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Interaction of barley *tweaky spike* and *laxatum* mutations in F_1 hybrids

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Only few genes are known to regulate the development of flower lodicules in *Poacea* plants. Among them are *lax-a* and *tw*. Ectopic expression of both mutant genes gives conversion of lodicules to stamens. By a comparative examination of the action of *lax-a* and *tw* genes on ear and flower structure and especially by a complementation test it has been proven that *tw* and *lax a* are in different loci. F_1 hybrids between various *lax a* alleles and *tw* have a normal structure of flowers. Two alleles from Nordic Gene Bank have a stronger expression on flower structure in heterozygous state, but that phenomenon has been displayed only in 10% of the flowers tested.

Key words: complementation, lodicule development, genes in different loci, different expression of alleles, barley

INTRODUCTION

Mutations causing changes in the fate of organ primordia are central to studies of flower developmental genetics. Among such may also be barley mutants *tweaky spike* (*tw*) type with lodicules converted to stamens and/or carpels. The homeotic conversion of lodicules is accompanied by alteration of the number of flower organs [1, 2]. Numerous barley developmental mutants are known, but only few of them have homeotic transformations of lodicules. Among such are mutants in the *laxatum-a* locus. In their flowers lodicules are converted only to stamens, and flowers have 5 stamens instead of the normal number of 3 [3, 4]. In previous work [5], interaction of *tw* type mutants with various *Hooded* type mutants was investigated, and influence of the *tw* gene was observed on the development of an extra flower of inverse polarity on the lemma instead of awn or on awn [5]. More interesting is the investigation of the interaction of two mutants who have nearly the same phenotypic effect on conversion of lodicules to stamens, but a different action on the common ear structure as it have both *tw* and *lax a* barley mutants. The *tw* type mutants have ears of specific structure with well expressed gradient of mutant gene action [3]. Mutants *of laxatum* type are presented by very differing phenotypes and have been localizated by diallelic crosses to 26 different loci, but all *laxatum* mutants have reduced spike density [3, 6]. Among them only mutants in *lax a* locus act on the development of lodicules/stamens.

In the present work, the interaction between barley mutant *tw* and 19 different *lax* mutants was examined. The same was made also with two *tweaky* mutants from the USA – *tweaky and missing kernels* and *tweaky No 18.*

MATERIALS AND METHODS

The barley mutant *tw* used as the mother plant is of original origin induced by chemical mutagens in barley cv. “Auksiniai II”. The latter was primarily obtained from the Lithuanian Institute of Agriculture and was used in the present work as a *Wild Type* (*WT*). The *laxatum* mutants were of different genotypes, *a, aa, ab, ac, ae, ag, b, c,* and from two different collections: l*axatum aa* (1572), *ab* (1573), *ac* (1574), *ag* (1575), *a* (1775), *ae* (2041), *a* (2103), *lax* 298 (2275), *aa* (2276), *ab* (2277), *a1* (2278) – all from the USA, Dacota; *lax compact, purple 6-row* (1460), *lax* (625), *lax spike, long awn 2(564), tweaky and missing kernels* (1119), *tweaky No. 18* (111) – from Aberdeen, Idaho, USA (all that material presented by the National Small Grains Res. Facility Barley Genetic Stocks Collection, Aberdeen, Idaho, USA, numbers in parentheses – numbers of accessions in that collection). The other part of *laxatum* mutants was from the Nordic Gene Bank (Alnarp, Sweden). There were *lax a.01* (NGB116334), *b.1* (NGB116647), *a.54* (NGB116388), and *a.434* (NGB). All material was preliminary planted for propagation, hybridization was made and the hybrid mate-

