
Total	181	155		2.012	0.100–0.250		
Heterogeneity				1.056	0.750–0.900		
M 13 × (Chico × M 13)		17	26			1.883	0.100–0.250
M 13 × (M 13 × Chico)		13	8			1.190	0.250–0.500
M 13 × (Gangapuri × M 13)		57	47			0.961	0.250–0.500
M 13 × (M 13 × Gangapuri)		4	8			1.333	0.100–0.250
Total		91	89			0.022	0.750–0.900
Heterogeneity						5.345	0.100–0.250

ate types, and with M 13 the dip at 34 DAS separated intermediate and late types. Considering the criteria described earlier, and the peaks and dips in the F_2 and backcross generations, the plants which took up to 28 DAS ($\overline{X}$ + 1 SD of early parent) to first flower were classified as early-flowering, and those which took 35 or more DAS (> $\overline{X}$ - 1 SD of late parent) were classified as late flowering. The plants which flowered between 29–34 DAS ($\overline{X} \pm$ 1 SD of F_1 hybrid) comprised the intermediate flowering type.

In the F_2 generation of Chico × M 13 and its reciprocal, the number of early-, intermediate-, and late-flowering plants fitted well to a 1:2:1 ratio (Table 1) suggesting that days to flower is controlled by single gene with additive gene action. The number of early- and intermediate-flowering plants in Chico × (Chico × M 13) and Chico × (M 13 × Chico) and intermediate- and late-flowering types in M 13 × (Chico × M 13) and M 13 × (M 13 × Chico) fitted extremely well to a 1:1 ratio (Table 2), supporting the F_2 observation.

The cross involving Gangapuri and M 13 also followed the segregating pattern similar to that of Chico and M 13 (Tables 1, 2).

