Interaction of barley mutants *Hooded* and *tweaky spike* in F_1 hybrids

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The *Hooded* mutation of the barley gene *BKn3* causes ectopic development of additional flower instead of awn or on awn. Another barley developmental mutation, *tweaky spike* (*tw*), causes ectopic conversion of lodicules to stamens and/or carpels. The interaction of both mutations was investigated on 15 different *Hooded* type genotypes in F_1 (heterozygous state). The borderline between the action of both mutant genes is well expressed: *tw* acts on basic flower whereas the *Hooded* type mutants determine additional flower. The latter mutant gene doesn't display any effect on the basic flower, while *tw* shows a significant influence on the development of additional structures on the lemma/awn border. The effect depends on the type of *Hooded* mutation.

Key words: flower development, barley, homeotic mutations, *Hooded* and *tw* interaction

INTRODUCTION

Homeobox genes are involved in many important developmental processes of multicellular eukaryotes. They encode a large family of homeodomain proteins that are transcription factors and regulate the expression of the downstream cascade of target genes. Homeodomain is a highly conserved protein domain involving a helix-turn-helix motif for binding to nucleotide sequences [1–3]. Different homeodomain proteins have been grouped into separate families or classes based on either sequence identity within the homeodomain or conserved protein motifs outside the homeodomain, or the tissue or cells where homeobox genes are expressed.

The first family of homeobox genes was isolated by transposon tagging the morphological mutation *Knotted1* (*Kn1*) in maize [4, 5]. Originally *Kn1* was known only from dominant alleles that encoded knots of tissue over the veins, although some new recessive alleles of *Kn1* have been showed recently [6].

The *Kn1*-like homeobox gene family comprises two classes. The class I genes include maize *Kn1*, *rough sheath1*, *Arabidopsis STM-1*, rice *OSM1* and *OSM15*, barley *HvKnox 3*(or *BKn3*) are highly expressed in meristematic tissues. In addition, *Kn1* like genes are expressed throughout the corpus of the inflorescence meristem and in spikelet and floral meristems, but are not expressed in lateral organs such as leaf or glume primordia, or floral organs

[6]. Ectopic expression of the class I genes results in formation of ectopic meristems. Class I genes belong to the three amino acid (proline – tyrosine – proline) loop extension (TALE) superclass of homeobox genes.

In contrast, class II genes are expressed in most of the tissues studied [7, 8]. Sentoku et al. [9] single out in the rice genome the third class of *Kn1* type genes represented by *OSM3*, which is expressed only in early embryo and inflorescence meristems, but not in vegetative or floral ones.

The homeodomain zipper (*HD-Zip*) class of homeobox genes is characterized by the leucine zipper dimerization motif adjacent to the homeodomain and is essential for vascular development [10]. The plant homeodomain finger (*PHD finger*) class is distinguished by a conserved cysteine-rich motif and is represented by a pathogenesis-related homeodomain determining *PRM* genes [11]. *GLABRA2* like (*HD-GL2*) class is expressed during embryonic pattern formation and trichome development. GLABRA protein is similar to HD-ZYP, but does not have the Leu zipper [12, 13]. The *BELL1* family is represented by the photomorhogenic genes *cop1* and *det1* [14] or by genes involved in pattern formation of the ovule primordium [15]. Several plant homeobox genes have also a DNA box encoding about 24 a. a. ELK domain (from three amino acids – Glu, Leu, Lys) [8].

The interaction of different homeobox genes with one another and with regulating genes [7, 9, 6–12]

can provide for a high plant diversity as shown for different *Arabidopsis thaliana* ecotypes [16]. Epigenetic factors [18, 22, 29] as well as alternative splicing [24, 25] can be involved in different expression of developmental genes.

On the other hand, the same or pretty much the same phenotypes can be encoded by different genes, as was observed for barley *Hooded* and *calcaroides* mutations [26]. Interaction between two mutant developmental genes can also give a new phenotype. Zygomorphic flowers of *Antirrhinum majus* are exhibited in the arrangement of lateral organs around the floral axis and within individual organs. The *cycloidea* (*cyc*) or *dichotoma* (*dich*) mutations result in semipeloric flowers, whereas *cyc dich* double mutants have completely peloric (radially symmetrical) flowers [27].

