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Correlation Between Chiasma Frequency and Quantitative Traits in Upland Cotton (*Gossypium hirsutum* L.)

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Summary. Four locally adapted and high yielding cultivars of upland cotton were examined in order to elucidate the relationship between total chiasma frequency and quantitative traits, including yield and fiber properties. Total chiasma frequency per nucleus was found to correlate positively with boll number ($r = 0.4041$), seed cotton yield ($r = 0.6003$), seed index ($r = 0.4624$), lint yield ($r = 0.7325$), and lint index ($r = 0.9534$). The data are discussed from the point of view that the heterozygosity caused by increased chiasma frequency in inbreeding cotton cultivars is an important compensating mechanism for enhancing effective recombination and genetic variability.

Key words: Chiasma frequency – Quantitative traits – Genetic correlations – Genetic variability

Introduction

The genetic variability of a species is to a large extent controlled by the recombination of genes or gene complexes between homologous chromosomes. The chiasma is a visible expression of genetical crossing-over and, as such, serves as a potential marker of the degree of recombination between linked genes. The frequency and distribution of crossovers are measured directly by observing chiasmata at the diplotene stage of meiotic prophase. Although for a given species the number of chiasmata per nucleus deviates little from the average (Shaw et al. 1976), chiasma frequency differences between genotypes (Srivastava and Malik 1974; Murray 1976) and between male and female reproductive cells (Traut 1977) of the same species have been observed. Some individual differences can also be caused by mutations (Tease and Jones 1976), B-chromosomes (Patton 1977), chromosome rearrangements (Baker et al. 1976), amounts of heterochromatin (Rhoades 1978), or environmental factors (Couzin and Fox 1974).

Significant genetic association of chiasma frequency in relation to heterosis (Srivastava and Balyan 1977; Srivastava 1979) has been demonstrated. The present study was undertaken in four locally adapted and high yielding cultivars of cotton to determine whether (a) these varieties differ in mean chiasma frequency and (b) correlations exist between chiasma frequency and quantitative traits. An attempt has been made to study the correlation of chiasma frequency to a number of quantitative characters, such as boll number per plant, plant height, cotton seed yield, lint yield, seed index and lint index, and the results provide evidence to support the hypothesis that excessive genetic homogeneity of inbreeding cultivars is compensated for by enhanced chiasma frequency.

Material and Methods

Four cotton cultivars, namely, 'Stroman 254', 'Del Cerro', 'Acala 1517-70' and 'Acala 1517-BR2' were grown in randomized blocks with three replications. There were three rows each of ten plants, with 60 cm between rows and 45 cm between plants within each row, per plot. The recommended cultural and spraying practices were followed during the crop season. Young flower buds at the appropriate stage were taken from fifteen randomly selected plants per cultivar between the hours of 8 a.m. and 10 a.m. and fixed in Carnoy's solution (6 parts absolute alcohol: 3 parts chloroform: 1 part glacial acetic acid). In order to obtain better transparency of the cytoplasmic background, the anthers were subjected to a short pretreatment in 1 N HCl (24°C, 1-2 min.) and thereafter washed thoroughly with distilled water to remove excess acid and acid-soluble materials. For cytogenetical studies, pollen mother cells (PMC's) from pretreated anthers were stained and examined using the conventional iron-aceto-carmine or iron-propiono-carmine squash techniques. Because of the relatively small size of the cotton chromosomes and the related technical difficulty in identifying different stages of meiotic prophase I, most of the cytological studies concerning chiasma frequency in cotton have so far concentrated on recording the number of bivalents from metaphase I cells (Phillips 1974 and personal communication). In this study, only PMC's in the diplotene stage were carefully scored for chiasmata. All terminal chiasmata in bivalents

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Table 1. Estimates of mean, standard deviation (S.D.), and coefficient of variation (C.V.) for various quantitative traits in four cultivars of upland cotton

