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CHIASMA FREQUENCY AND TERMINALIZATION IN *CAPSICUM* SPECIES

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ABSTRACT

Comparative analysis of chiasma frequencies at late diplotene/early diakinesis in 15 species/varieties of *Capsicum* indicates invariably 12 bivalents in all the types. Conspicuous variations in number of chiasmata and bivalent length/cell have been observed. The number of bivalents with zero chiasma was highest in the cultivated species, *C. annuum* and *C. frutescens*, whereas bivalents with three chiasmata were more in the wild species, *C. baccatum*. Significant correlation between number of bivalents and bivalent length was noted in *C. chacoense*, *C. chinense*, *C. pendulum* and *C. baccatum*. Chiasma terminalization also appeared to be maximum in the wild species. All these observations suggest random distribution of chiasmata and their free terminalization in wild species; whereas in cultivated species chiasmata appear to be localized. Heterogeneity test applied to paired samples revealed *C. baccatum* and *C. pendulum* to be relatively less heterogeneous, supporting the above findings.

Key words: Chiasma frequency, chiasma terminalization, differential condensation.

Genus *Capsicum* is native of tropical America. Normal meiotic chromosome behaviour with 12 bivalents in *C. annuum* has been reported by Huskins and La-Cour [1] and Dixit [2]. Detailed analysis has been done by Vazart [3, 4] and Abdel-Maksoud [5]. The last author [5] observed maximum number of three chiasmata per bivalent mostly restricted to the achromatic regions of chromosomes. Swaminathan et al. [6] noted ring type bivalents with chiasmata in both arms. However, Sinha [7] noted sterility due to irregular chromosome behaviour. Similar irregularities have been reported by Raman et al. [8]. They have suggested the role of hybridity in the formation of *C. frutescens*. These findings have been supported by Ohta [9] and Shopova [10]. Based on cytogenetic relationships among three *Capsicum* species, Egawa et al. [11] have treated *C. chinense* and *C. frutescens* as two different varieties of a single species and not two distinct species. Thus, the information available on meiotic chromosome behaviour in *Capsicum* appears to be meagre. Hence, in continuation of karyomorphological analysis [12], the present authors have studied chiasma frequency in 15 species/varieties of *Capsicum*.

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MATERIALS AND METHODS

Capsicum species/varieties used and sources are given below:

Species/variety	*Source*
C. annuum Local Diwani	Maharashtra, India
C. annuum EC 149804	Afghanistan
C. annuum EC 149808	Argentina
C. annuum EC 149807	Turkey
C. baccatum EC 149813	Bolivia
C. chacoense EC 149820	Bolivia
C. chacoense EC 149821	USA
C. chacoense EC 149823	Argentina
C. chinense EC 149815	Peru
C. chinense EC 149816	Costa Rica
C. frutescens EC 149827	Ethiopia
C. microcarpum EC 149830	Mexico
C. pendulum EC 149840	India
C. pubescens EC 149832	Colombia
C. pubescens EC 149835	Equador

Flower buds of proper size and stage were fixed separately from different plants in Carnoy's fixative between 9.30 to 11.00 A.M. and anthers were squashed in 1% propionocarmine with traces of iron. Pollen mother cells (PMC) with well separated bivalents at late diplotene/early diakinesis were selected. Camera lucida drawings of two PMCs from each slide/plant were sketched and data recorded from such semipermanent slides. Data on number of bivalents with 0 to 4 chiasmata have been processed by applying Brandt and Snedecors' formula (cf. [13]) to test the heterogeneity in paired samples.

RESULTS

The data on number of bivalents with 0–4 chiasmata, total number of chiasmata and total length of bivalents in the above species/varieties are presented in Table 1.

All the 15 types invariably had 12 bivalents. The range of total number of chiasmata/PMC was 17.7–24.3. Maximum number of chiasmata (24.3) was observed in *C. baccatum* EC 149813, followed by *C. chacoense* EC 149823 (23.0), *C. chinense* EC 149815 (22.6), and minimum in cultivated species *C. annuum* EC 149804 (17.7).

