Cereal Research Communications 46(4), pp. 697–706 (2018)
DOI: 10.1556/0806.46.2018.036
Published Online: August 16, 2018

Grain Filling Variation in Winter Wheat, Barley and Triticale in Pannonian Environments

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(Received 20 March; Accepted 13 April;
Communicated by T. Harangozó and M. Taylor)

Knowledge about the comparative development and grain filling of winter cereals under different environmental conditions is important for stable and high yielding crop production. The objective of this work was to compare patterns of grain filling in bread wheat, barley and triticale grown in the Pannonian region, as well as to investigate relationships among grain filling parameters, time to anthesis and grain yield. The trials with 12 winter cereal genotypes were carried out in four successive seasons at the location Novi Sad, Serbia. Results of this study showed that all studied grain filling parameters were significantly influenced by species, cultivar, growing season, and species by growing season interaction. Longer duration of grain filling period and period to maximum grain filling were observed in triticale and wheat cultivars compared with six and two-rowed barley. Two-rowed barley cultivars had a higher grain filling rate than other cultivars. Furthermore, a negative association between time to anthesis and grain yield indicates that cultivars with the long pre-anthesis period are not recommended for the agro-ecological conditions of the Pannonian plain. Generally, medium early cultivars of small grain cereals had the highest grain weight within species and spike type, suggesting that medium early cultivars have a balanced ratio of pre-anthesis and grain filling period. High values of final grain weight in different growing seasons indicate that weather conditions in the Pannonian plain are mainly suitable for grain growth.

Keywords: cultivar, grain filling rate, grain filling duration, time to anthesis, winter cereals

Introduction

Serbia is one of the most important winter-cereal growing regions in the Pannonian Plain. Similarly to other regions of the Pannonian plain, such as Romania, Hungary and Croatia, wheat and barley are two of the most important winter cereals in the rain-fed system of northern Serbia, with a five-year average harvested area over 500,000 ha and 90,000 ha, respectively (FAOSTAT 2014). In addition to barley and wheat, triticale represents a less

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important or alternative small grain cereal, grown in unfavorable environments or low input systems. As the market demands shifted, winter triticale gradually gained in importance and the crop cultivation area has had a steady annual increase over the past decades (McGoverin et al. 2011). In cereals, grain number per unit area and grain weight represent two major grain yield components (Cossani et al. 2011). Although grain yield of major cereal crops is more correlated with grain number per unit area (Peltonen-Sainio et al. 2007), high and stable yields are often positively associated with increased grain weight (Pržulj et al. 2012; Sun et al. 2017). Grain weight is defined by two major parameters: rate and duration of grain filling. In the Pannonian plain, especially in spring cultivars, grain filling frequently occurs in unfavorable environments/seasons characterized by high temperature and limited water supply at the end of the grain filling period (Pržulj et al. 2015). Influence of high temperature and/or water deficit on grain filling parameters has been well documented (Voltas et al. 1999; Dias and Lindon 2009). Numerous studies have reported that the duration of the grain filling period is more affected by environmental factors than the grain filling rate (Tiwari et al. 2012; Gonzales et al. 2014). Furthermore, presence of genetic variability of developmental patterns among winter cereal crops and genotypes, including rate (Brdar et al. 2008; Koutroubas et al. 2014) and duration (Borràs et al. 2009; Jocković et al. 2014) of grain filling period, enables the development of different genotypes in a wide range of environmental conditions.

In addition to the grain filling period, time to anthesis and duration of pre-anthesis developmental phases have been recognized as important traits that allow adjustment of crop phenology with the available resources for grain growth (Reynolds et al. 2009). In temperate environments, including the Pannonian plain, the time to anthesis should occur late enough to avoid late frosts in the spring, and early enough to ensure that grain filling occurs before high temperatures and drought becomes too severe (Ceccarelli et al. 1989). Manipulation of cultivar phenology and time to anthesis could increase spike fertility and therefore represent a major breeding objective (Sanna et al. 2014).

Considering that triticale has expanded rapidly in the past three decades in Serbia and surrounding regions, there is still lack of information about the comparative development and grain filling of triticale and widely grown cereals (wheat and barley). Therefore, the main objectives of the present study were to (i) investigate genetic variability, and compare patterns of grain filling and its parameters in bread wheat, barley and triticale grown in the Pannonian plain; and (ii) to investigate relationships among the grain filling parameters, time to anthesis and grain yield.

