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Two types of revertants from the same homeotic barley mutants *tweaky spike*

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Two types of reversions from barley mutants denoted as N (normal) and C (compact ear) are compared. The revertant nature of the C type was confirmed by flower structure analysis. Reversions at that type arose only in the progeny of two allelic *tw* type mutants (tw_1 and tw_2). C-type revertants are more resistant to lodging. Some of the C-type revertants were resistant to *Erysiphe graminis* or had a higher protein content. Both N and C revertants from tw_1 were more resistant to kernel infection with *Cochliobolus sativus* and are interesting as a new source of genetic diversity. Most intriguing are the differences revealed between the allelic mutants tw_1 and tw_2.

Key words: barley revertants, revertant types, polymorphism, economic value, resistance to fungi

INTRODUCTION

Genetic instability was one of the peculiarities of the newly induced barley recessive pleiotropic mutants *tweaky spike*. Reversions to the normal type, $tw \rightarrow Tw$ arose with a high frequency, allowing us to gather a collection of revertants and to examine their peculiarities. Separate peculiarities, such as a higher protein content, have been preserved in revertants, therefore there is a perspective to use the revertants as the initial material for breeding purposes [3, 4].

The new turning point has been reached in the investigation of *tw* type mutants and their revertants when the homeotic nature of *tw* mutants was revealed [5]. Normally, a barley flower has two lodicules, three stamens and one pistil. Allelic mutants of *tw* type in the present work tested mostly in upper flowers, are characterized by conversion of lodicules to main part into stamens, but less frequently also into pistils, or mixed flower types are observed, even with excess of flower organs [5]. So, instability in the development of flower organs is also amongst the main characteristics of *tw* mutants. Despite the fact that all barley *tw* type mutants that arose from the initial cv. Auksiniai II [3], are allelic, their significant polymorphism has been observed [6]. One of the manifestations of polymorphism is that not only typical reversions to *WT* (*Tw*) arosed, but also plants with a more compact ear were detected, but only among the allelic mutants tw_1 and tw_2. That peculiarity was not observed among the other *tw* type allelic mutants [8]. The compactoid plants have been also preserved in the barley genetic collection, and a comparison of such plants with typical revertants of the normal phenotype is the main task of that investigation. Attention is focused on two peculiarities: flower structure and susceptibility to fungal infection. The significant immunodeficiency is also one of the common characteristics of allelic *tw* mutants [7].

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MATERIALS AND METHODS

Only mutants and revertants of original origin were tested in the present work. All the mutants were induced with chemical mutagens from the initial barley cultivar Auksiniai II. In the present work, cv. Auksiniai II is used as a wild type (*WT*). All revertants used in the investigation arose only from the allelic mutants tw_1 or tw_2. Both initial mutants, as well as *WT* and revertants, were propagated in the experimental field of the Botanical Garden of Vilnius University for a long time without pesticides. This allowed us to escape genetic instability which is so frequent among the newly arisen mutants and revertants.

Flower structure determination. Flowers were fixed in Carnoy's solution (3:1) and analyzed on a stereozoom microscope (Motic). All parts of flower were examined in detail after the lemma had been removed. The number of the flower organs, their homeotic conversion and the number of mosaic organs were registered [5].

Evaluation of quantitative characters. Thirty or more plants from each genetical sample were analyzed. For the measurements, mature plants and their parts were used. The productivity of plants was determined in 2 m^2 plots in three repeats. Morphological properties were evaluated and described according to the IPGRI descriptor list for barley [8]. The relative content of crude protein was estimated in kernels. Determination of nitrogen was made by the standard micro-Kjeldahl method in 5–6 repeats.

Susceptibility to diseases was expressed in % of affected plants. It was determined in field conditions. Susceptibility to *Claviceps purpurea* (Fr.:Fr.)Tul., *Ustilago nuda* (Jens.) Rostr., *Drechslera teres* (Sacc.)Shoem. (syn. *Helmintosporium teres* Sacc.), *Puccinia hordei* G. H. Otth. (syn. *P.simplex* (Koern.) Erikss. et Henn.), *Blumeria graminis* f.sp. *hordei* (syn. *Erysiphe graminis* DC ex Merat) was determined according to [9].

Internal micromycetes in barley kernels. Kernels were sterilized with 3% NaOCl for 2 min and washed with sterile distilled water three times for 2 min. Then the kernels were dried with sterile filter paper and placed onto Petri dishes with MEA substrate and streptomycin (250 mg/l) and kept at a temperature of 24 °C for seven days. Then the micromycetes were identified according to [10–13].

