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Breeding progress in grain filling and grain yield components of six-rowed winter barley

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Abstract

The objectives of this study were to quantify the grain yield breeding progress and identify the changes in numerical yield components and grain filling traits of six-rowed winter barley (*Hordeum vulgare* L.) cultivars under different nitrogen (N) fertilization treatments: 0 kg ha^{-1} N (0N, control) and 100 kg ha^{-1} N (100N). Field trials were conducted during two (2015–2016 and 2016–2017) growing seasons in a southern Pannonian location, Novi Sad, Serbia with fifteen six-rowed winter barley cultivars. The rate of genetic gain in grain yield was 0.055 t ha^{-1} yr^{-1} at 0N, while at 100N genetic gain was 0.061 t ha^{-1} yr^{-1}, indicating that modern winter barley cultivars use the applied N fertilizer more efficiently than older cultivars. Grain yield progress was mainly associated with increased grain number per unit area, grain number per spike, grain weight and harvest index. A positive linear correlation was determined between fruiting efficiency and the year of cultivar release, while changes in spike dry weight at anthesis as influenced by the year of cultivar release were not significant. Breeding progress in grain weight was more related with grain filling and maximum grain filling rate, while grain weight association with grain filling duration was less pronounced.

Therefore, further grain yield improvement in six-rowed winter barley should be achieved by simultaneous increase in grain weight and grain number per spike, while maintaining high values of harvest index.

Key words*:* genetic gain, grain growth, *Hordeum vulgare*, nitrogen, yield components, yield improvement.

Introduction

Common barley (*Hordeum vulgare* L.) is one of the most important cereal crops worldwide, ranking fourth after wheat, maize and rice (FAO, http://faostat.fao.org/). In the Pannonian countries, winter barley is the second most important winter crop, mainly grown for animal feed, while about one third of its production is directed for the malting industry (Pržulj et al., 2010). In the southern part of the Pannonian region, growers and breeders prefer two-rowed winter barley as malting barley, while six-rowed cultivars are mainly used for animal feed. Since the quality parameters for feed barley are less defined and demanding than those for malting barley, the main objective of six-rowed winter barley improvement programs in the Pannonian region is the development of cultivars with high and stable grain yields, mainly characterized by higher grain protein content.

In Serbia, the current on-farm ten-year average winter barley grain yield is 3.43 t ha^{-1} and has more than doubled compared to 1950s (Statistical Office of the Republic of Serbia, http://www.stat.gov.rs/WebSite/Default.aspx). In the past 50 years, grain yield of cereal crops, including winter barley, has constantly increased due to the introduction of new high-yielding cultivars and improved production technology (Peltonen-Sainio et al., 2009). Contemporary studies of the physiological basis of grain yield progress in different cereal crops have reported that number of grains per unit area is one of the main traits related to grain yield improvement (Abeledo et al., 2003; Zhou et al., 2014). However, small grain cereals differ significantly in grain number per unit area and grain yield determination (Mirosavljević et al., 2018), since two-rowed winter barley grain number variation is more related to spike number per unit area, while in wheat, grain number is associated with both grain number per spike and spike number per unit area (Prado et al., 2017). Also, grain yield in cereal crops is related to an average grain weight, especially under less favourable environmental conditions (Lizana, Calderini, 2013; Sun et al., 2017).

In cereal crops, grain weight is determined by two major parameters, namely duration and rate of grain filling. As previously reported (Kandić et al., 2018;

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Dodig et al., 2019), environmental factors had a strong influence on grain weight, grain filling rate and duration in Pannonian cereal crops. Environmental conditions in the Pannonian Plain are characterized by appearance of high temperatures and water deficit after anthesis, resulting in decreased duration of grain filling period and grain weight reduction (Pržulj et al., 2015). Although grain weight and grain filling parameters varied between the genotypes, there is a lack of information about contribution of breeding to the grain filling duration and rate in six-rowed winter barley in the Pannonian Plain. Knowledge about the relationship between grain yield and grain filling parameters is required for further improvement in winter barley breeding and production under conditions of the Pannonian Plain.

An assessment of the changes in physiological traits associated with genetic progress in grain yield improvement within a specific period is necessary to identify yield limiting factors and adjust further breeding strategies. Studies of grain yield progress in a set of historical cultivars showed an increase in grain yield in different cereal crops, maize (Mitrović et al., 2016), durum wheat (Álvaro et al., 2008) and bread wheat (Sanchez-Garcia et al., 2013), where only few studies analysed genetic progress in winter barley grain yield (Abeledo et al., 2003; Bingham et al., 2012). Moreover, studies on the genetic gains in winter barley breeding were mainly restricted to two-rowed winter barley cultivars (Mirosavljević et al., 2016) or limited to non-Pannonian environments, such as Nordic European countries (Bertholdsson, Kolodinska Brantestam, 2009), the United Kingdom (Bingham et al., 2012) or South America (Abeledo et al., 2003).

Since the information about grain yield progress of six-rowed winter barley in southern Pannonian Plain is scarce, the aims of this study were to (i) quantify yield breeding progress and (ii) identify changes in grain filling and grain yield components in six-rowed winter barley cultivars under different nitrogen (N) fertilization treatments.

