Peculiarities of Inheritance of Traits in Hybrids of the Second Generation Obtained by Crossing Georgian Endemic Species and Aboriginal Varieties of Wheat


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ABSTRACT. It is shown in the present paper that in plants surviving from lethal genetic phenomena (effect of lethal genes) inheritance of dominant morphological traits of paternal plants is of monogenic nature (single gene inheritance) and the obtained segregation corresponds to theoretically expected one at the following ratio 3(dominant):1(recessive). It was established that early heading (early ear formation) time dominates in the second generation, while in hybrids obtained with participation of endemic species heading time characteristic of endemic species dominates. Resistance to yellow and brown rust dominates in plants of the second generation obtained with participation of endemic species. It is also shown that inheritance of plant height in plants segregated in the second generation is controlled by two genes – tallness is a dominant trait and the obtained segregation corresponds to theoretically expected one: 13(tall-stemmed):3(short-stemmed) or 15(tall-stemmed):1(short-stemmed). Diversity of biotypes is segregated in hybrid populations of the second generation and the peculiarities of inheritance of ear spike length, number of spikelets developed on the spike, number of grains in the spike, weight of a single spike and 1000 grains have been established in these plants. © 2012 Bull. Georg. Natl. Acad. Sci.

Key words: transgression, matrocliny, segregation.

Introduction. First investigations on crosses between species belonging to the genus Triticum are dated to the 19th century. Research in this direction became intensive only in the 1860s-70s in Germany (Rhimpau) and France (Vilmoren Company) and later in Australia (Farera) and USA (Mc Faden). Quite valuable wheat varieties (Marquillo, Kanred, Thatcher, etc.) have been developed by geneticists and breeders working in these countries. Application of this method in Saratov (the Agricultural Institute of the South-West) yielded globally accepted results. The first interspecific hybrid varieties of wheat (Sarrubra and Sarroza), were developed by A.I. Stebut (1930-1947). Later as a result of complex gradual crosses
performed by P. Shekurdin and V. Mamontov a series of spring varieties was released [1,2]. Among them “Saratovskaya-29”, which was grown on more than 18.4 million ha area in 1974 holding the first position in the world by the area occupied. Using this method the famous varieties of hard wheat (Michurinka, Novomichurinka) and others have been developed for the first time by F.G. Kirichenko at the All-Union Institute of Plant Breeding and Genetics in Odessa. Using the method of interspecific hybridization, varieties of winter wheat, as well as spring and facultative varieties of wheat have been developed in different countries of the world. Georgian endemic species of wheat, in particular Chelta Zanduri (T. timopheevi) and wheat Dika (T. carthlicum) are successfully applied in interspecific hybridization. Many immune varieties of wheat (Tinvera, Timstein, Timgalan, Mengavi, Mendes, Lee, Timvin, Melanopus 5, Melanopus 6, Melanopus 7 and others) have been obtained on the basis of T. timopheevi. Chelta Zanduri is applied for solving the problem of development of sterile analogs. The following varieties have been created on the basis of wheat Dika - T. carthlicum: ELS in Germany; Rong in Sweden; two varieties - Runar and Rolla have been developed in Norway; in England the lines (races) TR 309 A and TR 315/2 resistant to powdery mildew have been obtained. In France with participation of wheat Dika - T. carthlicum the varieties Capelle and Desrez resistant to septoriosis and cephotyperiosis were developed; in Italy (in San Angeulo Lodigiano Breeding Station) highly productive early varieties of hard wheat with horn-like consistency have been obtained [1-4].

Highly productive and immune initial breeding material has been obtained in Georgia via crossing Dika – T. carthlicum with the varieties Capelle and Desrez resistant to septoriosis and cephotyperiosis were developed; in Georgia (in San Angeulo Lodigiano Breeding Station) highly productive early varieties of hard wheat with horn-like consistency have been obtained [1-4].

Comprehensive investigation of Georgian endemic species of wheat has revealed that these species have played a significant role in the evolution of the genus Triticum and wheat breeding at a global scale. Not only new species and varieties (sorts) have been developed on their basis, but also new agricultural crop Triticale. Their genotype contains such genes and gene blocks which ensure the obtaining of high quality, highly adaptive, immune, ecologically safe production, highly productive varieties with stable yield. Thus knowledge of the peculiarities of inheritance of morphological, biological and economic traits and regularities of inheritance of manifestation of these traits is of paramount importance while genetic and breeding work on the second and further hybrid generations obtained as a result of crossing Georgian endemic species of wheat with other species and aboriginal varieties of wheat, as success of interspecific hybridization in wheat genetics and breeding is to a great extent determined by these indices.

