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Interaction of three homeotic barley genes involved in flower development

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Flowers of Poaceae plants have a specific structure of the lemma and palea and two lodicules. Their genetical control has been investigated insufficiently, and the interaction of homeotic mutants introduced in the development of those organs, is of interest. In the present work, the interaction of two groups of homeotic mutants, attributed in previous and present investigations to four different loci, was examined: *tw* and *lax* (belonging to two loci, *lax-a* and *lax-c*) controlling the development of lodicules characterized by homeotic conversion of lodicules to stamens, and *tw* – also to carpels; in *Hooded* (*K*) mutants, an additional inverted flower develops at the site of transition between the lemma and the awn or on the awn. The *Hooded, lax-a* and *tw* give an independent phenotypic effect, while an interaction between *lax-c* and *lax-a* loci was observed. It has been supposed that *lax-c* is a slight suppressor of *lax-a* mutation.

Key words: Poaceae flower control, lodicule development, homeotic gene interaction, hooded (*K*) mutants, *lax* mutants, *tw* mutants

INTRODUCTION

In general, the flower development of grasses (Poaceae) is controlled by genes attributed to classes according to the ABCE model, the first being applied to eudicots [1, 2]. However, inflorescences and flowers of grasses have a characteristic structure differing distinctly from that of eudicots. The floret of grasses has specific organs – lodicules – and is protected by two leafy organs, the lemma and the palea, both representing reduced vegetative leaves [3–5]. The normal floret of barley has two lodicules, three stamens, one carpel (2L3S1C), and the upper part of the lemma in most cultivars develops into the awn, a long distal appendage. However, in the barely dominant mutant *Hooded* (*K*), an extra flower develops at the site of transition between the lemma and the awn or on the awn. Ectopic floral organs differentiate in an inverted orientation with respect to the lemma proper [6]. Periclinal cell divisions in the subepidermal layer of the awn primordium give rise to flower meristematic cushion [6, 7].

The barley mutants *laxatum-a* (*lax-a*) and *tweaky spike* (*tw*) have another flower homeotic conversion. The lodicules of *lax-a* are converted to stamens, and the typical flower formula of that mutant is 0L5S1P [8]. Contrary to *lax-a*, in the barley mutant *tw* only about half or even less flowers have lodicules converted to stamens, and other disturbances of normal flower development are also observed. In some of flowers, lodicule(s) are converted to carpels [9, 10].

The genetical ground of the *Hooded* (*K*), *lax-a* and *tw* mutants is different.

All *Hooded* mutants, despite significant phenotype variations, have 305 bp duplication in intron IV of the homeobox gene *BKn3*, which is a member of the *Knox*

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plant homeodomain family [6]. The constitutive expression of maize transgene *Kn1* in barley reproduces the *Hooded* mutant phenotype. The protein and mRNA location of the transgene, driven by a constitutive promoter, is similar to the expression pattern of the *hvKnox3* intron. The regulatory function of this intron in flower meristem development was proposed [12] and proved experimentally [13]. When one or three copies of this 305 bp fragment were used as 'baits' in the yeast one hybrid screening system, four different cDNAs, binding to the 305 bp sequence, were isolated. These cDNAs encode barley proteins designed as BEIL, BAPL, BBR and BGRF. So, an interaction between transcription factors forming the heterodimer structures was shown [13].

The barley *lax-a* gene belongs to another family of transcription factors attributed to B class of flower organ identity genes determining sepals and petals [14]. The original mutants *tw* are non-allelic to both test mutants *Hooded* and *lax-a*, as well as to the other two mutants *tweaky and missing kernels* or *tweaky N* 18 [15].