Materials and methods

Plant material and experimental design. A collection of fifteen commercial six-rowed winter barley (*Hordeum vulgare* L.) cultivars widely grown in the last half century in southern part of the Pannonian region were used in this study. Common barley cultivars 'Majo' from Germany, released in 1972, 'Novosadski 27' and 'Novosadski 150' from Serbia, in 1973 and in 1976, 'Robur' from France, in 1973, 'Kredit' and 'Okal' from Czech Republic, in 1984 and in 1986, 'Novosadski 313', 'Novosadski 317' and 'Novosadski 703' from Serbia, in 1987, in 1988 and in 1992, respectively, 'Botond' and 'Attila' from Hungary, in 1992 and in 1993, 'Galeb', 'Nonius' and 'Rudnik' from Serbia, in 1993, in 2003 and in 2009, respectively, and 'Carmina' from France, in 2013 were investigated. The cultivars were grown under field conditions during two consecutive growing seasons under two nitrogen (N) fertilization levels: 0 kg ha^{-1} N (0N, control) and 100 kg ha^{-1} N (100N). The experiment was arranged in a split-plot design with three replicates; N treatment was randomized within the main plots and cultivars within sub-plots. Fertilizer N was applied as ammonium nitrate (NH_4NO_3) to the plots at a rate of 100 kg ha^{-1} N in two treatments: the first half 50 kg ha^{-1} N was applied prior to sowing, and the second was top-dressed at the start of stem elongation stage (BBCH 30).

Growing conditions. The experiment was conducted during the 2015–2016 and 2016–2017 growing seasons in the experimental field (45°20′ N, 19°51′ E) of Institute of Field and Vegetable Crops, Novi Sad, Serbia on a *Haplic Chernozem* (Aric) (WRB, 2014). The trials were sown on 8 October in 2015 and 10 October in 2016 (recommended sowing dates for agroecological conditions in southern Pannonian Plain) with a target density of 350 plants m^2. The plots were sown mechanically with a row seeder spaced at 10 cm, and each plot occupied an area of 5 m^2. All trials were fertilized prior to sowing with an average rate of *circa* 60 kg ha^{-1} P_2O_5 and 60 kg ha^{-1} K_2O. In trials, weeds were periodically manually removed, while pests (Decis 25 EC, a.i. deltamethrin, 20 ml ha^{-1}) and diseases (Prosaro, a.i. tebuconazole and protiokonazol, 1000 ml ha^{-1}) were controlled by appropriate chemical applications in spring.

Weather conditions. The weather data for 2015–2016, 2016–2017 and long-term (1961–2015) period were obtained from the meteorological station located near the experimental field (Fig. 1).

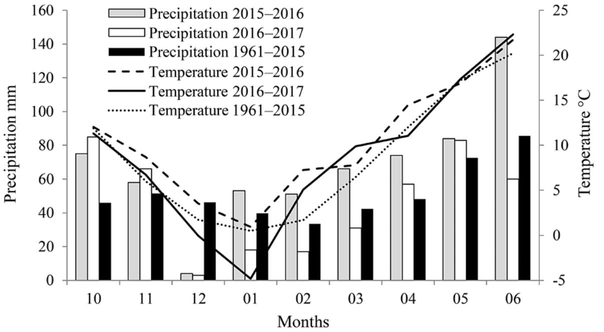


Figure 1. Monthly average daily precipitations and temperatures during 2015–2016, 2016–2017 and in the long-term period

During the growing season in 2015–2016 and 2016–2017 the mean temperature was 9.1°C and 7.5°C, respectively, and the sum of precipitation – 507 and 352 mm, respectively. In both growing seasons, October and November were characterized by mild air temperatures and precipitation that was on average higher than the long term average, resulting in fast plant emergence and early crop growth. In 2016–2017, the winter period (December and January) had lower temperatures compared to 2015–2016 and the long-term (1961–2015) period. However, the presence of snow cover enabled good winter survival of six-rowed winter barleys. Temperatures in February and March of both growing seasons were higher than the long-term average, resulting in earlier spring growth of winter barley. During the spring (April and May) in 2015–2016 and 2016–2017, long period of moderate temperatures close to the long-term average accompanied with high level of precipitation positively influenced crop growth during stem elongation, anthesis and early grain filling period. Increased precipitation in June 2015–2016, which occurred mostly in the second half of the month, did not disturb the harvest, as it was performed in the first ten-day of June with the favourable weather conditions.

Data recording. During the growing season, anthesis date and physiological maturity were recorded for each cultivar. At anthesis (BBCH 65) and physiological maturity (BBCH 89, 50% of peduncle yellow), 1 m long samples from two central rows (away from plot border) were cut at the ground level. From the samples taken at anthesis, biomass was divided into the spikes and the rest of the canopy. Samples were dried at 60°C temperature for 72 h and then weighed to calculate spike dry weight at anthesis (SDW). Harvest index, yield and its numerical components: grain number per unit area (GN), average grain weight (AGW), spike number per unit area (SN), grain number per spike (GNS), were determined from the samples taken at physiological maturity. Fruiting efficiency (FE) was calculated as the number of grains per spike divided by spike dry weight at anthesis (Slafer et al., 2015). Harvest index (HI) was calculated as the ratio of grain yield to total plant yield.

Ten days after anthesis, plant height (PH) was measured from the ground to the top of the spike without awns on ten main stems in each plot. At anthesis, 100 main spikes per plot with visible anthers were tagged and three spikes from each plot were randomly sampled twice a week, beginning 10 days after anthesis until harvest maturity. The ears were oven dried at 60°C temperature for 72 h, hand threshed, and the grains were counted and weighed.

Grain dry matter content per 3 or per 1 spike was expressed as function of accumulated growing degree days (GDD) from anthesis. The GDD was calculated from local daily minimum (T_{min}) and maximum (T_{max}) temperatures and base (b) temperature ($T_b = 0°C$) as $GDD = \Sigma ((T_{max} + T_{min}) / 2) - T_b°$.

The dry weight of the grains from each plot was fitted by the logistic curve (Darroch, Baker, 1990). The logistic curve was calculated by formula:

$$Y = W / (1 + eB - Cx),$$

where Y is the estimated dry grain weight, W – the maximum grain weight, e – exponent, B and C – empirical coefficients derived from the adjustment, x – the time from anthesis calculated in GDDs.