Cultivars	Statistical parameters	Chiasma frequency/ PMC	Plant height (cm)	Boll number/ plant	Seed cotton yield (g)	Seed index (g/100 seed)	Lint yield (g/plant)	Lint index (g/100 seed)
'Stroman 254'	Mean	21.20	115.9	16.57	71.4	12.19	43.34	7.62
	S.D. (±)	5.71	11.64	4.63	19.8	0.90	11.20	0.54
	C.V. (%)	26.95	10.03	27.98	28.0	7.45	25.80	7.28
'Del Cerro'	Mean	16.97	110.4	14.5	59.0	13.3	32.3	7.43
	S.D. (±)	4.35	13.9	3.61	14.4	1.1	8.25	0.78
	C.V. (%)	25.64	12.63	24.95	24.39	8.67	25.54	9.72
'Acala 1517-70'	Mean	13.13	134.5	16.16	64.03	11.69	35.56	6.42
	S.D. (±)	2.66	17.76	4.0	15.6	1.00	9.25	0.90
	C.V. (%)	20.27	13.20	24.8	24.34	9.60	26.04	14.0
'Acala 1517-BR2'	Mean	14.36	88.2	14.06	45.1	10.83	28.0	6.30
	S.D. (±)	5.30	13.63	3.32	10.2	0.90	6.31	0.64
	C.V. (%)	36.90	15.46	23.6	22.27	8.37	22.63	10.23

The data on chiasma frequency represent values from a range of 50-80 PMC's studied per cultivar; and those on quantitative traits represent values from 50 randomly selected plants examined per cultivar

Table 2. Analysis of variance for various traits in the four cultivars of upland cotton

Traits	F Value
Chiasma frequency/PMC	17.59[a]
Plant height (cm)	52.63[a]
Boll number/plant	2.92
Seed cotton yield (g)	15.56[a]
Seed index, g/100 seed	29.97[a]
Lint yield, g/plant	15.95[a]
Lint index, g/100 seed	16.86[a]

[a] Significant at the 0.01 level of probability

were scored with a frequency of 1 and 2; interstitial chiasmata in bivalents were recorded with 3. A minimum of 50 plants per cultivar per replication were selected for quantitative measurements and fiber properties. The following characters were evaluated in both the field and laboratory: (1) plant height in cm; (2) boll number/plant, the total number of bolls which accounted for the yield were counted and recorded; (3) total yield of seed cotton, the total produce of seed cotton/plant was weighed in g and recorded; (4) seed index, in g weight of 100 seeds; (5) lint yield, the total produce of lint/plant was weighed in g and recorded; and (6) lint index, in g of lint/100 seeds. The data based on individual plant observations were analysed as a randomized complete block following the standard statistical procedures (Steel and Torrie 1960).

Results and Discussion

Table 1 summarizes the estimates of mean, standard deviation, and coefficient of variation with respect to chiasma frequency and other quantitative traits, and Table 2 gives the analysis of variance for these characters. Differences among the four cotton cultivars are significant for all characters with the exception of boll number/plant. The F-value for differences in chiasma frequency and other quantitative traits is highly significant, indicating the existence of substantial differences between the cultivars. The two cultivars 'Stroman 254' and 'Del Cerro' possess relatively increased chiasma frequency, and this enchanced chromosome behaviour is reflected in other quantitative measurements and fiber properties, respectively. The other two cultivars 'Acala 1517-70' and 'Acala 1517-BR2' show low chiasma frequency which is further in concordance with various quantitative trait measurements; the cultivar 'Acala 1517-BR2' has the lowest values for mean chiasma frequency as well as for all quantitative measurements and fiber properties. Although these 'Acala' cultivars are taxonomically classified as *G. hirsutum*, their pedigrees reveal that each group has remained largely discrete during cultivar development (Ramey 1966; Quisenberry 1975). The progressive improvements of the original germplasm 'Acala 4-42' into distinct cultivars, obtained by selecting within material which had been inbred for several generations, may be related to their amphidiploid origin. The present cytogenetical and quantitative observations also suggest the effectiveness of individual cultivar selection within a given germplasm for progressive improvement and development of distinct cultivars.

The data on mean chiasma frequency along with its respective confidence interval are illustrated in Figure 1. The two cultivars 'Stroman 254' and 'Del Cerro' have a quite distinct confidence interval for their respective mean chiasma values suggesting their genetic divergence in terms

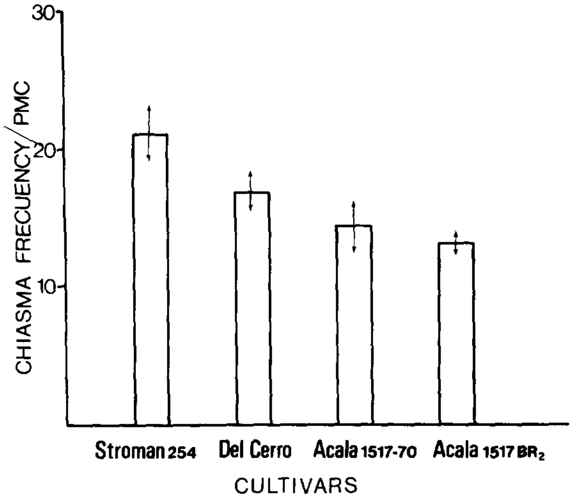

Fig. 1. Chiasma frequency variation in four cultivars of upland cotton. The arrow over each bar indicates confidence interval (± 2 S.D.) for the mean value