Statistical analysis. Results were evaluated usint the Excel program, and the significance of differences between the means was analyzed by Student's t test.

RESULTS AND DISCUSSION

Flower structure analysis confirmed our preposition that the plants attributed to the compactoid (C) group were really revertants in relation to the initial mutants tw_1 and tw_2 from which C-type plants arose (Table 1). Despite the high number of the flowers tested (in total 1184) they had a normal flower structure: 2 lodicules, 3 stamens and 1 pistil, like the revertants attributed to the N-group. In that group, a high number of flowers was also analyzed (in total 5217). In contrast, the upper flowers of both tw_1 and tw_2, mutants had various deviations from a normal flower structure. In most cases they were expressed in lodicule conversions to stamens or pistils, or one lodicule was converted to a stamen and the other to a pistil. Such flowers were absent in both groups of revertants (C and N). So, we may conclude that the C-type plants are really revertants according to flower structure.

A more compact ear structure of the plants under discussion is seen not only from the external ear view (Figure 1) but is also confirmed by a direct analysis of the ear (Table 2). The ears of R-C plants were shorter and denser independently of the mutant, tw_1 or tw_2, from which they arose. The difference according to the ear length between C-and N-type revertants was very clear. The ears of N-type revertants did not differ in length from those of *WT*. Both mutants, tw_1 and tw_2, have very short but not so dense ears as R-C-type plants.

Table 1. **Flower structure of barley revertants and initial mutants tw_1 and tw_2**

Characteristic of genotypes	Number tested		% of flowers	
	Revertants	Flowers	Normal[1]	Atypical
WT (AII)	–	62	93.6	6.4[2]
tw_1	–	60	50.0	50.0
R-N1-N25[3]	25	2512	100	0
R-C1-C3[3]	2	296	100	0
tw_2	–	95	87.4	12.6
R-N26-N52	27	2705	100	0
R-C4,C6-11,13,14	9	888	100	0

[1] Normal flower has 2 lodicules+ 3 stamens+1 pistil; [2] 4 flowers are sterile, [3] – name of revertant lines: R-N – with typical normal ear structure; R-C – with compacted ear structure

Fig. 1. Ear structure of various revertants and initial plants From left: four C-type revertants; two N-type revertants; barley mutant tw_2 and *WT* (cv. Auksiniai II).

Table 2. **Comparison of ear characteristics of the two types of barley revertants (average results from two years)**

Genotype	Number of R	Ear length, cm		Number of grains ear $^{-1}$		Density of ear	
		Average	Variation	Average	Variation	Average	Variation
WT (AII)	–	7.5 ± 0.09	–	26.1 ± 0.9	–	11.9 ± 0.09	–
tw_1	–	4.7 ± 0.09	–	15.1 ± 0.1	–	10.6 ± 0.04	–
R-N	8	7.7 ± 0.06	6.8 – 8.2	24.8 ± 0.04	22.9 – 25.5	11.9 ± 0.1	11.4 – 12.1
R-C	2	6.3 ± 0.2	5.8 – 6.7	24.1 ± 0.06	24.0 – 24.2	15.1 ± 0.4	14.3 – 15.8
tw_2	–	4.8 ± 0.2	–	15.3 ± 0.2	–	10.8 ± 0.2	–
R-N	7	7.6 ± 0.06	7.1 – 8.0	24.8 ± 0.6	23.7 – 26.2	12.0 ± 0.4	11.5 – 12.5
R-C	9	6.1 ± 0.2	4.7 – 6.6	23.0 ± 0.3	22.0 – 24.3	16.4 ± 0.6	13.6 – 20.3

R-N – revertant with ear and flower structure typical of *WT*; R-C – revertant with a compact ear type.

Barley plants with compact shorter ears have an advantage. They are more resistant to lodging. Results of lodging analysis are presented in Table 3. The lodging is expressed in scale numbers. The revertant most resistant to lodging was one of those belonging to the R-C type. Its scale number was 8.8, while the plants of the initial cv. 'Auksiniai II' had scale the number 5.8 and the present standard barley cultivar at 'Ula' only 5.5. One revertant of C-type with a high protein content in kernels was also revealed. The *tw* type mutants are characterised also by susceptibility to *Claviceps purpurea* and *Ustilago nuda.* The C-type revertants are resistant to these fungi. This fact confirms additionally the revertant nature of C-type plants. One revertant of C-type was found resistant to *Erysiphe graminis*. However, in both groups of revertants, N and C-type, we were unable to find a revertant resistant to *Drechslera teres.*

The distribution of micromycetes was examined in kernels of five N-type revertants and of three C-type revertants (Table 4). The results were compared with respective initial mutants tw_1 or tw_2 and with *WT* (AII).