Interaction between the genes determining flower development and structure, take place [3, 4, 17], and investigation of such interaction between different barley loci is of interest. In the previous works [15, 16], the interaction of *tw* with *lax-a* and *tw* with *Hooded* was examined. In the present work, the triple hybrids *tw lax-a Hooded* are examined, and a bigger collection of *lax-a* allelic mutants was introduced into the complementation test with the barley *tw* locus. The impetus for such investigation was given by the significant variation of *lax-a* alleles according to flower structure and the fact that *lax-c.21*, belonging to another locus, shows also lodicule conversion into stamen-like structures, though not so clearly expressed as in *lax-a.01* and several other *lax-a* alleles.

Table 1. **Flower structure of *lax-c.21*, different alleles of *lax-a* locus and their complementation test with mutant *tw***

lax genotipe	Number of flowers		Flower structure, %											
			2L3S1C		5S1C		5S'1C		5²S1C		Sum of 5S1C		2L3S5S1C		1L5S4S1C	
	lax	*lax* × *tw*	*lax*	*tw* × *lax*	*lax*	*tw* × *lax*	*lax*	*tw* × *lax*	*lax*	*tw* × *lax*	*lax*	*tw* × *lax*	*lax*	*tw* × *lax*	*lax*	*tw* × *lax*
lax-c.21	94	206	0	0	0	0	0	0	0	0	0	0	79.7	100	0	0
lax-a.01	159	208	0	100	96.2	0	1.3	0	0	0	97.5	0	0	0	2.5	0
lax-a.04	157	254	0	99.2	67.5	0	15.2	0	10.8	0	93.5	0	1.9	0.8	4.6	0
lax-a.08	96	21.9	0	94.1	52.1	0	34.4	0	13.5	0	100	0	0	0.9	0	4.1
lax-a.20	92	209	0	100	37.0	0	33.7	0	29.3	0	100	0	0	0	0	0
lax-a.37	116	209	0	99.0	25.0	0	53.4	0	21.6	0	100	0	0	0	0	1.0
lax-a.39	108	201	0	98.0	90.7	0	8.3	0	1.0	0	100	0	0	0	0	2.0
lax-a.54	116	213	0	98.6	22.4	0	25.9	0	51.7	0	100	0	0	0	0	1.4
lax-a.208	138	226	0	100	28.3	0	34.8	0	36.9	0	100	0	0	0	0	0
lax-a.218	105	223	100	99.5	0	0	0	0	0	0	0	0	0	0	0	0.5
lax-a.222	178	276	0	100	60.7	0	0	0	11.2	0	71.9	0	17.4	0	10.7	0
lax-a.278	106	222	0.9	100	0	0	8.6	0	45.3	0	53.9	0	22.6	0	22.6	0
lax-a.286	143	205	0	99.0	0	0	15.4	0	0	0	15.4	0	81.8	0	2.8	1.0
lax-a.373	101	200	73.3	100	0	0	0	0	0	0	0	0	26.7	0	0	0
lax-a.434	112	198	0	100	58.9	0	28.6	0	12.5	0	100	0	0	0	0	0
lax-a.450	172	243	0	95.5	73.8	0	18.6	0	7.6	0	100	0	0	1.2	0	0

The number of tested flowers of initial cultivars for induction of *lax* mutants (*WT*): 'Kristina' – 157; 'Foma' – 132; 'Bonus' – 201; the initial cv. for *tw* mutant induction was 'Auksiniai II'-177. In two hybrid combinations, flowers with a rare formula were observed: two flowers 1LS + 2S + 1C in *tw* × *lax-a.0.08*, one flower 1LS + 3S + 1C + 1SC in *tw* × *lax-a.450*, and seven flowers 1L1LS + 3S + 1C; 1 – one stamen is intermediate type with hairs, typical of lodicule, because typical stamens are not hairy; 2 – the same for both (two) converted stamens.