Materials and Methods

Experimental design

The trials were conducted during four growing seasons (2008/09–2011/12) in Rimski Šančevi Experimental Station of Institute of Field and Vegetable Crops, Novi Sad, a typical location within the Pannonian plain cereal production area in northern Serbia. Soil type of the experiment location was characterized as a non-carbonate chernozem, with soybean as a previous crop in each experimental season. The trials were arranged in a randomized complete block design with three replications in plots of 12 m^2. Each experimental plot was divided into two equal subplots, where one was used for destructive sampling and the other left intact for assessment of grain yield. Standard agricultural practices were conducted in each season. All trials were fertilized in doses consistent with good agricultural practice, based on soil agrochemical analysis. Pests and diseases were prevented or controlled by spraying recommended fungicides and insecticides, and weeds were periodically removed by hand. No artificial irrigation was applied.

Experimental material consisted of 12 winter cereal cultivars. The winter cereal genotypes were selected from the collection of cultivars widely grown in Serbia and other countries. Each species was represented by three cultivars divided into three maturity groups (E-early, ME-medium and L-late) in order to include a wide range of variability in developmental patterns. Two-rowed winter barley cultivars (NS 525 – E, NS 565 – ME, Monaco – L), six rowed winter barley cultivars (Dorat – E, Nonius – ME, NS 150 – L), winter wheat cultivars (Prima – E, Pobeda – ME, Diplomat – L) and winter triticale (Odisej – E, NS tritikale – ME, Garne – L) were sown in each growing season.

Data recording and analyses

The anthesis was recorded on each plot and expressed as the growing degree days (GDD) from emergence to anthesis. By definition, anthesis occurs when the central florets have shed their pollen (Zadoks stage 61). On that date, 150 main spikes per plot with visible anthers were tagged and three from each plot were randomly sampled twice a week, beginning 10 days after anthesis until harvest maturity. To determine dry weight, ten grains were removed from the middle of each of the three spikes and oven dried at 70 °C for 48 h. Dry matter accumulation was expressed as function of accumulated GDD from anthesis. Accumulated GDD was calculated as $GDD = \sum((T_{max} + T_{min})/2 - T_b$, where T_{max} is maximum daily temperature, T_{min} is minimum daily temperature, and T_b is the base temperature (0 °C). The limits for the maximum and minimum temperatures were established at 37 °C and 0 °C, respectively (Gallagher 1979).

Grain dry weight data were fitted to the logistic curve (Darroch and Baker 1990). The logistic curve was calculated by $Y = W/(1 + e^{B-Cx})$, where Y is the estimated dry grain weight, x is the time from anthesis calculated in growing degree days, W is the maximum grain weight, and B and C are empirical coefficients derived from the adjustment. The parameters of the grain filling curves were determined for each plot. Final grain weight (FGW) was expressed in mg. Grain filling duration (GFD) was considered to be the time in accumulated GDD required for grain weight to reach 0.95FGW. Grain filling rate (GFR) was calculated as ratio of FGW and GFD. The maximum rate of grain filling was mathematically determined from the curve parameters ($MGFR = (C \times FGW)/4$), and expressed as mg of grain GDD^{-1}. Time to maximum grain filling rate (TMGFR) was calculated from time to anthesis to the maximum grain filling rate and expressed in GDD. Grain yield was determined at maturity after mechanical harvesting of the intact plots.

Studied data were subjected to a combined analysis of variance, treating the growing season as the main plot and the species as the sub-plot. The cultivars were nested within species. Means were compared using the Tukey test ($P < 0.05$). Principal component analysis (PCA) was performed on the correlation matrix, calculated on the mean data of studied cultivars across environments. All analyses were performed in STATISTICA 10.