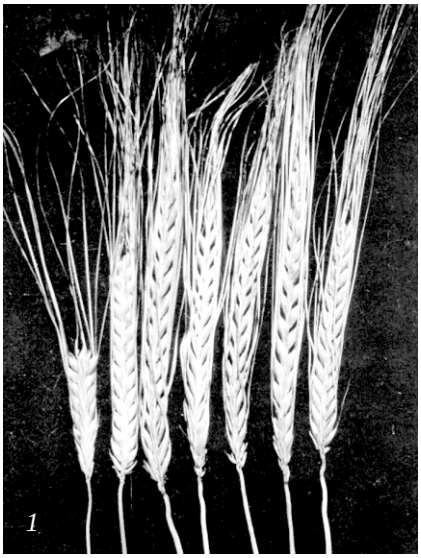

Fig. 1. Diversity of barley *laxatum* mutants used in the current work:
1 – (from left): *tw*, *WT* (cv. 'Auksiniai II'), *lax a.01*, *lax a.54*, *lax a.*434, *lax b.1*, *lax c.21* (all from NGB);
2 – (from left): *tw*, *WT* (cv. 'Auksiniai II'), *lax aa* (1572), *lax ab* (1573), *lax ac* (1574), *lax ag* (1575), *lax a* (1775), *lax a* (2103) – all from USA;
3 – (from left): *tw*, *WT* (cv. 'Auksiniai II'), *lax spike, long awn*; *lax* (625); *lax compact, purple 6-row*; *lax a1* (2278) – all from USA.

Table 1. **Flower structure of parent stocks and complementation test results in F_1 of hybrids with barley mutant *tw* as mother plants and various *laxatum* alleles as father plants**

Mutant	Structure of flower					
	Parent plant		F_1 of hybrids with *tw* x as a mother plant			
	n	Flower formula[1]	n	Flower formula[1]	Altered flowers	
					n	%
a locus						
lax a (1775. USA)	80	5S+1C[7]	143	2L+3S+1C(N)[3]	3	2.1[8]
lax a (2103.USA)	48	5S+1C	227	2L+3S+1C(N)	0	0
lax a 1 (2278.USA)	68	5S+1C	165	2L+3S+1C(N)	15	9.1[9]
lax a 54 (338NGB)	97	5S+1C	250	2L+3S+1C(N)	24	9.6[10]
lax a 434 (647NGB)	98	5S+1C	197	2L+3S+1C(N)	0	0
Others						
lax aa (1572.USA)	64	2L+3S+1C(N)	68	2L+3S+1C(N)	0	0
lax ab (1573.USA)	86	2L+3S+1C(N)	122	2L+3S+1C(N)	0	0
lax compact and purple 6-row	114	2L+3S+1C(N)	295	2L+3S+1C(N)	0	0
Reciprocal combination			69	2L+3S+1C(N)	0	0
tweaky N. 18[2]	209	About 25% of altered flowers [2]	114	2L+3S+1C(N)	0	0
Reciprocal combination			51	2L+3S+1C(N)	0	0
tweaky and missing kernels[4]	128	7.8% of altered flowers[4]	79	2L+3S+1C(N)	0	0
Reciprocal combination			76	2L+3S+1C(N)	1	1.3[11]
tw[5]		see[5]				
WT (c. 'Auksiniai II')[6]		2L+3S+1C(N)		2L+3S+1C(N)		

1 – normal flowers have 2 lodicules (L) + 3 stamens (S) + 1 carpel (C); **2** – *tweaky No 18* – from 209 analysed flowers (fls) 157 fls were normal: 2L+3S+1C; the others 52 (25.4%) fls with various alterations in L, S and C number: 11 fls with 1 L, among those were 1 fl. with 4S and 3 fls with 2S; 1 fl. – with 3 L; 1 fl. – without sexual organs; the flowers, which had normal number of lodicules (2L) were with other alterations in flower structure: 1 fl. – 1S+1C; 5 fls – 4S+2C; 1 fl. –4S+1C; 2 fls – 3S+0C and others; **3** – N – normal flower phenotype (2L+3S+1C) means complementation phenomenon, and that there are different non-allelic genes; **4** – from 128 fls tested the 10 (7.8%) were with alterations: 3 fls without sexual organs and L; 7 fls – only glume; **5** – *tw* (*tweaky spike*) according to [1] had 26.4% of flowers with both L converted to S; 21.35% of fls – one L converted to S; 11.9% fls – one L – to S, the other – to C; 3.8% fls – both L converted to C; **6** – *WT* according to [1, 5] had N flowers – 2L+3S+1C; **7** – Two altered flowers (2.5%), both had lodicules: 1 fl. – 1L, the other – 2L; **8** – 3 fls have a normal number of L (2); **9** – even 11 fls. have 1 L, but 3S; the other 4 fls have 5S as father plant; **10** – even 22 fls have 1L and 3S; 2 fls – 5S + 1C as father plant; **11** – 1 fl. has 4L+3S+1C