In the present work, the interaction between the two independently inherited barley developmental homeotic mutants, *Hooded* and *tweaky spike* (*tw*), was examined. The *Hooded* is a mutation in the homeobox gene *HvKnox3* (*BKn3*) and is caused by a 305-base pair duplication in intron 4. The dominant mutation *Hooded* (also named *Kap*) induces the appearance of an extra flower of inverse polarity on the lemma [26, 28]. The barley recessive mutants *tweaky spike* (*tw, tw₁, tw₂* and others) have a specific form of the ear and show a conversion of lodicules to stamens and/or carpel. In those mutants, homeosis of flower organs is accompanied by a variation in the number of flower organs [29].

MATERIALS AND METHODS

Both barley *tweaky spike* (*tw₂ and tw*) mutants used as the mother plants are 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 W*ild Type* (*WT*). The barley *Hooded* type used as a mother plant was obtained from VIR (Sanct Petersburg, Russia) in 1990 as a collection No 15550 *Bt2* (*Brittle rachis*) Colsess. All that plant material had been cultivated for a long time without pesticides in the Botanical Garden of Vilnius University as was also the material used as father plants. The main characteristics of the mother plant are represented in Table 1. To escape the influence of a different cytoplasm, the same stock was used as the mother plant with various father plants, and as the father plant was used material obtained in 2002 only from one place – The National Small Grains Res. Facility Barley Genetic Stocks Collection (Aberdeen, Idaho, USA), but two specimens of that collection used in our work were from other states of USA: from the North Dakota (*Brittle rachis*) and from Colorado (*Hooded lemma*). All that material was also cultivated in the Botanical Garden. Hybridization was made and the hybrid material was planted in the experimental field of the Botanical Garden and in the greenhouse of the Department of Botany and Genetics.

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. Additional flower on the lemma-awn transition region or on awn was also analysed in detail. The number of flower organs, their homeotic conversion and the number of mosaic organs were registered.

For evaluation of the quantitative traits (plant height and ear length), 30 (or more) plants in each

Table 1. **Characteristics of the main barley genotypes used for analysis**				
Character	Auksiniai II	*Hooded*[1]	*tw*	*tw₂*
Structure of basic flower	Normal (2L+3S+1C)[2]	Normal	Lodicules converted to S or C [29]	
Structure of additional flower/conversion of awn	Normal awn	Additional inverted flower	Normal awn	
Plant height, cm	63.3 ± 1.3	65.7 ± 2.3	69.3 ± 0.7	77.5 ± 2.5
Ear length, cm	7.3 ± 0.2	4.8 ± 0.2	5.1 ± 0.1	5.3 ± 0.2
Number of grains per ear	25.7 ± 0.5	28.5 ± 0.6	15.0 ± 0.4	15.6 ± 0.4
Number of rows in the ear	2	6	2	2
Mass of 1000 grains, g	33.7 ± 0.3	34.0 ± 0.02	39.0 ± 0.03	38.7 ± 0.7
Productivity (g/2 m²)	625 ± 25	923 ± 86	490 ± 38	410 ± 60
Protein content (%)	13.5 ± 0.3	–	15.1 ± 0.1	17.9 ± 0.3
Days till heading	55.3 ± 3.9	50.3 ± 0.2	61.3 ± 0.3	60.3 ± 0.3
Days till maturation	98.5 ± 2.0	96.5 ± 0.3	101.0 ± 4.0	101.0 ± 4.0
Resistance to lodging (in numbers)	6.5 ± 0.5	9.0 ± 0.0	9..0 ± 0.0	9.0 ± 0.0
Sensitivity to *Claviceps purpurea* (%)	0.65 ± 0.29	0.98 ± 0.07	4.81 ± 0.11	4.18 ± 0.25
L – lodicule, S – stamen, C – carpel; 1– *Hooded* from St. Petersburg; 2 – average results from 30 plants.				