MATERIALS AND METHODS

The barley mutant *tw*, used as the mother plant, is of specific origin induced by chemical mutagens in barley cv. "Auksiniai II". The latter had been obtained from the Lithuanian Institute of Agriculture and was used in the present work as a wild type (*WT*). The *laxatum* mutants were from the Nordic Gene Bank (Alnarp, Sweden) and all except *lax-c.21* belong to the *lax-a* locus. Mutants with two figure indices are induced in the barley cultivar 'Bonus' and with higher indices in the cultivars 'Foma' and 'Kristina'. Only four allelic mutants of different origin were examined in the previous work [15]. The mutant *Hooded* was from VIR (Sanct Petersburg, Russia). All initial material and hybrids were planted in the Botanical Garden of Vilnius University. For triple hybrids, stable hybrid forms were selected in F_5–F_6 of hybrids *tw* × *Hooded* and used for hybridization with different *lax-a* allelic mutants and also with *lac-c.21*; because it was an unexpected finding that *lax-c.21* has also lodicules converted into stamen-like structures, special attention was given to complementation analysis between *lax-c.21* and different *lax-a* alleles.

Flowers were fixed in Carnoy's solution (3 : 1) and analysed with 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 evolution of the quantitative traits, 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

Introduction of a longer list of *lax-a* allelic mutants of more monotypous origin (all from the Nordic Gene Bank) in the investigation of flower structure, as well as for the complementation test with the *tw* mutant, allowed to reveal significant differences among different alleles in the same *lax-a* locus (Table 1). Generally, most of the test *lax-a* alleles had the flower formula 5S1C (five stamens and one carpel). Especially it is characteristic of the *lax-a* mutants arisen from the initial cv. 'Bonus'. However, the expression of that peculiarity significantly varied if a stamen more differentiated in time was applied. Significant part of stamens converted from lodicules preserves the peculiarity of lodicules – hairs on the top of stamens. The frequency of such hairy stamens varies in different *lax-a* mutants, even in *lax-a* mutants developed from cv. 'Bonus' (Table 1).

Two allelic mutants, *lax-a.218* and *lax-a.373*, need further investigation. In *lax-a.218*, all flowers had a normal, typical of a barley flower formula 2L3S1C (two lodicules, three stamens and one carpel). In the mutant *lax-a.373*, a significant part of flowers had the formula 2LS3S1C, i. e. both lodicules, only partially converted into stamens, had hairs typical of lodicules.

The reason for such a great difference of *lax-a.218* and *lax-a.373* mutants from the other *lax-a* alleles in the same locus may be differences in the conditions of Lithuania and Sweden or dependence of mutant allele expression on vegetation conditions in the different years of reproduction.

The complementation test has confirmed our previous conclusion [15] that *lax-a* and *tw* are different loci, despite lodicule conversion into stamens common for both of them (Table 2).

Table 2. **Complementation test between *lax-c.21* and various *lax-a* allelic mutans**

Mutant or F_1 hybrid	n	Type of flowers and their frequency, %					
		2L3S1C	1L1LS3S1C	2LS3S1C	5S1C	3S1C2SC	4S1C1SC
lax-c.21	206	0	0.5	99.5	0	0	0
lax-a.01	187	0	0	0	81.8	7.5	10.7
lax-a.37	176	0	0	0	64.3	22.2	12.5
lax-a.54	188	0	0	0	73.4	9.6	17.0
lax-a.208	160	0	0	0	84.4	5.0	11.3
lax-a.434	184	0	0	0	62.0	20.7	17.3
***lax-c.21* × with *lax-a* alleles**							
lax-a.01	188	28.7	27.2	43.6	0.5	0	0
lax-a.37	211	30.3	33.6	36.1	0	0	0
lax-a.54	198	31.8	20.2	48.0	0	0	0
lax-a.208	196	59.2	23.5	17.3	0	0	0
lax-a.434	202	27.2	30.2	41.6	0.5	0	0.5

Table 3. **Quantitative spike traits of *lax* mutants and their hybrids with *tw***

