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BEHAVIOR OF UNIVALENT CHROMOSOMES FROM A PENTAPLOID WHEAT HYBRID[1)]

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SUMMARY

A computer program has been developed to simulate meiotic behavior of a pentaploid wheat hybrid, in order to test the randomness of univalent disjunction at the second anaphase. For the simulations, several other parameter values for univalent behavior were obtained from experimental data. When simulated at an average disjunction ratio of 30 : 70, the frequency distribution of chromosome numbers in produced gametes is flattened, and is in a good agreement with observed data so far reported. It seems likely, therefore, that the non-random disjunction of univalent chromosomes prevails in meiosis of plants with odd numbers of genomes.

INTRODUCTION

The behavior of univalent chromosomes from wheat monosomics and interspecific hybrids between different ploidy levels has been investigated by Kihara (1924), Morrison (1953), and Sears (1953a). Matsumura (1936), Alston and Jones (1968), Makino (1974), Tsuji and Maan (1981), and others have studied the frequency distributions of chromosome numbers in pollen grains or egg cells from pentaploid hybrids between emmer and common wheats (2n=5x=35, genome AABBD), and have found a significant deviation from the expected distribution based on random disjunction and 50% elimination of univalent chromatids in the second meiotic division. This may be attributed to the non-random distribution of univalents instead of the expected 50 : 50 disjunction, as suggested by Sears (1953b). We have preliminarily reported a computer simulation for the pentaploid univalent behavior (Tsuji and Nagasawa 1982), and suggested an average disjunction ratio of 30 : 70 and a 15–20% elimination. It is certain, however, that the real situation is more complex than was modeled by us. We know that it is not an easy task to observe and understand the univalent disjunction in the second division. For a better understanding of the univalent behavior, therefore, we have attempted to simulate it with several parameter values, and the results are presented below.

MATERIALS AND METHODS

The course of meiotic events involving univalent chromosomes affects their transmission to gametes. In the pentaploid wheat hybrids, a majority of metaphase I (MI) cells has

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7′+14″ (Kihara 1924). The presence of nonhomologous pairing of an AB-genome chromosome (parameter p_1) or homoeologous pairing between a D-genome chromosome and an AB-genome chromosome (p_2) leads to an MI configuration other than 7′+14″, and determine a transmission characteristics in a meiocyte. At anaphase I (AI), most of the univalents move to the equator, and the daughter chromatids disjoin. However, some univalents precociously move undivided to one pole (p_3); and some others fail to reach the equator and are eliminated as dyad micronuclei (p_4). At telophase I (TI), a part of the disjoined univalent chromatids fail to be included in telophase nuclei and form micronuclei (p_5). At AII of meiosis, the univalent chromatids move to opposite poles without splitting, but some of them fail to be included in tetrad nuclei (p_6).

These parameters can be estimated by observing different meiotic stages and counting the number of univalents (average: a_1) and trivalents (a_2) at MI, univalents near the equator at AI (a_3), dyad micronuclei from undivided univalents (a_4) and from divided univalent chromatids (a_5), and tetrad micronuclei (a_6). The average numbers for p_1 and p_2 and the average probabilities for p_3 to p_6 can be estimated in the following ways:

Nonhomologous pairing at MI: $p_1=(a_1+a_2-7)/2$
Homoeologous pairing at MI: $p_2=a_2$
Non-disjunction at AI: $p_3=(a_1-a_3-a_4)/a_1$
Elimination at AI: $p_4=a_4/a_1$
Elimination at TI: $p_5=a_5/2a_3$
Elimination at TII: $p_6=(a_6-a_4-a_5)/(2a_3-a_5)$

To obtain the values for these parameters, meiosis was observed in pollen mother cells (PMCs) from a pentaploid hybrid between *Triticum aestivum* L. cv. Chinese Spring (2n=6x=42, AABBDD) and *T. durum* Desf. cv. Stewart (2n=4x=28, AABB). Data on the MI configuration indicate that each of homoeologous and nonhomologous pairing follows a Poisson distribution. This is why we calculate average numbers as the estimates for p_1 and p_2. Since the distributions of univalents and micronuclei at the other stages are not clear, it is tentatively assumed that each of them is determined by a series of Bernoulli trials (that is, binomial distribution) with a given probability. The trivalent distribution and the non-disjunction of univalents at AI are assumed to be random. On this basis, we developed a BASIC computer program which generates the random numbers following a theoretical distribution in each meiotic stage in order to determine how many chromosomes are transmitted to gametes. As observed by Makino (1974), univalents from the present pentaploid also misdivide at AI to some degree; however, this factor is neglected in the computer program for the sake of simplicity. After the key-entry of the six parameter values into our NEC personal computer PC-8001, 2,500 meiocytes resulting in 10,000 gametophytes were examined at various values for disjunction rate at AII of meiosis.