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

It has been possible to examine the interaction of our original *tweaky spike* barley mutants with *Hooded* type mutants as both genes are involved in flower development. In *tw* type mutants not only lodicules are homeotically converted to stamens or/and carpels, but also the number of flower organs varies. The latter peculiarity of *tw* mutants has a well expressed polarity to the upper part of the ear [29]. The conversion of lodicules to sexual organs of flower shows rather that floral development genes of the class C [30] are expressed irregularly, or the expression of class B genes is blocked, or even it is more likely that the new class of E genes having a wider expression throughout flower and ovule development [31] are engaged in the case of *tw* type mutations.

In the case of *Hooded*, an additional flower ectopically develops on the upper end of the lemma converting the awn to a flower in inverse polarity [26, 32]. However, not only 305 bp duplication in intron 4 [28] but also overexpression of maize transgene *Kn1* in the barley genome gives the *Hooded* phenotype, showing that post-transcriptional regulation is involved in the development of the *Hooded* phenotype [33]. Recently several suppressor genes for *BKn3* have been identified [34] as an interaction of *BKn3* gene with other class I and II *Knox* genes (*BKn-1*; *BKn-7*, *JuBel1*, *JuBel2*) [35].

However, various barley *Hooded* type accessions differ significantly (Figure), and differences in the phenotype must be fixed in the structure of the *BKn3* gene. For these reasons the interaction of *tw* was examined with various, most different in our collection *Hooded* type accessions (Table 2), as well as an interaction among various *Hooded* genotypes (Table 3).

The main borderline helping the analysis of results is that ectopic action of *tw* mutation manifests in the structure of the basic flower, while development of additional flower must be fully attributed to the *BKn3* gene. This pecularity of the different expression of *tw* and *Hooded* genes allows us to determine the action of different *Hooded* alleles on the *tw* gene in heterozygous state in F₁ or, *vice versa*, the influence of the mutant *tw* gene (*tw₂*) on various *Hooded* genotypes (Table 2).

Despite the significant differences of *Hooded* phenotypes, in F₁ all hybrid combinations the basic flowers have a normal structure: 2 lodicules, 3 sta-
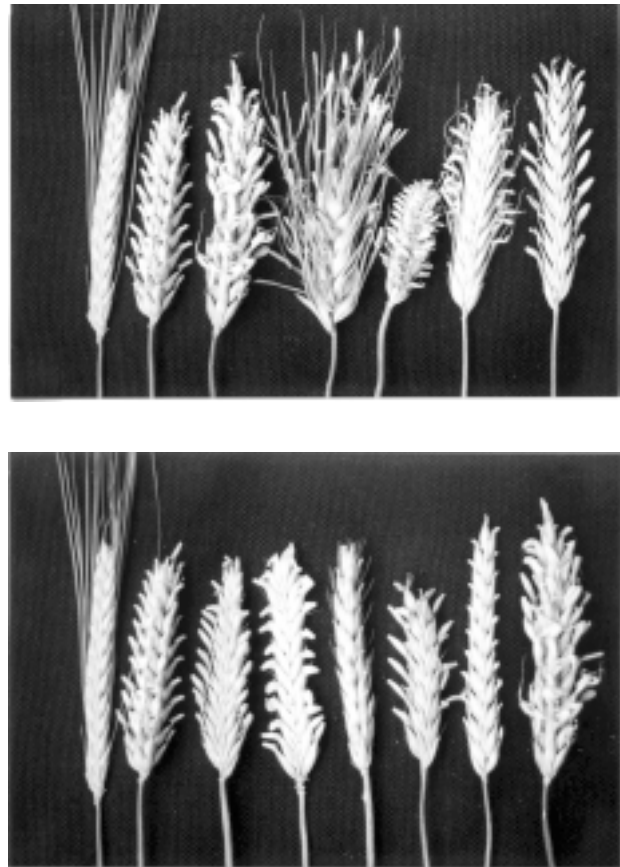

Figure. Diversity of *Hooded* type mutants in ear structure Lower row: (from left) *Wild Type* (*WT*) cv. 'Auksiniai II' (normal ear), *Hooded* (St. Petersburg), *2-row hooded* (Idaho, Aberdeen, 1445), *Hooded 2-row*, *Hoods on center spikelet, 2-row hooded* (Idaho, Aberdeen, 1441), *Hooded lemma* (North Dakota), Colsess II; Upper row: (from left) *WT*, *Hooded* (St. Petersburg), Colsess II, *Lemma hooded*, *Dense wing hood*, *Hood awn*, *Hooded lemma* (Colorado).

mens and 1 carpel, as it must be in the heterozygote *Twtw*, where *Tw* is dominant and *tw* is recessive (Table 2).