of chromosome pairing and cross-over behaviors. The other two 'Acala' cultivars appear to be genetically less diverged from each other with respect to chiasma frequency, as the values of confidence interval for their means coincide. The similarity in chiasma frequency of these two cultivars could be interpreted in the sense that they both share original 'Acala 1517' germplasm, and sufficient selection pressure for their progressive improvement and divergent evolution into two distinct cultivars has not yet occurred. It is worth noting that the two 'Acala' cultivars, i.e., '1517-70' and '1517-BR2', represent relatively new selections based on local adaptations and yielding attributes from 'Acala 1517'. The data concerning position and frequency distribution of chiasmata in the four cultivars are presented in Table 3. Most of the small chromosomes which were scored for chiasmata had a single chiasma. A few other chromosomes showed a distribution of two chiasmata per bivalent. Some bivalents with three chiasmata were scored, but it was rather difficult to score bivalents beyond three chiasmata in these cultivars. Although all the cultivars with the exception of 'Acala 1517-BR2' possessed 8-17% interstitial chiasmata, the majority of chiasmata consisted of a terminal type. There have been specific studies on position and frequency distribution of chiasmata in populations of *Capaea hortensis* (Price 1975) and *Phaseolus vulgaris* (Srivastava 1979), indicating that interstitial chiasmata are more important in producing effective recombination and directly determine the release of variability in the population. While this relationship may also be true in the case of cotton cultivars which possess interstitial chiasmata, a strong claim relating to interstitially distributed chiasmata and their possible role in maintaining population genetic variability can not yet be made because of apparent technical difficulties in making counts of bivalents having three or more chiasmata in cotton. It is imperative, therefore, to study meiotic chromosome behavior in cotton at the electron microscopic level in order to have more detailed understanding of the ultrastructural position distribution of chiasmata.

There is strong evidence, based on ultrastructural studies of the frequency and distribution of chiasmata, that meiotic crossing-over invariably occurs in the presence of the synaptonemal complex (SC), and models of crossing-over now attempt to integrate the SC into the process (Gillies 1975; Holliday 1977). Direct electron microscopic observations of chiasmata in bivalents at diplotene reveal nodule like structures called 'SC remnants' as sites of crossing-over (Moens 1978). The most extensive observation on the correlation between chiasmata and SC remnants has been reported by Zickler (1977) in the fungus *Sordaria macrospora*. Light microscopy of cells in diplotene show that on the average there are 18 chiasmata/nucleus for 20 nuclei scored; electron microscopic observation of completely reconstructed diplotene nuclei exhibit a range of 17 to 21 SC remnants/nucleus. As the cultivars of *G. hirsutum* are amphidiploids containing multiple sized chromosomes, an additional ultrastructural analysis at the electron microscopic level may give more accurate information on the position and frequency distri-

Table 3. Cytogenical data obtained on position and frequency distribution of chiasmata in four cultivars of upland cotton. The data represent values from a range of 50-90 PMC's studied per cultivar

Cultivar	Mean[a] chiasmata frequency/PMC	Bivalents distribution with different number of chiasmata (%)				Position distribution of chiasmata (%)	
		0	1	2	3	Terminal	Interstitial
'Stroman 254'	21.2	39.78	43.0	11.92	5.3	82.93	17.07
'Del Cerro'	16.9	45.26	39.3	9.64	5.8	89.40	10.60
'Acala 1517-70'	14.4	52.89	30.13	13.18	3.8	91.93	8.06
'Acala 1517-BR2'	13.1	64.48	21.4	14.12	–	100.0	–

[a] The data in this column is repeated for convenience of making comparison

Table 4. Estimates of simple correlation coefficients and their standard errors between chiasma frequency and some quantitative traits in upland cotton. S.E. is given in parenthesis for each r value

Trait	Plant height	Boll number per plant	Seed cotton yield	Seed index	Lint yield	Lint index
Chiasma frequency	–0.03613	+ 0.4041[a]	+ 0.6003[b]	+ 0.4624[a]	+ 0.7325[b]	+ 0.9534[b]
	(0.0188)	(0.172)	(0.1138)	(0.1678)	(0.1291)	(0.1020)

[a, b]significant at the 0.01 and 0.05 levels of probability, respectively

bution of chiasmata/bivalent in terms of SC nodules or SC remnants. A generalization could, however, be made that there is a correspondence between chiasmata and SC remnants; both possibly reflect site-specific crossing-over and recombinant events.

