

VARIATION OF CURRENT MORPHOLOGICAL CHARACTERS IN WINTER BARLEY, *Hordeum vulgare* L.

Nicolae IONESCU¹, Mihaela Ioana GEORGESCU², Aurelian PENESCU²,
Elena SĂVULESCU², Maria VOICA¹, Alexandru LAZĂR¹

¹Agricultural Research and Development Station Pitești, 5 Pitești-Slatina Road,
117030, Pitești, România

²University of Agronomic Sciences and Veterinary Medicine of Bucharest,
59 Marasti Blvd, 011464, District 1, Bucharest, Romania

Corresponding author email: nicolaeionescu50@gmail.com

Abstract

Various studies on morphological, biochemical, molecular (Martinez, Esparza-Fostre, 1998) could be used in the progress of improvement in new barley varieties. Board genetic dowry and barley culture conditions usually result in the characteristic expression of plant morphology. In the case of winter barley, there were some differences in the two forms: two rows (distichon-D) and six rows (hexastichon-H). By comparison the average values were 62-76 cm (D-H) straw length, 10.5 cm/3.2 mm-11.1 cm/3.8 mm length/ diameter of the basal internode, 28-36 cm length of the apical internode, 7.5 cm/1.45 g-7.5 cm/ 2.51 mm length/ weight of the ear, 25/10.6 mm-56/11.3 mm number and length of the spikelets, 2.8-14.5 number of sterile spikelets in a ear, 15.9-14.7 cm awn length, 22.5/1.18 g- 41.9/2.05 number and grain weights in an spike (ear), 52.3-48.6 g thousand grains weight (TGW) and 8.63/3.96 mm-9.13/3.75 mm grain sizes (length/thickness/width). Between the main morphological caries studied, significant positive correlations were obtained, which demonstrates the good adaptability of the plant to the crop area, both two- and six- rows barley.

Key words: ear, *Hordeum vulgare*, spikelet, straw, variation.

INTRODUCTION

Having a long history, barley (*Hordeum vulgare* L., pro syn *H. sativum* Jessn., common barley, cereal barley, barley) is an important crop plant (Pickering, Johnson, 2005). Barley comes from Old English *baere* (similar to *farina- flour*) derived from adj. *barley*, originally from North Scotland. It is expressed as *beer* in the description of the specific form of the six-row barley (the one growing in the region). As a surface into the World, barley follows maize, rice and wheat, and is met in a multitude of conditions (Delhaize et al., 2004). The purpose of its cultivation is the production of feed (as vegetable material and grains), for the production of beer (*ale* beer from two-rows barley, and *lager* beer from six-rows barley), seed production and human food. The grains contain starch (59-65%), crude protein (9-11%), fats (2-3%), cellulose (4-7%), ash (2-3%) (Bîlteanu, Bârnaure, 1989), and a variety of other phenolic compounds (*caffeic acid*, *p-coumaric acid*), *ferulic acid*, *8,5-diferulic acid*, flavonoids (*catechin-7-O-glucozide*, *saponarin*,

catechin, *procyanidin B₃* and *C₂*, *prodelphinidin B₃*), and alkalioids (*hordenine*) (Friedrich, Galensa, 2002). In the course of time, the plant has evolved through various forms and characteristics (Strelchenko et al., 1999; Mayer et al., 2012). Thus, barley is considered one of the most diverse cereal from a genetic point of view, with winter and spring types, with two and six rows, with both grained and an-grained fruits. In fact, the genome consists of seven pairs of chromosomes (type 1H, 2H, 3H, 4H, 5H, 6H and 7H) with $2n = 14$. The existence of a gene, *vrs1*, which is responsible for the transition from two-row to six-row forms of barley (Komantsuda et al., 1999; Tano et al., 2002) has recently been demonstrated. The inflorescence of the plant is an ear consisting of spikelets attached directly to the central shaft (rachis). At each node of the rachis are three spikelets colled triplets. They alternate in opposite places of the ear. Each spikelet has up to two glumes in the form of bracts, palea and lemmas. Depending on the variety, the lemma expands like an awn and it is rarely like a hood. In same varieties glumes of

sterile grains can be awnless. Varieties of awnless barley are not well known. When the palea and lemma stick to the grain, it gets dressed. At six-rows barley, the entire set of triplets is fertile and thus grows grains. The central grain is usually round and the lateral ones are slightly asymmetrical. In barley two-rows only the central spikelet is fertile, while the two sides pieces are reduced, with rudimentary stamens, ovary and stigma. Due to the fact that the two collars spikelets are sterile and only the central grain is formed, the ear has the flat aspect. Each ear can produce 16-30 grains in the form of two-rows and 25-60 grains