Table 2. **Plant height (cm) of F_1 hybrids between barley *tw* and *laxatum* type mutants**

Parental plant genotype	Parental plants		*tw* x as a mother plant		*laxatum* x as a mother plant	
	Average	Variation min–max	Average	Variation min–max	Average	Variation min–max
laxatum – a (1775)	51.0 ± 2.2	38–61	70.8 ± 2.6	58–85	58.3 ± 1.6	50–69
laxatum – a (2103)	58.1 ± 2.4	44–74	74.0 ± 2.2	61–84	73.0 ± 2.4	59–83
laxatum a1 (2278)	80.0 ± 1.8	66–87	77.6 ± 2.4	63–90	76.1 ± 2.3	62–89
laxatum a.1	58.3 ± 1.6	50–69	78.0 ± 1.6	70–88	73.0 ± 2.2	63–82
laxatum a.54	58.9 ± 1.4	50–66	79.4 ± 1.9	68–91	–	–
laxatum a.434	54.6 ± 1.9	45–64	87.7 ± 2.2	79–100	73.7 ± 2.0	65–86
laxatum aa (1572)	64.3 ± 2.4	52–80	84.0 ± 2.2	69–97	86.1 ± 2.4	75–96
laxatum aa (2276)	73.1 ± 1.4	64–80	70.7 ± 1.9	60–85	73.8 ± 1.6	65–81
laxatum ab (1573)	57.3 ± 1.3	49–63	72.7 ± 2.2	62–90	66.6 ± 2.1	59–80
laxatum ab (2277)	78.1 ± 2.2	65–87	74.5 ± 1.7	63–85	71.7 ± 2.9	50–83
laxatum ac (1574)	73.1 ± 1.5	64–84	79.7 ± 2.5	65–91	76.7 ± 1.7	65–85
laxatum ae (2041)	60.4 ± 2.2	50–72	76.2 ± 2.0	65–90	74.6 ± 1.3	65–83
laxatum ag (1575)	38.0 ± 1.4	29–44	70.0 ± 1.6	61–79	60.1 ± 1.9	50–68
laxatum b.1	69.8 ± 2.3	56–86	80.5 ± 2.2	70–91	75.3 ± 1.6	69–84
laxatum c.21	60.9 ± 1.7	52–74	79.9 ± 1.7	69–89	75.6 ± 2.0	68–90
laxatum 298 (2275)	66.3 ± 2.6	51–80	68.1 ± 2.0	57–77	67.8 ± 2.2	53–79
lax (625)	90.7 ± 4.7	60–112	103.5 ± 2.1	94–114	102.4 ± 2.2	92–114
lax spike, long awn	84.2 ± 3.5	64–97	98.5 ± 2.4	85–112	98.1 ± 1.5	90–106
lax compact purple 6-row	53.8 ± 2.3	41–68	83.9 ± 1.7	74–95	77.9 ± 3.7	55–92
tweaky and missing kernels	84.3 ± 5.5	54–101	96.0 ± 1.9	83–106	98.0 ± 1.9	83–109
tweaky no18	88.4 ± 3.1	63–100	98.8 ± 3.2	65–108	95.6 ± 2.4	75–107
AII (WT)	72.1 ± 2.4	56–86	–	–	–	–
tw	69.3 ± 0.7	–	–	–	–	–

rial was examined in the experimental field of Botanical Garden of Vilnius University.