Results

Weather conditions

Weather data were collected from the meteorological station located at the experimental field (Fig. S1a and S1b). Climate conditions, especially the amount and distribution of precipitation and average daily temperature, varied remarkably across the growing seasons. Grain filling took place mainly in June and coincided with the relatively warm weather. Average daily temperatures were slightly higher for the cultivars with late anthesis date. Air temperatures prior to anthesis and from anthesis to maturity were similar in 2008/09, 2009/2010, and 2010/11. Temperatures during grain filling in 2011/12 were higher compared to those recorded in the first three seasons. Furthermore, total precipitation during crop growth cycle was 470 mm, 812 mm, 445 mm, and 400 mm in the 2008/09, 2009/10, 2010/11, and 2011/12 growing season, respectively. A higher level of precipitation during the period after anthesis was recorded in seasons 2008/09 and 2009/10 compared to seasons 2010/11 and 2011/12.

Time to anthesis and final grain weight

The grain-filling parameters calculated by fitting the data of grain weight into the logistic model (Daroch and Baker 1990) are shown in Table S1–S3*. The values of R^2 coefficient for the fitted curve derived from the model (data not shown) were in most cases higher than 98%, indicating that grain growth was appropriately described by the logistic equitation.

The final grain weight (FGW), estimated from the logistic curves, was significantly affected by the species, cultivar, growing season and $S \times GS$ interaction (Table S1). Across growing seasons, winter triticale genotypes had higher FGW than barley and wheat (Table S2). Averaged over species, the FGW was highest in 2009/10, and lowest in 2008/09. The cultivar with the overall highest FGW was NS Tritikale (56.13 mg), followed by Garne, Odisej and two-rowed winter barley cultivars NS 565 and Monaco (Table S3). All studied two-rowed winter barley cultivars had higher FGW compared to six-rowed cultivars. Furthermore, the lowest FGW was recorded in early wheat variety Prima (41.09 mg) and late wheat variety Diplomat (41.38 mg).

Cultivars differed significantly in the duration of time to anthesis. Although two-rowed winter barley had shorter duration of pre-anthesis period than the six-rowed (Table S2), there was no significant difference between cultivars that belong to the same maturity

*Further details about the Electronic Supplementary Material (ESM) can be found at the end of the article.

group Table S3). On average, the highest duration of pre-anthesis period was recorded in 2011/12, and the shortest in 2010/11. The range in the duration of time from emergence to anthesis (TA) among cultivars was from 1003 GDD to 1331 GDD. The late wheat variety Diplomat had the longest period to anthesis. On the other hand, the early two-rowed barley cultivar NS 525 and the early triticale cultivar Odisej were characterized by the shortest TA.

Period to maximum grain filling rate and grain filling duration

Variation in the duration of the period to maximum grain filling rate (TMGFR) and maximum grain weight (GFD) was mainly influenced by species and environmental conditions (Table S1). Across growing seasons, triticale cultivars had a higher duration of the grain-filling period than barley and wheat (Table S2). The shortest GFD for each species was recorded in the 2011/12 growing season. There was no significant difference in GFD among triticale cultivars (Table S3). The shortest GFD was recorded in the two-rowed barley cultivar

Monaco (650.4 GDD) followed by the remaining two-rowed and six-rowed barley cultivars. Also, triticale consistently needed longer periods to reach maximum grain filling rate in each growing seasons, reaching a peak of 396.4 GDD in 2008/09, while the shortest duration was recorded in two-rowed barley cultivars.

Maximum grain filling and grain filling rate

Variation in maximum grain filling rate (MGFR) was significantly affected by all factors, species, cultivar, growing season, and S × GS interaction, with the highest contribution of the species (Table S1). The values of MGFR calculated by the model were highest in 2011/12 for each species (Table S2). There was no significant difference in MGFR between wheat and six-rowed barley cultivars (Table S3). The late triticale cultivar Garne showed the highest maximum grain filling rate across growing seasons. Grain filling rate (GFR) depended mainly on the species, but the effect of the growing season, interaction between the growing season and species, as well as the cultivars, also had significant influences on the grain filling rate. On average, two-rowed winter barley cultivars had the highest, while wheat cultivars had the lowest GFR in each season. Across cultivars, the highest GFR was recorded in 2011/12. Among the two-rowed winter barley cultivars, the highest GFR was reported in the late cultivar Monaco. There was no significant difference in GFR between triticale and six-rowed barley cultivars (Table S3).

Trait associations

The biplot of the principal component analysis (PCA) illustrates the relationships between the means of the following variables, date of anthesis, grain filling parameters, and yield (Fig. 1). Together, both axes accounted 81.32% of the total variation in the data.