On the contrary, action of the mutant *tw* allele on several *Hooded* genotypes is obvious (Table 2). In hybrids *tw₂ × Hooded wide outer glume* lodicules may be converted to glume and additional flowers have often 3 or even 4 glumes. The several accession tested must be attributed to *calcaroides* as are *Hoods on the center spikelet*. In Vilnius conditions, only small undifferentiated appendices were observed on the central spikelets. In hybrids with *tw₂* additional flower structures were expressed more clearly. The influence of *tw₂* allele is also obvious for hybrids *tw₂ × Sessile hood*, *tw₂ × Brittle rachis*, *tw₂ × Dense wing hood*, *tw₂ × Hooded 2-row*. The latter hybrids have additional flowers in a specific 90°-angle position to the basic flower. However, the same is also true for hybrids *Hooded* (St. Petersburg) × *Hooded 2-row* (Table 3, 16). Influence of the mot-

Table 2. **Comparison of basic and additional flowers in barley F_1 hybrids between tw_2 and various *Hooded* type plants**

Hybrid combination	Additional flower (ad. fl.)		Basic flower		Additional information (see comments)
	n	Flower structure (fs)	n	fs	
tw_2 × *Hooded* [1]	42	V[2] (L 2, r. 4, can be fused; S 1+1,1+1+1, fr. 2; C common number till 5; C 1, r. 2)	60	N[3]	4
tw_2 × Lemma hooded	36	V (L 1–3; S 2–5 or. 3,1+1; C 1–4)	40	N	5
tw_2 × Colsess II	22	V (L 1–4, fr. fused; S 1–8, fr. fused 1+1, 1+1+1; C 0–4, fr. 2)	22	N	6
tw_2 × Hooded lemma	21	V (L 0–3, S 0–3, can be fused 1+1, 1+1+1; C 0–1)	30	N	7
tw_2 × Hoods on center spikelet	18	Sterile or has 1L, or all flower parts are fused into undifferentiated structure	26	N	8
tw_2 × Brittle rachis	51	V (L 0–3, fr. converted to S; S 0–5, can be 1+1: C 0–1–2)	48	N	9
tw_2 × 2-row hooded	21	V (L 0–4; S 0–5, can be fused 1+1; C 0–3, fr. 1)	19	N	10
tw_2 × Elevated hood	36	V (L 0, r. 2–3; S 0–5, fr. 1+1, C 0–3)	32		11
tw_2 × Sessile hood	50	V (L 1, fr. 2; S 4–8, fr. 1+1 or 1+1+1; C 1, r. 2)	40	N	12
tw_2 × Hooded wide outer glume	38	V (L 2–4 fr. L can be converted to glumes; S 3–7, fr. 1+1 or 1+1+1; C 1–3, fr. 1)	66	N	13
tw_2 × Multiflorous	60	Pure differentiated, but with awn; V (L 0–3, grown into glume; S 2–6, sometimes 1+1+1+1+1; C 0–3)	24	N	14
tw_2 × Dense wing hood	45	Only on upper part of ear; V (L 0–4, r. converted to S; S 3–8, fr. 1+1; C 0–4)	45	N	15
tw_2 × Hooded 2-row	106	Have awn; r. on additional flower have extra flower; V (L 1–6, very fr. grown into glume; S 3–7, fr. 1+1 or 1+1+1, C 0–3)	150	N	16