Flowers were fixed in Carnoy's solution (3:1) and analysed on a stereozoom microscope (Motic). All parts of basic flowers were examined in detail after the lemma had been removed. The number of flower organs, their homeotic conversion and the number of mosaic organs were registered.

For evaluation of the quantitative traits (plant height, ear length and the number of kernels per ear), 30 (or more) plants in each sample were analysed. For these measurements we used mature plants and their parts. Statistical analysis was performed using the Excel and Statistic programs.

RESULTS AND DISCUSSION

The preliminary tested collection of *laxatum* mutants differs significantly according to the phenotypic expression of mutant characters of ear structure (Fig. 1), but only mutant alleles in the *laxatum a* locus act on ectopic conversion of lodicules to stamens [3, 4]. Our results of investigation of the different *lax* mutants

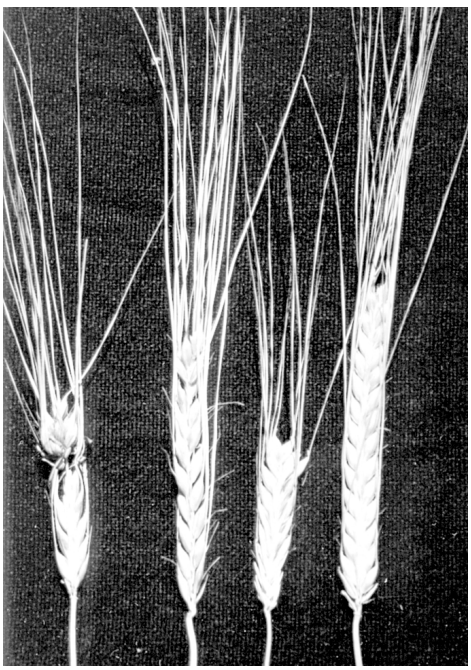

Fig. 2. Ear comparison of different *tweaky* mutants of barley: from left – *tweaky No. 18, tweaky and missing kernels, tw* (our), *WT* (cv. 'Auksiniai II')

Table 3. **The length of the ear (cm) of F_1 hybrids between barley *tw* and *laxatum* type mutants**

Parental plant genotype	Parental plants		*tw* x as a mother plant		*laxatum* x as a mother plant	
	Average	Variation min–max	Average	Variation min–max	Average	Variation min–max
laxatum – a (1775)	11.9 ± 1.8	6–13.5	8.4 ± 1.3	5–11	9.4 ± 1.2	7–12
laxatum – a (2103)	10.5 ± 1.5	5–10.5	7.9 ± 1.1	6–10	7.3 ± 0.9	5.5–9
laxatum a1 (2278)	10.0 ± 1.1	4.5–9	8.1 ± 1.0	6.5–10	7.4 ± 0.8	6–8.5
laxatum a.1	10.45 ± 1.8	6–13	9.3 ± 0.8	7–11	8.8 ± 1.1	6–10.5
laxatum a.54	8.9 ± 1.5	5–11	8.2 ± 1.1	5–10	8.5 ± 1.5	6–12
laxatum a.434	9.2 ± 1.8	5–12	10.4 ± 0.7	9–12	9.8 ± 1.4	7–13
laxatum aa (1572)	13.5 ± 2.5	7.5–17	8.8 ± 1.0	6–10.5	10.0 ± 1.2	7–12
laxatum aa (2276)	9.4 ± 1.1	4.5–9	7.2 ± 1.1	4–9.5	7.1 ± 0.8	6–9
laxatum ab (1573)	9.9 ± 1.8	4.5–11	6.3 ± 0.8	5–8.5	5.9 ± 0.8	4.5–7.5
laxatum ab (2277)	8.9 ± 0.8	4.5–8	7.2 ± 1.0	5–9	6.8 ± 1.3	3.5–9
laxatum ac (1574)	11.8 ± 1.1	7.5–11	10.2 ± 2.9	6–13	8.4 ± 0.8	7–10
laxatum ae (2041)	9.1 ± 0.8	5–8	6.7 ± 0.8	4–8.5	6.7 ± 1.2	5–9.5
laxatum ag (1575)	9.6 ± 1.1	5.5–9	7.8 ± 1.5	5–10	8.6 ± 1.1	6.5–10.5
laxatum b.1	8.2 ± 0.9	6.5–10	8.8 ± 0.9	7–11	–	–
laxatum c.21	8.8 ± 1.1	7–11.5	8.8 ± 0.7	7–10	8.4 ± 0.8	7–10
laxatum 298 (2275)	9.3 ± 0.9	4–8	6.5 ± 1.0	4–8	5.9 ± 1.3	1.5–8
lax (625)	5.4 ± 0.6	1–4	7.3 ± 1.5	5–10	6.6 ± 1.1	5–9.5
lax spike, long awn	8.1 ± 1.4	3–9	8.5 ± 1.0	6.5–11	8.2 ± 1.1	6–10.5
lax compact purple 6-row	5.4 ± 0.9	1–4	5.6 ± 0.9	4–7.5	5.4 ± 1.1	3.5–7.5
tweaky and missing kernels	9.2 ± 1.9	4.5–12	8.7 ± 0.7	7.5–10	8.8 ± 1.4	5–10.5
tweaky no18	7.4 ± 1.8	3–10.5	9.9 ± 1.2	7.5–13	9.7 ± 1.5	6–12
AII (WT)	7.5 ± 0.9	6–9	–	–	–	–
tw	4.1 ± 3.8	3–7	–	–	–	–

