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Threshold Concentration of Plasmon-sensitive Polygenes in the Expression of Quantitative Characters of Maize (*Zea mays* L.)*

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Summary. Reciprocal crosses between varieties of maize were developed in such a way that the genome of one variety was introduced into the cytoplasm of the other in fractions of 25, 50, and 75 per cent. Cytoplasmic effects on yield, maturity, plant height, and ear height were measured at each of the three nuclear constitutions. The results indicated that the cytoplasmic effects on quantitative characters were not consistently produced irrespective of the nuclear constitution and some relationship existed between the number of polygenes introduced and the cytoplasmic effects. The hypothesis was put forward that cytoplasmic effects on quantitative characters would be expressed only when the genes of one parent remained below a certain threshold concentration in the hybrid nucleus. Once this level was crossed by increasing the number of genes alien to the cytoplasm the cytoplasmic effects disappeared.

1. Introduction

Following the pioneering work of Fleming, Kozelnicky, and Browne (1960), a number of workers (Bhat and Dhawan, 1968a, 1969; Brown, 1961; Singh, 1965, 1966), using maize, have shown that in addition to simply inherited traits like male-sterility, the expression of polygenically inherited characters is also under cytoplasmic control. All these workers studied the cytoplasmic effects in reciprocal crosses by transferring either the whole or a part of the genome of one line into the cytoplasm of the other. For example, Fleming *et al.* (1960) and Bhat and Dhawan (1969) studied the cytoplasmic effects between reciprocal $F1$ crosses i.e. after reciprocally transferring only 50 per cent of the genome. Brown (1961) substituted the WF9 genome for the whole P_2 genome and studied the cytoplasmic effect. Singh (1965), on the other hand, compared exotic cytoplasm stocks with corn belt cytoplasm stocks by reciprocally transferring only 96.875 per cent of corn belt genome into the two cytoplasmic types. None of these workers studied the cytoplasmic effects after transferring a particular genome in fractions into an alien cytoplasm. This would seem to be very important in view of the fact that we are dealing with cytoplasmic effects on characters polygenically inherited. It would be expected that with the introduction of each fraction of the genome into an alien cytoplasm there would be a proportionate increase in the number of polygenes from the donor and it would be interesting to observe whether this increase in the polygenes nullifies the cytoplasmic effects.

The present investigation was undertaken to study the cytoplasmic effects after reciprocally transferring into alien cytoplasms genomes of different varieties of maize in fractions of 25, 50, and 75 per cent.

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2. Materials and Methods

Two sets of materials were developed. In set one, four varieties — Llera III (L III), Yellow Tuxpan (YT), Eto Amarillo (EA), and San Andres Tuxtla (SAT) — were each crossed with Sikkim Primitive 2 (SP 2) to develop reciprocal F_1 and backcrosses as indicated in Table 1. In this way the genome of one variety was introduced into the cytoplasm of the other in fractions of 25, 50, and 75 per cent. The three nuclear constitutions (levels) were designated N_1, N_2, and N_3, respectively. In the second set, each of the four varieties SP 2, Pira Blanco (PB), Pollo Segregaciones (PS), and Pollo Amarillo (PA) was crossed with Colorado (Co) in the same way as in set one. In all, eight groups were developed with eight entries in each group (Table 1).

The eight entries within each group were planted in a split-plot design with four main plots and two sub-plots within each main plot. The three nuclear levels and the parents constituted the main plots and the two cytoplas-

Table 1. *Crossing plan of the materials studied*

Entry No.	Pedigree	Nucleus: Nuclear constitution (%)	Nucleus: Code	Cytoplasmic source
1	*A**	*A* (100)	P_1	A
2	*B**	*B* (100)	P_2	B
3	(A × B) × *A*	*A*:*B* (75) (25)	N_1	A
4	(*B* × *A*) × *A*	*A*:*B* (75) (25)	N_1	B
5	*A* × *B*	*A*:*B* (50) (50)	N_2	A
6	*B* × *A*	*A*:*B* (50) (50)	N_2	B
7	(*A* × *B*) × *B*	*A*:*B* (25) (75)	N_3	A
8	(*B* × *A*) × *B*	*A*:*B* (25) (75)	N_3	B

