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CULTIVAR AND YEAR EFFECT ON GRAIN FILLING OF WINTER BARLEY

ABSTRACT

Kernel weight and grain yield depend on the rate and duration of grain filling (GF). Rate of GF represents the rate of dry matter accumulation per kernel and GF period duration from anthesis to physiological maturity. In order to study the relationships among grain yield and yield components and the rate and duration of GF in winter barley, field experiments were conducted during the 1995-1998 period. A quadratic polynomial was used to describe the relationship between kernel weight and time from anthesis and a linear equation to describe the relationship between kernel water content and time from anthesis. Accumulated growing-degree days (GDD) from anthesis were used as a time scale. The rate and duration of GF were obtained from the fitted curve. Depending on the cultivar and year, rate of GF ranged from 0.058 to 0.082 mg \times kernel⁻¹ \times GDD⁻¹ and the duration of GF from 505 to 887 GDD. Rate positively (r=0.70) and duration of GF negatively $(r=-0.57)$ effected grain yield. Both rate and duration of GF to a large extent were influenced by environmental factors. The correlation between rate and duration of GF was negative. The positive correlations between the rate of GF and kernel weight as well as kernel weight and yield enable indirect selection for yield and a high rate of GF via breeding for a larger kernel.

Key words: correlation, grain filling, Hordeum vulgare, winter barley, yield

INTRODUCTION

After spike number and kernel number per spike have been determined during the vegetative phase, cereal grain yields become proportional to kernel weight, which is a function of the rate and duration of grain filling (GF) (Wiegand and Cuellar 1981). The GF is the result of the translocation of photosynthate from source to kernels. Rate of GF represents the rate of dry matter accumulation per kernel during the period of GF. The GF period represents the duration from anthesis to physiological maturity. Physiological maturity represents the point at the end of GF beyond which there is no significant increase in kernel dry matter.

Rate of GF depends on the number of endosperm cells formed during the first two weeks after anthesis (Brocklehurst 1977) and, to a lesser extent, on increased temperature in that period (Sofield et al. 1997a, 1977b).

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Duration of GF is in strong negative correlation with temperature (Spiertz 1977, Wardlaw et al. 1980, Wiegand and Cuellar 1981, Wych et al. 1982, Van Sanford 1985, Stapper and Fischer 1990). Lengthening of the duration of GF can be achieved through the selection of genotypes that have earlier anthesis (Metzger et al. 1984) or genotypes that are relatively insensitive to high temperatures and continue photosynthesis under high temperature conditions (Van Sanford 1985). Genetic factors to a large extent determine the rate of GF, and environmental factors, first of all temperature to a large extent determine duration of GF (Wardlaw et al. 1980, Van Sanford 1985, Bruckner and Frohberg 1987, Campbell et al. 1990, Triboi 1990, Hunt et al. 1991). An increase in temperature up to a certain point does not negatively affect yield, since the intensification of physiological processes can compensate for the shortening of GF (Sofield et al. 1977b). Longer duration of high temperature reduces GF period to such a large extent that faster rate of GF cannot prevent yield losses (Wardlaw et al. 1980). When duration of GF is severely limited by temperature, final kernel weight is proportional to the rate of GF (Wiegand and Cuellar 1981).

Investigations have shown the existence of genetic variation for both the rate and duration of GF within different species (Daynard et al. 1971, Nass and Reiser 1975, Sofield et al. 1977a, Gebeyehou et al. 1982, Dofing and Knight 1994). Sofield et al. (1977a), Fussell and Pearson (1978), and Darroch and Baker (1990) found that high kernel weight in wheat is associated with intensive rate of GF, while Wiegand and Cuellar (1981), Sayed and Gadallah (1983), and Wong and Baker (1986) emphasized the importance of duration of GF. Optimum temperature for wheat and barley kernel development is about 12-15°C. Each 1°C increase in mean daily temperature above the optimum temperature during GF decreased the period of filling by 3.1 days and reduced kernel weight by 3-5% or 2.8mg (Chowdhury and Wardlaw 1978, Wiegand and Cuellar 1981, Wardlaw et al. 1989).

Researchers have established that linear (Housley et al. 1982, Van Sanford 1985, Hunt et al. 1991, Gouis 1993, Takahashi et al. 1993), quadratic (Nass and Reiser 1975, Bruckner and Frohberg 1987) or cubic (Gebeyehou et al. 1982, Bauer et al. 1985) polynomial equations can describe GF. Suitable growth curve can be used to calculate the rate and duration of GF. In the literature many papers clarify GF in wheat (Sofield et al. 1977a, Chowdhury and Wardlaw 1978, Gebeyehou et al. 1982, Bruckner and Frohberg 1987, Darroch and Baker 1990), corn (Daynard et al. 1971, Cross 1975), and some other crops, while relatively few papers explain GF in barley (Metzger et al. 1984, Dofing and Knight 1994). The objectives of this study were to examine (i) effect of cultivar and year on rate and duration of GF, (ii) correlations between kernel growth characters and yield components, and (iii) kinetics of water during the GF process in winter barley.