As regards plant disease, microorganisms can be differentiated into three categories: good organisms, which play a role in the ecological processes that reduce diseases; bad organisms, which cause diseases either directly or indirectly, and organisms that do not have an obvious role in disease enhancement or suppression [14]. *Cochliobolus sativus* (S. Ito et Kurib.) Drechsler ex Dastur (anamorph. *Bipolaris sorokiniana* (Sacc.) Schoemaker) and fungi of the genus *Fusarium* Link are among the bad organisms of prime importance in the barley disease complex.

Our results are in full agreement with the conclusion of other investigators that the main micromycete to infect barley kernels is *Cochliobolus sativus*. In *WT*, even 93% of the kernels were infected with *C. sativus* (Table 4). According the investigations of the other authors [15, 16], the infection level of kernels as high as 90–100% was registered. The difference between both allelic mutants, tw_1 and tw_2, was very clear. The level of infection for tw_2 was about the same as for *WT*, while the kernels of tw_1 were not susceptible to *C. sativus* as tw_2 kernels. The frequency of infected kernels of the tw_1 mutant is significantly lower as for *WT* or tw_2. About the same level of infection with *C. sativus* was also observed in all revertants arisen from tw_1, independently of reversion type – R-N or R-C.

Cochliobolus sativus is a causal agent of common rot and crown rot, node cancers, head and seedling blights, grain black point and foliar spot blotch of barley world-wide. The development of barley genotypes resistant or tolerant to spot blotch is considered to be the most economic way for controlling this disease [17], and reversions from the mutant tw_1 and, even partially, from tw_2 are a promising source for obtaining genotypes resistant to *C. sativus*. However, it is also obvious that even allelic mutants of the same gene are not equally suitable for that purpose. The influence of the mutant from which the reversions have been arisen is very clear. This dependence is not accidental and needs further investigations. This conclusion is corroborated by the results of our previous work [18] in which the activity of salicylic acid was tested on two groups of *tw* mutants arisen from two different initial barley cultivars, Auksiniai II or Auksiniai 3, and the results depended mainly on the history of tw mutants, namely on the characteristics of the initial cultivar from which a mutant arose.

One of the common peculiarities of *tw* type mutants is also an increased frequency of moldy germinating kernels [6]. The results of the present work may be a clue to the explanation of that phenomenon. Significant differences between *WT* and tw_1 or tw_2 have been observed as regards infection with *Fusarium equiseti*. The level of kernel infection with *F. equiseti* of the tw_1 and tw_2 mutants was about the three times as high as of *WT* (Table 4). Recovery to normal type amongst both types of revertants is in well agreement with the decreased frequencies of *F. equiseti* in revertants. It does not depend on the nature of reversion type – R-N or R-C (Table 4).

Fungi of the genus *Fusarium* also belong to the bad micromycetes. They are responsible for two forms of disease: 'foot rot' which affects roots and crows and may cause seedling blight at early stages; and 'head blight',

Table 3. **Several quantative characters of barley revertants R-C-type in comparison to *WT* and initial mutants tw_1 and tw_2**