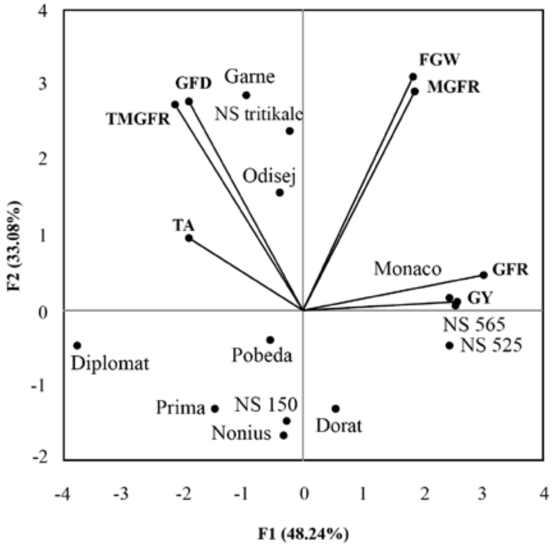

Figure 1. PCA analysis of trait association (Final grain weight – FGW. Time to anthesis – TA. Grain filling duration – GFD. Time of maximum grain filling rate – TMGFR. Maximum grain filling rate – MGFR. Grain filling rate – GFR. Grain yield –GY) in winter barley, wheat and triticale across four growing seasons

According to the biplot, PCA1 relates predominantly to GFR and GY, while PCA2 was mostly related to MGFR and FGW.

TA, GFD and TMGFR were negatively associated with GY and GFR. TA had the shortest vector length, indicating a lower influence in relation to the other studied traits. Further, MGFR and GFR were in positive association with FGW. PCA showed that GY had a weak positive relationship with FGW. The distribution of the points represents the means of the studied cultivars across the growing seasons. The biplot for this data showed that wheat cultivars had lower, while two-rowed barley had higher GFR than other crops. Six-rowed barley had lower and triticale had higher values of TMGFR and GFR.

Discussion

Grain development and filling is a complex physiological process, involving the growth of both the endosperm and the embryo. Assimilates for grain growth are provided by current photosynthesis and remobilization of temporarily deposited reserves in the vegetative parts (Barraclough et al. 2014). Different models can be used to describe many crop and soil processes, including grain filling (Archontoulis and Miguez 2015). In our study, logistic nonlinear equation was used to estimate grain filling parameters of different cereal crops grown in the Pannonian climate. According to our investigation high values of coefficient of determination, exceeding 0.96 in all cases (data not shown), indicate that the logistic curve provided a good fit to the grain filling data for all 12 winter cereal cultivars grown across four growing seasons.

Rate and duration of grain filling (GFR and GFD) and other parameters obtained from the logistic curve (MGFR and TMGFR) are commonly used to describe the complex nature of this process. In our research, all studied grain filling parameters were significantly influenced by species, cultivar, growing season, and species by growing season interaction. In general, triticale and wheat cultivars had longer duration of grain filling period and period to maximum grain filling compared with six and two-rowed barley. Furthermore, two-rowed barley cultivars had higher grain filling rate compared to wheat, triticale and six-rowed barley. Our data confirm the findings of different studies which state that barley has shorter grain filling duration than wheat (Cossani et al. 2011) and triticale (Royo et al. 1997). In 2011/12, cultivars had lower values of GFD and TMGFR and higher values of GFR and MGFR, which could be the result of higher temperatures during the grain filling period in this season. It was widely accepted that high temperatures decrease the duration and increase the rate of grain filling (Dias and Lindon 2009). Moreover, Semenov et al. (2009) found that increased duration of the grain filling period is favorable only when terminal stress is escaped.

