

Inheritance of the branching in hybrid populations among tetraploid wheat species and the new branched spike line 166-Schakheli

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Abstract The new branched spike form of wheat was synthesized from a cross between a complex wheat line 171ACS $\{[(T. durum \text{ Desf.} \times Ae. tauschii \text{ Coss.}) \times S. cereale \text{ L. ssp. segetale Zhuk.}] \times T. aestivum \text{ L. 'Chinese Spring'}\}$ ($2n = 6x = 42$, AABBDD) and durum wheat variety *T. durum* Desf. 'Bereketli-95' ($2n = 4x = 28$, AABB). This branched spike form is distinguished significantly from the other branched spike forms known so far. Later on basis of these plants have been developed the branched spike lines. This study was aimed to generate the segregating populations from reciprocal (F_1 – F_3) and backcross (BC_1F_1 – BC_1F_3) crosses between one of such lines—166-Schakheli ($2n = 4x = 28$, AABB) and tetraploid wheat species (*T. polonicum* L., *T. turanicum* Jakubz., *T. durum* Desf.) for revealing the inheritance character of this branching trait and study meiotic behavior in reciprocal (F_1 , F_2) and backcross (BC_1F_1) progenies. Results showed that this trait is controlled by a single recessive gene despite certain irregularity against Mendelian law in F_2 generations and does not depend on gene dosage, i.e., number of chromosomes.

Keywords Branched spike · Inheritance · Meiosis · Recessive gene · Segregation ratio · Tetraploid wheat

Introduction

Wheat (*Triticum* L.) is one of the most important food crops. Because arable land is gradually being decreased, improving the yield of this crop is essential. Wheat scientists consider the change of the wheat spike architecture as one possible way to contribute to yield increases. One way of changing the spike morphology is to increase the number of spikelets in the spike, i.e., making selection towards producing wheat forms with a branched spike or supernumerary spikelets (SS). According to many scientists (Koric 1969; Salunke and Asana 1971; Rawson and Ruwali 1972; Li and Zhao 2000), this technique allows to increase the productivity of the crop.

Wheat with branched spikes has been known since ancient times. Already Pliny mentioned *ramosum* and *centigranum* wheat. In 1774, Carl von Linné described branched wheat as *T. compositum* L. species. Later, taxonomists have included it in a special group of *T. turgidum* L. "Branching" is one of the traits in wheat classification that distinguishes *T. turgidum* L., *T. jakubzineri* Udacz. et Schachm. and *T. vavilovii* Jakubz. from other wheat species. So far, two types of branching have been reported: *turgidum* (regular) and *vavilovii* (irregular). The first one is specific for spike of *T. turgidum* L., and the last one for *T. jakubzineri*

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Udacz. et Schachm. and *T. vavilovii* Jakubz. In the first case, additional spikelets emerge at a rachis node, but in the second case—an extended rachilla. In order to distinguish these two types from each other, the turgidum type branching was called supernumerary spikelet (Percival 1921; Coffman 1924) and the vavilovii type—branched spike (Sharman 1944; Koric 1966). There is a tendency to combine both types of branching under the term “supernumerary spikelet” (Kadkol and Halloran 1987; Peng et al. 2004).

The spike branching in our case is similar to the vavilovii type, but differs significantly by the more extended rachilla. The aim of this study was to reveal an inheritance character of this branching type in generated populations and to find out whether this trait is influenced by number and configuration of chromosomes in meiosis.

Materials and methods

As research materials were used reciprocal F_1 – F_3 hybrids obtained from crosses among tetraploid wheat species *T. polonicum* L., *T. turanicum* Jakubz., *T. durum* Desf. (local varieties: ‘Alinja-84’, ‘Arandeni’) and the new branched spike line 166-Schakheli, also BC_1F_1 – BC_1F_3 populations obtained by backcrosses of F_1 plants ($2n = 28$) with both parents. Hybridization has been done in accordance with the conventional methodology (Gorin et al. 1968). Hybrid seeds have been germinated in Petri dishes and the seedlings were transferred to the experimental plot for further observation. The feeding area per plant was 5×20 cm. The plants were harvested with roots.