Materials and methods. The following Georgian endemic species of wheat (T. timopheevi, T. georgicum, T. carthlicum, T. zhukovskyi, T. macha) and varieties var. timopheevi, var. viticulosum, var. chvamlicum, var. stramineum, var. rubiginosum, var. fuliginosum, var. zhukoskyi, var. subletschunicum, var. macha, var. paleoimereticum, var. coerulescens, var. striatum, var. vilosum, var. rufum, var. arabicum) of other wheat species T. durum, T. turgidum, T. polonicum, T. dicoccoides and also 32 aboriginal and selection varieties of Georgian soft wheat were chosen as initial material for developing interspecific hybrids.

Methods of interspecific crossing, back-crossing and genetic analysis were applied in the research. Castrated spikes were pollinated by means of natural (free), artificial (forced) and artificial-natural (forced-free) pollination. 100-100 flowers were castrated and pollinated to obtain each combination. In total 495 reciprocal combinations were obtained.

Sowing of grains of F_2 hybrid generation, their growth, observation, monitoring, study of inheritance of traits and scoring were performed according to conventionally accepted techniques.

Results and discussion. In the second generation of simple hybrid combinations obtained as a result of
Table 1. Segregation by the presence of awn in the second generation

<table>
<thead>
<tr>
<th>#</th>
<th>Hybrid combination</th>
<th>Number of analyzed plants</th>
<th>Segregation into black- and white spike plants</th>
<th>Ratio</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Khulugo X Coerulescens 19/28</td>
<td>404</td>
<td>296:108</td>
<td>303:101</td>
<td>3:1</td>
</tr>
<tr>
<td>2</td>
<td>Lagodekhis grdzeltavtava (long-spiked wheat) X Coerulescens 19/28</td>
<td>390</td>
<td>290:100</td>
<td>292:98</td>
<td>3:1</td>
</tr>
<tr>
<td>3</td>
<td>Bezostaya 1 X Coerulescens 19/28</td>
<td>465</td>
<td>344:121</td>
<td>349:116</td>
<td>3:1</td>
</tr>
<tr>
<td>4</td>
<td>Khulugo X Turgidum</td>
<td>322</td>
<td>236:86</td>
<td>241:81</td>
<td>3:1</td>
</tr>
<tr>
<td>5</td>
<td>Lagodekhis grdzeltavtava (long-spiked wheat) X Turgidum</td>
<td>310</td>
<td>228:82</td>
<td>232:78</td>
<td>3:1</td>
</tr>
<tr>
<td>6</td>
<td>Bezostaya 1 X Turgidum</td>
<td>333</td>
<td>247:86</td>
<td>250:83</td>
<td>3:1</td>
</tr>
<tr>
<td>7</td>
<td>Khulugo Dika X Dika 9/14</td>
<td>255</td>
<td>195:60</td>
<td>191:64</td>
<td>3:1</td>
</tr>
<tr>
<td>8</td>
<td>Bezostaya 1 X Dika 9/14</td>
<td>246</td>
<td>189:57</td>
<td>185:61</td>
<td>3:1</td>
</tr>
</tbody>
</table>

Table 2. Segregation by grain color in the second generation

<table>
<thead>
<tr>
<th>#</th>
<th>Hybrid combination</th>
<th>Number of analyzed plants</th>
<th>Segregation into black- and white spike plants</th>
<th>Ratio</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Dolis Puri X Coerulescens 19/28</td>
<td>420</td>
<td>320:100</td>
<td>315:105</td>
<td>3:1</td>
</tr>
<tr>
<td>2</td>
<td>Tetri Ipkli X Coerulescens 19/28</td>
<td>445</td>
<td>336:109</td>
<td>334:110</td>
<td>3:1</td>
</tr>
<tr>
<td>3</td>
<td>Motsinave X Coerulescens 19/28</td>
<td>405</td>
<td>309:102</td>
<td>303:102</td>
<td>3:1</td>
</tr>
<tr>
<td>4</td>
<td>Tbilisuri 5 X Coerulescens 19/28</td>
<td>490</td>
<td>371:119</td>
<td>368:122</td>
<td>3:1</td>
</tr>
</tbody>
</table>

The reciprocal crossing of Georgian endemic species of wheat with other wheat species, with aboriginal variety-populations (landraces) of soft wheat and selection sorts of soft wheat a fairly great number of plants was lost as a result of hybrid necrosis (genetic system $N_e^1+N_e^2$), red hybrid chlorosis (genetic system $C_h^1+C_h^2$) [9,10], hybrid dwarfness (genetic system $D_1^1+D_2^2$). Due to this it became impossible to establish the regularities of behavior of hybrids in the second generation.