have confirmed also the effect on lodicule conversion only of mutations in the *lax a* locus. All the five mutant alleles tested, *lax a* (1775), *lax a* (2103) *lax a.01*, *lax a.54* and *lax a.434*, developed flowers without lodicules, but with 5 stamens instead of normal 3 (Table 1), despite of a different origin of the mutants: two first were from the USA, and the others three from Nordic Gene Bank (Sweden).

At the presentations of results about barley mutants *tw* type at the EPSO Conference [7, 8] and at the 6th Getersleben Conference [9] the question about the attribution of *tweaky spike* mutants also to *laxatum a* alleles was discussed. Results of previous investigations [1, 2] and especially a comparative examination of *tw* and *lax a* alleles in the present work show clearly that it is not so. Barley mutants *tweaky spike* belong to another new gene which acts specifically on identification of flower organs. Normally they have to act on the development of lodicules, but in mutant form they cause ectopic conversion of lodicules to sexual organs, more frequently to stamens, but also to carpels [2]. A polarity of expression of mutant characters is also observed. A stronger expression of a mutant allele is observed in the upper part of the ear, in which multiflower structures are fixed. The better development of kernels also takes place on the upper part of the ear [2, 5]. These statements have been confirmed also in the present work. Besides, all mutants of *tw* type are pleiotropic. Many traits are affected. Conversion of lodicules is only one of them [10].

However, decisive facts on the different genetic nature of *laxatum a* and *tweaky spike* have been obtained from the complementation test (Table 1). In all hybrid combinations of *tw* with *lax a* mutant alleles, in F_1 the normal phenotype, *i.e.* the complementation effect, is observed. In all five combinations *tw* with *lax a* alleles the F_1 hybrids had the normal flower structure – 2L + 3S + 1C.

The general conclusion has been made that *tw* and *lax a* mutants belong to different loci. They are non-allelic mutations. So, the *tw* is the separate locus which regulates development of floral organs of Poaceae plants.

