VARIABILITY OF GRAIN FILLING PARAMETERS IN WHEAT GENOTYPES OF DIFFERENT EARLINESS

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ABSTRACT: Final grain dry weight (W) is dependent on the two parameters: rate (R) and duration (T) of grain filling. The study was undertaken to compare W with R and T in four groups of genotypes which are different in earliness, and control group of high – yielding NS cultivars. A logistic equation was used for estimation W, R and T. Stepwise multivariate analysis showed differences between groups for all three estimated parameters. Groups with the highest grain dry weights had high maximum rates and short durations of grain filling in common environment. In unfavorable environment long grain filling duration had adventage.

Key words: wheat, grain filling duration, grain filling rate, earliness

INTRODUCTION

Grain yield of wheat (*Triticum aestivum* L.) depends on number of grains per unit area and grain weight. Final grain weight is a product of grain filling process, which can be described by two parameters: rate and duration. Although both of them are influenced by genotype and environment (Gebeyehou et al. 1982, Bruckner and Frohberg 1987), it is generally accepted that genetic factors largely determine grain filling rate and environmental factors (temperature) largely determine grain filling duration (Hunt et al. 1991). However, some authors suggested stronger relations between grain weight and duration than with rate of grain filling (eg. Evans et al. 1975), and the others (Whan et al. 1996, Calderini and Reynolds 2000) favor grain filling rate. Gebeyehou et al. (1982) found positive connections between both grain filling parameters and grain yield. Although grain filling can be described with quadratic (Bruckner and Frohberg 1987) and cubic (Gebeyehou et al. 1982) equation or with linear regression (Van Sanford 1985), it seems that multivariate analysis of variance (MANOVA) of nonlinear regression estimated parameters, suggested by Darroch and Baker (1990), is more appropriate aproach. The use of stepwise MANOVA (Keuls and Garretsen 1982) provides the identification of the relative importance of this various parameters in a growth curve. The objective of this study was to compare grain weight with rate and duration of grain filling in four groups of genotypes which are different in earliness, and control group of high – yielding NS cultivars. Development of early cultivars possessing optimal duration and rate of grain

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filling is one of the goals of wheat breeding in Vojvodina (Kobiljski et al. 2000), and the results of this study can be used in this efforts.

MATERIALS AND METHODS

16 wheat genotypes were used in this study. 12 genotypes were selected in four groups: extra early (Vrn 7, Vrn 8, Vrn 9), medium early (Lerma Rojo, Inia 66, Argentina 80/5216), medium late (Bankut 1205, Phoenix, Odeska 51) and late (F 54 – 70, Purdue 5392, Stepnjačka 30). The fifth (control) group was made of 4 high – yielding NS cultivars: Pobeda, Renesansa, Evropa 90, Sonata. The trial was conducted at the experimental field Rimski Šančevi, Institute of Field and Vegetable Crops, Novi Sad, in 2001 and 2002. The plot areas were $5m^2$ and each of them was sown in a four replications. The standard agrotechnic procedures were applied. Rimski Šančevi meteorological station data (temperature, precipitation) were used. Sampling was initiated 14 days afther anthesis and continued at 7 – days intervals in first 3 weeks, and approximately 2 – days intervals after, until maturity (13% moisture in grain). Random samples of 20 spikes per plot were harvested on each sampling date, selected in four replications. 10 grains from the middle of each of the 20 spikes were removed and oven dried at 80^oC for 24h. The grains were weighed before and after drying. The following traits were analysed: observed final grain dry weight – M (mg), observed maximum grain filling rate – IN_{max} (mg dm $^oC^{-1}grain^{-1}$), observed grain filling duration – D (gdd), nonlinear regression estimated final grain dry weight – W (mg), nonlinear regression estimated max grain filling rate – R (mg dm $^oC^{-1}grain^{-1}$), nonlinear regression estimated grain filling duration (gdd). Dry matter accumulation was expressed as a function of accumulated growing degree days (gdd) from anthesis. Gdd were calculated as a summ of daily degree days (T_n), which was determined by: $T_n = \{(T_{max} + T_{min}) / 2\}T_b$, where T_{max} and T_{min} are the maximum and minimum daily temperatures, and T_b is the base temperature (0^oC). Below the base temperature plants are unable to develop (Duguid and Brûlé – Babel 1994). The data from each plot were fitted by nonlinear regression to a logistic curve: $y = W / \{1 + \exp(B – Cx)\}$, where y was average grain weight (mg) and x was accumulated gdd from anthesis. W estimates the final grain weight (mg), B is related to both duration and rate of grain filling, and C is related to grain filling rate. Estimates of W, B and C were determined by nonlinear regression, using STATISTICA software package. The maximum rate of grain filling (R) was calculated using the derivative of the logistic curve: $dy / dx = Cy (W – y) / W$, where dy / dx represents the instantaneous grain filling rate. This value reaches a maximum when y = 0,5 W. So the maximum rate (R) can be calculated as R = CW / 4. Theoretically, grain dry weight will never reach its asymptotic maximum W, so grain filling was considered to be complete when y = 0,95 W. Based on this assumption, an estimate of the grain filling duration (T) was calculated by substituting 0,95 W for y in the derivative of the logistic curve and solving for x: $x = T = (B + 2{,}944) / C$ (Darroch and Baker 1990). The variables W, R and T are first analysed by ANOVA. Since all three variables define the shape of each growth curve, the stepwise MANOVA method described by Keuls and Garretsen (1982) was considered to be more appropriate than ANOVA for comparisons of growth curves. The procedure was used in order to determine which of the estimated variables (W, R, T) is the most important in characterizing the grain filling curves. The variable with the