Total bivalent length per PMC was highest in *C. chacoense* EC 149821 (56.2 μm) and lowest in *C. chinense* EC 149815 (35.2 μm). The difference in total bivalent

Table 1. Chiasma frequency in *Capsicum* species/varieties at diplotene/diakinesis

Species or variety	Total PMC	Mean No. of bivalents with chiasmata 0	1	2	3	4	Total no. of chiasmata/ per PMC	Total bivalent length per PMC (V)	Mean bivalent length per unit chiasma (μm)	No. of chiasmata per bivalent	No. of chiasmata 100 μm bivalent length	Correlation coefficient between No. of chiasmata and bivalent length
C. annuum												
Local Diwani	10	0.40	3.80	7.60	0.20	—	19.6	42.9	2.19	1.63	45.6	0.32
EC 149804	20	1.05	4.95	5.25	0.70	0.05	17.7	48.9	2.75	1.48	36.3	0.61*
EC 149808	20	0.70	3.20	7.40	0.65	0.05	19.6	50.7	2.58	1.64	38.7	0.01
EC 149807	20	0.75	3.30	6.35	1.30	0.20	20.8	56.0	2.69	1.73	37.1	0.02
C. baccatum												
EC 149813	20	0.25	1.60	8.10	1.70	0.35	24.3	49.7	2.05	2.03	48.9	0.58*
C. chacoense												
EC 149820	20	0.20	2.60	8.20	0.80	0.20	22.2	51.4	2.32	1.85	43.2	0.79*
EC 149821	20	0.45	2.65	8.05	0.75	0.10	21.4	56.2	2.63	1.78	38.1	0.03
EC 149823	20	0.10	1.30	10.05	0.55	—	23.0	42.9	1.86	1.92	53.8	0.07
C. chinense												
EC 149815	20	0.05	2.30	8.75	0.75	0.15	22.6	35.2	1.55	1.89	64.3	0.53*
EC 149816	20	0.20	2.30	9.10	0.40	—	21.7	38.5	1.78	1.81	66.3	0.39
C. frutescens												
EC 149827	20	1.45	3.20	6.70	1.35	0.15	19.5	46.9	2.40	1.63	41.7	0.04
C. microcarpum												
EC 149830	20	0.75	2.45	7.95	0.80	0.05	20.9	55.9	2.67	1.74	37.5	0.42
C. pendulum												
EC 149840	20	0.35	2.50	7.90	1.15	0.10	22.1	56.1	2.53	1.85	39.5	0.51*
C. pubescens												
EC 149832	20	0.60	4.15	6.05	1.00	0.20	20.0	53.9	2.69	1.67	37.2	0.89*
EC 149835	20	0.50	2.50	7.60	1.35	0.05	21.9	56.0	2.55	1.83	39.2	0.01

* Significant at 0.05 level.

lengths of individual species appears to be conspicuous. This variation may be due to (1) observational errors in selecting PMC at diplotene/early diakinesis, which may not be comparable, and (2) differential degree of spiralization and condensation of bivalents. Though attempts were made to select PMC with comparable phases, it is difficult to exclude the source of error under (1). The chiasmata per bivalent recorded were 0–4. The mean number of bivalents with 0 chiasma was maximum in the cultivated species, *C. annuum* (0.40–1.05) and *C. frutescens* (1.45), and minimum in the wild species *C. chacoense* and *C. baccatum*. Number of bivalents with one chiasma was highest (4.95) in *C. annuum* EC 149804, and lowest in *C. chacoense* EC 149823 (1.30) and *C. baccatum* (1.60). On the other hand, bivalents with three chiasmata were maximum in *C. baccatum* (1.70) and lowest in *C. annuum* var. Local Diwani (0.2). Similar trend was also observed for the number of bivalents with four chiasmata.

Table 2. Coefficient of terminalization in *Capsicum* species

Species/variety		Mean chiasma frequency at diplotene/diakinesis			Coefficient of terminalization (interstitial/total chiasmata)
		interstitial chiasmata	terminal chiasmata	total chiasmata	
C. annuum					
Local Diwani		0.20	19.4	19.6	0.99
EC 149804		0.80	16.9	17.7	0.95
EC 149808		0.75	18.7	19.6	0.95
EC 149807		1.70	19.1	20.8	0.92
C. baccatum					
EC 149813		2.40	21.9	24.3	0.90
C. chacoense					
EC 149820		1.20	21.0	22.2	0.95
EC 149821		0.95	20.4	21.4	0.96
EC 149823		0.55	22.5	23.0	0.97
C. chinense					
EC 149815		1.05	21.6	22.6	0.95
EC 149816		0.40	21.3	21.7	0.98
C. frutescens	EC 149827	1.65	17.9	19.5	0.91
C. microcarpum	EC 149830	0.90	20.0	20.9	0.96
C. pendulum	EC 149840	1.35	20.8	22.1	0.94
C. pubescens	EC 149832	1.40	18.6	20.0	0.93
	EC 149835	1.45	20.5	21.9	0.93

