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CHARACTERIZATION OF VEGETATIVE AND GRAIN FILLING PERIODS OF WINTER WHEAT BY STEPWISE REGRESSION PROCEDURE. II. GRAIN FILLING PERIOD

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In wheat, rate and duration of dry matter accumulation and remobilization depend on genotype and growing conditions. The objective of this study was to determine the most appropriate polynomial regression of stepwise regression procedure for describing grain filling period in three winter wheat cultivars. The stepwise regression procedure showed that grain filling is a complex biological process and that it is difficult to offer a simple and appropriate polynomial equation that fits the pattern of changes in dry matter accumulation during the grain filling period, i.e., from anthesis to maximum grain weight, in winter wheat. If grain filling is to be represented with a high power polynomial, quartic and quintic equations showed to be most appropriate. In spite of certain disadvantages, a cubic equation of stepwise regression could be used for describing the pattern of winter wheat grain filling.

Key words: dry matter accumulation, model, stepwise regression analysis, grain filling period

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INTRODUCTION

Yield of wheat depends mainly on the processes of starch synthesis and accumulation (PAN *et al.,* 2007). Sink capacity determines the rate and duration of starch accumulation during grain filling under optimal growing conditions, i.e., the accumulation, transformation and partitioning of carbohydrates between grain and biomass. The rate of grain starch accumulation and grain weight are affected by photosynthate assimilation, dry matter accumulation, dry matter remobilization and starch accumulation capacity on one side and growing conditions, i.e., temperature, available nitrogen and moisture on the other (PRŽULJ and MOMČILOVIĆ, 2001; DENNIS, 2004).

In conditions when assimilates from current photosynthesis become unavailable due to stress such as drought, high temperature or low light influx, grain filling depends to a high extent on remobilized resources (PRŽULJ and MOMČILOVIĆ, 2003; MAYDUP *et al*., 2010). Under drought conditions, photosynthetic capacity of leaves is decreased and at the same time the demand for current photosynthates is increased, i.e., for both, grain filling and respiration. Water deficit brings about a lower accumulation of stem reserves and reduced amounts of remobilized stem reserves into grain (EHDAIE *et al*., 2006). Reduction in grain growth depends on water deficit intensity and the phase of grain development (MASONI *et al*., 2007). When water deficit occurs during early stages of grain development, the grain sink capacity is diminished (RAJALA *et al.,* 2009).

The effects of various factors on specific crop traits can be efficiently simulated (MICHELE *et al*., 2003; PAN *et al.,* 2006). Several models have been developed which simulate the growth and dry matter accumulation in wheat (ASSENG *et al*., 2002).

Several mathematical models have been used to estimate grain filling parameters in small grains. PEPLER *et al.* (2006) applied the linear regression for rate of grain filling determination, but he dealt only with the linear phase of grain filling, while omitting the first or accelerating phase and the third or saturation phase. PRŽULJ (2001) fitted a quadratic and EGLI (2004) a cubic polynomial to the data of wheat grain filling. SANTIVERI *et al*. (2002) found that a logistic equation could describe the relationship between grain weight and accumulated growing degree days very well.

The objective of this study was to test the stepwise regression procedure as a method for determining the polynomial regression that describes most appropriately the grain filling in winter wheat.

MATERIALS AND METHODS

The experimental design, measurements, and statistical analysis was described in detail in our previous paper (PRŽULJ and MOMČILOVIĆ, 2011). Briefly, a 5-year field trial, during 2002/03-2006/07 growing seasons, was conducted under rainfed conditions on the calcareous chernozem soil. Three winter wheat cultivars were used in the study, Prima (early-maturing), Pobeda (medium-maturing), and Diplomat (late-maturing).

In each plot we tagged 100 main tillers from fourth and fifth rows, which flowered on the same day. Three tagged tillers per plot were collected in plastic bags at 2-4 day intervals from anthesis until physiological maturity, weighed in the lab and oven-dried at 80°C for 48 hours to constant weight. The accumulated growing-degree days (GDD) were used as the time scale.