Abbreviations: 1 – H – *Hooded* from St.Petersburg; 2 – V – variation; 3 – N – normal flower structure: L2 S 3 C 1, fs. – flower structure; fr. – frequent; r. – rare; 1+1 or 1+1+1 – fused parts of flower; L – lodicule, S – stamen, C – carpel; ad. fls – additional flowers; as *WT* (*Wild Type*) is cv. 'Auksiniai II', has normal flower structure (L2 S 3 C 1) without ad. fls; *tw* – V, but in 70.8% flowers two (44.2%) or one L are converted to S or C [29]; 4 – ad. fls sometimes have awn; 5 – ad. fls are open type with awn on the end of ad. fl.; 6 – very well developed ad. fls; 7 – ad. fls are of a very open type and have very expressed wings of ad. fls; 8 – very long ear, longer than in parents, ad. fls only on central flowers; we propose it is *calcaroides*, father plants don't have ad. fls in Vilnius conditions (see Figure); 9 – ad. fls bigger than in father plants, lateral flowers are similar to flower glumes; 10 – most of ad. fls are sterile, but with awn at the end of ad. fl; 11 – ad. fls are only on central flowers, have awn, exhibit big wings, open, on the top of the ear ad.fls are sterile; 12 – ad. fls are only on central flowers, have small awn, big wings, inside of ad. fl. structures are mostly undetectable or the flower is without sexual organs; 13 – often ad. fls have 3, even 4 flower glumes, when the *WT* has 2, in the top of the ear ad. fls have undifferentiated flower structures, in the middle of the ear ad. fls have very well identified structures, all ad. fls have big wings, rare lodicules can be converted to glume; 14 – proposed that both hybrid and father plants are *calcaroides*, ad. fls are badly differentiated, but the flowers have very long awns (see also 14 of Table 3); 15 – ad. fls have 3, even 4 glumes, big wings and long awn, displaced only on central flowers, on the upper part of ear ad. fls have awn; 16 – ad. fls are displaced at an angle of 90° to the basic flower, have well expressed awns, r. ad. fls have awn.

her plant *Hooded* (Colsess) from St. Petersburg was also observed in several cases. It was more pronounced in *Hooded* × *2-row hooded* hybrids (cf. comments 10 in Table 2 and 12 in Table 3).

All these exclusive cases shown in comments of Tables 2 and 3 necessitate more detailed investigations. Preliminarily we suppose that the gene *BKn3* is downstream the *calcaroides* genes in determination of meristems, and in some hybrid combinations downstream the *calcaroides* genes are suppressed.

In contrast to our observations, suppressive genes analysed by Roig et al. [34], showed a different phenotype. All *BKn3* suppressed mutants have a short awn. The relation of *tw* to *BKn3* and to different *cal* genes [26] remains to be determined. According to Price and Stebbins (1971), between the phenotypic expression of *calcaroides* and *Hooded* there is a well expressed boarderline: the *calcaroides* mutation exerts a pleiotropic effect on awn and leaf while *Hooded* only on awn development. We did not ob-

Table 3. **Comparison of basic and additional flowers in barley F$_1$ hybrids between *Hooded* (St. Petersburg) and others**