On the other hand, another interesting phenomenon was observed in F_1 of *tw* crossed with two tested *lax a* alleles. An examination of the floral structure of F_1 hybrids showed that various alleles in the *lax a* locus have a different penetrance acti-

Table 4. **Number of kernels per ear of F_1 hybrids between barely *tw* and *laxatum* type mutants**

Parental plant genotype	Parental plants		*tw* x as a mother plant		*laxatum* x as a mother plant	
	Average	Variation min–max	Average	Variation min–max	Average	Variation min–max
laxatum – a (1775)	22.9 ± 3.2	14–27	22.9 ± 3.3	13–28	20.2 ± 4.5	12–27
laxatum – a (2103)	18.6 ± 2.9	9–21	20.8 ± 2.8	13–25	20.9 ± 2.8	13–25
laxatum a1 (2278)	16.7 ± 2.1	10–17	23.7 ± 2.6	18–29	21.3 ± 2.9	15–26
laxatum a.1	16.6 ± 3.5	8–25	21 ± 4.1	11–28	15.4 ± 7.8	2–28
laxatum a.54	18.6 ± 3.9	11–25	21.4 ± 4.1	12–28	9.1 ± 7.0	1–24
laxatum a.434	14.0 ± 1.6	6–21	23.9 ± 2.8	19–28	16.7 ± 7.1	4–29
laxatum aa (1572)	10.4 ± 3.9	2–18	19.1 ± 3.0	12–23	18.1 ± 3.8	8–24
laxatum aa (2276)	15.8 ± 2.3	9–18	20.2 ± 2.4	13–24	18.8 ± 2.3	14–25
laxatum ab (1573)	9.0 ± 5.7	0–19	15.5 ± 2.0	12–21	14.2 ± 1.9	8–17
laxatum ab (2277)	15.9 ± 1.4	10–17	19.7 ± 2.4	14–24	19.1 ± 3.2	11–23
laxatum ac (1574)	26.8 ± 2.9	19–32	23.3 ± 4.3	10–29	23.4 ± 2.9	14–28
laxatum ae (2041)	22.1 ± 1.7	15–22	20 ± 3.8	6–25	19.7 ± 4.1	2–25
laxatum ag (1575)	22.3 ± 2.9	14–26	21.9 ± 3.5	14–27	20.5 ± 5.0	7–28
laxatum b.1	16.6 ± 3.4	7–22	23.0 ± 3.0	14–26	20.5 ± 5	7–28
laxatum c.21	19.2 ± 4.8	7–27	24.0 ± 2.9	15–25	19 ± 4.4	7–10
laxatum 298 (2275)	20.1 ± 2.2	12–22	20.2 ± 3.2	11–25	16.7 ± 4.2	6–24
lax (625)	33.2 ± 5.9	22–49	15.3 ± 5.2	2–23	16.3 ± 4.1	7–24
lax spike, long awn	22.9 ± 11.8	3–44	8.5 ± 1.0	13–32	19.9 ± 3.5	13–26
lax compact purple 6-row	23.2 ± 6.9	6–31	16 ± 3.5	7–22	14.9 ± 1.2	6–23
tweaky and missing kernels	15.5 ± 4.0	3–23	21.9 ± 2.6	17–27	22.0 ± 4.0	10–26
tweaky no18	14.8 ± 5.0	4–24	23.9 ± 3.3	18–31	22.7 ± 3.1	16–29
AII (WT)	20.3 ± 2.4	15–24	–	–	–	–
tw	10.5 ± 3.8	0–18	–	–	–	–

vity in the heterozygous state *tw*$^+$*tw lax a*$^+$ *lax a*. Especially it is obvious for two alleles, *lax a.01* and *lax a.54* (both from NGB). Despite the fact that the main part, about 90%, of the tested flowers in hybrid state had a normal structure, there were about 10% of flowers with expression of the mutant phenotype, *i.e* with five stamens (Table 1). That effect needs of further investigations and is not known from literature data.

Our investigation with a complementation test showed also that *tw* (from VU) differed from two other barley mutants of *tweaky* phenotype (Fig. 2). The mutant *tweaky No. 18* had a significant part (25.4%) of altered structure flowers (see Table 1, comment 2). However, those alterations disappeared in F_1 hybrids, and in F_1 hybrids between *tw* and *tweaky No 18* all flowers were of normal phenotype – 2L + 3S + 1C. The same was observed in both (reciprocal) combinations. The normal phenotype was observed also in reciprocal crosses of F_1 hybrids between *tw* and *tweaky and missing kernels*. In homozygous state, that mutant had only 7.8% of altered flowers, but alterations have been of different character, in quite the opposite manner as of the mutant *tweaky No. 18*. These flowers did not have sexual organs at all, while in our *tw* mutant sexual organs were in abundance.