As the F values for differences between cultivars with respect to chiasma frequency and five economically important quantitative traits were highly significant at the 1% level of probability, the genetic correlation coefficients between the chiasma frequency and these quantitative measurements could be calculated; the relevant results are presented in Table 4. The correlation coefficients between chiasma frequency and five characters, e.g., boll number, seed cotton yield, seed index, lint yield, and lint index, were all positive and significant at both the 5% and 1% levels of probability. There was no correlation (r = –0.03613) between chiasma frequency and plant height. The negative correlation between height and chiasma frequency must be considered relative to the fact that height is not a yield-contributing trait in upland cotton; semi-dwarf cultivars have been developed to meet the requirements of narrow-row, high-population cotton production (Quisenberry 1977). Diallel analysis indicates that the genetic variation for plant height is primarily additive, with a small, although significant, dominance component associated with it (Singh et al. 1972b). The genetic association between chiasma frequency and yield and fiber characters appears to be direct and positive, as the correlation coefficients for seed cotton yield and lint yield were relatively high. These findings are in concordance with those of earlier workers (Muntzing and Akdik 1948; Tehrani and Wricke 1977; Srivastava and Balyan 1977) where some positive genetic associations between chiasma frequency and several agronomically and physiologically important traits have been established.

How could the results of correlations between chiasma frequency and quantitative traits be interpreted in genetic terms? The estimates of the genetic variances reveal that both additive and non-additive (dominance and epistatic genes) genetic components are important for most yield and fiber characters in upland cotton (Singh et al. 1972a; Culp and Harrel 1975). Chiasma frequency also shows a typical attribute of polygenic traits (Simchen and Stamberg 1969) and, as such, is supposed to be controlled by a polygenic system. Inbred lines exhibit lower frequencies of chiasmata (Rees and Thomson 1956; Srivastava 1979), and there is a steady decrease in chiasma frequency as inbreeding increases (Sybenga 1958). Total chiasma frequency seems to correlate strongly with boll number, seed cotton yield, seed index, lint yield and lint index in the four cultivars of upland cotton studied. Chiasmata along with their SC remnants are presumably important in recombining lengths of homologous chromosomes, and if gene loci are heterozygous they may lead to a more diverse array of gametes and thus effective genetic recombination. Hence the occurrence of a high chiasma frequency may be an important compensating mechanism for enhancing effective recombination in cotton and other self-fertilized crops. It is of interest that the two cultivars 'Stroman 256' and 'Del Cerro', besides being higher for all the key quantitative traits, exhibit a higher degree of chiasma frequency than the other two cultivar populations. In an amphidiploid species like cotton, which is now fully diploidized, exhibiting monomeric inheritance for almost all the characters, one would expect the greatest differences in variability between cultivars from different varieties; cultivars from the same variety should be quite similar except for the extremely rare exception of gene mutations and chromosome aberrations. Within population variability in terms of heterozygosity or homozygosity for yield and fiber properties has been demonstrated in experimental populations of the individual plants or of the cultivar in cotton (Meyer and Meyer 1970). It is suggested that some level of heterozygosity caused by increased chiasma frequency might have important effects on the maintenance of genetic variability in these cotton cultivars. The positive correlations between chiasmata and quantitative traits are most likely due to dispersed genes on the chromosomes possessing combined additive and epistatic genes which are brought together after crossing-over in linked favorable gene complexes.

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Literature

Baker, B.S.; Carpenter, A.T.C.; Espisito, M.S.; Espisito, R.E.; Sandler, L.: The genetic control of Meiosis. Ann. Rev. Genet. **10**, 53-134 (1976)

Couzin, D.A.; Fox, D.P.: Variation in chiasma frequency during tulip anther development. Chromosoma **46**, 173-179 (1974)

Culp, T.W.; Harrell, D.C.: Influence of lint percentage, boll size, and seed size on lint yield of upland cotton with high fiber strength. Crop Sci. **15**, 741-746 (1975)

Gillies, C.B.: Synaptonemal complex and chromosome structure. Ann. Rev. Genet. **9**, 91-110 (1975)

Holliday, R.: Recombination and meiosis. Philos. Trans. Roy. Soc. (Lond.) Ser. B **277**, 359-370 (1977)