All morphologically analyzed spikes were classified into branched and normal spike types. The contingency χ^2 -test (Lakin 1990) was used to analyze the segregation results for branching in the second and third hybrid generations. For studying of meiosis in reciprocal F_1 , F_2 and backcross BC_1F_1 hybrids, its spikes were fixed in Carnoy’s fixative I (a 3:1 mixture of absolute alcohol and glacial acetic acid) for at least 24 h. After 1 day, the spikes were transferred to 80% ethanol and stored in a refrigerator (Pauscheva 1988). Analysis of meiotic behavior was performed by the standard acetocarmine squash techniques. Cytogenetic observations were made using a Leitz Orthoplan microscope. Statistical data manipulation was done according to Dospekhov (1979).

Results

The reciprocal crosses were made among the branched spike line 166-Schakheli and normal spiked tetraploid wheat species—*T. polonicum* L., *T. turanicum* Jakubz., *T. durum* Desf. (local varieties: ‘Alinja-84’ and ‘Arandeni’) for studying the new branching type inheritance. Seed sets for these hybrid combinations were low and ranged between 0.82 and 27.78%. Then obtained F_1 plants were backcrossed with 166-Schakheli and tetraploid wheat species.

Obtained reciprocal F_1 – F_3 and backcross BC_1F_1 – BC_1F_3 hybrid populations were analyzed morphogenetically (Table 1).

As Table 1 shows, all the F_1 hybrids (32 plants) obtained from crosses among 166-Schakheli and tetraploid wheat species were homomorphic. In the F_2 generation instead of the expected segregation ratio 3:1, the numbers of normal and branched spike plants were equal, but in the F_3 generation, the segregation ratio was 5:3.

The morphotype variability was more intensive in reciprocal hybrid populations from crosses between *T. polonicum* L. and 166-Schakheli. Progenies were differentiated significantly by the occurrence of the new interesting morphotypes (Fig. 1).

The different results were observed in BC_1F_1 hybrids among branched spike line 166-Schakheli and tetraploid wheat species depending on the backcrosses’ direction. All the BC_1F_1 plants had the normal spikes when the F_1 plants were backcrossed with tetraploid wheat species. When backcrosses were made with branched spike line 166-Schakheli, the normal and branched spike plants were obtained in a ratio of 1:1, as expected theoretically. In the F_2 , the expected segregation ratio deviated significantly in all backcross combinations, except BC_1F_2 plants belonging to the combination (166-Schakheli \times *T. polonicum*) \times *T. polonicum*.

The expected segregation ratios of all backcross populations have again been restored in the third generation. So, in BC_1F_3 populations obtained from the backcrossing F_1 hybrids with tetraploid wheat species, the segregation ratio of normal and branched spike plants has been 13:3, but in BC_1F_3 populations obtained from backcrossing F_1 hybrids with the line 166-Schakheli—5:11, respectively.

Furthermore, the results of cytogenetic analysis revealed that the meiosis proceeded normally in all

Table 1 Segregation ratios for spike morphotype in F₁-F₃ and BC₁F₁-BC₁F₃ hybrid populations obtained from crosses among tetraploid wheat species and the new branched spike line 166-Schakheli