Final grain weight (FGW) was expressed in mg. Grain filling duration (GFD) was calculated from the logistic equation and considered to be the time required for grain weight to reach 95% of its final grain weight. Grain filling rate (GFR) was calculated as a ratio of final grain weight to grain filling duration. The maximum grain filling rate (MGFR) was mathematically determined from the curve parameters as MGFR = (C × FGW) / 4, and expressed as mg of grain GDD^{-1}. Time to maximum grain filling rate (TMGFR) was calculated from the non-linear equation as time from anthesis to the maximum grain filling rate and expressed in GDD. Rate of grain growth (RGG) was calculated according to Dodig et al. (2019). Grain yield (GY) in t ha^{-1} was determined at maturity after mechanical harvesting and adjusted to 13% moisture.

Statistical analysis was conducted by analysis of variance (ANOVA) in a factorial design with two growing seasons, two levels of N application and fifteen cultivars. Treatment means were compared using the Tukey test. To partition the total variation, ANOVA for individual N treatment was performed using generalized linear model along with environments (year), replications within environments, blocks within environments and their interactions. All stated factors were treated as random effects. Absolute and relative genetic gains were computed as the slope of the linear regression between the absolute or relative value of the trait and the year of release (YOR) of the cultivar. Relative values were computed for each cultivar as a percentage to the average values of all the cultivars according to Royo et al. (2007). Principal components analysis (PCA), linear regression and Pearson's correlation were calculated using mean values of three replicates using software *InfoStat* (Di Rienzo et al., 2011).

Results

Grain yield and grain yield components. Results from Table 1 indicate that the effect of the growing season was significant for all traits except harvest index. For most traits (GY, GN, SN, SDW, FE, PH, GFD, time to maximum GFR and RGG), growing season had the greatest impact, accounting for >50% of total variability in spike number per unit area, plant height and time to maximum GFR. The effects of N fertilization were not significant on spike dry weight at anthesis and time to maximum GFR, but significant for all other traits. The cultivars significantly differed for all traits. The greatest genotypic effect was observed in final grain weight (64.75% of variability), followed by average grain weight (64.62%) and maximum grain filling rate (61.36%). The effect of interaction between growing season and N fertilization was significant for GY, GW, GNS, HI, FGW, GFD, GFR, MGFR, TMGFR and RGG. The interaction effect of the genotype and the growing season was significant for all traits except plant height. The contribution of genotype and fertilization interaction was significant for all traits except grain number per spike, while interaction of growing season, N fertilization and genotype was significant for all traits except grain number per spike and plant height.

Grain yield showed a significant linear relationship ($P < 0.01$) with the year of cultivar release under both N fertilization treatments. The slope of the relationship varied between N treatments. At 0N, the genetic progress in terms of grain yield was 0.055 t ha^{-1} yr^{-1}, while at 100N it was clearly higher compared to the 0N and reached 0.061 t ha^{-1} yr^{-1}. At 0N, grain yield ranged from 7.00 t ha^{-1} ('Majo') to 9.32 t ha^{-1} ('Rudnik') with the average of 8.25 t ha^{-1} (Table 2). The average grain yield

Table 1. Relative contribution to total sum of squares and significance level of source of variation for studied traits of six-rowed winter barley genotypes (G) released from 1972 to 2013 grown at two nitrogen (N) fertilization treatments in 2015–2016 and 2016–2017 growing seasons (GS)

Trait	Unit	Source of variation						
		GS	N	G	GS × N	GS × G	N × G	GS × N × G
GY	t ha^{-1}	33.06***	24.40***	32.36***	0.32***	4.09***	3.09***	2.68***
AGW	mg	3.43***	3.32***	64.62***	1.75***	9.58***	9.20***	8.09***
GN	m^{-2}	45.30***	16.21***	17.65***	0.02 ns	7.57***	5.66***	7.59***
SN	m^{-2}	60.36***	8.30***	12.44***	0.13 ns	6.56****	4.80**	7.41***
GNS		21.56***	16.57***	31.26***	4.49**	12.3*	6.25 ns	7.56 ns
SDW	g	43.62***	0.63 ns	20.79***	0.16 ns	16.69***	6.61**	11.50***
FE		44.21***	2.96**	20.52***	0.77 ns	11.8***	6.10*	13.62***
PH	cm	60.39***	1.61***	29.1***	0.17 ns	1.23 ns	6.30***	1.11 ns
HI	%	0.45 ns	12.56***	45.74***	5.83***	23.32***	5.83*	6.28*
FGW	mg	3.4***	6.32***	64.75***	0.67*	7.31***	10.09***	7.47***
GFD	GDD	45.87***	0.78*	25.79***	0.67*	7.29***	9.93***	9.67***
GFR	mg GDD^{-1}	26.31***	1.46***	38.00***	0.61*	8.77***	5.85***	19.00***
MGFR	mg GDD^{-1}	3.41***	6.82***	61.36***	1.14*	7.95***	11.36***	7.95***
TMGFR	GDD	65.82***	0.00 ns	19.11***	0.27***	9.37***	2.35***	3.08***
RGG	mg GDD^{-1}	46.58***	5.48***	26.71***	0.68***	8.22***	3.42***	8.90***

GY – grain yield, AGW – average grain weight, GN – grain number per unit area, SN – spike number per unit area, GNS – grain number per spike, SDW – spike dry weight at anthesis, FE – fruiting efficiency, PH – plant height, HI – harvest index, FGW – final grain weight, GFD – grain filling duration, GFR – grain filling rate, MGFR – maximum grain filling rate, TMGFR – time to maximum GFR, RGG – rate of grain growth; GDD – growing degree days; *, **, *** – significant at the 0.05, 0.01, and 0.001 probability levels, respectively, ns – not significant