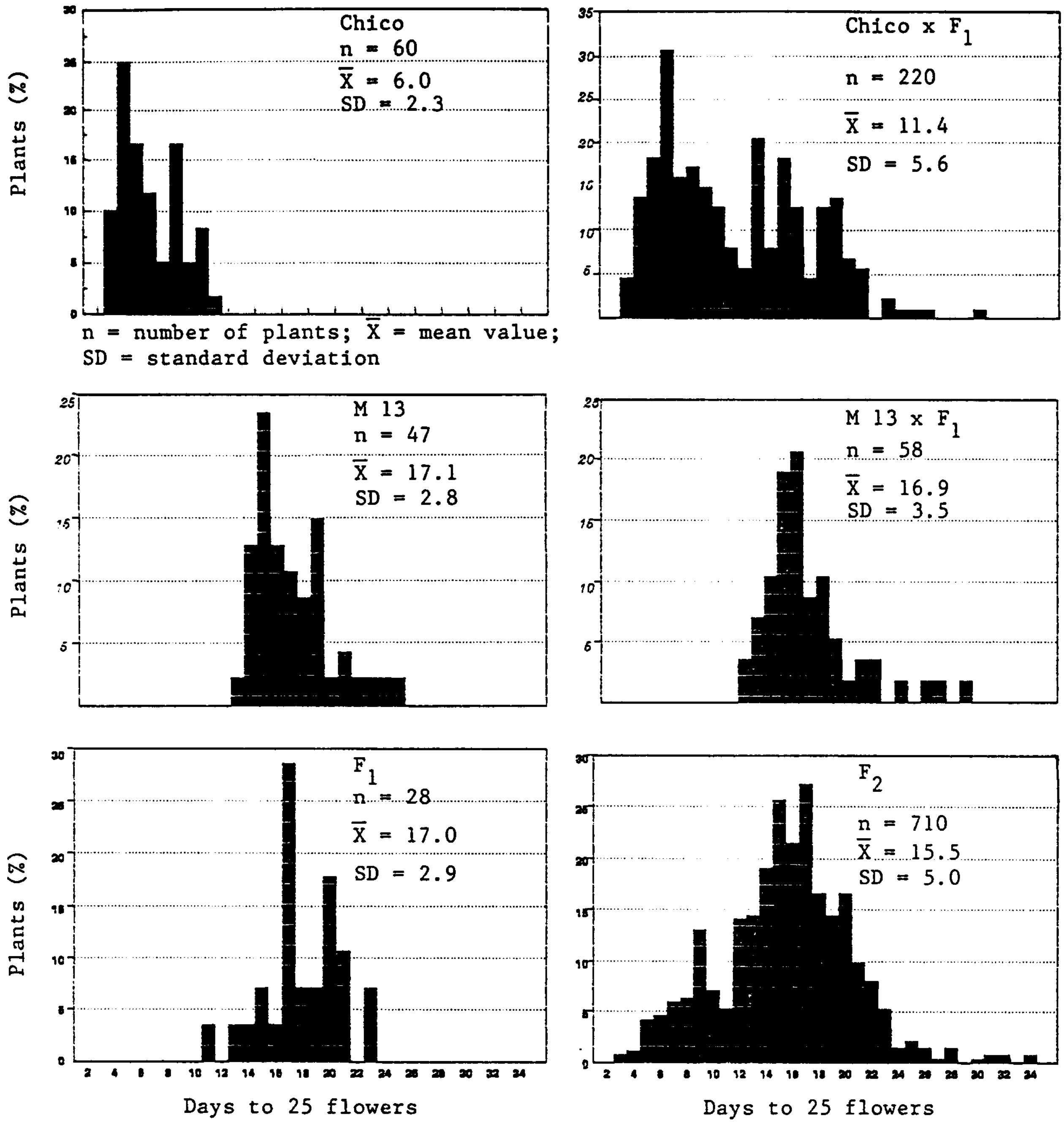

Fig. 2. Distribution of plants (%) for number of days from appearance of first flower to accumulation of 25 flowers in groundnut genotypes Chico and M 13, and their F_1, F_2, and backcross generations.

The frequency distributions of Chico, Gangapuri, and their F_1, F_2, and backcross generations were almost similar. The differences of the mean values of F_1, F_2, and backcross generations from the parental mean were nonsignificant. This indicated that Chico and Gangapuri probably possess the same allele for early flowering.

Of the 120 F_3 progenies from crosses involving Chico and Gangapuri with M 13, some did not germinate and many others had few plants. In instances where a population is expected to segregate into a 1:2:1 ratio of early-, intermediate-, and late-flowering types, it requires ≥ 5 individuals to have an acceptable probability (0.05) of detecting at least one parental type (early or late) (Hanson, 1959). Sixty-four F_3 progenies of Chico × M 13 and 24 of Gangapuri × M 13 had ≥ 5 plants at the time of recording observations on appearance of first flower. Thirty-seven F_3 progenies of the cross Chico × M 13 showed segregation for days to flowering, 12 were uniformly early flowering, and 15 were uniformly late. This fitted well to an expected ratio of 1 non-segregating early:2 segregating:1 non-segregating late progenies (χ^2 = 1.844; P = 0.250–0.500). The progenies in the cross Gangapuri × M 13, followed a similar pattern (χ^2 = 5.583; P = 0.050–0.100). Only 47 F_3 progenies in these two crosses had sufficient population (11 or more) for detecting both parental types. Twenty-two of these progenies did not show any segregation, with 11 each being uniformly early- and late-flowering types. The remaining 25 segregated for days to first flower. This again fitted well to a 1:2:1 ratio (χ^2 = 0.192; P = 0.900–0.950).

All but two of the 25 segregating F_3 progenies showed a good fit to 1:2:1 ratio of early-, intermediate-, and late-flowering plants. This further indicated that days to first flower is controlled by a single gene with additive gene action.

Days to accumulation of 25 flowers. Chico and Gangapuri took less time than M 13 to accumulate 25 flowers. The mean number of days were 6.0 ± 0.29 for Chico, 6.8 ± 0.21 for Gangapuri, and 17.1 ± 0.41 for M 13.

There was no significant difference between Chico × M 13 F_1 hybrid and its reciprocal (M 13 × Chico), and the F_1 took 17.0 ± 0.54 days, similar to that of M 13, to accumulate 25 flowers. This indicated the absence of maternal effects, and the presence of complete dominance of lateness over earliness in the control of this trait. The mean of the backcross generations with Chico lay between the means of Chico and M 13. The mean of the backcross generation with M 13 (16.9 ± 0.46) was similar to that of M 13. The F_2 mean of Chico × M 13 (15.5 ± 0.29 days) and M 13 × Chico (15.4 ± 0.23 days) did not differ significantly from each other, reconfirming the absence of reciprocal differences observed in the F_1 generation.