lowest Wilks' λ – value is considered first. It is the most significant variable. Next, the most significant pair of variables that includes the first variable is considered. Finally, the set can be extended to all three variables. Each addition of another variable to the set is considered to be important only if the new variable adds information not already contained in the previous set (Darroch and Baker 1990).

RESULTS AND DISCUSSION

The logistic curve provided a good fit to the grain filling data in all cases. Combined ANOVA of all trials showed that there were significant differences between groups, environments and significant group – environment interactions for most of the analysed observed and estimated traits. Exceptions were nonsignificant group – environment interactions for observed grain filling duration and nonsignificant differences between environments and group – environment interactions for estimated maximum rate of grain filling. Analyses of variance conducted on individual trials indicated that there were significant group differences for all estimated and observed variables in both environments (Table 1.). Therefore, the results from ANOVA conducted on individual trials imply that all analysed traits (final grain dry weight, rate and duratin of grain filling) were important in determining the group differences in grain filling.

Table 1. Summary of significance of group mean squares for individual ANOVA for observed (M, IN_{max}, D) and variables estimated from grain filling curves (W, R, T) for five groups of genotypes of different earliness

	Traits						
	Observed				Estimated		
	M	IN_{max}	D		W	R	T
Environments							
2001	**	**	**		**	**	**
2002	**	**	**		**	**	**

M – observed final grain dry weight (mg), IN_{max} – observed maximum rate of grain filling (mg dm °C^{-1} grain^{-1}), D – obsedved duration of grain filling (gdd), W – estimated final grain dry weight (mg), R – estimated maximum rate of grain filling (mg dm °C^{-1} grain^{-1}), estimated grain filling duration (gdd)

** - significant at the 0,01 level of probability

The logistic equation overestimated the final grain dry weight (W), but a ranking of groups was similar to observed. Grain filling duration (D) was underestimated in all groups, similar to results obtained by Duguid and Brûlé-Babel (1994). They assumed those differences are a consequences of differences in the method of measurement. The observed grain filling duration is a time in gdd from anthesis to maturity (13% moisture in grain). In contrast, the estimation of grain filling duration was based on the logistic curve, which is largely determined by final grain dry weight. Overestimated maximum grain filling rates (R) occurred as a consequences of underestimated durations of grain filling (Table 2.). However, MANOVA is required to obtain a more complete analysis of group differences, because it accounts for correlations among the variables (Darroch and Baker 1990). MANOVA was used in both environments (2001, 2002) to determine the significance of group effects for the complete set of estimated variables (W, R, T) and all their possible subsets. Stepwise MANOVA (Keuls and Garretsen 1982) provided the determination of the smallest set of variables that contribute information to group grain filling curves in both environments. In 2001 (wett growing season, delayed and long grain filling, low temperatures) the most significant variable in differentiating among group grain filling curves was T, followed by W and R. In 2002 (common for our region) the most important variable was W, and the set also was extended by R and T (Tables 3. and 4.).