* *A* and *B* are arbitrary varietal names

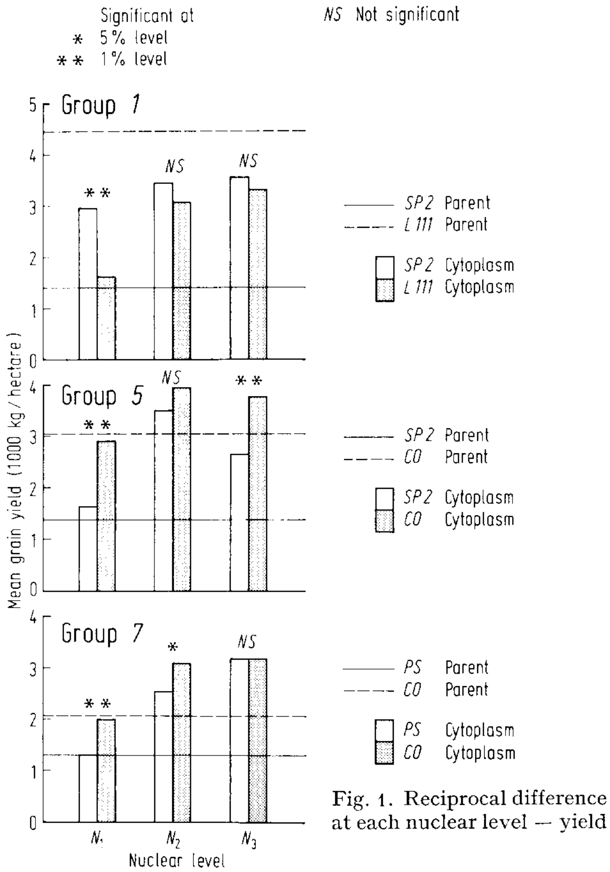

Fig. 1. Reciprocal difference at each nuclear level — yield

mic sources constituted the sub-plots. The experiment was conducted during the summer 1965 at the Division of Genetics, I.A.R.I., New Delhi, and was replicated four times. Plot size was one row 9 metres long. Row-to-row spacing was 0.75 metres and plant-to-plant spacing within a row was 25 cm.

Data were recorded on four quantitative characters, grain yield, number of days to 75 per cent silking (maturity), plant height, and ear height, in the manner described by Bhat and Dhawan (1969).

The significance of the difference between reciprocal crosses at each of the three nuclear levels was calculated for only those groups in which the analysis of variance for split-plot design revealed cytoplasmic effect and/or "nuclear × cytoplasm" interaction to be significant.

3. Results

The cytoplasmic effect on grain yield was significant in groups 1, 5, and 7. The reciprocal differences were significant at: N_1 nuclear level in group 1; N_1 and N_3 nuclear levels in group 5; N_1 and N_2 nuclear levels in group 7 (Fig. 1).

Maturity was significantly influenced by the cytoplasm in groups 1, 2, 5, 7, and 8, while "nuclear × cytoplasm" interaction was significant in groups 1, 2, 4, 5, and 8. The reciprocal differences were significant at: N_1 nuclear level in groups 1 and 5; N_1 and N_2 nuclear levels in group 2; N_3 nuclear level in groups 4 and 8; all the three nuclear levels in group 7 (Fig. 2).