MATERIALS AND METH°DS

Two two-rowed, Novosadski 183 and Astrid, and two six-rowed, Galeb and Botond, winter barley cultivars were used for investigations. The cultivars Novosadski 183 and Galeb were released by the Institute of Field and Vegetable Crops, Novi Sad, Yugoslavia. The cultivar Novosadski 183 was derived from the cross Ager/Emir and the cultivar Galeb from the cross L.2-89/NS.305. The cultivar Astrid was derived from the cross Weih.8264 (Malta-Emir-818-Tria) × Weih.5907 (4095-Malta) and released by BPZ/Dörfler, Germany. The cultivar Botond was selected from the cross KFD-4/K-79-4 and released by the Agricultural Research Institute GATE "Fleischmann Rudolf" Kompolt, Hungary. Novosadski 183 is the leading winter malting barley cultivar in Yugoslavia and it is grown on more than 50% of acreage sown with this crop. Astrid is a German cultivar with good agronomic performance in the Yugoslav environmental conditions. The six-rowed cultivars Galeb and Botond are new cultivars with good and stable grain yield. These four cultivars were grown in the field at Novi Sad from 1994/95 till 1997/98 in two identical trials with three replications for each trial in all the studied years. Each trial followed a fertilized crop of soybean and fertilized with 45 kg N \times ha⁻¹, 45 kg P₂O₅ \times ha⁻¹, and 45 kg K₂O \times ha⁻¹ at sowing. The cultural practices applied were those regularly used for large-scale winter barley production (Przulj and Momcilovic 1998). The first trial was used for GF parameters determination and the second for yield and yield components determination. Rate and duration of GF and the yield parameters were estimated for each replication during the four years. The trials were sown on non-calcareous chernozem soil at Novi Sad (45°20 N, 15°51 E, 86 m asl) on 15 October 1994, 20 October 1995, 12 October 1996, and 17 October 1997 at a planting rate of 350 viable seeds per square metre, in two identical trials with three replications. Plots were 5m long and consisted of 6 rows, 20 cm apart.

At anthesis 60 main spikes from each plot of the first trial that flowered on the same day were tagged. Samples of four tagged spikes were collected from each plot at 3-4 day intervals beginning about 5-10 days after anthesis and continuing past harvest maturity. Spikes were weighed immediately after sampling, oven-dried at 70 C for 48h to water content determination, then hand thrashed in bulk to determine average kernel dry weight. Accumulated growing-degree days (GDD) from anthesis were used as the time scale. Daily degree-days were calculated as

$$
T_n = \frac{(T_7 + T_{14} + 2 \times T_{21})}{4}
$$

where T_7 , T_{14} , and T_{21} are temperatures at 7 a.m., 14 p.m. and 21 p.m., respectively. Rate of GF was expressed as milligrams per kernel per GDD.

The relation between kernel weight and accumulated GDD from anthesis for each plot was presented by fitting a quadratic polynomial

$$
W = a + bt + ct^2
$$

where W is kernel dry weight (mg) , t is time (GDD) from anthesis and a, b , and c are regression coefficients. The instantaneous rate of grain filling dW/dt can be calculated from the derivative of the polynomial (Nass and Reiser 1975, Gebeyehou et al. 1982).

$$
\frac{dW}{dt} = b + 2ct
$$

When kernel weight has reached its maximum then $dW/dt=0$. Solving for t in $dW/dt=0$ gives t_2 as the estimated point of the end of GF duration. Anthesis, i. e. beginning of GF (t_1) calculated for W=0 and predicted GF duration obtained as t_2-t_1 . The average of GF rate in the interval from t_1 to t_2 can be defined (Radford 1967) as

$$
\frac{1}{\left(t_2-t_1\right)\int_{t_1}^{t_2} \left(dW_{dt}'\right)dt} = \frac{W_2-W_1}{\left(W_2-t_1\right)}\left(\frac{W_2-W_1}{t_2-t_1}\right)
$$

where W1 and W_2 are the predicted kernel weights at times t_1 and t_2 . Mean rates of GF were estimated as predicted maximum grain dry weight divided by duration of GF. The relation between kernel water proportion and accumulated GDD from anthesis for each plot was presented by fitting a linear equation

$$
M = a + bt
$$

where M is percentage of kernel moisture content, t is time (GDD) from anthesis and a and b regression coefficients. For percentage of kernel moisture content arc $sin \sqrt{percentage}$ transformation was used.