Plant character	Number of years	*WT*		tw_1	R-C from tw_1		tw_2	R-C from tw_2	
		AII	Ula[1]		Average[2]	Variation		Average[3]	Variation
Productivity, g/2 m^2	6	901 ± 94	1030 ± 279	501 ± 39	830 ± 68	762 – 898	510 ± 43	746 ± 44	428 – 888
- only of years in which protein content was determined	4	807 ± 107	751 ± 117	463 ± 49	742 ± 65	682 – 801	453 ± 44	636 ± 45	326 – 801
Protein, %	4	12.9 ± 0.3	14.2 ± 0.1	16.3 ± 0.3	13.7 ± 0.9	12.8 – 14.6	16.5 ± 0.5	14.4 ± 0.4	11.8 – 16.2
Lodging, scale number	5	5.8 ± 1.0	5.4 ± 2.1	8.1 ± 0.7	6.2 ± 0.3	5.6 – 6.7	7.9 ± 0.8	6.6 ± 0.4	5.0 – 8.8
Weight of 1000 kernels, g	5	40.0 ± 3.3	43.5 ± 4.0	40.1 ± 2.4	39.6 ± 2.3	35.5 – 43.6	40.9 ± 1.9	39.6 ± 2.3	37.6 – 42.0
Susceptibility % to:									
Claviceps purpurea	1	0.02 ± 0.02	0	2.81 ± 0.12	0	–	2.76 ± 0.15	0.03 ± 0.03	0 – 0.06
Ustilago nuda	1	0.05 ± 0.05	1.20 ± 0.24	1.10 ± 0.23	0.75 ± 0.19	–	0.30 ± 0.12	0.05 ± 0.03	0 – 0.15
Drechslera teres	4	10.4 ± 1.5	9.5 ± 2.9	11.9 ± 1.6	10.5 ± 1.5	10.1 – 10.9	10.6 ± 1.5	11.5 ± 1.6	8.9 – 15.7
Puccinia hordei	4	0.1 ± 0.1	0	0.2 ± 0.2	0.9 ± 0.5	0.7 – 1.1	0.8 ± 0.4	1.3 ± 0.6	0 – 3.4
Erysiphe graminis	4	3.6 ± 0.9	2.5 ± 1.6	3.6 ± 0.9	3.4 ± 0.9	2.4 – 4.3	7.7 ± 1.3	2.3 ± 0.8	0.25 – 7.7

[1] – barley cv. Ula tested only for two years; [2] – average from two R-C-type revertants; [3] – average from nine R-C-type revertants

Table 4. **Distribution of micromycetes in internal grain tissues of barley revertants and in initial material, 2003 year data**

Micromycetes	Genotypes/revertants										
	WT/AII	tw_1	N1	N13	C1	tw_2	N30	N46	N48	C6	C7
Distribution, %											
Acremonium strictum	0	0	1 ± 1	1 ± 1	0	0	0	0	0	0	0
Alternaria alternata	1 ± 1	2 ± 1	11 ± 3^{2b}	7 ± 2^{2a}	6 ± 2^{a}	3 ± 2	11 ± 3^{2a}	10 ± 3^{2a}	17 ± 4^{2c}	5 ± 2	5 ± 2
Aspergillus sp.	0	1 ± 1	0	0	0	0	0	1 ± 1	0	0	0
Cochliobolus sativus	93 ± 3	79 ± 4^{2}	80 ± 4^{2}	83 ± 4^{1}	84 ± 3^{1}	91 ± 3	93 ± 2	87 ± 3	80 ± 4^{2}	89 ± 3	94 ± 2
Fusarium equiseti	8 ± 3	24 ± 4^{1}	13 ± 2^{b}	11 ± 3^{b}	7 ± 3^{c}	22 ± 4^{1}	9 ± 3^{b}	7 ± 2^{c}	10 ± 3^{a}	7 ± 2^{c}	7 ± 2^{c}
F. poae	1 ± 1	0	0	0	1 ± 1	1 ± 1	0	0	0	1 ± 1	0
F. sambucinum var. *minus*	1 ± 1	6 ± 2^{1}	4 ± 2	0	1 ± 1	1 ± 1	2 ± 1	0	7 ± 2^{2}	1 ± 1	1 ± 1
Mucor sp.	1 ± 1	1 ± 1	0	1 ± 1	1 ± 1	0	3 ± 2	0	0	1 ± 1	0
Mycelia sterilia	2 ± 1	2 ± 1	4 ± 2^{a}	1 ± 1	1 ± 1	2 ± 1	4 ± 2	7 ± 2^{1a}	6 ± 2^{1a}	1 ± 1	2 ± 1
Penicillium spp.	7 ± 2	2 ± 1^{1}	4 ± 2	4 ± 2	1 ± 1^{2}	6 ± 2	0^{3b}	2 ± 1^{a}	0^{b}	1 ± 1^{a}	0^{b}
Sordaria fimicola	0	2 ± 1	0	0	0	0	0	3 ± 2	3 ± 2	0	0
Ulocladium consortiale	0	0	0	0	0	0	0	2 ± 1	0	0	0
Trichotecium roseum	0	0	0	0	0	1 ± 1	0	0	0	0	2 ± 1

1,a - P<0.05; 2,b - P<0.01; 3,c - P<0.001.
1,2,3 – compared with *WT* (Auksiniai II); a,b,c – compared with tw_1 or *tw2,* respectively; *WT*/AII – initial cv. Auksiniai II

Continuation of table 4. **Distribution of micromycetes in internal grain tissues of barley revertants and in initial material, 2003 year data**