Generally, medium early small grain cultivars – triticale (NS Tritikale), wheat (Pobeda), two-rowed (NS 565) and six-rowed barley (Nonius) had the highest grain weight within species and spike type, suggesting that medium early cultivars have a balanced ratio of pre-anthesis and grain filling period. Additionally, Borràs et al. (2009) emphasized the importance of adjustment of crop developmental phases for the achievement of increased grain weight and grain yield. Despite the presence of significant variation across growing seasons, the final grain weight was relatively stable and ranged from 47.19 mg (2008/09) to 51.30 mg (2009/10). These results confirm the findings of different studies (Sadras 2007; Griffiths et al. 2015) where FGW displayed low levels of variability in relation to other traits. Even in the season 2011/12, characterized by increased temperature during grain filling, cultivars had high values of FGW, which were mainly the result of increased GFR and MGFR. Furthermore, translocation of assimilates accumulated in vegetative tissues prior to anthesis can significantly contribute grain development (Mirosavljević et al. 2015), both in favorable and unfavorable environmental conditions (Koutroubas et al. 2014).

It was observed that FGW were closely associated with GFR and MGFR, while the association between FGW and GFD was near zero. These data are consistent with previous studies (Jocković et al. 2014; Xie et al. 2015), indicating that the rate of synthesis of storage products in the growing grain is more important than the duration of this period. Presence of a negative correlation between GFD and GFR, that was also reported in other studies (Wang et al. 2009; Jocković et al. 2014).

Variation in the duration of pre-anthesis was influenced by the cultivar, growing season and S × GS interaction. On average, two- and six-rowed barley cultivars had shorter periods from emergence to anthesis than wheat and triticale. The presence of high genotypic variation, that could be successfully used to adjust development patterns and selection of appropriate cultivars to particular environments, has also been reported in different cereal crops (Blum 2011; Pržulj et al. 2012). According to the PCA biplot, the time to anthesis was negatively associated with grain yield and GFR, indicating the importance of earlier beginning of grain filling. The differences in time of anthesis resulted in the untimely occurrence of the second half of grain filling of late cultivars, under the conditions of higher temperatures when grain growth and yield can be reduced even with full irrigation (Pradhan et al. 2012). Nevertheless, Mirosavljević et al. (2015) stated that cultivars with early anthesis had lower yield potential, mainly as a result of shorter pre- and post-anthesis development.

The results of the present study indicate that growing season, species, cultivar, and S × GS interaction significantly influence the studied grain filling parameters. High values of FGW in different growing seasons indicate that weather conditions in the Pannonian plain are mainly favorable for grain growth. Generally, wheat and triticale had later time of anthesis than the barley cultivars, and needed longer periods to reach MGFR and FGW. Further, a negative association between the time to anthesis, and grain yield and GFR indicates that cultivars with the long pre-anthesis period are not recommended for the agro-ecological conditions of the Pannonian plain. Medium cultivars had the highest final grain weight because of the suitable duration of the pre-anthesis and grain filling periods, which enable appropriate vegetative and grain development and growth, and escape from high temperatures at the end of the growth cycle. Furthermore, the presence of the observed genotypic variation indicates that breeding for higher GFR and MGFR in different winter cereals should enable the development of new cultivars characterized by higher grain weight and yield.

Acknowledgements

This paper presents the results of the project TR-31066 “Modern breeding of small grains for present and future needs”, supported by the Ministry of Education, Science and Technological Development of the Republic of Serbia.

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Electronic Supplementary Material (ESM)

Electronic Supplementary Material (ESM) associated with this article can be found at the website of CRC at https://akademiai.com/loi/0806

Electronic Supplementary *Table S1*. ANOVA for the analyzed traits (final grain weight – FGW; time to anthesis – TA; grain filling duration – GFD; time to maximum grain filling rate – TMGFR; maximum grain filling rate – MGFR; grain filling rate – GFR)[a]

Electronic Supplementary *Table S2*. Mean final grain weight (FGW), time to anthesis (TA), grain filling duration (GFD), time to maximum grain filling rate (TMGFR), maximum grain filling rate (MGFR) and grain filling rate (GFR) of two-rowed barley, six-rowed barley, wheat and triticale averaged in four growing season

Electronic Supplementary *Table S3*. Mean final grain weight (FGW), time to anthesis (AD), grain filling duration (GFD), time to maximum grain filling rate (TMGFR), maximum grain filling rate (MGFR) and grain filling rate (GFR) of two-rowed barley, six-rowed barley, wheat and triticale, wheat and triticale cultivars averaged over four growing seasons

Electronic Supplementary *Figure S1*. Monthly average temperature (a) and precipitation (b) during the four growing seasons (2008/09–2011/12)