Hybrid combination	Additional flower (ad. fl.)		Basic flower		Additional information (see comments)
	n	Flower structure (fs)	n	fs	
H.[1] × Lemma hooded	38	V[2] (L 0–2, grown into glume or separate; S 1–6; C 1–3)	60	N[3]	4
H. × Brittle rachis	3	Undifferentiated. Detected ad. fls have L2; S1 or 4; C1	50	N	5
H. × Hooded lemma	18	V (L fr. 2, r. 4; S 1–6; C 1–3)	30	N	6
H. × 2 – row hooded	30	Only 14 have differentiated structures; V (L 0–2; S 4–10, fr. 1+1 or 1+1+1; C fr. 2, r. 1)	83	N	7
H. x Colsess II	22	V (L 1–4 grown into each other or with glume; S 1–8, fr. 1+1 or 1+1+1; C 0–4, fr. 2)	22	N	8
H. × Hoods on center spikelet	33	V (L 0–4, fr. 2; S 1–6; C 1–2)	67	N	9
H. × Hooded wide outer glume	23	V (L 1–5, fr. grown into glume; S till 8, fr. 1+1 or 1+1+1; C fr. 2, r. 1)	90	N	10
H. × Elevated hood	25	V (L 0–4, fr. grown into glume; S 4–5, fr. 1+1; C 1–2)	73	N	11
H. × 2 – row hooded	34	V (L 0–4, fr. grown into glume; S till 8, fr. 1+1; C 1–2, r. 3)	75	N	12
H. × Sessile hood	31	Only 5 with sexual organs; V (L 0–4; S 2–4; C 1–3)	56	N	13
H. × Multiflorous	20	V (L 0–6, fr. grown into glume; S 2–10, fr. 1+1 or 1+1+1; C 0–3, fr. 1)	80	N	14
H. × Dense wing hood	37	V (L 0–3, fr. 1 and grown into glume; S 3–4, fr. 1+1 or 1+1+1; C fr. 1, r. 2)	40	N	15
H. × Hooded 2 – row	38	V (L 1–3, fr. 1 or 3; S 3–7, fr. 1+1; C 1–3, fr. 1)	38	N	16
Hooded	30	V (L 2, fr. 1 grown into glume or converted 1L to 1S or 1C)	40	N	

Abbreviations: 1 – *H.* – *Hooded* from St. Petersburg; 2 – V – variation; 3 – N – normal flower structure: L2 S 3 C 1; fs – flower structure; fr. – frequent; r. – rare; 1+1 or 1+1+1 – fused parts of flower; L – lodicule, S – stamen, C – carpel; as *WT* is cv. 'Auksiniai II', has normal flower structure (L2 S 3 C 1) without additional flowers (ad. fls); 4 – ad. fls are mostly without sexual organs; 5 – ad. fls are undeveloped, undifferentiated, it is difficult to examine flower structure with microscope; 6 – ad. fls are of a very open type, have big wings; 7 – ad. fls are only on basal flowers, r. on basal flower can be detected 2 ad. fls; 8 – ad. fls are bigger than in the father plants, lodicules fr. are grown into glume; 9 – the father plants have very purely developed ad flower structures, while all hybrids have ad flowers, but most are without sexual organs, with one glume (*calcaroides*?), in the center of several ad. fls there is additional derivative called "TV tower", awn has no antocian, rare C can be green (it was observed in 4 flowers) while normal C is white; 10 – ad. fls are of a very open type, it is difficult to count the number of rows (2- or 6-row ear); 11 – ad. fls are only on central flowers, ad. fls are of open or semiopen type, well expressed wings; 12 – ad. fls have well expressed awn, is of a close type, and flower glume is coalescent, but most flowers don't have differentiated and separated flower organs (can be of *calcaroides* type); 13 – ad. fls are on lateral and basal flowers, close type, frequently have undifferentiated structures or are sterile (can be of *calcaroides* type); 14 – ad. fls are best expressed in the middle of ear, lodicule can be converted into glumes; 15 – ad. fls best expressed in the middle of ear, ad. fls are on central flowers; 16 – sometimes on basal flowers can be detected 2 ad. fls which grow from one point, ad.fls are displaced in at an angle of 90° to basal flower.

serve any case of the influence of hybrids '*calcaroides*' on leaf development. The effect was restricted only by lemma-awn derivates.

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 genes. Relative pleiotropy can show both types of interaction, activation or suppression, of the non-allelic, independently inherited genes. For these reasons two quantitative characters, plant height (Table 4) and ear length (Table 5), were analyzed on the same hybrid material in F$_1$. Dwarf plants are also of economical interest because of their resistance to lodging.