Study of inheritance of paternal traits in surviving hybrid plants of the second generation obtained as a result of reciprocal and back-crossing of Georgian endemic wheat species with other species of wheat and aboriginal and selection varieties of Georgian soft wheat has demonstrated that such morphological characteristics as presence or absence of awn and coloration of spike are traits of special ecological importance. At the same time they are of great value for selection work.

Study of inheritance of morphological traits in hybrids of the second generation has shown that traits characteristic of parents – such as absence of awn, red or black coloration, hairiness of leaves, fragility of awn rachis are dominant characteristics and are being inherited in a monogenic (single gene) way. Segregation obtained in the second generation corresponds to theoretically expected one 3(dominant): 1(recessive) [8] (Tables 1 and 2). The results presented in these Tables show that matrocliny – dominant role of female organism in inheriting (passing) of morphological traits – does not seem to be a case in these crosses.

Great diversity is found within the hybrid combination of the second generation in terms of heading (early-forming) time. Plants which differ from parental forms by heading time are obtained. Some of them are characterized by early heading, while some by late heading. In hybrid population the number of early-heading plants dominates in combinations raised with participation of early heading variety of soft wheat. In combinations obtained with participation of wheat $T. timopheevi$ and $T. zhukovskyi$ plants prevail whose heading time is the same as for the mentioned species.

By the time of heading (earing) plants obtained as a result of crosses between species with equal
chromosome numbers stay within the frames characteristic of initial species. In hybrids of this group formation of new forms in terms of heading time does not take place. New transgression forms with early heading time are obtained in crosses between species with different chromosome numbers.

In the second generation segregation in terms of resistance or susceptibility to yellow and brown rust was revealed. At the same time plants of such biotypes are segregated which differ from initial parental forms by the resistance or susceptibility to brown rust. In the second generation segregation of transgression type takes place both in crosses between species with equal chromosome numbers and species with different chromosome numbers. Segregation of transgression type is the case also in such crosses where initial forms are characterized by high or weak susceptibility to diseases.

Study of plants segregated in the second generation of hybrid combinations has shown that in the second generation obtained as a result of crossing varieties of Georgian aboriginal and selection varieties of soft wheat with varieties of Georgian endemic and other species of wheat segregation by plant height takes place. Segregation by this trait is of dihybrid character. Hybrids of the second generation obtained as a result of crossing varieties of Georgian endemic and other species of wheat with the varieties of soft wheat are split into two main groups: hybrids of the first group raised with participation of the following varieties of soft wheat: Motsinave, Khulugo, Bezostaya 1, Tbilisuri 5, Tbilisuri 8, Tbilisuri 10, Tbilisuri 11, Tbilisuri 12 and the varieties of tetraploid wheat species – Dika 9/14 and Coerulescens19/28 – segregation at the following ratio takes place: 13(tall-stemmed):3 (short-stemmed). Segregation in the second generation of hybrid combinations as a result of crosses between the following varieties of soft wheat: Dolis Puri 35-4, Dolis Puri 18-46, Lagodekhis grdzeltavtava (long spiked wheat), Kakhuri Dolis Puri, Tetri (white) and Tsiteli (red) Ipiki, Kartlis Tetri (white) and Tsiteli (red) Dolis Puri, Dzalisuri 35-3 with Georgian endemic and other species of wheat corresponds to the ratio 15(tall-stemmed):1(short-stemmed) [6].

In the second generation of hybrids the segregation by spike length, number of spikelets on a spike and also by spike fertility level has been revealed. Positive transgression towards increase of spike length as well as negative transgression towards decrease of spike length was marked. Individuals the spike length of which exceeded that of the parent form by 10 cm were found among segregated plants; also individuals with 1.5 times reduced spike lengths as compared to initial forms were found and plants, with reduced spikes not longer than 4-6 cm. Plants with sharply reduced spikelet numbers have been segregated which by this index lagged behind not only initial forms but also hybrids of the first generation. In parallel to plants of such biotypes plants with sharply developed spikelets, highly fertile ones and those with sterile spikes were found among segregated plants. The greatest number of highly fertile plants was obtained as a result of direct crosses (soft wheat served as a female parent).

Plants segregated in the second generation of hybrids raised with participation of varieties of soft wheat split into three groups according to the density of spike: 1) plants with spikes of the same density as in parental forms; 2) plants with thin spikes; 3) plants with dense spikes. Besides that among segregated plants an insignificant number of plants with compact spikes as well as sparse spikes was found.

Regularity of inheritance in terms of the density of spike is not evident, but difference in numbers of each group of plants is marked, depending on the female parent used in hybrid obtaining. When the female form with dense spike is used in crosses a tendency to the decrease of thin spiked plants and increase of dense spiked plants is observed.