Mutant	Spike length		Number of grains in spike		Density of spikes	
	mutant	*tw* × *lax*	mutant	*tw* × *lax*	mutant	*tw* × *lax*
tw	5.04 ± 0.84	–	13.0 ± 2.1	–	9.80 ± 0.79	–
lax a.04	10.57 ± 2.15	11.11 ± 2.02	25.6 ± 3.3	25.3 ± 4.6	8.80 ± 1.14	8.90 ± 0.74
lax a.08	10.88 ± 1.80	10.58 ± 1.92	25.3 ± 2.7	24.8 ± 2.6	8.80 ± 0.42	9.30 ± 1.25
lax a.20	10.77 ± 1.88	9.72 ± 2.20	25.5 ± 3.6	25.3 ± 3.1	9.00 ± 0.67	9.20 ± 1.14
lax a.37	10.05 ± 1.69	8.33 ± 1.95	24.9 ± 2.9	22.3 ± 2.9	8.80 ± 0.79	10.90 ± 1.20
lax a.39	9.83 ± 1.54	9.95 ± 1.87	24.3 ± 2.5	23.7 ± 3.7	9.30 ± 0.67	9.30 ± 0.48
lax a.208	9.82 ± 1.38	9.98 ± 2.05	25.1 ± 2.6	23.4 ± 4.4	9.30 ± 0.82	8.90 ± 0.88
lax a.222	9.02 ± 1.84	10.28 ± 1.55	24.6 ± 3.5	26.8 ± 3.3	9.40 ± 0.84	9.80 ± 0.79
lax a.278	9.77 ± 1.86	10.15 ± 1.29	26.0 ± 3.8	25.6 ± 2.2	10.40 ± 0.52	10.00 ± 0.82
lax a.286	9.82 ± 1.67	9.47 ± 2.04	25.1 ± 3.5	23.4 ± 4.5	9.90 ± 0.74	10.00 ± 1.05
lax a.373	8.40 ± 1.10	9.12 ± 1.99	25.0 ± 2.4	23.4 ± 3.7	11.30 ± 0.67	10.10 ± 0.99
lax a.434	11.87 ± 1.78	10.60 ± 0.72	28.8 ± 3.0	27.7 ± 2.0	9.00 ± 0.47	10.20 ± 0.92
lax a.450	12.48 ± 2.48	9.22 ± 2.07	28.3 ± 3.6	22.4 ± 4.9	8.20 ± 0.92	9.20 ± 1.03

Table 4. **Characteristic triple hybrids (*tw* × *Hooded*) × *lax-a*: comparison with selected stable hybrids *tw* × *Hooded* (*K*)**

Stable selected *(tw × K)* hybrid with *lax*	Spike characteristics			Flower characteristics			
	Length	Row number	*tweaky* form	Additional	n	*WT* type	Others
2 × *lax-a.0.1*	L	2	–	+	184	46.6 ± 3.7	53.4 ± 3.7
× *lax-a.37*	L	2	–	+	186	57.5 ± 3.6	42.5 ± 3.6
× *lax-a.54*	L	2	–	+	180	58.3 ± 3.7	41.7 ± 3.7
× *lax-a.373*	M	2	–	+	177	55.9 ± 3.7	44.1 ± 3.7
× *lax-a.434*	L	2	–	+	180	56.1 ± 3.7	43.8 ± 3.7
× *lax-c.21*	L	2	–	+	197	55.3 ± 3.6	44.7 ± 3.6
3 × *lax-a.0.1*	LN	2	–	+	176	55.7 ± 3.8	44.3 ± 3.8
× *lax-a.37*	LN	2	–	+	171	56.7 ± 3.8	43.3 ± 3.8
× *lax-a.54*	LN	2	–	+	192	55.2 ± 3.6	44.8 ± 3.6
× *lax-a.373*	LN	2	–	+	200	57.0 ± 3.5	43.0 ± 3.5
× *lax-a.450*	LN	2	–	+	197	56.4 ± 3.5	43.7 ± 3.5
× *lax-c.21*	LN	2	–	+	186	50.0 ± 3.7	50.0 ± 3.7
5A × *lax-a.01*	LN	2	–	+	167	56.3 ± 3.9	43.7 ± 3.9
× *lax-a.37*	LN	2	–	+	182	50.0 ± 3.7	50.0 ± 3.7
× *lax-a.54*	LN	2	–	+	170	57.7 ± 3.8	42.4 ± 3.8
× *lax-c.373*	LN	2	–	+	180	50.0 ± 3.7	50.0 ± 3.7
× *lax-c.21*	LN	2	–	+	180	50.0 ± 3.7	50.0 ± 3.7
7 × *lax-a.208*	L	2	–	+	193	44.0 ± 3.6	56.0 ± 3.6
3 × *lax-a.373*	L	2	–	+	181	56.4 ± 3.7	43.7 ± 3.7
× *lax-c.21*	L	2	–	±	259	52.1 ± 3.1	47.9 ± 3.1
var 2 (*tw* × *K*)	S	I	+[1]	+	262	46.6 ± 3.1	53.4 ± 3.1
var 3 (*tw* × *K*)	LSp	I	+	+	182	52.8 ± 3.7	47.3 ± 3.7
var 5 (*tw* × *K*)	S	2	+	±	159	46.5 ± 4.0	53.5 ± 4.0
var 7 (*tw* × *K*)	LN	2	–	±	174	51.2 ± 3.8	48.8 ± 3.8