Figure 1. Two-rows barley plants, 'Trasco' variety

in the form of six-rows. The plant generally forms stems with heights between 60 and 120 cm, and their appearance in the crop is characteristic (Figure 1 and Figure 2).

The research carried out to determine the variation of plant characters of the two barley forms consisted of: i) the strain by the total length of the straw, the length of the apical internode, the length and thickness of the basal internode; ii) the length and weight of the ear; iii) the number and length of spikelets, the number of sterile spikelets, awn length; iv) the number of grains, their weight, the thousand grain weight (TGW) and the size of grains.



Figure 2. Six-rows barley plants, 'Sistem' variety

MATERIALS AND METHODS

The variants have been cultivated over the past two years with two-row barley 'Trasco' variety and six-row barley 'Sistem' variety, like winter forms. The experience set up by the block method has the variants of 25 m² in 4 replicates. The crop technology used was the one recommended by the resort. At the full maturity, 25 plants/stems from each replicates (total 100 stems) were randomly picked and brought to the laboratory. The 100 strains were measured and determined the total length of the straw, the length and thickness of the down internode, the length of the apical internode, the length and weight of the ears, the number of spikelets in the ear and their length, the awn length, the number of grains from ear and their weight, thousand grains weight (TGW), the size of grains: the length and thickness.

The morphological characters obtained were analyzed by the histogram method (frequency polygons, %, FP). In their expression were used the class ranges established according to the specific values obtained. The study revealed

several aspects, namely: i) the modal values (with the highest frequencies); ii) the limits of the variability ranges of the studied characters; iii) the specificity of each character of the barley ecotypes in the analyzed area. Graphs have a comparative character between the two forms of autumn barley, with 2-rows and 4-rows of grains in each ear.

Between the analyzed characters the correlations were established, with the help of which they were able to observe their tendencies within the studied ecotypes.

The Excel program was used to express the values. The significance of the correlation coefficients obtained was compared to the r_{\max} values (Erna Weber, 1961) for the 5%, 1% and 0.1% levels of transgression probabilities.

In the statistical calculation of the all values obtained we used variance analysis (Anova test) on the variation rows.

Statistical parameters were calculated using the formulas:

$$\bar{a} = \frac{\sum x}{n}, \text{ where: } \bar{a} = \text{media of determinations,} \\ x = \text{the values;}$$

$$S^2 \text{ (variance)} = \frac{1}{n-1} \left[\sum x^2 - \frac{(\sum x)^2}{n} \right], S \text{ (standard error)} = \sqrt{S^2}, \text{ and } S \% \text{ (variation coefficient)} = \frac{S}{\bar{x}} \cdot 100.$$

RESULTS AND DISCUSSIONS

Variability of barley straw sizes. The stalk/straw of barley consists of several internodes (usually 5-7) with increasing lengths to the ear. Generally, the straw has lengths between 50 (60) cm and 100 cm. At harvest maturity, the plants exhibit heights considered modest due to the necessarily manifested appearance. The measurements showed that the straw of two-row barley was between 49 and 80 cm. The high frequency had straws of 61-64 cm (29%), followed by 57-60 cm (27%). Smaller and larger lengths together had 10% of the strains, the other being intermediate (Figure 3). In six-row barley the straw ranged from 61 to 92 cm, with a higher frequency between 73-80

cm (26% at 73-76 cm and 26% at 77-80 cm). The graph shows the obvious difference between straw lengths/stems between the two winter forms. The internode under the ear (apical) is usually the longest. Thus, in the two-row barley it was between 17 and 41 cm, and in the six-row barley between 23 and 47 cm. The highest frequencies were 29-32 cm (32% in two-row and 35-38 cm (29%) in six-row (Figure 4). The internode at the base (considered the third at the top), being much shorter, had dimensions between 7 and 15 cm in both forms. However, the higher frequency was 10-11 cm (30%) for two-row and 11-12 cm (28%) for six-row (Figure 5). The diameter of the base internode was instead different. At the two-row it ranged from 2.1 to 4.4 mm, with a higher frequency at 3.0-3.2 mm (55%). Six-row diameter of this internode was 3.0-5.0 mm, with high frequency at 3.9-4.1 mm (39%) (Figure 6).