So, as in the case of *lax a* alleles, the complementation test showed that *tw* and other mutations of *tweaky* phenotype are in different loci (Table 1), because the complementation effect was observed in hybrids of our *tw* with both mutants *tweaky* phenotype tested: *tweaky No. 18* and the other – *tweaky and missing kernels.*

Attention is attracted attracts also by the fact that all the duplicate genotypes tested, *lax aa* or *lax ab*, do not show a mutant flower phenotype in F_1 hybrids with *tw* or in homozygous state (Table 1), despite the presence of the mutant *lax a* allele. We suppose that the transcriptional gene silencing [11–13] takes place. Such hybrids had a normal flower phenotype (2L+3S+1C) without deviations specific for *tw* or *tweaky No. 18.*

Of economical value may be the appearance of new specific flower phenotypes. It may be expected in F_1 hybrids between developmental mutants as it was in the case of F_1 hybrids between several *Ho-*

oded type and *tw*$_1$ barley mutants [5]. However, the new phenotypes have been absent in F_1 hybrids of *tw* × *laxatum*. More interesting results of the economical value were obtained on quantitative characters. As in the case of F_1 hybrids between *Hooded* and *tw* mutants [5], the effect of interaction of different genes in heterozygous state on quantitative characters is of interest not only for heterosis, but it can also show the character of interaction between the tested genes. Relative pleiotropy can show all types of gene interaction on various quantitative characters – activation or suppression of the non-allelic, independently inherited genes. For these reasons three quantitative characters – plant height (Table 2), ear length (Table 3) and the number of kernels per ear (Table 4) – were analyzed in reciprocal crosses between *tw* and various *laxatum* mutants and also among the various *tweaky* type mutants. Interaction of *tw* with various *laxatum* mutants was studied on the more numerous material than it was for analysis of the flower structure.

With hybrids between *tw* and various *laxatum* mutants there were more incidents that may be attributed to heterosis than when barley *tw* was hybridized with various *Hooded* mutants [5]. Even in nine combinations from 21 tested, the hybrid plants excelled both parental mutant stocks. Such effect was observed in combinations of *tw* as the mother plant with *lax a1, lax a.54, lax a.434, lax aa, lax b1, lax c.21, lax; lax spike, long awn; lax compact purple 6-row* mutants as the father plant. It is also obvious that such cases are significantly lesser if *laxatum* type mutants have been used as the mother plant. In these combinations there were only three cases when F_1 hybrids excelled in height both parental mutant stocks. Such result was observed with *lax aa, lax; lax spike, long awn*. All those reciprocal combinations gave the same phenotypic effect. Only in the case of *tw* combination with *lax a* (1775) the maternal effect has been observed.

The ear length of F_1 hybrids was less in the most hybrid combinations than in parental *laxatum* stocks (Table 3). Heterosis was not observed at all.

The number of kernels per ear is a very important character. It can show normalization of *laxatum* phenotype of F_1 hybrids. In general, this tendency was observed (Table 4), but the high variation of individual plants from semisterile or even fully sterile to plants with a significant number of kernels per ear does not allow to determine a statistically significant effect.

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MIEÞIØ MUTACIJØ *TWEAKY SPIKE* IR *LAXATUM* SÀVEIKA F_1 HIBRIDUOSE

Santrauka

Ðiame darbe iðtirti mieþiø mutantai, kurie ektopiðkai keièia lodikuliø raidà. Komplementacijos bandiniu nustatyta, kad tirti *lax a* ir *tweaky spike* mutantai yra skirtingø genø mutacijos. Ðie mutantai skiriasi ir raiðka homozigotose. Árodyta, kad originalûs *tw* mutantai yra naujo geno, reguliuojanèio þiedo organø raidà, mutacijos.