Table 2. Mean values of grain yield (GY), average grain weight (AGW), grain number per unit area (GN), spike number per unit area (SN), grain number per spike (GNS) of six-rowed winter barley cultivars released from 1972 to 2013 at two nitrogen (N) levels

Cultivar	GY t ha^{-1}		AGW mg		GN m^{-2}		SN m^{-2}		GNS	
	0N	100N	0N	100N	0N	100N	0N	100N	0N	100N
Majo	7.00 e	8.65 gh	36.1 e	40.9 i	19580 abc	21171 bc	406 a	417 abc	48.3 b	51.2 abc
Novosadski 27	7.30 e	9.29 efg	45.8 bcd	43.2 gh	16147 f	21535 bc	338 de	434 ab	48.1 b	49.8 c
Robur	7.44 e	8.71 fgh	42.8 d	42.2 hi	17468 def	20608 cde	352 cde	406 abcd	49.7 ab	50.9 abc
Novosadski 150	7.56 de	8.43 h	43.3 cd	45.6 def	17473 def	18470 fg	354 bcd	354 e	49.6 ab	52.2 abc
Kredit	8.03 cd	8.34 h	44.6 bcd	45.2 ef	18029 cde	18438 g	361 abcde	355 e	50.0 ab	52.1 abc
Okal	7.57 de	9.44 def	45.8 bcd	45.6 def	16499 ef	20759 bcd	324 e	388 bcde	50.9 ab	53.7 ab
Novosadski 313	8.31 c	8.97 fgh	45.4 bcd	47.7 bc	18321 bcd	18783 efg	356 bcde	368 de	51.6 ab	51.6 abc
Novosadski 317	8.06 cd	9.41 def	45.7 bcd	49.3 ab	17628 def	19081 defg	347 de	377 cde	50.8 ab	50.8 abc
Attila	8.50 bc	9.75 cde	46.2 bc	48.1 bc	18433 bcd	20347 cdef	367 abcde	385 cde	50.4 ab	53.1 abc
Novosadski 703	8.50 bc	10.03 bcde	42.8 d	46.7 cde	19863 ab	21557 bc	398 b	424 abc	50.0 ab	51.5 abc
Botond	8.95 ab	10.11 bcd	47.2 ab	46.7 cde	19018 bcd	21859 bc	370 abcd	419 abc	51.4 ab	52.6 abc
Galeb	9.03 ab	9.98 bcde	46.5 abc	48.1 bc	19500 abc	20776 bcd	377 abcd	401 abcde	51.9 ab	51.9 abc
Nonius	8.99 ab	10.44 bc	47.2 ab	47.4 cde	19107 bcd	22073 bc	374 abcd	409 abcd	51.2 ab	53.9 ab
Rudnik	9.32 a	11.37 a	49.7 a	50.4 a	18858 bcd	22554 ab	371 abcd	421 abc	50.8 ab	53.7 ab
Carmina	9.27 a	10.73 ab	45.0 bcd	44.7 fg	20911 a	24145 a	396 abc	442 a	53.1a	54.5 a
Average	8.25 b	9.58 a	44.9 b	46.1 a	18456 b	20810 a	366 b	400 a	50.5b	52.2a
Gain	0.055	0.061	0.148	0.145	66.108	76.072	0.747	0.737	0.082	0.083
Gain %	0.67	0.64	0.33	0.31	0.36	0.37	0.20	0.18	0.16	0.16
Correlation with YOR	0.93	0.88	0.61	0.68	0.62	0.59	0.36	0.34	0.79	0.79
Significance	**	**	*	**	**	*	ns	ns	**	**

Note. YOR – year of release of the cultivar; means followed by the same letter were not significantly different at $P = 0.05$ by the Tukey test;*, **, *** – significant at the 0.05, 0.01 and 0.001 probability levels, respectively, ns – not significant.

at 100N was 9.58 t ha^{-1} and varied from 8.34 ('Kredit') to 11.37 t ha^{-1} ('Rudnik'). The average grain yield at 0N was significantly lower (1.33 t ha^{-1}) than at 100N. On average, application of 100N fertilizer average grain weight increased for 1.2 mg compared to 0N (control) treatment. Older cultivars 'Majo' and 'Robur' had the lowest average grain weight under both fertilization treatments. Average grain weight increased at the rate of 0.148 mg yr^{-1} at 0N, while at 100N the rate of grain weight increase was slightly lower (0.145 mg yr^{-1}) than at 0N.

The average grain number per unit area of the tested cultivars per m^2 was 18456 and 20810 at 0N and 100N, respectively. At 0N, grain number per unit area increased from 16147 for the 'Novosadski 27' (released in 1973) to 20911 for 'Carmina' (2013), while at 100N grain number per unit area also increased from 18438 from 'Kredit' (1984) to 24145 'Carmina' (2013). Grain number per unit area was positively correlated with year of cultivar release at both N levels, demonstrating an increase of 66 and 76 grain yr^{-1} at 0N and 100N, respectively. Spike number per unit area at 0N fertilization are ranged from 324 to 406 m^{-2} and at 100N – from 354 to 442 m^{-2}. There was no significant linear relationship between year of release of cultivar and spike number per unit area at both N levels. The average grain number per spike of tested cultivars was 50.5, ranging from 48.1 ('Novosadski 27') to 53.1 ('Carmina') at 0N. Moreover, at 100N grain number per spike varied between 49.8 ('Novosadski 27') and 54.5 ('Carmina') with the average of 52.2. Grain number per spike significantly increased with years of cultivars release, with the genetic gain of 0.08 and 0.083 grain yr^{-1} at 0N and 100N fertilization treatments, respectively.