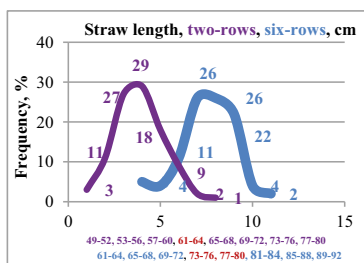


Figure 3. Frequency of straw lengths, cm

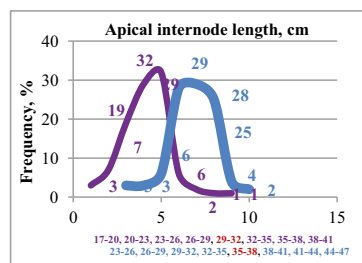


Figure 4. Frequency of apical internode lengths, cm

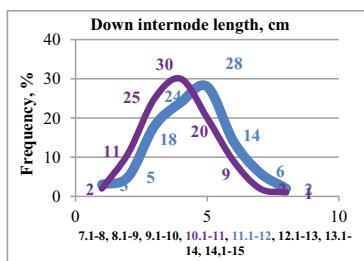


Figure 5. Frequency of down internode lengths, cm

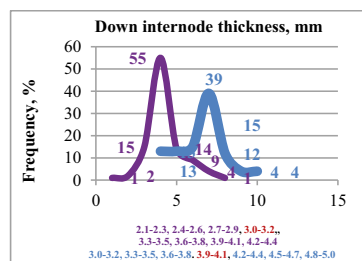


Figure 6. Frequency of down internode thickness, mm

Variability of barley ear/spikes. The appearance and dimensions of the barley spike are characteristic. Thus, its length was between 5 and 10 cm. In the two-row, the lengths of 7.1-8 cm (49%) were dominated, while in six-row the highest values were at 6.1-7 cm (30%), but with high values close to 8.1-9 cm (29-26%)

(Figure 7). The awns that the spikelets form have the obvious characteristic length. Between the two forms there found some differences in length. Thus, the two-row awns ranged from 12 to 21 cm, with a maximum of 15.7-17.4 cm (46%), while the six-row were between 8.5 and 22.8 cm, with a maximum of 13.9-15.6 cm

(34%). Given the modal value of the two forms, it was found that the two-row were slightly longer than the six-row type (Figure 8). The number of spikelets in a ear/spike is different due to the configuration of the two forms. Thus, in two-row ear they formed between 15 and 34 spikelets. Higher frequency was obtained at 25-29 spikelets (58%). Barley six-row ranged from 35 to over 70 spikelets. The higher frequency was obtained at 50-54 (24%), although spikes with 60-64 spikelets were numerous (20%)

