

Influence of gametocidal chromosome 4S¹ on the segregation ratio in genetic analysis of the common wheat lines.

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ABSTRACT

The character "hairy leaf sheath" was studied in two groups of introgressive common wheat lines and shown to be under control of dominant gene *Hs* being situated in chromosomes 4S¹ and 4D of *Aegilops sharonensis* and *Triticum miguschovae* (AAGDD), respectively. Using experimental data on genetic analysis of introgressive lines for character "hairy leaf sheath" controlled by the gene of "cuckoo" chromosome 4S¹, the algorithm for calculation the theoretical segregation ratio in F₂ was developed. Segregation distortion is caused by non-viability of majority of gametes lacking 4S¹. Frequency of functioning gametes without 4S¹ is determined by the probability p . Then, the ratio 7 nonviable : 9 viable zygotes is formed as $0.7p - 0.5p^2 : 0.25 + 0.5p + 0.25p^2$. Since segregation involves two characters, gamete viability and hairiness, not monogenic ratio 3:1 but ratio 15 hairy : 1 hairless was used as a base for search of frequency p by maximum-likelihood method. Using 16 populations F₂ from crossing lines differing in character studied, it was shown that theoretically expected ratio is equal to 0.9676:0.0325 and 0.9787:0.0213 in two different years. Judging by the χ^2 criterion, actual segregation ratios do not differ from theoretical ones calculated using p , the frequency of functioning gametes lacking the "cuckoo" chromosome.

INTRODUCTION

A number of factors hamper the progress of transfer of useful genes from related taxa into common wheat, among which the gametocidal action of several chromosomes takes not last place. To date, the gametocidal chromosomes are revealed in the 2nd, 3rd, 4th, and 6th homoeologous groups of chromosomes in several *Aegilops* species. The presence of this chromosome in the introgressive line genome simultaneously with the gene, which is of interest for researcher, can decrease essentially chance of successful introgression. In addition, it is the factor that distorts the ratio of classes in phenotypical segregation in hybridological analysis. Our investigation is aimed at studying the dependence of ratio of phenotypical classes of segregation in genetic analysis with respect to alien character on the presence of gametocidal chromosome in the genome analyzed.

MATERIALS AND METHODS

As an object of genetic analysis, introgressive common wheat lines with alien chromosomes from species *Aegilops sharonensis* Eig., which substituted homoeologous chromosomes of the wheat D subgenome with hairy and hairless border of leaf sheath (the last character gradation is inherent in recurrent genotype, i.e., the common wheat variety Aurora, genome AABBDD), F₁ and F₂ from crossing the lines possessing the contrast character gradations, including the recurrent genotype, with each other, and genome-substitution form Aurosis

(AABBS¹S¹, 2n=42 where S¹S¹ is the genome of diploid species *A.e sharonensis* Eig.) were used. In April before booting, under field conditions, the plants were assessed visually for the characters hairy leaf sheath border.

RESULTS AND DISCUSSION

Earlier, we demonstrated that the gene for hairy leaf sheath border, *Hs*, is situated in wheat chromosome 4D, as well as in 4S¹ chromosome of *Ae. sharonensis*. Presence of hairiness dominates its absence and the character is controlled by single gene (Vdovychenko et al., 2001). Instead of a quarter of plant without hairiness (hairless) in F₂, quite other ratio of phenotypical classes was observed. Lack of correspondence between actual and theoretically expected segregation ratios was supposed to be a consequence of preferred transmission of gametes with chromosome 4S¹, well known as gametocidal chromosome (Endo, 1985).

The gametocidal action of chromosome 4S¹ is displayed as differential vital capacity: the gametes lacking gametocidal chromosome are lacking vitality. However, appearance of plants without hairiness in F₂ indicates the functioning of portion of viable gametes lacking chromosome 4S¹ involving the *Hs* gene. To base the experience data on calculation of the frequency p of that rare event, which is keeping gametes lacking gametocidal chromosome, the formal assumption was made: let for the gametes with chromosome 4D, but without chromosome 4S¹, a certain probability p to take part in forming viable zygote is present. Formalization of our argumentation is aimed to use the maximal-likelihood method in calculations. It consists in speculative linkage of the factors for lack of vitality, L , with the wheat 4D chromosome. To ensure the gamete viability, linkage $D-L$ should be broken and substituted by combination $D-l$. The probability of this rare event is equal p . The l factor in initial cross component is assumed to be linked with chromosome 4S¹. Then, from cross 4S¹4S¹ X 4DL4DL, the hybrid 4S¹4DL with gametocidal chromosome and hairy border of leaf sheath was derived. The hybrid forms nonviable gametes DL with probability $0.5(1-p)$, all the rest gamete types are viable.