The cytoplasmic effect on plant height was significant in groups 3, 5 and 6 and "nuclear × cyto-

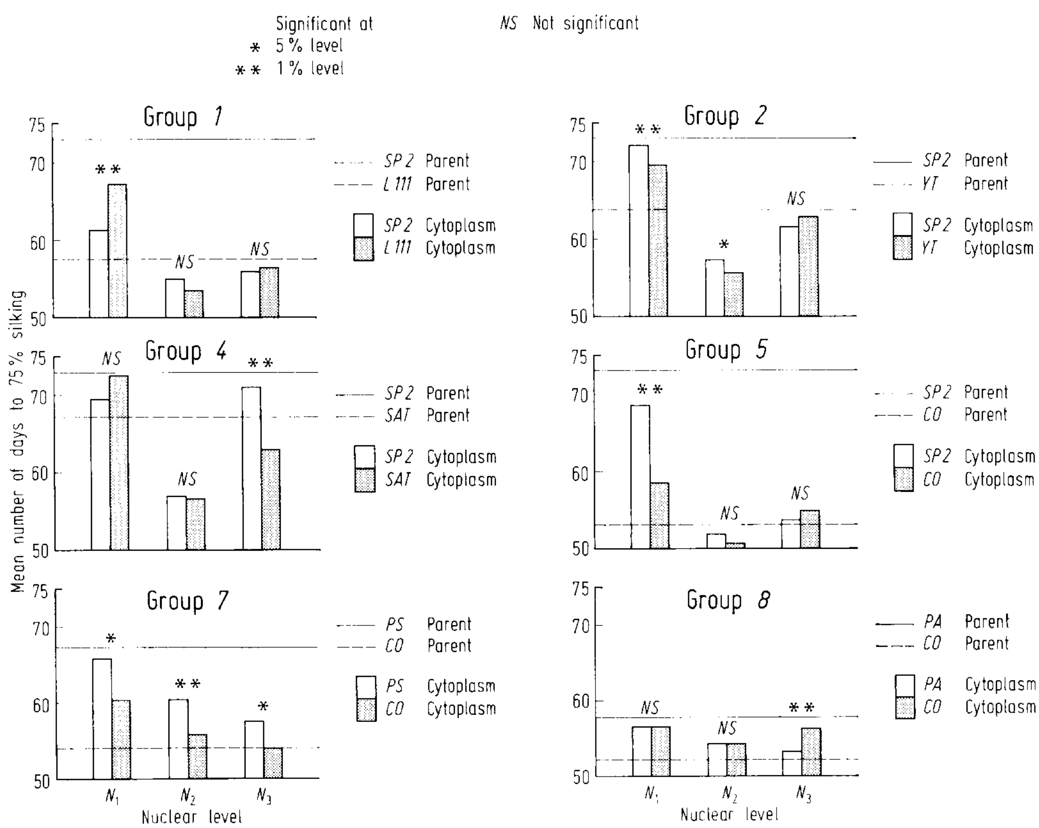

Fig. 2. Reciprocal difference at each nuclear level — maturity

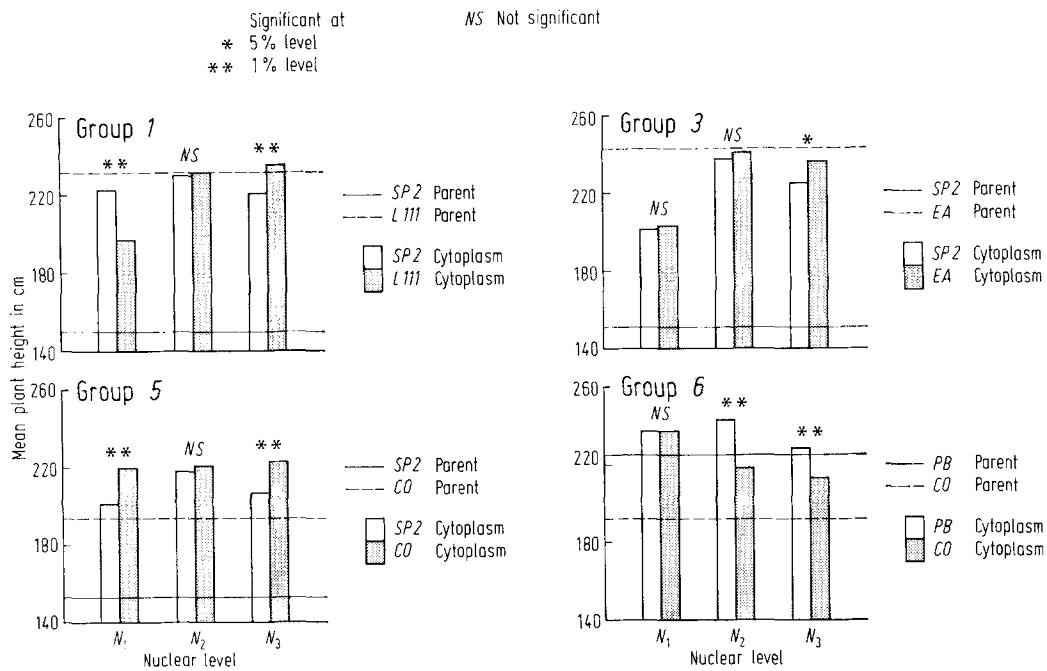

Fig. 3. Reciprocal difference at each nuclear level — plant height

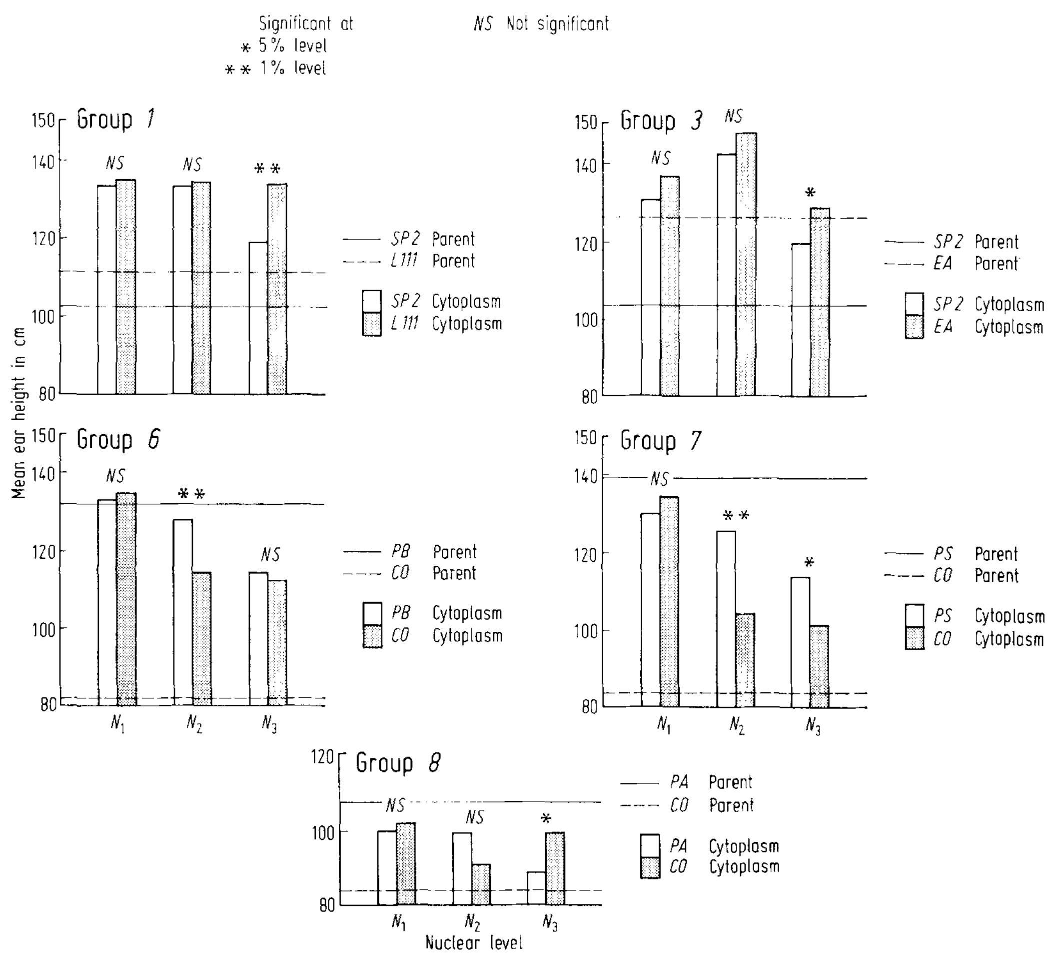

Fig. 4. Reciprocal difference at each nuclear level — ear height

plasm" interaction was significant in groups 1, 5, and 6. The difference between reciprocal crosses was significant at: N_1 and N_3 nuclear levels in groups 1 and 5; N_2 and N_3 nuclear levels in group 6; N_3 nuclear level in group 3 (Fig. 3).

The analysis of variance of ear height revealed that the cytoplasmic effect and "nuclear × cytoplasm" interaction were significant in groups 1, 3, 6, and 7, and 1, 6, 7, and 8, respectively. The reciprocal cross differences were significant at: N_3 nuclear level in groups 1, 3, and 8; N_2 nuclear level in group 6; N_2 and N_3 nuclear levels in group 7 (Fig. 4).

4. Discussion

Extensive studies by Michaelis (1954) on *Epilobium* have shown that even though the cytoplasms of two strains are different the quality and quantity of plasmon-sensitive genes should be sufficient in the F_1 or backcross plants for the manifestation of these differences. In maize, ample data has been reported on the first aspect of the study (Bhat and Dhawan, 1968a, 1969, 1970a, b; Fleming *et al.