RESULTS AND DISCUSSION

The experimental data obtained from the pentaploid between Chinese Spring and Stewart are as follows: (The number of PMCs observed is given in parentheses.) An average MI configuration is 7.238′+13.678″+0.136‴ (487). At AI (108), an average

Table 1. Simulations for the transmission of univalent chromosomes from a pentaploid hybrid between *Triticum aestivum* cv. Chinese Spring and *T. durum* cv. Stewart.

Disjunction rate	Disjunction ratio	% Gametes with different chromosome numbers											
		12	13	14	15	16	17	18	19	20	21	22	23
0.0	0:100	0.5	5.9	29.9	9.6	3.4	1.7	4.5	11.5	17.4	13.0	2.2	0.3
0.1	10: 90	0.2	2.5	19.1	17.0	8.1	5.7	9.5	15.2	14.1	7.4	1.0	0.1
0.2	20: 80	0.1	1.4	11.2	17.0	14.6	11.8	14.1	15.4	10.2	3.4	0.6	0.1
0.3	30: 70	0.0	0.5	5.6	14.9	19.2	20.0	17.5	13.5	6.9	1.6	0.3	0.0
0.4	40: 60	—	0.2	3.3	10.7	22.2	26.0	20.3	11.6	4.4	1.1	0.2	—
0.5	50: 50	—	0.1	2.7	10.8	22.5	27.2	21.3	10.9	3.8	0.7	0.1	0.0

Note 1. See text for description of parameters used.

Note 2. A total of 10,000 gametes were examined for univalent transmission in each simulation at a different value for disjunction rate.

of 6.611 univalents lies near the equator, suggesting that 91.3% of the univalents observed at MI divide at AI. The remaining 8.7% of the univalents are considered to move undivided to one pole, or to form dyad micronuclei. At interkinesis (225), there are 0.911 micronuclei per dyad, among which 14.6% and 85.4% are estimated from their size to be originated from the failure of univalents to reach the equator, and from the failure of divided univalent chromatids to be incorporated into dyad nuclei, respectively. Then, 2.125 micronuclei are observed per microspore tetrad (200). (Dyad and tetrad micronuclei which might be due to misdivision were excluded from the calculation.)

From these data obtained, the values for the six parameters are estimated as follows: 0.187 (p_1), 0.136 (p_2), 0.064 (p_3), 0.023 (p_4), 0.059 (p_5), and 0.095 (p_6). The p_6 value is probably underestimated because large micronuclei observed frequently at TII may consist of more than one univalent chromatid. Simulation results with these parameter values are presented in Table 1. We have not yet obtained the experimental data on the frequency distribution of chromosome numbers in gametes from the present pentaploid; therefore, the simulated distributions were compared with the observed data so far reported (Makino 1974; Kihara 1975). At values of 0.0, 0.1 and 0.2 for disjunction rate (disjunction ratios 0:100, 10:90 and 20:80, respectively), there are two peaks in the frequency distributions in which the gametes with 14–15 and 19–21 chromosomes have very high frequencies. Apparently, the univalent disjunction with any of such rates is unrealistic. The simulation at an average disjunction ratio of 30:70 produces a flattened distribution. It should be noted that this simulated pattern is in a good agreement with the actual distribution patterns from other pentaploids (Kihara 1975), although direct comparisons can not be made because of the differences in parameter values between these pentaploids. With increasing values for disjunction rate, the distribution patterns become skewed and the frequencies of gametes with 14 and 21 chromosomes decrease. Actually, their frequencies are very low in a disjunction rate of 0.5.

These results indicate that the observed flattened distributions can be explained by the non-random disjunction of univalent chromatids at AII. Probably the univalents have some affinity with one another, and an entire set of univalents frequently passes to one of

the two poles, as suggested by Sears (1953b) and Kihara (1975). If such is the case, we can say that the univalent chromatids disjoin at AII with an average ratio of 30:70. We have drawn a similar conclusion in our preliminary report (Tsuji and Nagasawa 1982). This suggests that a transmission pattern of the univalent chromosomes from a pentaploid hybrid or a plant with odd-numbered genomes can be characterized or predicted mainly by two parameters of elimination rate and disjunction rate.

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