The distribution of Chico, M 13, and their F_1, F_2, and backcross generations for days to accumulation of 25 flowers is given in Fig. 2. For this trait also there was no overlap of distribution of Chico and M 13. The dip at 11 days from appearance of first flower to accumulation of 25 flowers in the F_2, and the backcross generation with Chico indicated the point of separation of early and late groups. The backcross with M 13 followed a distribution similar to that of M 13. Considering the criteria described earlier, and the distribution patterns of the F_2 and backcross generations, the plants which took up to 11 days ($\overline{X}$ + 2 SD of early parent) to accumulate 25 flowers were included in the early category, and those which took 12 or more days (> $\overline{X}$ - 2 SD of late parent) were classified as late.

Seventy-one out of 353 plants in Chico × M 13 and 66 out of 357 plants in M 13 × Chico F_2 generations were classified as early. The remaining F_2 plants, 282 in Chico × M 13, and 291 in M 13 × Chico were categorized as late. This segregation pattern fitted well to a 13 late:3 early ratio (Table 3). This ratio could be expected in the case of the dominant-recessive epistasis between two independently segregating genes wherein one gene when dominant is epistatic to the second, and the second gene when homozygous recessive is epistatic to the first gene. The backcross progenies with early parent Chico showed a good fit to an expected 1 late:1 early ratio, and all the backcross progenies with M 13 (late parent) were the late type (Fig. 2; Table 4).

In the F_2 generation of Gangapuri × M13, 208 plants were late and 53 were early (χ^2 = 0.415, P = 0.500–0.750), and in the reciprocal F_2, 252 were late, and 72 were early (χ^2 = 2.564, P = 0.100–0.250), which fitted well to a 13 late:3 early ratio, observed earlier in the crosses involving Chico and M 13 (Table 3). The backcross generation of Gangapuri × M 13 also followed a pattern similar to that of Chico × M 13 cross (Table 4).

Only 36 F_3 progenies of Chico and M 13 cross had 11 or more plants until the accumulation of 25 flowers. Of these progenies, 20 were non-segregating and 16 showed segregation. This fitted well to an expected 1 non-segregating:1 segregating ratio (χ^2 = 0.444, P = 0.500–0.750). In Gangapuri × M 13 cross also similar pattern was observed (χ^2 = 0.50, P = 0.250–0.500). In 3 of the 23 non-segregating progenies of these two crosses, all the plants were early types. The remainder progenies were late types. This again fitted to a ratio of 7 late:1 early non-segregating progenies, expected in the F_3 generation (χ^2 = 0.006, P = > 0.95). The 21 segregating progenies of these two crosses showed two types of segregation patterns. In 9 of these progenies the frequency of late plants was less than the early

Table 3. The chi-square values and probabilities of goodness of fit for epistatic F_2 ratios (13 late:3 early and 1 late:15 early) for days to accumulation of 25 flowers in the F_2 generation of crosses involving Chico, Gangapuri, and M 13

Cross	Number of plants		Epistatic ratios			
	Late	Early	(13 late:3 early)		(1 late:15 early)	
			χ^2	P	χ^2	P
Chico × M 13	282	71	0.430	0.500–0.750		
M 13 × Chico	291	66	0.016	0.900–0.950		
Total	573	137	0.138	0.500–0.750		
Heterogeneity			0.308	0.500–0.750		
Gangapuri × M 13	208	53	0.415	0.500–0.750		
M 13 × Gangapuri	252	72	2.564	0.100–0.250		
Total	460	125	2.630	0.100–0.250		
Heterogeneity			0.349	0.500–0.750		
Chico × Gangapuri	29	327			2.185	0.100–0.250
Gangapuri × Chico	28	329			1.548	0.100–0.250
Total	57	656			3.704	0.050–0.100
Heterogeneity					0.029	0.750–0.900

Table 4. The chi-square values and probabilities of goodness of fit for an expected ratio of 1 late:1 early in accumulation of 25 flowers in the backcross generations of crosses of M 13 with Chico and Gangapuri