No.	Hybrid combinations	F	No. of plants with normal spike	No. of plants with branched spike	Actual segregation	Theoretical segregation	χ^2
1	<i>T. polonicum</i> × 166-Schakheli	F ₁	3	–	1:0	1:0	
2	“_ “_ “_ “_ “_	F₂	93	59	1.6 : 1.0**	3:1	
3	“_ “_ “_ “_ “_	F ₃	309	162	5:3	5:3	1.93
4	(<i>T. polonicum</i> × 166-Schakheli) × 166-Schakheli	BC ₁ F ₁	2	2	1:1	1:1	
5	“_ “_ “_ “_ “_	BC₁F₂	82	68	1.2 : 1.0**	3:5	
6	“_ “_ “_ “_ “_	BC ₁ F ₃	14	36	5:11	5:11	0.23
7	166-Schakheli × <i>T. polonicum</i>	F ₁	7	–	1:0	1:0	
8	“_ “_ “_ “_ “_	F₂	201	218	1:1**	3:1	
9	“_ “_ “_ “_ “_	F ₃	540	321	5:3	5:3	0.02
10	(166-Schakheli × <i>T. polonicum</i>) × <i>T. polonicum</i>	BC ₁ F ₁	5	–	1:0	1:0	
11	“_ “_ “_ “_ “_	BC₁F₂	85	5	7:1	7:1	3.97*
12	“_ “_ “_ “_ “_	BC ₁ F ₃	72	11	13:3	13:3	1.67
13	<i>T. turanicum</i> × 166-Schakheli	F ₁	3	–	1:0	1:0	
14	“_ “_ “_ “_ “_	F₂	110	75	1.5 : 1.0**	3:1	
15	“_ “_ “_ “_ “_	F ₃	452	270	5:3	5:3	0.003
16	(<i>T. turanicum</i> × 166-Schakheli) × 166-Schakheli	BC ₁ F ₁	1	2	1:1	1:1	
17	“_ “_ “_ “_ “_	BC₁F₂	107	81	1.3 : 1.0**	3:5	
18	“_ “_ “_ “_ “_	BC ₁ F ₃	23	65	5:11	5:11	1.08
19	166-Schakheli × <i>T. turanicum</i>	F ₁	2	–	1:0	1:0	
20	“_ “_ “_ “_ “_	F₂	117	103	1:1**	3:1	
21	“_ “_ “_ “_ “_	F ₃	365	233	5:3	5:3	0.54
22	(166-Schakheli × <i>T. turanicum</i>) × <i>T. turanicum</i>	BC ₁ F ₁	15	–	1:0	1:0	
23	“_ “_ “_ “_ “_	BC₁F₂	117	45	2.6 : 1.0**	7:1	
24	“_ “_ “_ “_ “_	BC ₁ F ₃	134	39	13:3	13:3	1.65
25	‘Alinja-84’ × 166-Schakheli	F ₁	2	–	1:0	1:0	
26	“_ “_ “_ “_ “_	F₂	59	39	1.5 : 1.0**	3:1	
27	“_ “_ “_ “_ “_	F ₃	184	128	5:3	5:3	1.65
28	(‘Alinja-84’ × 166-Schakheli) × 166-Schakheli	BC ₁ F ₁	1	–	1:0***	1:1	
29	“_ “_ “_ “_ “_	BC₁F₂	126	151	1.0 : 1.2**	3:5	
30	“_ “_ “_ “_ “_	BC ₁ F ₃	106	187	5:11	5:11	3.29
31	166-Schakheli × ‘Alinja-84’	F ₁	7	–	1:0	1:0	
32	“_ “_ “_ “_ “_	F₂	157	149	1.1 : 1.0**	3:1	
33	“_ “_ “_ “_ “_	F ₃	243	158	5:3	5:3	0.61
34	‘Arandeni’ × 166-Schakheli	F ₁	3	–	1:0	1:0	
35	“_ “_ “_ “_ “_	F₂	67	64	1:1**	3:1	
36	“_ “_ “_ “_ “_	F ₃	197	106	5:3	5:3	0.81
37	(‘Arandeni’ × 166-Schakheli) × 166-Schakheli	BC ₁ F ₁	1	–	1:0***	1:1	
38	“_ “_ “_ “_ “_	BC₁F₂	66	50	1.3 : 1.0**	3:5	