Coefficient of correlation between total bivalent length and total number of chiasmata per PMC is highly significant in *C. pendulum* and *C. chacoense*. It is interesting to note that species/varieties showing significant correlations have relatively higher number of chiasmata per PMC. Such close association between bivalent length and chiasma frequency may suggest random distribution of chiasmata. Lack of association in some of the species perhaps indicates restricted localization of chiasmata.

The above data have been processed further and relative chiasma frequencies, distribution and terminalization of chiasmata during late diplotene/early diakinesis are presented in Table 2. Interstitial chiasmata at diplotene appear to be maximum in *C. baccatum* (2.40), followed by *C. annuum* EC 149807 (1.70), *C. frutescens* (1.65), and minimum in *C. annuum* var. Local Diwani (0.20). The coefficient of terminalization was lowest in *C. baccatum* (0.90), *C. frutescens* (0.91), and highest in *C. annuum* var. Local Diwani (0.99).

Table 3. Comparative heterogeneities for diplotene/diakinesis chiasma behaviour among *Capsicum* species

Species/ variety	Local Divani	EC 149804	EC 149808	EC 149807	EC 149813	EC 149820	EC 149821	EC 149823	EC 149815	EC 149816	EC 149827	EC 149830	EC 149840	EC 149832
C. annuum EC 149804	–													
C. annuum EC 149808	+	–												
C. annuum EC 149807	–	–	+											
C. baccatum EC 149813	–	–	+	–										
C. chacoense EC 149820	–	–	–	–	–									
C. chacoense EC 149821	+	–	+	–	–	+								
C. chacoense EC 149823	–	–	–	–	–	–	–							
C. chinense EC 149815	–	–	–	–	–	–	+	–						
C. chinense EC 149816	–	–	–	–	–	+	+	+	+					
C. frutescens EC 149827	–	–	–	+	–	–	–	–	–	–				
C. microcarpum EC 149830	–	–	+	–	–	+	+	–	–	–	–			
C. pendulum EC 149840	–	–	+	–	+	+	+	–	+	–	–	+		
C. pubescens EC 149832	–	+	–	+	–	–	–	–	–	–	–	–	–	
C. pubescens EC 149835	–	–	+	+	–	+	+	–	–	–	–	+	+	–

Significant for heterogeneity estimated at 0.05 level: + homogeneous, – heterogeneous.

Data on individual bivalents classified on the basis of number of chiasmata (0–4) were processed to estimate heterogeneity in paired samples by applying Brandt and Snedecor's formula (cf. [13]). Table 3 indicates that *C. annuum* EC 149804, *C. chacoense* EC 149823, and *C. frutescens* have heterogeneity with maximum number of paired samples. The minimum number of paired samples showing heterogeneity was exhibited by *C. chacoense* EC 149827 and *C. pendulum*. It is interesting to note that heterogeneity test applied to *C. baccatum* and *C. pendulum* suggests these two species to be relatively less heterogeneous.

DISCUSSION

The varieties of eight *Capsicum* species studied invariably had 12 bivalents. The total number of chiasmata per cell as well as per bivalent were maximum in the wild species, *C. baccatum, C. chacoense* and *C. microcarpum,* whereas in the remaining species reverse situation was observed. These observations suggest random distribution of chiasmata and their free terminalization in the wild species. On the contrary, localized chiasmata in the cultivated species, *C. annuum* and *C. frutescens,* suggest their interrupted linear homology. The possible reason for such differential chromosomal behaviour may be the highly restricted distribution of wild species within narrow ranges in or around the centre of origin, whereas, cultivated forms occupy extensive areas covering a wider range of ecological habitats resulting in the corresponding genotypic variations.

Cytogenetic studies on *C. frutescens* and *C. annuum* by Ohta [9] revealed more or less complete pairing at metaphase-I in the hybrid, thereby suggesting the chromosomes of both species to be semihomologous. This situation has been confirmed by the present studies, as the total number of chiasmata per cell, mean bivalent length per chiasma, and correlation coefficient between number of chiasmata and bivalent length in *C. annuum* and *C. frutescens* are similar.