However, plant height and ear length characteristics in F$_1$ depend on the character tested and on the

Table 4. Plant height (cm) of F₁ hybrids between barley *tw* and *Hooded* type mutants

Father plants genotype	Father plants		*tw* × as mother plant		*H*[3] × as mother plant	
	Average[1]	Variation min–max[1]	Average[1]	Variation min–max[1]	Average[1]	Variation min–max[1]
Sessile hood	85.1 ± 2.4	68–102	87.4 ± 2.3	72–103	75.0 ± 3.1	60–95
Lemma hooded	46.0 ± 1.4	40–55	66.4 ± 1.5	60–74	70.0 ± 1.7	60–79
Dense wing hood	55.2 ± 2.6	37–67	91.5 ± 2.6[2]	81–105	74.9 ± 2.6	63–87
Colsess II	78.5 ± 2.2	65–87	88.2 ± 2.0[2]	78–97	74.1 ± 2.2	60–87
Hoods on center spikelet	96.3 ± 2.9	79–113	101.6 ± 4.3	70–122	90.7 ± 3.3	73–106
Elevated hooded	73.3 ± 2.9	54–88	73.1 ± 1.5	63–82	79.0 ± 2.3	68–87
Hooded wide outer glume	76.8 ± 4.8	48–99	75.6 ± 2.8	60–90	78.8 ± 2.7	65–92
Hooded 2-row	74.3 ± 2.4	54–93	79.8 ± 3.5	65–103	90.3 ± 3.0	66–92
2-row hooded	71.8 ± 2.2	57–85	69.1 ± 2.3	60–90	68.3 ± 1.9	58–79
2-row hooded	58.8 ± 2.7	40–70	76.8 ± 2.2	65–87	73.8 ± 2.4	60–87
Hooded lemma	77.4 ± 3.3	59–91	77.4 ± 3.3	65–90	80.1 ± 1.8	63–86
Brittle rachis	38.9 ± 1.8	30–47	60.2 ± 1.6	51–75	50.5 ± 1.9	43–64
Hood awn	75.5 ± 2.9	59–90	72.7 ± 1.7	64–80	75.5 ± 3.0	55–96
Multiflorous	63.6 ± 2.1	54–78	83.6 ± 2.3	73–95	78.5 ± 2.2	65–87
Hooded (mother plant)	–	–	–	–	78.8 ± 3.8	53–94
tw (mother plant)	–	–	77.4 ± 2.2	59–99	–	–

1 – average results from 30 plants; 2 – heterosis is observed; 3 – *H* – the mother plant is *Hooded* from St. Petersburg.

Table 5. Ear length (cm) of F₁ hybrids between barely *tw* and *Hooded* type mutants

Father plants genotype	Father plants		*tw* × as mother plant		*H*[3] × as mother plant	
	Average[1]	Variation min–max	Average[1]	Variation min–max	Average[1]	Variation min–max
Sessile hood	6.03 ± 1.04	4–8	5.08 ± 0.77	3.5–6	8.02 ± 0.91[2]	6–9.5
Lemma hooded	5.15 ± 1.20	2–7	5.20 ± 0.78	3–7	7.22 ± 0.93[2]	5.5–9.5
Dense wing hood	3.25 ± 0.60	2–4	4.57 ± 0.97	3–6.5	8.55 ± 0.53[2]	7.5–9.5
Colsess II	6.37 ± 0.68	5–7.5	5.62 ± 0.87	4–7.5	9.03 ± 1.11[2]	7–12
Multiflorous	4.48 ± 0.64	3–5.5	6.58 ± 1.25	4–9	8.75 ± 1.19[2]	6.5–11
Hood awn	6.15 ± 1.18	3.5–8	4.85 ± 0.77	3–6	6.42 ± 0.78	5–7.5
Hoods on center spikelet	7.67 ± 1.42	5–10.5	5.87 ± 1.47	3–8	9.61 ± 0.97[2]	7.5–11.5
Elevated hood	7.17 ± 0.93	5.5–9	5.62 ± 0.78	3–7	6.65 ± 0.91	4–8.5
Hooded wide outer glume	7.13 ± 1.07	4–9.5	5.07 ± 1.29	3–7	7.45 ± 1.10	5–9.5
Hooded 2-row	6.65 ± 1.17	4–9	5.75 ± 1.01	4–8	9.18 ± 0.95[2]	6–11
2-row hooded	5.78 ± 1.10	4–8	–	–	6.70 ± 0.68	5–8
2-row hooded	6.78 ± 0.69	5.5–8	6.62 ± 0.90	5–8	8.70 ± 0.64[2]	7–9.5
Brittle rachis	3.80 ± 0.35	2–3.5	2.85 ± 0.72[4]	1–4	3.78 ± 0.64	2.5–5
Hooded lemma	7.88 ± 1.20	6–10.5	4.87 ± 0.95	3–7	7.07 ± 0.99	8.5–4.5
Hooded	3.78 ± 1.34	1.5–7	8.13 ± 0.93[2]	5–9	–	–
tw₂	5.48 ± 0.64	4–6.5	–	–	–	–

