Variation in Chiasma Frequencies in *Secale*, *Vicia* and *Tradescantia*

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Darlington (1933) has found a higher chiasma frequency in the meiotic chromosomes of *Secale cereale* than was previously reported by the writer. The chromosomes of *Secale* are very favorable for detailed studies of chiasma frequencies, and there is little chance that the differences obtained can be attributed to differences in interpretation. Darlington's data were obtained from an aneuploid variety of *Secale* grown in Japan, while my preparations were obtained from a normal diploid grown in a greenhouse at the Arnold Arboretum (Sax 1930). It is reasonable to assume that the differences in chiasma frequency can be attributed to differences in varieties or strains of the species, or to differences in environmental conditions.

In an attempt to determine the factors involved, we have obtained the chiasma frequencies in five varieties of *Secale*. These varieties were obtained from Dr. E. F. Gaines of Washington State College. The plants were grown in a cool greenhouse and meiotic divisions were obtained in early April. The chiasma frequencies were obtained from all chromosomes in twenty microspore mother cells of each variety. The statistical data are shown in Table 1. The chiasma frequencies per bivalent ranged from 1 to 3 with an average of 1.9 to 2.0. These values are somewhat lower than those obtained by

Table 1. Chiasma frequencies in meiotic chromosomes of *Secale cereale*.
(W) winter rye. (S) spring rye.

Variety	Chiasmata per II				
	1	2	3	N.	Ave.
Washington 2715 (W)	21	117	2	140	1.9
Rosen rye (W)	9	126	5	140	2.0
Omskaia (W)	15	107	18	140	2.0
Washington 2714 (W)	13	121	6	140	1.9
Prolific (S)	18	115	7	140	1.9
Total	76	586	38	700	1.9

Darlington, who found from 0 to 4 chiasmata in the normal chromosomes, with an average of 2.4 chiasmata per bivalent. Photographs illustrating the typical meiotic chromosomes of *Secale cereale* are shown in figure 1.

Although no significant varietal differences in chiasma frequency were obtained from varieties grown under the same environmental

Fig. 1. Meiotic chromosomes of *Secale cereale* showing chiasma distribution.

conditions, it is possible that such differences exist. If variation in chiasma frequencies are caused by differences in environmental conditions, a further comparison of data from different regions should serve as a check, and artificial control of environmental conditions should permit a study of the factors involved. Both methods have been used to a limited extent.

Considerable data on chiasma frequency has been obtained for *Vicia faba* grown in Japan. Maeda (1930) found an average of 8.1 chiasmata for the long "M" chromosome, and an average of 3.5 chiasmata for each of the five short chromosomes.

Barrett (1932) found in *Vicia faba*, grown at the Bussey Institution, only 5 or 6 chiasmata in the "M" chromosome. This low chiasma frequency was attributed to the low temperatures in the late fall when the material was collected.

We have also studied chiasma frequencies of the chromosomes of *Vicia faba*. The plants were grown in a greenhouse and the preparations were made in March and April. The anthers were smeared on a dry slide, and the preparation was then immersed in 20 percent alcohol containing a few drops of ammonia water for 20 seconds before fixing with Flemming's solution. The crystal violet iodine stain was used. Typical metaphase plates illustrating chiasma distribution are shown in figure 2.

The average chiasma frequency was found to be 6.7 for the long chromosome and 2.6 for the short chromosomes. The short chromosomes have subterminal fiber attachment points and there is often a chiasma on the long arm near the fiber and a terminal association of chromatids in the short arm. This terminal association of chromatids does not appear to result from an interstitial chiasma by

terminalization. However, such terminal associations have been classed as chiasmata. In some cases it was difficult to determine whether one or two chiasmata were present near the spindle fiber attachment points in the short chromosomes, but in general the chiasma frequencies could be obtained with little difficulty.

Fig. 2. Meiotic chromosomes of *Vicia faba* showing chiasma frequencies in the long "M" chromosome and in the five short chromosomes. The coiled chromonemata can be observed in the figure at the right. The insertion at the left shows the "M" chromosome photographed at a different level.