*, 1960; Singh, 1965, 1966), while the present investigation was designed to find out whether any relationship existed between the quantity of plasmon-sensitive polygenes and cytoplasmic effects.

Our results indicated that cytoplasmic effects on quantitative characters were not consistently produced irrespective of the nuclear constitution and some relationship existed between the number of polygenes introduced and the cytoplasmic effects. A hypothesis to explain these results is proposed below.

In the case of quantitative characters, where the genes have simple, small and supplementary action (Mather, 1949), it appears that the cytoplasmic effect is expressed only when the genes of one parent remain below a certain threshold concentration in the hybrid nucleus. Once this level was crossed by increasing the number of genes alien to the cytoplasm the cytoplasmic effect disappeared. In the terminology of v. Wettstein (quoted from Caspari, 1948), "antecedent" cytoplasm would become "recedent" on increasing the polygenes alien to the antecedent cytoplasm. The hypothesis was first proposed by us in 1968 (Bhat and Dhawan, 1968b) and is elaborated here.

Before discussing the hypothesis in the light of our results, it would be important to know whether the reciprocal cross differences were due to the cytoplasm of variety *A* or variety *B* or cytoplasms of both the varieties *A* and *B*. Our previous studies with the reciprocal crosses reported here (Bhat and Dhawan, 1970a, b) have shown that all the three situations exist. Therefore, the disappearance of the cytoplasmic effects on grain yield at the N_2 and N_3 nuclear levels in the crosses between SP 2 and L III might have been the result of the genes from the L III parent crossing the threshold limit beyond the N_1 nuclear level. It may be recalled that the N_1, N_2, and N_3 nuclear levels had, respectively, 25, 50, and 75 per cent genomes from the L III parent and a significant cytoplasmic effect was produced only when the proportion of the L III genome in SP 2 cytoplasm remained less than 25 per cent. Once this proportion was increased to 50 and 75 per cent the cytoplasmic effect disappeared.

In certain crosses the cytoplasm of both varieties provided an unsuitable substrate for the action of each others' genes. For example, the genes controlling grain yield in the crosses of SP 2 and Co were below the threshold limit at the N_1 and N_3 nuclear levels thus producing a significant cytoplasmic effect. Once this limit was crossed at the N_2 nuclear level no significant effect was produced. The cytoplasmic effect on various characters obtained in other groups could also be explained on the basis of this hypothesis of a threshold concentration of plasmon-sensitive polygenes.

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