Abrreviations: length: S – short, L – long, Sp – sparse, N – narrow, M – middle; row number: I – intermedium, 1 – frequently two additional flowers on both lemma and palea.

Table 5. **Characteristics of triple hybrids (*tw* × *Hooded*) × *lax* according to spike quantitative traits in comparison with selected stable *tw* × *Hooded* hybrids**

Triple hybrid or stable (*tw* × *K*) hybrid	Spike length	Number of grains in spike	Density of spikes	Triple hybrid	Spike length	Number of grains in spike	Density of spikes
var 2 × *lax.a01*	7.8 ± 1.4	20.6 ± 3.0	9.80 ± 0.70	var 5 × lax.a01	8.4 ± 1.4	21.1 ± 2.9	9.70 ± 0.84
var 2 × *lax.a04*	7.2 ± 1.6	19.8 ± 4.3	10.06 ± 0.64	var 5 × lax.a37	8.1 ± 1.8	21.3 ± 3.9	10.28 ± 0.75
var 2 × *lax.a20*	8.2 ± 1.3	21.8 ± 2.9	10.13 ± 0.78	var 5 × lax.a54	8.6 ± 1.4	22.3 ± 3.1	10.30 ± 0.70
var 2 × *lax.a39*	8.4 ± 1.3	22.0 ± 2.7	9.74 ± 0.66	var 5 × lax.a286	8.4 ± 1.6	22.7 ± 3.3	10.13 ± 0.86
var 2 × *lax.a54*	8.7 ± 1.1	22.5 ± 1.9	9.73 ± 0.74	var 5 × lax.a373	8.4 ± 1.2	23.9 ± 2.9	10.60 ± 0.72
var 2 × *lax.a373*	8.1 ± 1.2	22.0 ± 3.3	10.04 ± 0.66	var 5 × lax.c	7.8 ± 1.3	21.1 ± 2.9	10.50 ± 0.68
var 2 × *lax.a434*	8.8 ± 1.2	22.4 ± 2.6	9.77 ± 0.63	var 5 × lax.a08	8.2 ± 1.5	20.6 ± 2.8	11.22 ± 0.85
var 2 × *lax.c*	9.0 ± 1.3	23.4 ± 2.6	9.77 ± 0.73	var 5 × lax.a208	8.0 ± 1.3	21.7 ± 2.8	11.33 ± 0.84
var 3 × *lax.a01*	7.5 ± 0.3	19.1 ± 0.7	10.30 ± 0.15	var 5 × lax.a278	7.9 ± 2.3	20.2 ± 3.9	11.56 ± 1.04
var 3 × *lax.a37*	8.1 ± 0.4	20.4 ± 0.8	10.20 ± 0.20	var 7 × lax a.37	9.1 ± 1.9	23.81 ± 4.2	9.78 ± 0.51
var 3 × *laxa.54*	7.8 ± 0.4	18.9 ± 0.9	9.56 ± 0.18	var 7 × lax a.208	8.0 ± 1.6	22.5 ± 3.9	10.37 ± 0.89
var × *lax.a373*	7.6 ± 0.3	19.6 ± 0.6	10.70 ± 0.26	var 7 × lax a.278	8.5 ± 1.4	22.9 ± 3.7	10.41 ± 0.51
var 3 × *lax.a450*	8.2 ± 0.2	20.3 ± 0.6	10.40 ± 0.16	var 7 × lax a 286	6.7 ± 1.5	20.0 ± 4.3	11.42 ± 0.96
var 3 × *lax.c21*	8.8 ± 0.3	22.4 ± 0.5	10.10 ± 0.23	var 7 × lax a.373	6.6 ± 1.4	18.1 ± 3.7	10.58 ± 1.10
tw × *K* (*Hooded*)							
var 2	5.9 ± 0.1	21.8 ± 0.9	13.83 ± 0.68				
var 3	5.5 ± 0.2	18.0 ± 1.2	17.30 ± 0.66				
var 5	4.7 ± 0.1	10.0 ± 0.3	8.73 ± 0.28				
var 7	4.8 ± 0.1	10.3 ± 0.4	8.25 ± 0.35				