Based on cytogenetic and taximetric analysis of *Capsicum*, Eshbaugh [14] suggested *pendulum* and *microcarpum* species to be relatively inseparable in their quantitative characters, though both are distinct qualitatively. He also reported fertile hybrids between these two species, exhibiting normal chromosome pairing. Therefore, he proposed to combine the two taxa into a single wild taxon, *C. baccatum* var. *baccatum* (earlier *microcarpum*), and called the cultigen as *baccatum* var. *pendulum* (earlier *pendulum).* The present study on chiasma frequency suggests these two species to be closely related. Similarly, the application of heterogeneity test revealed *pendulum, baccatum* and *microcarpum* as members of a homogeneous group. These observations, to some extent, support those of Eshbaugh [14].

Recently, Egawa et al. [11] suggested, on the basis of cytogenetic relationships, that *C. chinense* and *C. frutescens* are not different species, but both are varieties of the same species. However, the present authors differ from this suggestion as both these species vary in the total number of chiasmata per cell, mean number of bivalents with 1–4 chiasmata, bivalent length per PMC, etc. Even the correlation coefficient between chiasma number and bivalent length appears to be conspicuously more in *chinense* than in *frutescens.* These observations clearly support the treatment of two species as separate taxa.

The above account of comparative chiasma frequencies at diplotene/diakinesis revealed that the intra- as well as interspecific variations in the 15 types studied may be due to conspicuous differences in chiasma frequency, distribution and localization in wild as well as cultivated species. Similar conclusions were made earlier from the karyotypes of wild and cultivated species of *Capsicum* [12].

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REFERENCES

1. C. L. Huskins and L. La-Cour. 1930. Chromosome numbers in *Capsicum*. Amer. Nat., **64:** 382–383.
2. P. D. Dixit. 1931. A cytological study of *Capsicum annuum*. Indian J. agric. Sci., **1**(4): 419–433.
3. J. Vazart. 1950. On the existence of polyploid pollen grains in *Capsicum annuum* L. Compt. Rend. Acad. Sci. Paris, **231:** 1244–1245.
4. J. Vazart. 1951. Nouvellers observations sur les noyaux a calotte: etude caryologique comparee de *Hordeum vulgare* L., *Capsicum annuum* L., *Pastinaca urens* Req. et *Solanum ovigerum* Dun. II. La meiose et la formation due pollen Chez *Capsicum annuum* L. Rev. Gen. Bot., **58:** 42–61.
5. Abdel-Maksoud and M. Mohamed. 1953. Cytogenetics of Hybrids between *Capsicum annuum* and *C. frutescens*. Ph.D. Thesis. University of California, Davis, U.S.A.: 61.
6. M. S. Swaminathan, T. Ninan and M. L. Magoon. 1959. Effects of virus infection in microsporogenesis and seed fertility in *Capsicum*. Genetica, **30:** 63–69.
7. N. P. Sinha. 1950. The somatic chromosomes and meiosis in *Capsicum*. Indian J. Genet., **10:** 36–42.
8. V. C. Raman, P. C. Kesavan and Balasubrmaniyan. 1963. Cytology, fertility and viability in *Capsicum frutescens* L. var. *baccatum*. Indian J. Genet., **29:** 168–173.
9. Y. Ohta. 1961. Cytogenetical studies in the genes *Capsicum* L., *C. frutescens* × *C. annuum*. Jap. J. Genet., **36:** 105–111.
10. M. Shopova. 1966. Studies in the genus *Capsicum*. I. Species differentiation. Chromosoma (Berl.), **19:** 340–348.
11. Y. Egawa and T. Masatake. 1984. Cytogenetic relationships among three species of chilli peppers, *Capsicum chinense*, *C. frutescens* and *C. baccatum*. Jap. J. Breed., **34**(1): 50–56.
12. V. K. Nijasure. 1986. Karyomorphological and Chiasma Frequency Studies in Chillies. M.Sc. Thesis. University of Poona, Poona.
13. N. T. J. Bailey. 1961. Statistical Methods in Biology. John Wiley and Sons, Inc., New York: 200.
14. W. H. Eshbaugh. 1964. A Numerical Taxonomic and Cytogenetic Study of Certain Species of the Genus *Capsicum*. Ph.d. Thesis. Indiana University, Bloomington: 112.