Grain yield, productive tiller density per square meter, kernel number per spike, and kernel weight were determined for each plot and year in the second trial. Analysis of variance for each character was conducted. The trial was calculated by using MASTAT-C program (Crop & Soil Sciences Dept., Michigen St. Univ.) Variance components were estimated using expected mean squares to compare the relative magnitude of main effect and interaction variances (Comstock and Moll 1963), while the percentage of the variability which they accounted for was calculated according to Borojević (1990). Simple and path correlation coefficients among the estimated GF parameters and associated agronomic characters were calculated.

RESULTS AND DISCUSSION

The quadratic polynomial, used to describe kernel growth from anthesis to physiological maturity, provided a good description of GF for the studied cultivars. Kernel weight and GDD data have fitted the model well and r^2 values exceeded 0.97 in all cases (Fig. 1). Only for the cultivar Botond in 1997 the linear equation gave a better description of GF for all three replications, with r^2 value higher than 0.97 (Fig. 1d). In the cultivar Novosadski 183, the rate of GF ranged from 0.071 mg \times kernel⁻¹ \times GDD⁻¹ in 1995 and 1996 to 0.080mg \times kernel⁻¹ \times GDD⁻¹ in 1997. The rate of GF dynamics in 1995 and 1996 were approximately the same up to the kernel weight of about 20-25mg, or 300 GDD (Fig. 1a) despite the difference of 6.7° C (-3.1 $^{\circ}$ C in 1995 and +3.6 $^{\circ}$ C in 1996) in mean daily temperatures during the period (Table 1). The reason for the equal rate of GF values in the first half of the GF stage in these two ecologically different years was that in 1996 the initial GF stage was shortened due to high temperatures and the plants entered the early GF stage quickly, whereby later flowering was compensated for. The increase of kernel weight in the second half of the GF stage was more rapid in 1996 than in 1995, so the yield and kernel weight were higher in 1996 (Table 2). The GF curves for Novosadski 183 were almost identical in 1997 and 1998 (the duration of GF was 568 GDD in 1997 and 626 GDD in 1998) (Table 2). High mean daily temperatures in the second ten-day period of May, 1997 (+4.9 relative to the long-term average) speeded up the process of GF, which is why in this cultivar the rate of GF was higher in 1997 than in 1998. In 1997, flowering started seven days later, so the sum of GDD was lower and the rate of GF about 10% higher than in 1998. The yield in the year with later flowering and faster GF was higher than in the year with earlier flowering and slower GF, although the difference was not statistically significant (Table 2).

In the cultivar Astrid, the rate of GF ranged from 0.068 mg \times kernel⁻¹ \times GDD^{-1} in 1996 to 0.082 mg \times kernel⁻¹ \times GDD⁻¹ in 1997. The GF models in 1995 and 1998 were identical (Fig. 1b), although the two years differed with regard to the temperature deviation from the long-term average (Table 1). In both years, flowering occurred on May 5 and there was no significant difference between the rate of GF, GF duration, yield, and number of spikes per m^2 (Table 2). The larger kernel size in 1998 than in 1995 was a result of the compensatory relations between kernel weight, spike number, and grain number per spike (Rasmusson and Cannell 1970). In 1996, the rate of GF was the lowest and the duration of GF the longest (778 GDD). In 1997, on the other hand, GF was the fastest but also the shortest, with the highest yield and largest 1000-kernel weight (Table 2).

The rate of GF in Galeb ranged between 0.058 mg \times kernel⁻¹ \times GDD⁻¹ in 1998 and $0.080 \text{ mg} \times \text{kernel}^{-1} \times \text{GDD}^{-1}$ in 1997 (Table 2). The rates of GF in 1995 and 1997 were similar, while the duration of GF in 1997 was 76 GDD, or about five days, longer than that in 1995. The longer duration of

Fig. 1 Effect of year on rate and duration of grain filling (GF) in four winter barley cultivars