Micromycetes	Genotypes/revertants									
	WT/AII	tw_1	N1	N13	C1	tw_2	N30	N46	N48	C6	C7
	% from common isolate number										
Acremonium strictum	0	0	0.9 ± 0.9	0.9 ± 0.9	0	0	0	0	0	0	0
Alternaria alternata	0.9 ± 0.9	1.7 ± 1.2	9.4 ± 2.7[2b]	6.5 ± 2.9	5.3 ± 2.1	2.4 ± 1.4	9.0 ± 2.6[2a]	8.4 ± 2.6[2a]	3.7 ± 3.1[3b]	4.7 ± 2.1	4.5 ± 2.0
Aspergillus sp.	0	0.9 ± 0.9	0	0	0	0	0	0	0	0	0
Cochliobolus sativus	81.6 ± 3.7	67.5 ± 4.4[2]	68.4 ± 4.3	76.9 ± 4.1	73.7 ± 4.1	71.7 ± 4.0[2]	76.2 ± 3.9	73.1 ± 4.1	64.5 ± 4.3	84 ± 3.6[a]	84.7 ± 3.4[a]
Fusarium equiseti	7.0 ± 2.7	20.5 ± 3.8[2]	11.1 ± 2.9	10.2 ± 2.9	9.6 ± 2.8	17.3 ± 3.4	7.4 ± 2.4	5.9 ± 2.2	8.1 ± 2.5	6.6 ± 2.4	6.3 ± 2.3
F. poae	0.9 ± 0.9	0	0	0	0	0.8 ± 0.8	0	0	0	0.9 ± 0.9	0
F. sambucinum var. minus	0.9 ± 0.9	5.1 ± 2.0[1a]	3.4 ± 1.7	0	6.1 ± 2.3[1a]	0.8 ± 0.8	1.6 ± 1.1	0	5.6 ± 2.1[1a]	0.9 ± 0.9	0.9 ± 0.9
Mucor sp.	0.9 ± 0.9	0.9 ± 0.9	0	0.9 ± 0.9	0	0	2.5 ± 1.4	0	0	0.9 ± 0.9	0
Mycelia sterilia	1.8 ± 1.2	0	3.4 ± 1.7	0.9 ± 0.9	3.5 ± 1.7	1.6 ± 1.1	3.3 ± 1.6	5.9 ± 2.2	4.8 ± 1.9	0.9 ± 0.9	1.8 ± 1.3
Penicillium spp.	6.1 ± 2.3	1.7 ± 1.2	3.4 ± 1.7	3.6 ± 1.8	0.9 ± 0.9[1]	4.7 ± 1.9	0[1a]	1.7 ± 1.2	0[1a]	0.9 ± 0.9[1]	0[1a]
Sordaria fimicola	0	1.7 ± 1.2	0	0	0	0	0	2.5 ± 1.4	2.4 ± 1.4	0	0
Ulocladium consortiale	0	0	0	0	0	0	0	1.7 ± 1.2	0	0	0
Trichotecium roseum	0	0	0	0	0	0.8 ± 0.8	0	0	0	0	1.8 ± 1.3
Number of isolates	114	117	117	97	114	127	122	119	124	106	111

1,a - P<0.05; 2,b - P<0.01; 3,c - P<0.001.
1,2,3 – compared with *WT* (Auksiniai II); a,b,c – compared with tw_1 or *tw2*, respectively; *WT*/AII – initial cv. Auksiniai II

which affects individual kernels, single ear spikelets or entire heads, and results in 'scab' of the kernels [19, 20]. On the ground of the present investigation it may be proposed that the lower frequency of germinating kernels of *tw* type mutants partly could due to the action of *Fusarium* on the young roots of the germinating seeds.

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DU REVERTANTŲ TIPAI IŠ TŲ PAČIŲ MIEŽIŲ HOMEOZINIŲ MUTANTŲ *TWEAKY SPIKE*

Santrauka

Iš 11 turimų *tw* tipo miežių mutantų tik tw_1 ir tw_2 mutantuose aptikti dviejų tipų revertantai normalios (N) ir kompaktiškos (C) varpos. Pastaroji reversija įrodyta žiedo struktūros tyrimais. Tarp C tipo revertantų rasta atsparesnių *Erysiphe graminis* infekcijai, su padidėjusiu baltymų kiekiu grūduose. Specifiškai tik iš tw_1 kilusių abiejų grupių revertantų grūdai buvo atsparesni *Cochliobolus sativus* infekcijai. Abu revertantų tipai yra būdas padidinti augalų genetinę įvairovę.