Cross	Number of plants		χ^2	P
	Late	Early		
Chico × (Chico × M 13)	29	27	0.071	0.750–0.090
Chico × (M 13 × Chico)	72	92	2.439	0.100–0.250
Total	101	119	1.473	0.100–0.250
Heterogeneity			1.038	0.250–0.500
Gangapuri × (Gangapuri × M13)	26	36	1.613	0.100–0.250
Gangapuri × (M 13 × Gangapuri)	17	18	0.029	0.750–0.900
Total	43	54	1.247	0.250–0.500
Heterogeneity			0.395	0.500–0.750

plants, and in the remaining 12 progenies the frequency of late was more than that of the early plants. The segregating F_3 progenies, derived from an F_2 population segregating for a 13 late:3 early ratio, are expected to segregate in 13:3, 3:1, and 1:3, late and early ratios with frequencies of 4, 2 and 2, respectively. Further, in the F_3 progeny rows it is not practically feasible to differentiate between 13:3 and 3:1 ratio, as it requires a minimum of 667 plants in a population to differentiate between these two ratios at an acceptable probability of 0.05. Therefore to test the ratios between the segregating F_3 progenies, those segregating for 13:3 and 3:1::late:early were clubbed together, and those with 1 late:3 early ratio were kept separately. The 9 F_3 progenies which had a smaller frequency of late plants were classified to belong to 1 late:3 early ratio and the remaining 12 progenies could belong either to 13 late:3 early or 3 late:1 early ratio. This fitted well to a 6 (13:3 + 3:1::late:early):2(1 late:3 early) ratio (χ^2 = 3.571, P = 0.050–0.100).

The data in the F_3 generation of crosses of Chico and Gangapuri with M 13 were also analyzed by pooling the first 7 plants from each progeny which had 7 or more plants. This population was tested for an expect-