Fig. 1 Continued

| Year | Date of anthesis | | | | $1 - 10$ | Dev. from | $11 - 20$ | Dev. from | $21 - 31$ | Dev. from | $1 - 10$ | Dev. from |
|------|------------------|--------|--|---|-----------------------------|---------------------------|-----------------------------|---------------------------|---------------------|---------------------------|----------------------|---------------------------|
| | NS183 | Astrid | | Galeb Botond | May \lceil °C \rceil | $long-$ term period | May \lceil °C \rceil | $long-$ term period | May \lceil °Cl | $long-$ term period | June \lceil °Cl | $long-$ term period |
| | | | | 1995 May 3 May 5 May 16 May 13 14.1 -1.3 19.2 | | | | -3.1 | -24.1 | 1.2 | 19.0 | 0.6 |
| | | | | 1996 May 10 May 13 May 17 May 16 18.9 | | $3.6\,$ | 20.0 | 3.6 | 16.3 | -0.8 | 22.5 | 4.1 |
| | | | | 1997 May 12 May 13 May 16 May 16 16.8 | | $1.5\,$ | 21.2 | 4.9 | 14.9 | -2.2 | 17.6 | -0.8 |
| | 1998 May 5 | May 5 | | May 11 May 11 15.4 | | 0.1 | $15.8\,$ | -0.5 | 16.8 | -0.3 | 23.0 | 4.6 |

Table 2. Means of yield components, grain filling parameters and rate of water release in four winter barley cultivars during four years

*LSD at a=0.05, **LSD at a=0.01

SN–number of spikes per m², KN– kernel number per spike, KW–1000–kernel weight [g], Y– yield
[kg × ha⁻¹], GFR– rate of grain filling [mg × kernel⁻¹ × GDD⁻¹], GFD– duration of grain fill– ing [GDD], WRR- rate of water release $[\%$ kernel⁻¹ × GDD⁻¹]

GF in 1997 was a result of lower temperatures in late May and early June, i. e. at the late stage of GF (period from the milk ripe stage till ces-

 $\left[\text{mag} \times \text{kerne} \right]^{-1} \times \text{GDD}^{-1}$], GFD- duration of grain filling [GDD]

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sation of photosynthesis) and final stage of GF (period from the cessation of photosynthesis till maturity). In 1998 in Galeb, GF was the slowest and lasted the longest (Fig. 1c). This was a result of an earlier flowering (5-6 days) relative to the other years as well as of lower temperatures in the first half of GF (Table 1).

The fastest rate of GF and shortest duration of GF in the cultivar Botond was recorded in 1997 (0.078 mg \times kernel⁻¹ \times GDD⁻¹ and 505 GDD, respectively). Temperatures at the late and final GF stages were moderate and did not represent a limiting factor for a longer GF. The shortening of duration of GF was due to high temperatures in mid-May and the shortening of the initial and early stages of GF. The slowest rate (0.065 $mg \times \text{kernel}^{-1} \times \text{GDD}^{-1}$ and longest duration of GF in Botond was recorded in 1996 (Table 2). High temperatures in 1996 at the late and final stages of grain filling did not shorten the duration of GF, so both the actual (the largest kernel weight obtained by measurement) and predicted (kernel weight in dW/dt=0) kernel weight were achieved at 850 GDD. In the other two years, the rate and duration of GF were in between those recorded in 1996 and 1997 (Fig. 1d).

Kernel water content and GDD fitted the linear model well, and the r^2 values generally ranged from 0.83 to 0.99 (data not shown). Only in two replicates for the cultivar Novosadski 183 r^2 was low (0.74 and 0.82). The rate of water release (WR) depended on the cultivar, year and cultivar x year interaction (Table 3). Two-rowed barley faster released water than six-rowed barley. The fastest WR was in 1995, 0.0570% kernel⁻¹ \times GDD⁻¹ and the slowest in the 1996, 0.0505% kernel⁻¹ \times GDD⁻¹.

The fastest rate of GF for all four cultivars and the shortest duration of GF in three cultivars were recorded in 1997. In that year rate of GF was about 0.080 mg × kernel⁻¹ × GDD⁻¹ and the duration of GF less then 600 GDD. Compared with the other years, 1997 was characterized by the very high mean daily temperatures in the early stages of the kernel development. High temperatures at flowering shortened the initial phase of GF and consequently duration of GF, but did not decrease the yield. Indeed, the highest yield and kernel weight where in this year, i. e. with high temperatures during early grain filling and moderate temperature in the relative short remainder of the GF stage, during which rapid filling of grain occurred. The significant contribution of the year to the GF rate is supported by the variance analysis data as well (Table 3). The influence of the cultivar on rate of GF was manifested through significant genotype x year interaction. Duration of GF was the shortest in the early two-rowed cultivar Novosadski 183 and the longest in the six-rowed cultivar Galeb. The longest duration of GF was in 1996 although in this year high temperatures in beginning and end of GF took place. It can be explained by specific reaction of each genotype to environment. This statement supported high C x Y interaction in total variability of duration of GF (Table 3). A large number of authors (Bruckner and Frohberg 1987, Campbell et al. 1990, Hunt et al. 1991), however, report finding the effect of the

cultivar to be the most important in the variance of rate of GF and that of year, i. e. environmental factors, in the case of duration of GF.