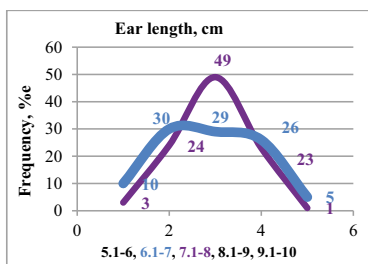


Figure 7. Frequency of barley ear lengths, cm

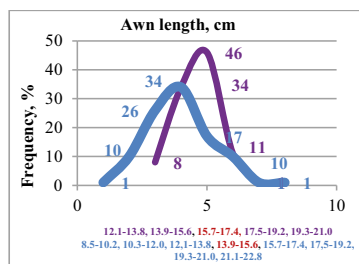


Figure 8. Frequency of barley awn lengths, cm

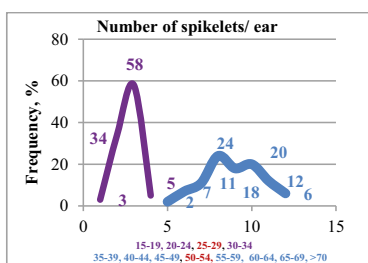


Figure 9. Frequency of spikelets number/ear

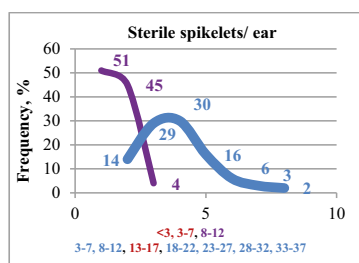


Figure 10. Frequency of sterile spikelets/ear



Figure 11. Two-rows barley characters, 'Trasco' variety



Figure 12. Six-rows barley characters, 'Sistem' variety

Variability of barley grains. The grains (caryopsis type) that are formed have specific characters: they are dressed in the lower palea and the upper palea (also called the lemma), with dimensions between 8-12 mm in length, 2.0-4.5 mm in thickness, in elongated shape and having a thousand grains weight in wide

range: 23-58 g (Fox et al., 2006). From the determinations it appeared that between the two forms there were some differences (Figure 11 and Figure 12).

The weight of the grains formed in a ear ranged between 0.53 g and 1.97 g in barley two-row form. The highest frequency was obtained at

0.90-1.25 g (49%). In barley six-row form, the grains in an ear weighed between 0.90 and 3.71 g. The highest frequency was between 2.34 and 2.69 g. The data shows the great difference due to the two forms of autumn barley (Figure 13). The thousand grains weight (TGW) showed slight differences. Thus, at two-row, the grains had an TGW of between 35 and 70 g, with a modal value of 50.1-55 g (44%) (Figure 14). The six-row form has a TGW of between 35 and 60 g, with the maximum frequency at 45.1-50 g (40%). From these data it results that the two-row has generally formed grains with TGW larger by about 5 g.

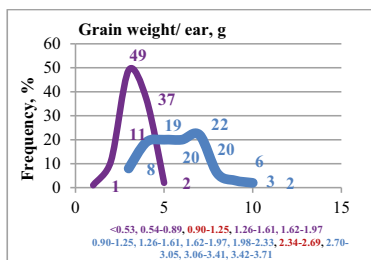


Figure 13. Frequency of grains weight/ear, g

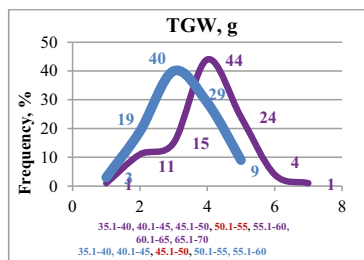


Figure 14. Frequency of barley TGW, g

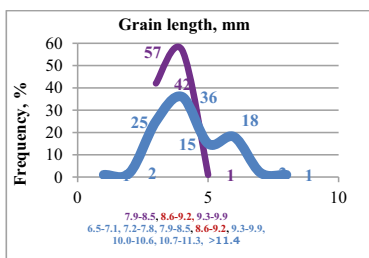


Figure 15. Frequency of grain length, mm

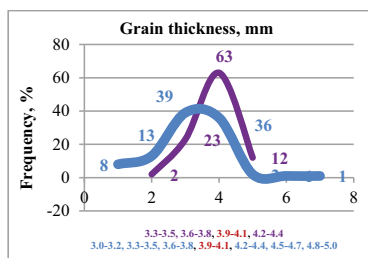


Figure 16. Frequency of grain thickness, mm

Correlations between the main characters If we look at the whole set of correlations between all the analyzed characters, we find mostly positive and statistically significant assurance. The situation is favorable for both the two-row form and the six-row form. In addition, there are small differences between the two forms, but which show nothing but that winter barley, in both forms, is well suited to the crop area.

Thus, at two-row form, the length of the straw correlated best with the number of grains in the ear ($r=0.304^{**}$). The spike's length was very closely related to the weight of the spike, the number of spikelets in the ear, the length of the

spikelet, the number of grains in the ear/spike, the weight of the grains/ ear, the weight of the grains/ ear, the TGW and the size of the grain. The weight of the ear correlated positively with the other characters and correlated negatively with the number of sterile spikelets in an ear ($r=-0.323^{000}$). The number of spikelets in an ear correlated positively with the other characters, less obvious with the number of sterile spikelets ($r=0.164$). Similarly, it was obtained in the case of spikelet length, and the exception was found to correlation with sterile spikelets ($r=0.053$). The number of sterile spikelets bindings correlated negatively with most of the

characters except in the size of the grains (insignificant positive correlations). The awn length has been positively and clearly correlated with all the grain characters. The number of grains in the ear has positively correlated with the length of the grain ($r=0.126$). The length of the grain in this type of barley correlated positively but insignificantly with the grain thickness ($r=0.160$), which means that there is only a small dependence between these two characters (Table 1.a).