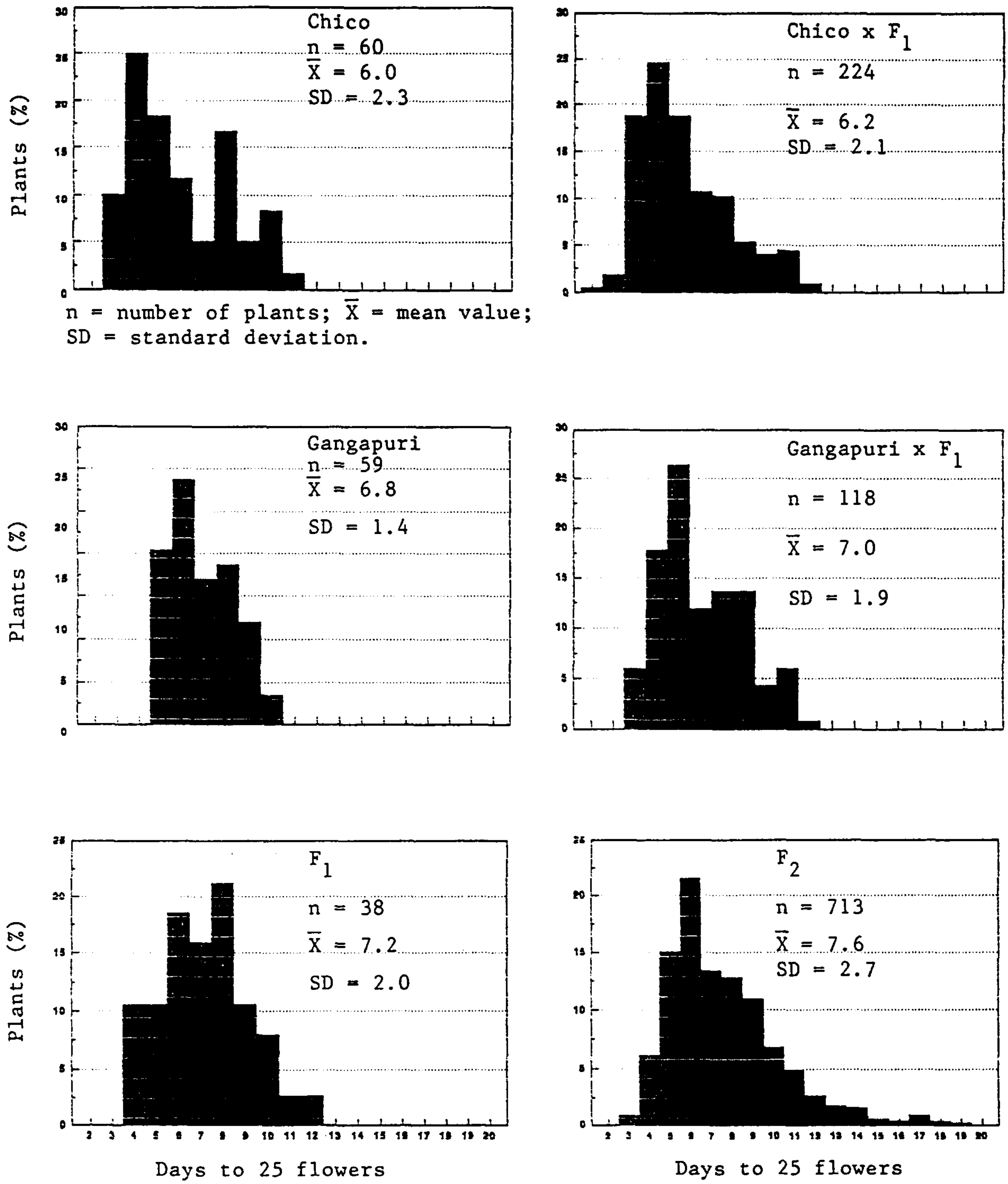

Fig. 3. Distribution of plants (%) for number of days from appearance of first flower to accumulation of 25 flowers in groundnut genotypes Chico and Gangapuri, and their F_1, F_2, and backcross generations.

ed 49 late:15 early ratio. Out of 350 plants, 75 fell in the early category and the remaining 275 in the late category, giving a good fit to the ratio ($\chi^2 = 0.787$, P = 0.250–0.500).

Figure 3 shows the frequency distribution of early parents, Chico and Gangapuri, and their F_1, F_2, and backcross generations. In the F_2 generation, 29 plants out of 356 in Chico × Gangapuri cross, and 28 out of 357 plants in the reciprocal cross were late in accumulating 25 flowers. The remaining plants, 327 in Chico × Gangapuri and 329 in its reciprocal (Gangapuri × Chico), were early types. This fitted well to a 1 late:15 early ratio (Table 3), suggesting that earliness in accumulation of 25 flowers in Chico and Gangapuri is controlled by two dominant genes without cumulative effects, with double recessive being late. All the plants in the backcross generations were early, similar to Chico or Gangapuri or their F_1 generation.

Sixteen out of 26 F_3 progenies, which had sufficient populations in the Chico × Gangapuri cross showed segregation, and the remaining 10 were of non-segregating type fitting well to a 1 non-segregating:1 segregating ratio (χ^2= 1.385, P = 0.100–0.250). Further, the non-segregating progenies contained 2 progenies which had all the late plants giving a good fit to a 1 late:7 early ratio (χ^2 = 0.514, P = 0.250–0.500). Among the 16 segregating progenies, 11 progenies showed an excellent fit to 1 late:3 early ratio, individually as well as on pooled basis (χ^2 = 0.373, P = 0.500–0.750), and 5 progenies fitted well to a 1 late:15 early ratio, individually as well as on pooled basis (χ^2 = 2.218, P = 0.100–0.250). This also agreed with an expected 1:1 ratio between progenies segregating for 1 late:15 early and 1 late:3 early ratios (χ^2 = 2.250, P = 0.100–0.250).

Further, the pooled data from the first 7 plants from each F_3 progeny, when tested for a pooled 9 late:55 early ratio, showed an excellent fit (χ^2 = 0.699, P = 0.250–0.500), further indicating that the days to accumulation of 25 flowers in two early parents Chico and Gangapuri is governed by two duplicate-dominant genes. The segregation pattern of Chico × M 13, Gangapuri × M 13, and Chico × Gangapuri crosses suggest that 3 different genes are involved in the control of accumulation of 25 flowers in these parents with 2 of them interacting in any given combination.

Undoubtedly the inheritance of early maturity in groundnut is not simple. The two components of earliness, days to first flower and days to accumulation of 25 flowers, are inherited in different manners. The former is controlled by a single gene with additive gene action. For the latter, 3 genes with two types of epistases: dominant-recessive and duplicate-dominant, are involved. Obviously, the segregation for lateness in the F_2 generation of a cross between two early parents (Table 3) introduces a new element in the selection program for early maturity. Genetic studies involving other parents are in progress at ICRISAT Asia Center, Patancheru, India.

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