The variation of spike number per square metre and kernel number per spike depended on the cultivar, year and cultivar \times year interactions (Table 3). The contribution of the cultivar genotype for determination of these two characters was the most important and accounted more than 90% in total variation. Kernel size depended also on the main factors and their interaction likewise; the year contribution was the most important (Table 3).

Once the numbers of spikes per square metre and kernels per spike have been determined, cereal grain yield is proportional to kernel weight (Wiegand and Cuellar 1981), which is a function of the rate and duration of GF. The interrelationships of the estimated parameters of GF, from one side, and yield components and yield, from the other side, were described by the simple coefficient of correlation and path coefficient (Table 4). In our study, yield was positively correlated with the rate of GF, so the highest yield in all cultivars was recorded in the year with the highest rate of GF but also the lowest duration of GF. Path coefficient analysis gives different picture then does simple correlation analysis. Simple correlation between yield and duration of $GF (r=-0.57)$ gives the misleading impression the duration of GF had very strong negative influence on yield, whereas the path analysis expose no negative effects (Table 4). Path coefficient shows that direct effect of rate of GF does not have so strong influence on yield as simple correlation coefficient shows. The more prominent example for different meaning of these two coefficients is very strong direct effect of spike number per m² and kernel number per spike on yield (Table 4) obtained by path analysis, while simple correlation coefficient showed their insignificance in control of grain yield. The apparent different values between the two analyses come from the fact that these methods define different things. Simple correlation measures mutual association without regard to causation, the path analysis specifies the causes and defines their relative importance.

Although kernel number per spike forms during the vegetative stage and depends on the sensitivity of morphogenesis of generative organs during the process of ontogenesis, the final number is still determined at grain fill, since poorly filled grains are lost during combine harvesting and in fact do not represent yield at all. If the period of GF lasts longer, the less developed kernels may not complete the filling process due to a sudden rise in temperatures and diseases, which could explain the negative correlation between GFD and grain number per spike.

What is important for breeders is the state that the rate and duration of GF exerted an opposite influence on grain yield. The similar judgment in the investigation with six-rowed winter barley we have obtained in our previous paper (Pržulj et al. 2000). Since a favorable relationship existed between rate of GF and yield more emphasis should be placed on rate of

GF than on duration of GF. These conclusions may only be valid when applied to similar environments of growing.

The correlation between the rate and duration of GF was negative although most other authors (Sofield et al. 1977a, Wardlaw et al. 1980, Sayed and Gadallah 1983, Van Sanford 1985) report a lack of association. Bruckner and Frohberg (1987) found a strong negative environmental correlation between these two traits, which indicates that the environmental conditions favor a high rate and short duration of GF. Consequently, the relationships we obtained in the present study can be attributed to the strong negative environmental correlation. The breeding program on winter barley for the similar growing conditions should favor genotypes with a larger grain, a high rate of GF and a moderate to shorter duration of GF. Sofield et al. (1977a), Gebeyehou et al. (1982), Van Sanford (1985) and Darroch and Baker (1990) pointed out that high kernel weight is associated with a rapid rate of GF, while Nass and Reiser (1975), Gebeyehou et al. (1982) and Wong and Baker (1986) reported positive correlations between an effective filling period and grain yield. Indeed, during the latter part of GF, genotypes with a long duration of GF may enter a period of high temperatures (Pržulj and Momčilovič 1998), which may significantly reduce yields and grain quality. The duration of the vegetative and generative phases should be balanced, since neither too early nor too late a flowering will bring maximum yields. The choice of genotypes with a high rate of GF whose developmental dynamics are suitable for particular growing conditions represents a safer way to develop stable, adaptable and high-yielding cultivars.

CONCLUSIONS

Earlier flowering and lower temperatures after anthesis effect lower rate and longer duration of GF. Shortening of GF duration is due to high temperatures during the first half of GF, while temperatures at the second half do not represent a limiting factor for kernel weight and grain yield.

Negative correlation exists between rate and duration of grain filling that have an opposite effect on grain yield. In semiarid conditions of growing environment favors a higher rate and shorter duration of GF, i. e. cultivars with faster rate and shorter duration of GF give higher yields.

Good ideotype of barley for semiarid conditions would be a cultivar with a higher rate and moderate duration of GF and larger grain.

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