In the case of the six-row form, the length of the straw correlated positively with the length of the spike, the length of the spikelet, the TGW and the length of the grain. The length of the ear correlated significantly positively with all the other characters analyzed. The ear's weight correlated very positively with most of the characters, less the length of the grain ($r=0.247^*$) and negative with the sterile spikelets ($r=-0.323^{000}$). High positive values of the coefficients were found for the number of spikelets/ ear and the length of the spikelets,

except in both cases the connection with the sterile spikelets ($r=0.164$ and $r=0.053$ respectively). Negative correlations of different levels were found between the number of sterile spikelets with most characters. However insignificant positive correlations were observed between sterile spikelets with grain dimensions ($r=0.087$ in length and $r=0.014$ in the grain thickness). The awn length had positive causal relationships with the other characters, but the closest was the length of the grain ($r=0.443^{***}$). The number of grains in an ear correlated positively but insignificantly with the length of the grain ($r=0.126$). Favorable situations were also observed between the weight of the grains/ ear with TGW and with the size of the grains. The thousand grains weight correlated closely with the grain size, especially the grain thickness ($r=0.381^{***}$), being different from the two-row form. Between the six-row grain dimensions the correlation was low ($r=0.160$) (Table 1.b), the same as in the two-row form.

Table 1.a. Correlations between different characters of *Hordeum vulgare distichon* form

Character	Straw length	Ear length	Ear weight	Spikelets no./ear	Spikelet length	Sterile spikelets	Awn length	Grains no/ear	Grains weight	TGW g	Grain length	Grain width
Straw length,cm	1	.169	.178	.208*	-.130	-.191 ⁰	.028	.304**	.211*	-.024	.180	.158
Ear length, cm		1	.708***	.797***	.379***	.042	.166	.641***	.682***	.435***	.252**	.213*
Ear weight, g			1	.672***	.243*	-.296 ⁰⁰	.175	.767***	.930***	.699***	.365***	.072
No. spikelets				1	.249*	.159	.045	.731***	.672***	.293**	.196	.077
Spikelet length, cm					1	.044	.170	.176	.207*	.141	.370***	.228*
Sterile spikelets						1	.172	-.550 ⁰⁰⁰	-.432 ⁰⁰⁰	-.057	-.215 ⁰	.007
Awn length, cm							1	-.079	.088	.295**	.232*	.065
No.grains/ear								1	.863***	.282**	.328***	.045
Grains weight/ear									1	.718***	.363***	.087
TGW, g										1	.256**	.133
Grain length, mm											1	.147
Grain width, mm												1

Table 1.b. Correlations between different characters of *Hordeum vulgare hexastichon* form

Character	Straw length	Ear length	Ear weight	Spikelets no./ear	Spikelet length	Sterile spikelets	Awn length	Grains no/ear	Grains weight	TGW g	Grain length	Grain width
Straw length,cm	1	.385***	.203*	.071	.277**	.157	.123	.089	.155	.194*	.432***	.090
Ear length, cm		1	.655***	.836***	.374***	.266**	.307**	.547***	.549**	.271**	.284**	.274**
Ear weight, g			1	.778***	.328***	-.323 ⁰⁰⁰	.289**	.888***	.962***	.663***	.247*	.358***
No. spikelets				1	.266**	.164	.240**	.757***	.726***	.302**	.212*	.268**
Spikelet length, cm					1	.053	.562***	.195*	.253**	.265**	.664***	.225*
Sterile spikelets						1	-.100	-.521 ⁰⁰⁰	-.473 ⁰⁰⁰	-.152	.087	.014
Awn length, cm							1	.141	.200*	.219*	.443***	.204*
No.grains/ear								1	.941***	.362***	.126	.223*
Grains weight/ear									1	.656***	.213*	.318**
TGW, g										1	.287**	.381***
Grain length, mm											1	.160
Grain width, mm												1

Statistical analysis of the variability of morphological characters in barley. The results obtained in the morphological analysis of some characters in winter barley have shown specific aspects. Thus, straw length measured 62 cm for

two-row barley and 76 cm for six-row barley (Table 2.a). Variability demonstrated medium coefficients at two-row (16.6%), and low coefficients at six-row (8.4%).