Table 1 continued

No.	Hybrid combinations	F	No. of plants with normal spike	No. of plants with branched spike	Actual segregation	Theoretical segregation	χ^2
39	"_ " " " "	BC ₁ F ₃	47	117	5:11	5:11	0.51
40	166-Schakheli × 'Arandeni'	F ₁	5	–	1:0	1:0	
41	"_ " " " "	F ₂	81	63	1.3 : 1**	3:1	
42	"_ " " " "	F ₃	197	128	5:3	5:3	0.48

* $P_{0.05} = 3,84$; $df = 1$

** Because of the lack of correspondence between the theoretical and actual segregation ratios, the results of the second generations were not put to the χ^2 test

*** Discrepancy between the theoretical and actual segregation ratios is connected with the representation of BC₁F₁ by only one plant

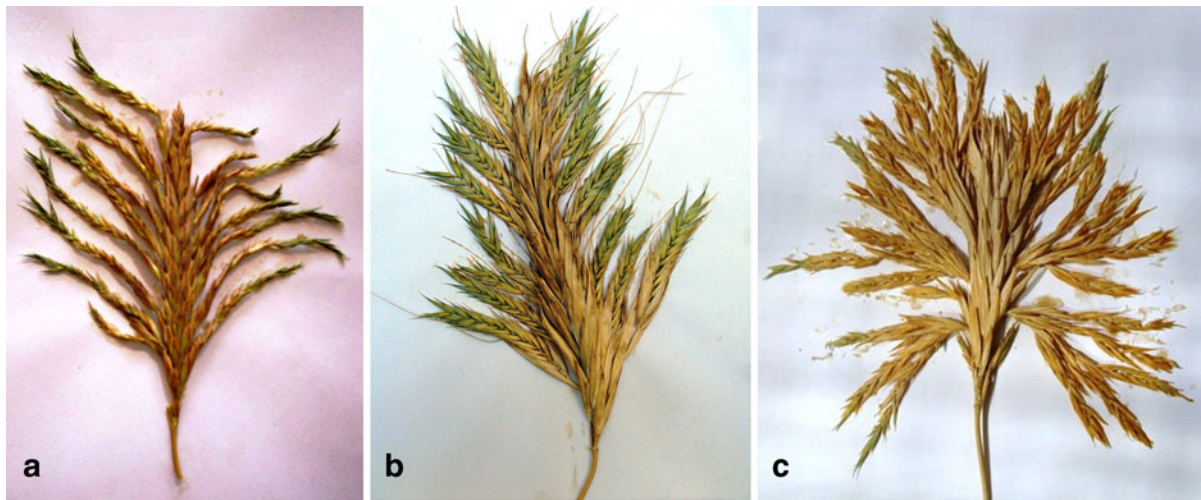


Fig. 1 The new interesting spike morphotypes appeared in the second (a), fourth (b), and fifth (c) generations of the cross *Triticum polonicum* × 166-Schakheli

reciprocal F₁, F₂, and BC₁F₁ plants and chromosome number of all investigated hybrids was $2n = 28$ (Table 2). The level of chromosome pairing and frequency of chiasm were high enough and the meiotic abnormalities were less than expected. The multivalent associations—quadrivalents have been detected only in the F₁ and F₂ plants from the cross *T. durum* 'Arandeni' × 166-Schakheli.

Discussion

The line 171ACS ($2n = 6x = 42$) was obtained by crossing trigeneric incomplete amphidiploid

Aegilotriticale [*T. durum* Desf. × *Ae. tauschii* Coss.] × *S. cereale* L. subsp. *segetale* Zhuk.] ($2n = 6x = 42$) with bread wheat variety 'Chinese Spring' ($2n = 6x = 42$, AABBDD). In 2002, we detected for the first time the new branched spike plants in the F₂ hybrid population from the cross between durum wheat variety 'Bereketli-95' ($2n = 4x = 28$, AABB) and 171ACS and considered it as a result of spontaneous mutation, not expecting it might be followed by recombination (Aliyeva and Aminov 2004).