1 – average from 30 plants; 2 – execeeding both parents; 3 – mother plant is *Hooded* from St. Petersburg; 4 – inhibitory effect.

mother plant, either *tw* or *Hooded*. It is clear after comparing the results of investigation of plant height and ear length.

In plant height investigations (Table 4), of interest can be only results with two F₁ hybrid combinations *tw₂* × *Dense wing hood* and *tw₂* × Colsess II when the mother plant is *tw₂*. Plants of F₁ in those combinations were higher than either of the parent plants. Those hybrids were also higher than *WT* (cv. 'Auksiniai II') (see Table 1). So, the observed effect can be attributed to heterosis. In all other combinations tested in our work, F₁ hybrids were equal in height to one of the parents or occupied an intermediate position between both parental mutants (Table 4).

Results of the ear length investigations are more interesting. Plants of both basic genotypes used as the mother plant, tw_2 and *Hooded* (St. Petersburg), have short ears, significantly shorter than in *WT* (cv. 'Auksiniai II') (Table 5). Even in 8 hybrid combinations where the mother plant was tw_2, the F₁ hybrids had the ears longer than in either of the parents. However, we are not prone to attribute this effect to heterosis. In all cases the ear length of F₁ hybrids does not exceed that of *WT* plants. The effect may be explained by the complementation effect between two independently inherited genes determining the shorter ear length in the mutant. However, all parent traits, including ear length, represent a specific complex of pleotropic traits characterizing the mutants tested and determined by one mutant gene. In the classical case, if complementation takes place, all mutant characters must be normalised in heterozygotes. The observed phenomenon needs further studies.

The effect depends very obviously on the mother plant tw_2. In the part of investigations where the mother plant was *Hooded* (St. Petersburg), it was only one case where ears of F₁ hybrids were longer than in parent plants, and it is a paradox that again tw_2 was engaged in the observed effect, because that hybrid combination was *Hooded* × tw_2 (Table 5). Such hybrids exceed slightly even *WT* (see Table 1).

More intriguing is the other hybrid combination – *Hooded* × *Brittle rachis*. It is the only case when ears are shorter in hybrids than in parent plants. The inhibitory effect observed in those heterozygotes is worth of further investigations.

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MIEŽIŲ MUTANTŲ *tweaky spike* IR *Hooded* SĄVEIKA F$_1$ HIBRIDUOSE

S a n t r a u k a

Vyraujanti miežių raidos *BKn3* geno *Hooded* mutacija lemia homeozinį (ne vietoje) papildomo žiedo atsiradimą žiedažvynio ir akuoto riboje arba ant akuoto. Homeozinio *tw* mutanto žiedo organai, lodikulės, virtusios kuokeliais ir/arba piestelėmis. Dėl šių dviejų mutantinių genų sąveikos gali atsirasti naujų fenotipų augalai. Ištirta 15 skirtingų *Hooded* tipo mutantų sąveika su *tw$_2$* mutantu ir su vienu iš *Hooded* tipo mutantų.

Pagrindinio žiedo raidai *Hooded* mutantinis genas hibriduose įtakos neturėjo, tuo tarpu *tw* mutanto poveikis kai kuriems *Hooded* tipo mutantams labai ryškus. Hibridai turi papildomo darinio struktūrą, labai artimą tai, kurią lemia *calcaroides* miežių mutacija. Aptiktas reiškinys bus tiriamas toliau. Stiprus *tw$_2$* poveikis pasireiškė ir hibridų varpos ilgiui. Jis buvo dvejopas – tiek slopinantis, tiek stimuliuojantis varpos raidą.