In general, spike dry weight varied from 0.44 to 0.58 g and from 0.45 to 0.55 g at 0N and 100N, respectively (Table 3). Changes in spike dry weight under both N fertilization treatments were not significantly related to year of cultivar release, indicating that spike dry weight played little role in winter barley grain yield increase. The lowest fruiting efficiency was recorded for 'Attila' and 'Kredit' at 0N and 100N, respectively. On the other hand, modern cultivars 'Rudnik' and 'Carmina' had consistently high fruiting efficiency under both N fertilization treatments. There was a linear improvement in winter barley fruiting efficiency with cultivar year of release with increase of 0.5 yr^{-1} at 0N and 0.33 yr^{-1} at 100N.

Plant height of winter barley cultivars, at 0N varied from 96.0 cm ('Majo') to 85 cm ('Botond') with the average of 89.9 cm. In addition, at 100N plant height ranged from 84.3 cm ('Rudnik') to 98.7 cm ('Majo') with the average of 91.2 cm. Plant height showed a linear trend of decrease with the year of release under both N fertilization treatments. Modern six-rowed winter barley cultivars showed a decline of 0.145 and 0.203 cm per year of release at 0N and 100 N, respectively. At 0N, average harvest index of the studied cultivars was 0.43 ranging from 0.39 ('Novosadski 150') to 0.48 ('Carmina'). At 100N, harvest index varied between 0.42 and 0.50 with the average of 0.45. Harvest index increased significantly with the year of cultivar release with improvement of 0.001 and 0.0016 per year of release at 0N and 100N, respectively.

Grain filling traits. The values of final grain weight calculated from the logistic curve were closely related to the values of the average grain weight determined from the harvested subsample at the physiological maturity. As in average grain weight, the main source of the variation in final grain weight was the cultivar, explaining almost two thirds of the variation in final grain weight. The lowest final grain weight was recorded for 'Majo', and the highest final grain weight was reported for modern cultivar 'Rudnik' at 0N and 100N (Table 4). Under both N fertilization treatments, cultivars had similar ranking as for final grain weight showing positive relationship with year of release of the cultivar. Grain filling duration varied between 572 GDD ('Novosadski 27') and 702 GDD ('Robur') at 0N, and between 597 GDD ('Novosadski 317') and 723 GDD ('Carmina') at 100N. In average, application of N fertilization increased grain filling duration for 11 GDD. Although there was significant variation in grain filling duration of six-rowed winter barley, there was no clear improvement trend according to the year of cultivar release. Modern cultivars ('Rudnik', 'Carmina' and 'Nonius') released in the past 20 years tend to have increased grain filling rate at 0N and 100N. On the other hand, their older counterparts ('Robur' and 'Majo') showed decreased rate of grain filling rate. There was

Table 3. Mean values of spike dry weight at anthesis (SDW), fruiting efficiency (FE), plant height (PH) and harvest index (HI) of six-rowed winter barley cultivars released from 1972 to 2013 at two nitrogen (N) levels

Cultivar	SDW g		FE		PH cm		HI %	
	0N	100N	0N	100N	0N	100N	0N	100N
Majo	0.55 ab	0.50 ab	89 c	109 ab	96.0 a	98.7 a	0.42 cdefg	0.46 abcd
Novosadski 27	0.49 bcd	0.50 ab	98 bc	102 ab	92.5 abc	93.8 bcd	0.40 defg	0.43 bcd
Robur	0.48 bcd	0.50 ab	104 bc	105 ab	88.7 cdef	94.3abc	0.42 cdefg	0.46 abcd
Novosadski 150	0.47 cd	0.46 b	108 bc	115 ab	91.0 bcd	90.5 cde	0.39 g	0.42 e
Kredit	0.52 abc	0.55 a	96 bc	95 b	89.8 bcde	90.0 cdef	0.43 bcdef	0.42 de
Okal	0.50 bcd	0.46 b	103 bc	116 a	89.0 bcdef	96.4 ab	0.46 abc	0.48 ab
Novosadski 313	0.49 bcd	0.45 b	106 bc	116 a	90.5 bcde	87.2 f	0.40 efg	0.43 cde
Novosadski 317	0.51 bcd	0.46 b	101 bc	112 ab	93.1 ab	91.0 cdef	0.40 fg	0.45 bcde
Attila	0.58 a	0.51 ab	88 c	105 ab	92.5 abc	92.2 bcde	0.47 ab	0.47 abcd
Novosadski 703	0.52 abc	0.52 ab	98 bc	103 ab	91.0 bcd	93.8 bcd	0.44 abcde	0.44 bcde
Botond	0.46 cd	0.48 ab	112 ab	110 ab	85.0 f	89.3 def	0.44 bcdef	0.47 abc
Galeb	0.49 bcd	0.48 ab	106 bc	108 ab	88.7 cdef	88.9 ef	0.41 defg	0.44 bcde
Nonius	0.49 bcd	0.51 ab	106 bc	108 ab	87.5 def	89.6 def	0.45 abc	0.46 abcde
Rudnik	0.46 cd	0.46 b	112 ab	121 a	86.7 ef	84.3 g	0.45 abcd	0.48 ab
Carmina	0.44 d	0.47 b	131 a	117 a	86.6 ef	87.9 ef	0.48 a	0.50 a
Average	0.50 a	0.49 a	104 b	110 a	89.9 b	91.2 a	0.43 b	0.45 a
Gain	−0.001	−0.001	0.505	0.329	−0.145	−0.203	0.002	0.001
Gain %	−0.20	−0.20	0.49	0.30	−0.16	−0.22	0.47	0.22
Correlation with YOR	−0.35	−0.18	0.61	0.69	−0.63	−0.69	0.68	0.59
Significance	ns	ns	*	*	**	**	**	*