However, further investigation revealed that branched spike forms appeared not only in the F₂ generation from the cross 'Bereketli-95' × 171ACS

Table 2 Results of meiosis process in hybrid populations obtained from the reciprocal and backcrossing crosses among tetraploid wheat species and a new branched spike line 166-Schakheli

Hybrid combinations		F	Total PMCs observed	Ring bivalents	Rod bivalents	Univalents	Quadrivalents	Chiasmata/PMC	2n
1	166-Schakheli		99	14.00 ± 0.00	–	–	–	28.00 ± 0.00	28
2	<i>T. polonicum</i> × 166-Schakheli	F ₁	145	13.04 ± 0.16	0.81 ± 0.12	0.30 ± 0.15	–	26.89 ± 0.20	28
3	(<i>T. polonicum</i> × 166-Schakheli) × 166-Schakheli	BC ₁ F ₁	121	12.34 ± 0.29	1.66 ± 0.29	–	–	26.34 ± 0.29	28
4	166-Schakheli × <i>T. polonicum</i>	F ₁	155	12.89 ± 0.19	0.95 ± 0.21	0.32 ± 0.14	–	26.73 ± 0.19	28
5	“ “ “ “ “ “	F ₂	115	12.24 ± 0.30	1.76 ± 0.30	–	–	26.24 ± 0.30	28
6	“ “ “ “ “ “	F ₂	137	12.37 ± 0.28	1.63 ± 0.28	–	–	26.37 ± 0.28	28
7	(166-Schakheli × <i>T. polonicum</i>) × <i>T. polonicum</i>	BC ₁ F ₁	134	13.13 ± 0.12	0.87 ± 0.12	–	–	27.13 ± 0.12	28
8	<i>T. turanicum</i> × 166-Schakheli	F ₁	193	12.40 ± 0.32	1.21 ± 0.32	0.79 ± 0.30	–	26.01 ± 0.38	28
9	(<i>T. turanicum</i> × 166-Schakheli) × 166-Schakheli	BC ₁ F ₁	136	12.86 ± 0.21	1.07 ± 0.22	0.07 ± 0.26	–	26.80 ± 0.28	28
10	166-Schakheli × <i>T. turanicum</i>	F ₁	188	12.39 ± 0.31	1.38 ± 0.35	0.23 ± 0.30	–	26.16 ± 0.43	28
11	(166-Schakheli × <i>T. turanicum</i>) × <i>T. turanicum</i>	BC ₁ F ₁	110	13.88 ± 0.09	0.12 ± 0.09	–	–	27.88 ± 0.09	28
12	<i>T. durum</i> ‘Alinjia-84’ × 166-Schakheli	F ₁	133	12.65 ± 0.15	1.24 ± 0.13	0.11 ± 0.18	–	26.55 ± 0.27	28
13	“ “ “ “ “ “	F ₂	143	11.76 ± 0.31	1.90 ± 0.26	0.70 ± 0.19	–	25.60 ± 0.31	28
14	(<i>T. durum</i> ‘Alinjia-84’ × 166-Schakheli) × 166-Schakheli	BC ₁ F ₁	190	13.00 ± 0.13	0.67 ± 0.12	0.66 ± 0.16	–	26.67 ± 0.17	28
15	<i>T. durum</i> ‘Arandeni’ × 166-Schakheli	F ₁	184	12.34 ± 0.33	0.61 ± 0.19	0.73 ± 0.33	0.34 ± 0.17	26.57 ± 0.40	28
16	“ “ “ “ “ “	F ₂	112	12.59 ± 0.22	0.91 ± 0.16	–	0.25 ± 0.11	27.09 ± 0.16	28
17	“ “ “ “ “ “	F ₂	143	12.70 ± 0.21	0.80 ± 0.14	0.41 ± 0.15	0.15 ± 0.10	26.79 ± 0.22	28
18	(<i>T. durum</i> ‘Arandeni’ × 166-Schakheli) × 166-Schakheli	BC ₁ F ₁	130	12.62 ± 0.15	1.18 ± 0.13	0.42 ± 0.15	–	26.41 ± 0.20	28