The internode at the base measured 10.5 cm in two-row and 11.1 cm in the six-row form. The coefficient of variability (CV) was medium and close in both cases (11 to 15%). The diameter of the basal segment was between 3.1 mm at the two-row and 3.8 mm at six-row. The variability in this character was similar, at about 11%.

The internode under ear (apical) measured 23.9 cm at two-row and 35.6 cm at six-row. The variability of character was over 20% in two-row and 12% in six-row.

The ear's length was about 7.5 cm in both forms, but with character variability between 10% (two-row) and 15% (six-row).

The ear weight was characteristic of the two forms: 1.45 g with 14% in two-row and 2.51 g with 26% in six-row variability.

In a similar way the number of spikelets/ ear was 25.4 with 5% in two-row barley variability, and 56.4 with 15% in six-row barley variability. The length of the spikelets was 10.6

mm at the two-row (6% CV) and 11.3 mm at the six-row (7% CV).

Sterile spikelets consisted of 2.8 of medium two-row barley and 14.5 per six-row barley. The variability of this character was 78% in the first case and 46% in the second case (Table 2.b). The awn length was 15.9 cm at the two-row and 14.7 cm in the six-row.

The character had variability of 9 to 15%. The number of grains formed in an ear was 22.5 for two-row and 41.9 for six-row. Character variability shows values of 14% in the first case and 24% in the second case.

The grain weight of an ear was 1.18 g for two-row barley, with the variability of 19%, and 2.05 g for six-row barley, with 28% variability. The thousand grain weight was 52.3 g in the two-row form and 48.6 g in the six-row form. The variability was similar, about 10%. The grains had average dimensions of 8.63/ 3.96 mm at the two-row barley and 9.13/ 3.75 mm in six-row barley. The variation in grain size of the two forms was small (less than 10%).

Table 2.a. Statistical indices of *Hordeum vulgare* plants

Indices	Straw length, cm	Base straw segment, cm		Up straw segment, cm	Ears		Spikelets	
		length, cm	width, mm		length, cm	weight, g	no./ear	length, mm
Winter barley <i>distichon</i> form								
Media, \bar{a}	62.08	10.52	3.183	28.14	7.510	1.450	25.41	10.59
Variance, s^2	27.12	1.379	0.118	45.06	0.599	0.042	1.739	0.409
Standard error, s	5.208	1.174	0.344	6.712	0.774	0.205	1.319	0.640
Variation coef., s%	8.39	11.16	10.81	23.85	10.31	14.10	5.19	6.04
Winter barley <i>hexastichon</i> form								
Media, \bar{a}	76.06	11.10	3.844	35.63	7.470	2.514	56.35	11.32
Variance, s^2	159.64	2.679	0.189	18.99	1.279	0.428	74.19	0.582
Standard error, s	12.625	1.637	0.435	4.358	1.131	0.654	8.613	0.763
Variation coef., s%	16.60	14.75	11.33	12.23	15.14	26.01	15.29	6.74

Table 2.b. Statistical indices of *Hordeum vulgare* plants

Indices	Sterile spikelets	Awn length, cm	No. grains/ear	Grains weight /ear, g	TGW, g	Grains, mm	
						length	width
Winter barley <i>distichon</i> form							
Media, \bar{a}	2.820	15.87	22.49	1.182	52.33	8.630	3.962
Variance, s^2	4.796	2.135	10.03	0.048	30.03	0.086	0.031
Standard error, s	2.190	1.461	3.167	0.220	5.480	0.292	0.176
Variation coef., s%	77.66	9.21	14.08	18.61	10.47	3.38	5.74
Winter barley <i>hexastichon</i> form							
Media, \bar{a}	14.47	14.71	41.88	2.051	48.58	9.129	3.747
Variance, s^2	43.48	5.055	99.08	0.337	21.98	0.762	0.096
Standard error, s	6.594	2.248	9.954	0.581	4.689	0.873	0.309
Variation coef., s%	45.57	15.28	23.76	28.32	9.65	9.56	8.25