Explanation under Table 2

Table 4. Mean values of final grain weight (FGW), grain filling duration (GFD) and grain filling rate (GFR) of six-rowed winter barley cultivars released from 1972 to 2013 at two nitrogen (N) levels

Cultivar	FGW mg		GFD (GDD)		GFR mg GDD^{-1}	
	0N	100N	0N	100N	0N	100N
Majo	36.5 d	40.3 g	627 abcde	598 c	0.058 e	0.068 ab
Novosadski 27	44.1 abc	42.3 efg	572 e	632 bc	0.069 abcd	0.068 ab
Robur	42.3 bc	41.2 fg	702 a	643 abc	0.061 de	0.065 b
Novosadski 150	42.2 c	43.9 def	587 de	647 abc	0.069 abcd	0.069 ab
Kredit	44.7 abc	43.9 def	668 abc	623 c	0.067 bcd	0.072 ab
Okal	44.9 abc	44.3 cdef	645 abcde	613 c	0.070 abc	0.073 ab
Novosadski 313	43.8 abc	46.9 abcd	607 abcde	660 abc	0.072 abc	0.072 ab
Novosadski 317	43.6 abc	47.2 abcd	596 cde	597 c	0.074 abc	0.073 ab
Attila	44.7 abc	47.5 abc	681 ab	706 ab	0.066 cde	0.068 ab
Novosadski 703	42.5 bc	45.1 bcde	644 abcde	638 bc	0.066 bcde	0.071 ab
Botond	46.2 ab	45.9 abcd	623 abcde	630 bc	0.075 ab	0.073 ab
Galeb	45.6 abc	47.9 ab	598 cde	640 bc	0.075 ab	0.075 a
Nonius	43.8 abc	45.0 bcde	591 cde	612 c	0.074 abc	0.073 ab
Rudnik	46.8 a	48.9 a	653 abcd	659 abc	0.070 abc	0.075 a
Carmina	45.4 abc	48.0 ab	668 abc	723 a	0.073 abc	0.074 a
Average	43.8 b	42.2 a	630 b	641 a	0.069 b	0.071 a
Gain	0.1257	0.173	0.5317	1.3727	0.0002	0.0001
Gain %	0.29	0.38	0.08	0.21	0.29	0.28
Correlation with YOR	0.62	0.83	0.17	0.49	0.59	0.78
Significance	*	**	ns	ns	*	**

Explanation under Table 2

a difference in grain filling rate between N fertilization treatments, and on average cultivars had higher grain filling rate at 100N treatment. There was positive correlation between grain filling rate and year of release of the cultivar, showing relative genetic gain of 0.29% and 0.28% at 0N and 100N, respectively.

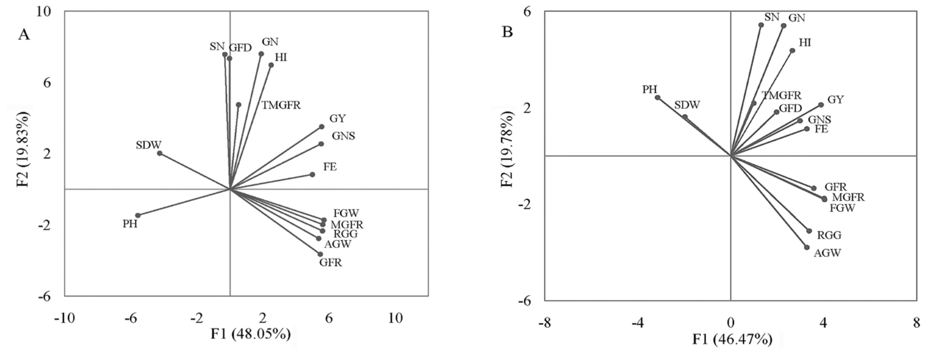
There was linear improvement in maximum grain filling rate under both fertilization treatments with relative genetic gain of 0.27% and 0.35% with year of release of the cultivar (Table 5). Application of 100N led to significant increase in maximum grain filling rate. Time to maximum grain filling rate varied significantly between the cultivars under both N fertilization treatments. However, time to maximum GFR did not vary between either N fertilization treatments. Also, there was no clear improvement in time to maximum GFR with year of cultivar release. The rate of growth varied from 0.063 mg GDD^{-1} ('Majo') to 0.082 mg GDD^{-1} ('Galeb') at 0N, and from 0.070 mg GDD^{-1} ('Robur') to 0.0886 mg GDD^{-1} ('Novosadski 317') at 100N, showing linear relationship with year of release of the cultivar. Also, average rate of grain growth at 0N was significantly lower than at 100N.

Relationship between traits. Associations between the studied grain yield determinants and grain filling traits were explored using PCA analysis (Fig. 2). At 0N, grain yield was positively related to main grain yield determinants and grain filling traits, but negatively related to spike dry weight and plant height. At 100N, grain yield mostly related to grain number per spike, harvest index, fruiting efficiency and grain filling duration, but less or not related to average grain weight and plant height and spike dry weight. Association of grain yield and average grain weight was higher at 0N, indicating importance of high grain weight in grain determination, especially under less favourable conditions. Under both N fertilization treatments, grain yield was more related to grain number per spike than to spike number per unit area. In six-rowed winter barley, spike dry weight was negatively related to fruiting efficiency at 0N and 100N. Fruiting efficiency was more related to grain number per spike than to spike number per unit area.