but also observed in all the F_2 progenies from the crosses among 171ACS and any durum wheat varieties or lines. Morphogenetic analysis of the F_2 progenies demonstrated a 3:1 segregation ratio of normal and branched spiked plants, respectively. Thus, this result suggested that this type of branching was possibly controlled by a single recessive gene.

Interestingly, this new branching type did not appear in the second and higher generations from the crosses among the line 171ACS and bread wheat varieties. Most probably the gene(s) belonging to the line 171ACS, which is(are) responsible for branching trait in durum wheat species, are suppressed by the D-genome of bread wheat. There is a report in the literature that the 2D gene inhibits the ‘branching’ genes (Klindworth et al. 1990).

Thus, the investigations carried out by us revealed that the new branched spike plants appear in all hybrid populations obtained from the reciprocal crosses of the line 171ACS to any durum wheat varieties and lines, starting from the F_2 generation. Hence, we concluded the line 171ACS is a source for a new type of branching spike only in durum wheat (Aliyeva 2009).

It was developed the new branched spike lines, including 166-Schakheli, on basis of the selected morphotypes from the cross 171ACS × ‘Bereketli-95’.

In general, the researchers studying branching inheritance have very different views on this matter. According to some authors, environmental factors (Sharman 1944; Swaminathan et al. 1966; Pennell and Halloran 1983), even sowing time (Hsan and Shigenaga 1990; Meena et al. 2008) exerts significant influence on expression of SS genes. Some researchers associated an occurrence of branching trait with changes in the number and configuration of chromosomes (Singh and Joshi 1983; Muramatsu 2009), while others identified that the branching trait has a hemizygote effect and did not depend on dosage, i.e., number of chromosomes (Kadkol and Halloran 1987; Peng et al. 1998).

It should be noted that a new branching trait neither depends on environmental factors nor sowing time. The results of meiotic analysis showed that there were no important changes related to chromosome configuration either in line 166-Schakheli or its reciprocal and backcross progenies. In general, meiosis proceeded normally in all hybrid plants with

normal and branched spike (Table 2). An insignificant amount of multivalent associations (quadrivalents) has been observed in F_2 hybrids of the cross *T. durum* ‘Arandani’ × 166-Schakheli. It might be supposed that these quadrivalents were the result of translocation that occurred between the chromosomes of ‘Arandani’ and line 166-Schakheli. Thus, we share the views of the above-mentioned scientists (Kadkol and Halloran 1987; Peng et al. 1998) and reached a similar conclusion that branching trait does not depend on gene dosage, i.e., the number of chromosomes.

Our recent study revealed that both lines—171ACS and 166-Schakheli had a different segregation character in crosses with durum wheat. F_1 hybrid plants of both lines had only the normal spikes, whereas the segregation ratio in the F_2 for the 171ACS hybrids was 3:1 (normal spiked to branched spiked) (Aliyeva 2009), but for the line 166-Schakheli hybrids—close to 1:1 (364 normal and 315 branched spike plants). The last ratio of 1:1 was also observed in the F_2 generation of line 166-Schakheli with *T. polonicum* and *T. turanicum* (521 normal and 455 branched spike plants) (Table 1). Therefore, we first supposed it was a 9:7 segregation ratio in the F_2 generation which occurred due to complementary effect of genes. In this case, the number of normal and branched spiked plants for the next generation had to be in a ratio of 25:39, as expected theoretically, but the segregation analysis of F_3 progenies showed a 5:3 ratio (2,487 normal and 1,504 branched spiked plants, respectively), which is consistent with Mendelian inheritance of a single gene.