However, in *tw* mutants, lodicules may also be converted to carpels. We may presume that both genes may be attributed to different subclasses of B class flower identity genes according to the ABCE model [1, 2].

Intriguing results were obtained by the complementation test between *lax-c.21* and five different alleles of *lax-a* locus. In general, the 'pure' *lax-a* (5S1C) flower phenotype was only an accidental case (Table 1). However, a significant part of flowers were not only *WT* (2L3S1C), but also had flowers in which lodicules were not fully converted to stamens – 2LS3S1C or 1L1LS3S1C. This result may imply that *lax-c.21* is a weak suppressor for *lax-a*.

Attribution of *lax-a* and *lax-c* to different loci was proven by Larsson who discovered even 29 *lax* loci after examination of 1273 *lax* type barley mutants [18].

Additional information on differences and interaction between *lax-a* and *tw* loci is given by the analysis of quantitative characters of spike, because *tw* has very characteristic spikes and not only shows a specific conversion of lodicules to stamens. Among the quantitative spike characteristics, in *tw* mutants it is a short spike and the low number of grains on the spike (Table 3). All F_1 hybrids after the complementation test had the quantitative character close to that of the *lax-a* parent (Table 3). The double-stable hybrids (F_5–F_6) *tw* × *Hooded* had the following basic phenotypic traits: typical spike structure for *tw* and inverted additional flower on awns or instead of awns (Figure).

In triple hybrids (*tw* × *Hooded*) × × *lax-a* alleles or *lax-c.21,* the dominant traits were developed in F_1 as a two row spike, a long normal form of spike (against the *tweaky* phenotype) (Figure), an additional flower instead of an awn (*Hooded* is dominant), but the structure of the main flower varied (Table 4). Nearly half of the flowers were not of the *WT* phenotype (2L3S1C), despite the fact that *lax-a* and *lax-c* are recessive mutations, and the interaction with *tw* gave a nor-

Figure. Initial forms of spikes used for interaction of *tw*, *Hooded* (*K*) and *lax* examination.
a: left – *tweaky spike* (*tw*), right – *Hooded* (St. Petersburg); b – *laxatum*; c – several stable dihybrids with *tw* spike phenotype and additional flowers on awns or in place of awns: from left: variants No 2, No 7, No 5, No 3; d – F_1 of triple hybrid (*tw* × *Hooded*) × *lax-a*

mal flower structure (compare with results in Table 1). This phenomenon needs further investigations.