Table 5. Mean values of maximum grain filling rate (MGFR), time to maximum GFR (TMGFR) and rate of grain growth (RGG) of six-rowed winter barley cultivars released from 1972 to 2013 at two nitrogen (N) levels

Cultivar	MGFR mg GDD^{-1}		TMGFR (GDD)		RGG mg GDD^{-1}	
	0N	100N	0N	100N	0N	100N
Majo	0.0912 c	0.1008 g	370 defg	381 cd	0.063 d	0.073 cd
Novosadski 27	0.1103 ab	0.1058 efg	352 fg	379 cd	0.069 bcd	0.074 cd
Robur	0.1059 ab	0.1029 fg	462 a	430 ab	0.066 cd	0.070 d
Novosadski 150	0.1056 b	0.1098 def	341 g	350 d	0.078 ab	0.077 abcd
Kredit	0.1117 ab	0.1098 def	426 abc	412 abc	0.071 bcd	0.076 bcd
Okal	0.1121 ab	0.1107 cdef	395 bcdef	377 cd	0.074 abc	0.079 abc
Novosadski 313	0.1095 ab	0.1171 abcd	401 bcdef	389 bcd	0.076 ab	0.082 abc
Novosadski 317	0.1090 ab	0.1181 abcd	394 bcdef	388 bcd	0.079 ab	0.086 a
Attila	0.1117 ab	0.1187 abc	442 ab	435 a	0.071 bcd	0.077 abcd
Novosadski 703	0.1061 ab	0.1129 bcde	380 cdefg	387 bcd	0.073 abcd	0.080 abc
Botond	0.1154 a	0.1148 abcd	389 cdefg	388 bcd	0.081 a	0.084 ab
Galeb	0.1140 ab	0.1198 ab	366 efg	400 abc	0.082 a	0.081 abc
Nonius	0.1095 ab	0.1113 cdef	420 abcd	403 abc	0.079 ab	0.081 abc
Rudnik	0.1129 ab	0.1221 a	409 bcde	405 abc	0.078 ab	0.084 ab
Carmina	0.1137 ab	0.1204 ab	388 cdefg	411 abc	0.079 ab	0.078 abcd
Average	0.1092 b	0.1130 a	395 a	396 a	0.075 b	0.079 a
Gain	0.0003	0.0004	0.4710	0.5293	0.0003	0.0002
Gain %	0.27	0.35	0.12	0.13	0.40	0.25
Correlation with YOR	0.57	0.82	0.18	0.33	0.65	0.63
Significance	*	**	ns	ns	**	*

Explanation under Table 2



Explanation under Table 1

Figure 2. Biplot for measured traits in 0N (A) and 100N (B) fertilization treatments for 15 six-rowed winter barley cultivars (mean of 2015–2016 and 2016–2017)

Discussion

In the present study, grain yield of six-rowed winter barley cultivars increased linearly by 0.055 t ha^{-1} yr^{-1} at 0N and by 0.061 t ha^{-1} yr^{-1} at 100N, indicating that the rate of genetic progress in six-rowed winter barley did not reach plateau in southern Pannonian Plain. Grain yield progress in six-rowed winter barley is slightly higher than that reported by Mirosavljević et al. (2016) in two-rowed winter barley, who reported grain yield progress of 0.046 t ha^{-1} yr^{-1} for cultivars released in the past 40 years in Serbia. Genetic improvement of winter barley grain yield has been reported to be 0.013 ± 0.003 t ha^{-1} yr^{-1} from 1942 and 1988 in Nordic countries (Ortiz et al., 2002) and 0.020 t ha^{-1} yr^{-1} from 1944 and 1998 in Argentina (Abeledo et al., 2003).

In the present paper, genetic grain yield progress in six-rowed winter barley was positively associated with both main grain yield determinants – grain number per unit area and grain weight. According to previous studies, in different cereal crops grain yield progress was mainly related to increase in grain number per unit area (Peltonen-Sainio et al., 2007; Zhou et al., 2014). More detailed analysis of grain number per unit area subcomponents in our study showed that grain yield improvement was mainly driven by the increase of grain number per spike, while association between grain yield and spike number per unit area was less pronounced. Also, spike number per unit area showed no relationship with year of cultivar release. The correlation between year of cultivar release and grain number per spike was also identified worldwide in durum wheat (De Vita et al., 2007) and bread wheat (Sanchez-Garcia et al., 2013).

A decrease in plant height has resulted in a decline in straw yield and an increase in harvest index, which favoured partitioning of dry matter during pre-anthesis development to spike and generally grain yield improvement in wheat (De Vita et al., 2007; Mladenov et al., 2011). Also, results of our experiment showed a significant reduction in plant height and improvement of harvest index in six-rowed winter barley. Although proposed theoretical maximum for harvest index in wheat is 0.62 (Austin et al., 1980), according to Fischer and Edmeades (2010), it is difficult to achieve values of harvest index higher than 0.50. Since the values of harvest index in modern winter barley cultivars in our study were already high (close to 0.5), further increase of values for these traits seems difficult. Therefore, additional grain yield increase should be achieved by increasing the biomass production while maintaining high values of harvest index (Zhou et al., 2014).

Although different studies reported that increase in spike dry weight at anthesis represents promising traits for further grain yield improvement (Miralles, Slafer, 2007; Reynolds et al., 2009), there was no significant change in spike dry weight with year release in our study. The unusual absence of spike dry weight improvement can be based on the fact that older cultivars already have optimal values of spike dry weight. Additionally, modern cultivars probably have higher resource allocation to fertile parts (developing florets) than in structural elements of spike (rachis, glume and awns), resulting in increased ovary size which is related to higher potential grain weight (Calderini, Reynolds, 2000). Therefore, fine tuning of fruiting efficiency and resource partitioning in fertile parts of florets could lead to simultaneous increase in grain number per spike and grain weight without significant changes in spike dry weight, as reported in our study.