In populations of the second generation of hybrid combinations transgression according to the number of grains in spike, weight of grains in a single spike and 1000-grain weight was observed towards
both decrease or increase of these indices. It is worth noting that by these elements the segregated plants of tetraploid biotype prevail over plants of soft wheat biotype. Plants with intermediate characters were revealed among plants of both biotypes. Individuals of soft wheat type were distinguished from intermediate plants by high indices. Hybrid combinations sharply differ from each other by the intensity of formation of the last biotype (soft wheat biotype), which is dependent on the soft wheat genotype which participates in crosses. Of tetraploid wheat species hard wheat and wheat turgidum manifest high combination-forming capacity when crossed with varieties of soft wheat. While crossing with the above-mentioned tetraploid species the following soft wheat varieties - Tbilisuri 5 and Bezostaya 1 and Khulugo from aboriginal varieties reveal high combination-forming capacity.

Sterile, half-sterile and completely fertile plants were segregated in the second generation. Such plants were registered in forms like soft wheat and tetraploid wheat as well as in forms of intermediate character. Among plants of the last type percentage of sterile plants was higher than among the plants of the remaining types. In different combinations percentage of sterile plants fluctuated between 2-4%.

In the second generation of hybrids produced as a result of crosses between species with equal chromosome numbers formation of forms with increased indices took place and the number of such plants prevailed. Highly productive plants of Carthlicum type were segregated. None of segregated plants were sterile.

Study of inheritance of grain number per spike, weight of a single spike and 1000-grain weight in interspecific hybrids of the second generation of Georgian wheat varieties has shown that a great variety of forms is segregated. Transgression forms according to the tendency towards increase or decrease of grain number per spike, weight of a single spike and 1000-grain weight segregated. Sterile plants are segregated as well, which is the case when crossing species with different chromosome numbers.

By studying protein content and content of essential amino acids – lysine and tryptophan in grains of wheat biotypes valuable in terms of genetics and selection segregated from hybrid populations of the second generation (obtained as a result of crossing Georgian endemic species of wheat with other species and Georgian aboriginal and selection varieties of soft wheat) it has been established that reciprocal combinations, obtained as a result of crosses between Georgian endemic species of wheat (T. carthlicum T. timopheevi, Tzhukovskyi, T. georgicum, T. macha) and other wheat species (hard wheat, wild fine-grained wheat) with Georgian aboriginal and selection varieties, are distinguished by the high content of protein and increased content of lysine and tryptophan.

Conclusions. Loss of a significant number of plants of the second generation of simple hybrid combinations, obtained as a result of crosses between Georgian endemic and other species of wheat with and Georgian aboriginal and selection varieties of soft wheat due to lethal genetic phenomena, in particular, hybrid necrosis, red hybrid chlorosis, hybrid dwarfness made impossible establishing to a full extent of regularities of behavior of hybrids of the second generation.

As a result of study of inheritance of parent traits in plants of the second generation, within each hybrid combination, surviving from lethal genetic phenomena, the following was established:

1. Such important morphological characteristics as absence of awn, red or white coloration of the grain, fragility of spike rachis, hairiness of the spike and leaves, red coloration of grain are dominant characters and these characters are inherited in the monogenic way. Actual segregation in the second generation corresponds with theoretically expected one at a ratio: 3(dominant):1(recessive).

2. Plants segregated in hybrid populations of the second generation differ from parental forms by the time of heading (ear-formation) – some are characterized by early heading, while some by late heading. In
combinations raised with participation of early-heading varieties of soft wheat early-heading plants dominate, while in the populations of the second generation raised with participation of Georgian endemic wheat species (T. carthlicum, T. timopheevi, T. georgicum, T. zhukoskyi, T. macha) plants with heading time characteristic of endemic species do.

3. In plants segregated in populations of the second generation raised on the basis of Georgian endemic wheat species resistance to yellow and brown rust dominates.

4. In plants segregated from hybrid combinations of the second generation inheritance of stem height is of digenic character and actual segregation corresponds to theoretically anticipated one at ratios – 13 (tall-stemmed):3 (short-stemmed) or 15 (tall-stemmed):1 (short-stemmed).

5. In populations of the second generation of all hybrid combinations diverse biotypes according to spike length, number of spikelets on a spike, number of grains per spike, weight of a single spike and 1000-grain weight have been revealed. Transgression according to all these indices towards increase or decrease of the mentioned characteristics was found. Besides these characteristic, individuals botanically distinct from the initial forms were found among segregated plants. This was especially notable in combinations obtained on the basis of Georgian endemic species of wheat.
Peculiarities of Inheritance of Characteristics and Traits in Hybrids

REFERENCES


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