Analysis of the quantitative traits of the spike gave about the same result as for F_1 of double *tw* hybrids with various *lax-a* alleles and *lax-c.21* (compare Tables 3 and 5). Despite the short *tw*-type spikes of double hybrids (Var 2, 3, 5, 7) *tw* × *Hooded*, in F_1 of triple hybrids the spikes were long. In all combinations of Var 2 with *lax-a* alleles hybrids whose spike density was equal to that of Var 2 were absent.

The triple hybrids will be of interest in future not only for stable composed of three genes introduced in flower development, but also as ornamental plants because of exotic forms of the spike.

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References

1. Weigel D, Meyerowitz EM. Cell 1994; 78: 203–9.
2. Coen ES, Meyerowitz EM. Nature 1991; 353: 31–7.
3. Kurata N, Miyoshi K, Nonomura K-J, Yamazaki Y, Ito Y. Plant Cell Physiol 2005; 46: 48–62.
4. Malcomber ST, Kellog EA. Tr Plant Sci 2005; 10: 427–35.
5. Soltis DE, Chanderbali AS, Kim S, Buzgo M, Soltis PS. Ann Bot 2007; 100: 659–76.
6. Müller KJ, Romano N, Gerstner O, Garcia-Maroto F, Pozzi C, Salamini F. Nature 1995; 374: 727–30.
7. Stebbins GL, Yagil E. Genetics 1966; 727–41.
8. Larsson HEB. Hereditas 1985; 103: 239–53.
9. Bieliūnienė A, Švėgždienė D, Rančelis V. Biologija 2003; 1: 21–5.
10. Rančelis V, Vaitkūnienė V. Biologija 2007; 53(4): 11–8.
11. Williams-Carrier RE, Lie YS, Hake S, Lemaux PG. Development 1997; 124: 3737–45.
12. Müller K, Pozzi C, Müller J, Salamini F, Rohde W. Eur J Physiol 2000; 439(Suppl): R14–5.
13. Roig C, Pozzi C, Santi L, Müller J, Wang Y, Stile MR, Rossini L, Stanca M, Salamini F. Genetics 2004; 167: 439–48.
14. Laurie DA, Pratchett N, Allen RL, Hantke SS. Theor Appl Genet 1996; 93: 81–5.
15. Vaitkūnienė V, Varnaitė A, Rančelis V. Biologija 2004; 4: 10–5.
16. Vaitkūnienė V, Varnaitė A, Rančelis V. Biologija 2004; 3: 13–20.
17. Theissen G, Melzer R. Ann Bot 2007; 100: 603–19.
18. Larsson HEB. Barley Genetics Newslet 1986; 16: 83–6.

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TRIJŲ HOMEOZINIŲ MIEŽIŲ GENŲ, KURIE KONTROLIUOJA ŽIEDO RAIDĄ, SĄVEIKA

Santrauka

Miglinių žiedas turi savitas žiedo dalis – žiedažvynius ir lodikules, kurių genetika yra nepakankamai ištirta. Tyrimus palengvina šių organų raidą kontroliuojančių genų mutacijos ir jų tarpusavio sąveikos tyrimai. Šiame darbe ištirti žiedo raidos homeoziniai mutantai, priklausantys skirtingiems lokusams: *lax-a* ir *lax-c*- kontroliuoja lodikulių raidą, tačiau skirtingi aleliai pasireiškia nevienodai – *tw* mutantuose lodikulės gali virsti kuokeliais arba / ir piestelėmis; *Hooded* mutantams vietoje akuoto arba ant jo atsiranda papildomas invertuotas žiedas. Darbe šių mutantų sąveika ištirta komplementacijos testu ir įrodytas *tw, Hooded* (*K*) ir *lax-a* lokusų nepriklausomas pasireiškimas; *lax-c.21* paveikia *lax-a* alelių raišką, todėl manoma, kad jis gali būti silpnas *lax-a* lokuso supresorius.

Raktažodžiai: homeoziniai mutantai, komplementacijos testas