Most previous studies reported that grain weight was not associated or even reduced with year of cultivar release in different cereal crops (Ortiz et al., 2002; Sanchez-Garcia et al., 2013; Zhou et al., 2014). However, some recent studies (Lopes et al., 2012; Beche et al., 2014; Aisawi et al., 2015) reported that the grain yield improvement was related to increase in average grain weight, especially when analysing narrow time period – past 40 years or less. Similarly, average grain weight as well as final grain weight increased in six-rowed winter barley with a rate of 0.148 and 0.145 mg yr^{-1} showing positive relationship with grain yield. Association of grain yield with average and final grain weight was higher at 0N, indicating importance of high grain weight in grain yield determination, especially under less favourable conditions. It should also be noted that demands of winter barley growers probably had an impact on definition of barley ideotype with increased average grain weight. Consequently, selection for higher grain weight in early segregating (F_2 and F_3) populations resulted in the development of modern cultivars with increased grain weight.

In our study, grain filling rate, maximum grain filling rate and rate of grain growth were increased as a result of breeding activities in six-rowed winter barley. Generally, high grain filling rate has been related to a greater terminal drought tolerance (Dias, Lidon, 2009). In the past 50 years in Pannonian barley, grain filling rate increased at rate of 0.29% and 0.28% at 0N and 100N, respectively. Environmental conditions in the Pannonian Plain are often unfavourable for grain growth, and increased grain filling rate could be important for formation of high and stable grain weight in modern cultivars. Also, in this study average grain weight and final grain weight were more related to grain filling rate than to grain filling duration confirming that the rate of assimilates synthesis is more important than duration of grain filling.

Grain filling duration and time to maximum grain filling rate were not modified by plant breeding in the past 50 years in the Pannonian Plain. There are several studies about changes in grain filling duration in different cereal crops as a result of breeding activities, with contrasting results. Thus modern bread wheat cultivars in Brazil had longer grain filling period than old cultivars, probably due to decrease in duration of pre-anthesis period (Beche et al., 2014), whereas modern Spanish durum cultivars had shorter grain filling period than older ones (Álvaro et al., 2008). Similar studies in durum wheat (Motzo et al., 2010) indicate that duration of grain filling period was not significantly changed by breeding in Italy. Absence of genetic gain in grain filling duration in our study was expected, since late maturity genotypes are not recommended for the Pannonian Plain due to reduced grain setting and grain weight (Mirosavljević et al., 2018). Also, increase of stay-green and grain filling period is often followed by decreased N remobilization to grain and grain protein content (Bingham et al., 2012). Therefore, further increase in grain weight would be also associated with changes in grain filling rate.

Conclusion

1. Grain yield improvement in six-rowed winter barley between 1972 and 2013 in the Pannonian Plain was strongly related with increased grain number per unit area (mainly grain number per spike), grain weight and harvest index during the studied period.

2. Genetic gain in grain weight was mainly the result of improvement in grain filling and maximum grain filling rate, while grain weight association with grain filling duration was less pronounced.

3. The increase in grain number per spike per year of cultivar release was followed by a positive trend in fruiting efficiency increase, while spike dry weight had no significant correlation with year of cultivar release.

4. Further improvements of six-rowed winter barley grain yield should be achieved by increasing both grain number per spike and grain weight, and maintaining high values of harvest index.

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Šešiaeilių miežių selekcijos pažanga grūdų pildymosi ir derliaus komponentų aspektu

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Santrauka

Tyrimo tikslas – kiekybiškai įvertinti šešiaeilio žieminio miežio (*Hordeum vulgare* L.) selekcinę pažangą pagal grūdų derlių ir nustatyti derliaus komponentų kiekybinius pokyčius bei grūdų pildymosi savybes tręšiant azotu (N) pagal du variantus: 0 kg ha^{-1} N (0N, kontrolinis) ir 100 kg ha^{-1} N (100N). Lauko eksperimentas su šešiaeilių žieminių miežių veislėmis buvo vykdytas du auginimo sezonus (2015–2016 ir 2016–2017 m.) Pietų Panonijoje (Novi Sad, Serbija). Dėl veislės genetinių savybių grūdų derliaus padidėjimas per metus buvo 0,055 t ha^{-1} esant 0N tręšimui, o tręšiant 100N – 0.061 t ha^{-1}. Tai rodo, kad šiuolaikinių veislių žieminiai miežiai azoto trąšas panaudoja efektyviau nei senųjų veislių. Grūdų derliaus pažanga labiausiai buvo susijusi su grūdų skaičiumi iš ploto vieneto, grūdų skaičiumi varpoje, 1000 grūdų mase ir derliaus indeksu. Nustatytas teigiamas priklausomumas tarp grūdų užmezgimo efektyvumo ir veislės sukūrimo metų. Priklausomai nuo veislės sukūrimo metų, varpų sausosios masės pokyčiai žydėjimo tarpsniu nebuvo reikšmingi. Dėl selekcijos įtakos 1000 grūdų masės padidėjimas buvo labiau susijęs su grūdų pildymusi ir maksimaliu grūdų užpildymo greičiu, o ryšys su grūdų pildymosi trukme nebuvo žymus.

Siekiant gausesnio šešiaeilių žieminių miežių grūdų derliaus, reikėtų didinti 1000 grūdų masę ir grūdų skaičių varpoje, išlaikant aukštas derliaus indekso vertes.

Reikšminiai žodžiai*:* *Hordeum vulgare*, genetinis indėlis, grūdų derliaus didinimas, derliaus komponentai, azotas.