CONCLUSIONS

The morphological characters of autumn barley were specific to the two forms: two-row and six-row. Thus, the strain/ straw had dominant lengths of 61-64 cm in the two-row barley and 73-80 cm in six-row barley. At the height of the

plant obviously contributed the apical internode, with lengths of 29-32 cm in the two-row and 35-38 cm in six-row. The basal internode has closely spaced lengths (10-12 cm), but with different diameters: 3.0-3.2 mm in two-row barley and 3.9-4.1 mm in six-row barley. The ear had close lengths (6-8 cm), with

longer awns at two-row form (2 cm more). Spikelets from an ear were on average between 25-29/two-row and 50-54/six-row. Sterile spikelets were found less than 3/two-row and 13-17/six-row. The grains in an average ear weighted 0.90-1.25 g/two-row and 2.34-2.69/six-row. TGW was higher at two-row barley: 50-55 g, vs. 45-50 g/six-row barley. The grains were similar in size: 8.6-9.2 mm in length and 3.9-4.1 mm in thickness.

Between all these characters were established simple correlations (r), with some specific differences to the two forms. Most of these were positive and statistically assured. The length of the two-row barley straw obviously correlated with the number of grains in the ear ($r=0.304^{**}$) and the lower correlations with ear length ($r=0.169$). The six-row barley have strong correlated in the straw length with grain length ($r=0.432^{***}$), and with ear length ($r=0.385^{***}$). The correlations obtained showed the level of adaptability of the two forms of winter barley in the southern area of territory.

The statistical indicators have demonstrated the average values obtained for each character studied. On the one hand, values were obtained that could characterize the morphology of the two-row barley and of the six-row barley. At the same time, the variability coefficients obtained had mostly low and medium values. There was only one exception to the high variability of the grain weights of a six-row barley (CV: 28.32%).

REFERENCES

- Bîlteanu G., Bîrmaure V., 1989. Fitotehnie (1). Ed. Ceres, București, 128-152.
- Delhaize E., Ryan P.R., Hebb D.M., Yamamoto Y., Sasaki T., Matsumoto H., 2004. Engineering high-level aluminium tolerance in barley with the ALMT1 gene. Proceedings National Academy of Science, USA, 101, 15249-15254.
- Fox P., Glen K., Poulsen D., Inkerman D., Andy H.R., 2006. Selectivity for increased barley grain size. Journal of Cereal Science, 43, 148-208.
- Friedrich W., Galensa R., 2002. Identification of a new flavanol glucoside from barley (*Hordeum vulgare*) and malt. European Food Research and Technology, 214 (5), 388-393.
- Komantsuda T., Tanno K., Salomon B., Bryngelsson T., VonBothmer R., 1999. Phylogeny in the genus *Hordeum* based on nucleotide sequences closely linked to the *vrs1* locus (row number of spikelets). Genome 42, 973-981.
- Martinez J.H., Esparza-Fostre A.E., 1998. Genetic analysis of heading date and other agronomic characters in barley (*Hordeum vulgare* L.). Euphytica, 99 (3), 145-153.
- Mayer K.F.X., Waugh R., Langridge P.C., Timothy J.W., Roger P., Graner A., Matsumoto T., Sato K., 2012. A physical, genetic and functional sequence assembly of the barley genome. Nature, 491, 711-716.
- Pickering R., Johnson P.A., 2005. Recent progress in barley improvement using wild species of *Hordeum*. Cytogenetic Genome Research, 109, 344-349.
- Strelchenko P., Kovalyova O., Okuno K., 1999. Interspecific hybridization with *Hordeum bulbosum* and development of hybrids and haploids. Hereditas, 106, 119-127.
- Tanno K., Takeda S., Takeda P., Komatsuda T., 2002. A DNA marker closely linked to the *vrs1* locus (row type gene) indicates multiple origins of six-rowed cultivated barley (*Hordeum vulgare* L.). Theoretical and Applied Genetic, 104, 54-60.