Meyer, V.G.; Meyer, J.R.: Some sources of variability in boll and fiber properties of cotton (*Gossypium hirsutum* L.). Crop Sci. **10**, 699-702 (1970)

Moens, P.B.: Ultrastructural studies of chiasma distribution. Ann. Rev. Genet. **12**, 433-450 (1978)

Muntzing, A.; Akdik, S.: Cytological disturbances in the first inbred generations of rye. Hereditas **34**, 485-509 (1948)

Murray, B.G.: The cytology of the genus *Briza* L. (Gramineae). II. Chiasma frequency, polyploidy and interchange heterozygosity. Chromosoma **57**, 81-93 (1976)

Patton, J.L.: B-chromosome systems in the pocket mouse, *Perognathus baileyi*: meiosis and c-band studies. Chromosoma **60**, 1-14 (1977)

Phillips, L.L.: Cotton (*Gossypium*). In: Handbook of Genetics, Vol. 2. (ed.: King, R.C.), pp. 111-133. New York: Plenum Press 1974

Price, D.J.: Chiasma frequency variation in *Cepaea hortensis* (Mull) and a comparison with *C. nemoralis* (L) Genetica **45**, 497-508 (1975)

Quisenberry, J.E.: Inheritance of fiber properties among crosses of Acala and high plains cultivars of upland cotton. Crop Sci. **15**, 20-204 (1975)

Quisenberry, J.E.: Inheritance of plant height in cotton. II. Diallel analyses among six semidwarf strains. Crop Sci. **17**, 347-350 (1977)

Ramey, H.H.: Historical review of cotton variety development. Cotton improvement conf., Proc. **18**, 310-326 (1966)

Rees, H.; Thompson, I.B.: Genotypic control of chromosome behavior in rye III. Chiasma frequency in homozygotes and heterozygotes. Heredity **10**, 409-424 (1956)

Rhoades, M.M.: The genetic effects of heterochromatin in maize. In: Proc. Int. Maize Symp. Genet. Breed. (ed.: Walden, D.B.) New York: Wiley-Interscience 1978

Shaw, D.D.; Knowles, G.R.: Comparative chiasma analysis using a computerized optical digitizer. Chromosoma **59**, 103-127 (1976)

Simchen, G.; Stamberg, J.: Genetic control of recombination in *Schizophyllum commune*: specific and independent regulation of adjacent and non-adjacent chromosomal regions. Heredity **24**, 269-381 (1969)

Singh, R.B.; Dahiya, R.P.; Jain, D.K.: Genetics of ginning and fiber characters in upland cotton. Ind. J. Genet. Pl. br. **32**, 125-137 (1972a)

Singh, R.B.; Jain, D.K.; Dahiya, R.P.: Genetic analysis of yield characters in upland cotton (*Gossypium hirsutum*). Ind. J. Genet. Plant Breed. **32**, 138-152 (1972b)

Srivastava, H.K.: Heterosis for chiasma frequency and quantitative traits in common beans (*Phaseolus vulgaris* L.). Theor. Appl. Genet. **56**, 25-29

Srivastava, H.K.; Baylan, H.S.: Increased chiasma frequency in some hybrids of pearl millet. J. Hered. **68**, 338-340 (1977)

Srivastava, H.K.; Malik, K.P.: Cytological studies in normal and mutagen treated strains of triticale (*Triticale hexaploide*, Lart.). Curr. Sci. **43**, 470-473 (1974)

Steel, R.G.D.; Torrie, J.A.: Principles and procedures of statistics, New York: McGraw Hill 1960

Sybenga, I.: Inbreeding effects in rye. Z. Vererbungsl. **89**, 338-354 (1958)

Tease, C.; Jones, G.H.: Chromosome-specific control of chiasma formation in *Crepis capillaris*. Chromosoma **57**, 33-49 (1976)

Tehrani, P.A.; Wricke, G.: Correlation between chiasma frequency and quantitative traits in rye (*Secale cercale* L.). Z. Pflanzenzücht. **79**, 1-5 (1977)

Traut, W.A.: Study of recombination, formation of chiasmata and synaptonemal complexes in female and male meiosis of *Ephestia kuchniella* (Lepidoptera). Genetica **47**, 135-142 (1977)

Zickler, D.: Development of the synaptonemal complex and the 'recombination nodules' during meiotic prophase in the seven bivalents of the fungus *Sordaria macrospora* Auersw. Chromosoma **61**, 289-316 (1977)

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