It should be noted that Tschermak (1910) for the first time put forward a conception that branching in *T. turgidum* L. species is a recessive trait and controlled by a single gene. Later on, other researchers (Sharman 1967; Klindworth et al. 1990; Peng et al. 1998; Goncharov 2002) also shared this conception and noted that the *bh* gene (*brahit* in latin) controlled branching trait had localized in the 2A chromosome. However, Pennell and Halloran (1983) reported that the branching trait is controlled by the two recessive genes.

For further studying of branching inheritance in our case, all F_1 plants derived from crosses between tetraploid wheat species *T. polonicum* L., *T. turanicum* Jakubz., *T. durum* Desf. (local varieties: ‘Alinja-84’, ‘Arandani’) and branched spike line 166-Schakheli

were involved to backcross hybridization to both parents and the same statistical irregularity for the segregation ratio was also observed in all the BC₁F₂ progenies. Depending on the direction of the backcrosses, i.e., whether the backcross was made with tetraploid wheat species or branched spike line 166-Schakheli, the results of segregation were different. So, in the first case, all BC₁F₁ plants had a normal spike (20 plants), but in the second case, the segregation ratio was 1:1, i.e., five plants had normal and six plants had branched spikes. The similarity of segregation ratios of the backcrossing and analyzing crossings confirmed that this new branching trait is actually controlled by a single recessive gene. In this case, the segregation ratio in the F₂ generation from backcrosses F₁ plants with tetraploid wheat species would be 7:1, with line 166-Schakheli—3:5. However, as seen from Table 1, by backcrossing of F₁ plants with *T. polonicum* in the BC₁F₂ were produced 85 normal and 5 branched-spike plants, i.e., the segregation ratio was 7:1, as theoretically expected, whereas in the BC₁F₂ population from backcrossing of F₁ plants with *T. turanicum* it was 2.6:1.0. In all BC₁F₂ populations derived from backcrossing F₁ plants with the line 166-Schakheli was again found the same irregularity against Mendelian law and numbers of plants with normal and branched spike were 381 and 350, respectively (i.e., the segregation ratio was close to 1:1 instead of 3:5). However, interestingly, the segregation ratios were again restored in all BC₁F₃ populations. So, the numbers of normal and branched-spike plants in BC₁F₃ populations from backcrossing of F₁ plants with tetraploid wheat species were 206 and 50, respectively (i.e., in a ratio of 13:3), with branched spike line 166-Schakheli—190 and 405 plants, respectively (i.e., in a ratio of 5:1) as expected for monohybrid inheritance.

So, all the segregation deviates observed in the F₂ generations of both reciprocal and backcross hybrid populations and their restoration in the F₃ generations is a rare phenomenon and its cause is still unknown. It could be explained by the complex hybrid origin of new branched spike line 166-Schakheli and we hope further investigations will shed light on this phenomenon.

It is important to note that an inheritance of the branching trait was also studied in bread wheat species and it was found out that the inheritance of branching in bread wheat differs from that of hard

wheat. So, according to Koric (1973) and Dencic (1988), there are two dominant genes or incomplete dominant genes promoting expression of SS trait in bread wheat, while Peng et al. (1998) reported that the SS trait is controlled by three genes—two recessive genes (*ss*) and one dominant gene (*Nr*), which inhibit an expression of this trait. Sun et al. (2009) have revealed that SS trait in bread wheat line 51885 is transferred by two dominant genes having complementary effect.

Thus, taking into consideration all the above-mentioned issues, we suggested that the new branched spike line 166-Schakheli and tetraploid wheat species have the different genotypes (they may conventionally be designated as *aa* and *AA*, respectively) for the studied branching trait. It was concluded that this trait has monogenic recessive inheritance in spite of observed certain irregularities against Mendelian law in the second generations of both reciprocal and backcross hybrid populations and does not depend on gene dosage, i.e., the number of chromosomes.

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