Differences in chiasma frequencies in *Tradescantia* are associated with differences in species and varieties and with environmental variations. For example the chiasma frequency was found to be 1.7 per bivalent for *T. edwardsiana* and 2.2 for *T. gigantea*. One plant of *T. gigantea* was found with a chiasma frequency of only 1.4 although there was no evidence of segmental interchange or other abnormality. This plant produces a high proportion of non-disjunction at times, and microspores with 7,8 or even 9 chromosomes are found frequently, but preparations obtained from the same plant at other times show no non-disjunction. Evidently slight environmental changes in the greenhouse are sufficient to cause considerable variation in chromosome pairing in certain plants. Environmental effects are also shown by the great variation in pollen sterility obtained from day to day in some of the plants under field conditions.

The artificial control of temperature has shown that temperatures, within the range of those experienced by the plants in nature, may cause great variation in chiasma frequencies. Plants of *Tradescantia* were placed in a constant temperature chamber at 33°C. Chiasma frequencies, obtained by Edward King at the Arnold Arboretum laboratory, were normal (about 2.1 per bivalent) during the first five days, but dropped to 0.2 on the sixth day. At 34°C, the chiasma frequency per bivalent dropped to 0.6 on the third day, and at 36°C the chiasma frequency was 0.2 at the end of 48 hours. Plants in nature would seldom experience such continuous high tempera-

tures, but the critical processes in chromosome pairing may occur frequently at these temperatures. Low temperatures may also inhibit chromosome pairing. (Shimotomai 1927 et al.)

Redfield (Morgan et al. 1933) has found that suppression of crossing-over in either chromosome I or III, or both, caused an increase in crossing-over in chromosome II in *Drosophila melanogaster*. If there is a direct correlation between chiasma frequency and crossing-over there should be a negative correlation between the chiasma frequency of a given chromosome and the chiasma frequency of the remaining chromosomes. Darlington (1933), inspired perhaps by Redfield's results in *Drosophila*, studied the interchromosomal chiasma frequencies in *Secale* and obtained a negative correlation ($r = -.33$) between the chiasma frequency of the fragment chromosome and the number of chiasmata in the seven normal chromosomes of the 8 chromosome strain of *Secale* which he examined. The data were obtained from only 36 cells and the maximum chiasma frequency in the fragment chromosome was 2. Such data are hardly adequate for a critical statistical analysis.

The chromosomes of *Vicia* are exceptionally favorable for a study of interchromosomal effects in chiasma formation. The chiasma frequency of the "M" chromosome of *Vicia faba* was found to vary from 5 to 11, while the total chiasma frequency of the five short chromosomes ranged from 10 to 18. Chiasma frequencies were obtained from 60 cells and the data obtained are shown in Table 2. It is obvious that there is no significant correlation between the chiasma frequency of the long chromosome and the chiasma frequencies of the five short chromosomes.

Table 2. Chiasma frequencies in meiotic chromosomes of *Vicia faba*. 60 p.m.c.

		Chiasma frequency—5 short chromosomes									
		10	11	12	13	14	15	16	17	18	
Chiasma frequency “M” chromosome	5		2	3	1	2	1		1	1	
	6	1	1	2	5	3	3	1			
	7	1	3	4	4	5	4				
	8		1	4		1		1			
	9					1					
	10			1					1		
	11			1	1						

Ave. Xta of short chromosomes = 2.63
Ave. Xta of long chromosome = 6.75
 $r = -.05 \pm .09$.

Summary

Chiasma frequencies obtained in *Secale cereale* and *Vicia faba* grown in Japan, were higher than those obtained for the same species grown in a greenhouse at the Arnold Arboretum. There is some evidence that such differences may be attributed to differences in environmental conditions, although inherent varietal differences within species doubtless occur. The variations found in *Tradescantia* show that both factors may be operative in a single species. The variations in environmental factors which influence chiasma formation may occur in nature.

No interchromosomal correlation was found in comparing the chiasma frequency of the long "M" chromosome with the chiasma frequency of the five short chromosomes of *Vicia faba*.

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