Taking into account the genotypes of viable gametes, which will take part in forming genotypes of F₂ hybrids, derived from crossing the lines with and without hairy border of leaf sheath, we consider the theoretical ratio 15 with hairiness : 1 without hairiness as appropriate for calculation of frequency p by maximal-likelihood method instead of ratio 3 hairy ; 1 hairless. On the other hand, nonviable gametes $0.5(1-p)DL$ ensure absence of seven portions of zygotes out of total number of portions 16, so that among the plants of the F₂ population these seven portions are absent and only nine portions out of 16 should be considered in calculations. Since the ratio of gametes and zygotes forms in given case depending on frequency p , the ratio 7 : 9 should be shown as $0.75 - 0.5p - 0.25p^2 : 0.25 + 0.5p + 0.25p^2$. For composition of equalization of estimation of value p and information value, the those were used that are given in Allard's tables (Allard, 1956) for F₂ segregation in ratio 15 dominant : 1 recessive, repulsion state: $(a+b+c)(-2p/4 - p^2) + d(2/p)$ for the equalization of estimation $p \pm s_p$ and $4/4 - p^2$ for calculation of information value (i_p) from each individual F₂. As sources of diversity for calculation of p by maximal-likelihood method, eight similar F₂ populations were used because in presence only two phenotypical classes in population segregating, the other source of diversity is absent. Value $(a+b+c)$ out the Allard's formulae represented really with the number of hairy plants contains eight portions of viable zygotes (we had and assessed these plants) and seven portions of non-viable zygotes (they take part in forming ratio 15 : 1, but do not appear as real plants because of their lack in vitality. Therefore, the total number of plants depends on the number of nonviable zygotes, which we did not observe, and is not the sum of hairy and not hairless plants. The value b varies

together with value p and is calculated according the formulae $(a + d) (0.75 - 0.5p - 0.25p^2) / (0.25 + 0.5p + 0.25p^2)$

Using value p , the frequencies of different genotypes were obtained. The frequency of plants with hairless leaf sheath does not correspond to the observed frequency. However, non-viable genotypes are absent, they do not take part in forming sample volume and should be excluded. After that, the sum of frequency of the residuary genotypes should be put to unity. The ratio 0.0325 hairless : 0.9676 hairy is the theoretically expected one on the base the p value, calculated by maximal-likelihood method for data of 2001 year and 0.0213 : 0.9787 for data of 2002 year. Taking into account value p , the theoretically expected in F_2 segregations were calculated (Table 1). Criterion χ^2 showed the homogeneity of actual distributions into phenotypical classes and the absence of differences between actual class volumes and theoretical ones calculated on the base of arising viable gametes without the gametocidal chromosome, p .

Table 1. Conformity testing the actual and theoretical ratios of two phenotypical classes in F_2

Frequencies in phenotypical classes							Frequencies in phenotypical classes						
Actual		Portion of	χ^2	Theoretical		χ^2	Actual		Portion of	χ^2	Theoretical		χ^2
Hai	no	hairless	3:1 ^{a)}	hai	no	^{a)}	hai	no	hairless	3:1 ^{a)}	hai	no	^{a)}
Data of 2001 year							Data of 2002 year						
76	4	0.050±0.028	15.6	77.4	2.6	0.77	152	6	0.050±0.028	37.9	154.6	3.37	2.1
36	0	0	12	35.2	0.77	0.78	102	1	0	31.7	100.8	2.19	0.7
28	2	0.07±0.045	5.38	29.4	0.64	2.96	101	1	0.07±0.045	29.2	99.8	2.17	0.6
31	1	0.031±0.031	8.17	31.3	0.68	0.15	231	1	0.031±0.031	74.7	227.1	4.94	3.2
45	2	0.043±0.029	10.9	46	1	1.01	179	3	0.043±0.029	52.9	178.1	3.88	0.2
82	4	0.047±0.023	20	84.2	1.83	2.62	112	2	0.047±0.023	32.9	111.6	2.43	0.1
41	0	0	13.7	40.1	0.87	0.89	312	7	0	88.5	312.2	6.79	0.0
56	2	0.034±0.024	14.4	56.8	1.24	0.48	104	6	0.034±0.024	22.4	107.7	2.34	5.8
The means for years:													
0.0366±0.009							0.0212±0.004						
* df = 1. $\chi^2_{0.05} = 3.84$													

Obtained by us estimations of transmission frequency of chromosome 4S¹ into hybrid progenies do not contrary to data of other researches. Distortion of segregation ratio 3 : 1 is caused by negative selection against gametes lacking the gametocidal chromosome, where the gene controlled the character under consideration is situated. The possibility of distortion of ratio of phenotypical classes due to action of gametocidal chromosome can be a cause of incorrect conclusions about the quantity and type of action of genes, which control the critical character. This possible must not be ruled out without purposeful examination when genetic analysis is carried out using the plant material of introgression origination.

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