Table 2. Nonlinear regression estimated final grain dry weight – W (mg), maximum rate of grain filling – R (mg dm $^oC^{-1}$ grain^{-1}), duration of grain filling – T (gdd) and observed final grain dry weight – M (mg), maximum rate of grain filling – IN_{max} (mg dm $^oC^{-1}$ grain^{-1}), duration of grain filling – D (gdd) in four groups of genotypes of different earlines and control group of NS cultivars

Environments	Groups	W	R	T	M	INmax	D
2001	extra early	41,9	0,0968	725	40,7	0,0624	971
	medium early	38	0,1042	689	35,7	0,0606	985
	medium late	38,5	0,1273	551,5	36,1	0,0761	898,5
	late	36,9	0,1272	570,5	34,1	0,0694	900,5
	NS cultivars	42,1	0,1304	601,5	40,6	0,0733	909
2002	extra early	39,3	0,0946	668,5	37,8	0,0624	855,5
	medium early	44,4	0,1061	677,5	41,3	0,0705	837
	medium late	49,6	0,1209	636	47,9	0,083	789,5
	late	45,6	0,1331	582,5	39,1	0,08	790
	NS cultivars	51	0,1092	692	47,9	0,0809	782

Extra early group and high – yielding NS cultivars were the groups with highest observed and estimated final grain dry weights in 2001. On contrast, in 2002 the highest estimated and observed grain dry weights were achieved in medium late and control group. Regardless of environment, one tendency is present: earlier genotypes have longer grain filling duration in gdd then the later.

The groups which had longer duration of grain filling also had lower maximum grain filling rates (Table 2.). In unfavorable environment (2001) high grain dry weight had group of extra early genotypes, because only they can compensate low grain filling rate with long grain filling duration. On contrast, in common environment (2002) high grain filling rate has adventage in comparison with duration: the group of medium late genotypes achieved high final grain dry weight. Grain filling is a complex process, and final grain dry weight is a result of its duration and rate. Those two parameters can not be studied separately, because both of them have certain influence on a dry matter accumulation, which is not the same in a different environments. For achievement of high grain dry weight is in our environments recommended medium earliness and relatively short grain filling with high rate, because of importance of avoiding terminal dry and temperature stress. Ability to compensate low grain filling rate with grain filling extension in unfavorable environments is crucial.

Table 3. Summary of tests of significance of group effects in MANOVA of estimated grain dry weight (W), maximum rate of grain filling (R) and duration of grain filling (T) from anthesis to 0,95W

	2001			2002		
set	**λ**	**df**	**F**	**λ**	**df**	**F**
W, R, T	0,1411	12, 151	13,8**	0,0897	12, 151	18,74**
W, R	0,4195	8, 116	7,89**	0,1105	8, 116	29,12**
W, T	0,2094	8, 116	17,19**	0,1119	8, 116	28,85**
R, T	0,2529	8, 116	14,33**	0,2745	8, 116	13,7**
W	0,5825	4,59	10,57**	0,2567	4,59	42,7**
R	0,751	4,59	4,88**	0,3971	4,59	22,39**
T	0,3427	4,59	28,28**	0,5777	4,59	10,78**

df – degrees of freedom, λ - Wilks' λ criterion, ** - significant at the 0,01 level of probability

Table 4. Determination of the smallest set of estimated variables (final grain dry weight (W), maximum rate (R) and duration (D) of grain filling) required to completely characterise the group grain filling curves

Environment	Cond. set	λ	df	F	Final set
2001	**T**	0,3427	4,59	28,29**	
	W \ T	0,6109	4,58	4,05**	**T, W, R**
	R \ TW	0,6739	4,57	6,9**	
2002	**W**	0,2567	4,59	42,7**	
	R \ W	0,4305	4,58	7,6**	**W, R, T**
	T \ WR	0,8112	4,57	3,32*	

Cond. set – conditional set, λ - Wilks' λ criterion, df – degrees of freedom, *, ** - significant at the 0,05 and 0,01 level of probability, respectively

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