The statistical analysis involved a special type of regression, the one that concerns a polynomial expression:

$$Y_i=\alpha+\beta_1 X_i+\beta_2 X_i^2+\beta_3 X_i^3+\ldots+\beta_m X_i^m+\varepsilon_i$$

and a model with parameters estimated in the expression:

$$\hat{Y}_i=a+b_1X_i+b_2 X_i^2+b_3 X_i^3+\ldots+b_mX_i^m \text{ (Zar, 1999).}$$

A stepwise regression procedure was used for determination of maximum power, m, where maximum power should not be greater than n-1 if a polynomial is to fit the data, and, more practically, not greater than *n-2* if statistical analysis is to be performed on the resulting polynomial fit (Zar, 1999). The procedure starts by fitting a linear regression ($\hat{Y}_i=a+bX_i$) to the data, followed by fitting a second degree polynomial to the data. Quadratic equation ($\hat{Y}_i=a+b_1X_i+b_2X_i^2$) is made by adding the quadratic term ($b_2X_i^2$) to the simple regression. To test whether the added quadratic term improves the precision of *Y* values prediction, the *t* test is applied. If the *t* test does not refute the null hypothesis, $H_0 : \beta = 0$, it means that the simple regression model characterizes the relationship between Y and X, i.e., that the quadratic term contributes insignificantly to this characterization. If the null hypothesis is refuted, fits are tried with polynomials of higher power, until the acceptable fit is found, which means that the polynomial with the m-1 term is the best model. For testing the significance of regression and coefficient values, a probability level α=0.05 and an appropriate degree of freedom were used. Stepwise regression was calculated and the curves plotted by the software package StatSoft Statistica 9.1

RESULTS AND DISCUSSION

The length of grain growth and grain weight are processes that are highly environment-dependent. Determination of the genetic base of these two traits/processes and their interactions with certain growing condition help breeders to develop new cultivars and growers to select a most appropriate cultivar for a specific environment. In plant simulation modeling, the growth dynamics should be predicted by an appropriate equation. A simple equation for characterization of grain filling duration and final weight is preferred (YIN *et al.,* 2003).

The life cycle of cereals is divided into two main periods, period till anthesis and grain filling period. From a practical point of view and considering the changes at the shoot apex, the period till anthesis can be divided in three phases: leaf initiation (vegetative phase), spikelet initiation (early reproductive phase) and spike growth (late reproductive phase) (SLAFER and WHITECHURCH, 2001). During the first 1-2 weeks, grain capacity for dry matter accumulation is established. The actual rate of dry matter accumulation in the grain is low in this phase and it can be presented by an exponential curve (WEISS and MORENO-SOTOMAYER, 2006). During the linear phase, which covers most of the period of grain filling and which indeed represents the period of actual grain filling, dry matter accumulation is almost constant per time unit and it can be presented by a linear equation. The third sub-phase or maturity phase, which is characterized by a decreased dry matter accumulation, can be presented by a convex equation. Instead of using these three equations sequentially, a curvilinear equation can be used which permits a gradual transition from one phase to another. So, the pattern of growth fits a sigmoid curve and the rate of growth a bell-shaped curve (YIN *et al*., 2003).

The linear model of dry matter accumulation proposed by PEPLER *et al*. (2006) can be questioned since it presents only a part of the grain filling, i.e., a period from the 10^{th} to the 26^{th} day after anthesis. Although most of the grain dry matter is accumulated during the linear period, it is difficult to evaluate the beginning and the end of this period and this method suffers from subjectivity. EHDAIE *et al*. (2008) have pointed out that not all grain filling curves that represented the second phase are linear, as some of them are sigmoid in shape. To minimize the influence of floret position on grain filling rate, many authors used grains at fixed positions (VOLTAS *et al.* 1999)

Different polynomial curves fitted the data of grain filling of the three winter wheat cultivars, ranging from cubic to septic (Tables 1, 2, 3). However, the cubic model correctly presented the grain filling process in all three cultivars since the coefficient of determination exceeded 99% in all cases. This model is the simplest and with a high value of the coefficient of determination. From the biological point, grain weight at anthesis is zero or very close to zero, while the estimated polynomials had the values different than zero, ranging from -4.8 to +4.7 (Tables 1, 2, 3). If coefficient a is zero, grain filling rate is also zero and the term b_1X_i can be omitted and substituted by the curve $\hat{Y}_i=b_2X_i^2+b_3X_i^3$ (Fu et al., 2009). PRŽULJ (2001) concluded that polynomial functions are appropriate in situations when grain weight decreases after reaching a maximum, which was not the case with the cultivars used in our investigation (Figure 1).

Many equations have been proposed to describe the sigmoid growth (SANTIVERI *et al.,* 2002). The logistic curve describes a situation in which grain weight does not necessarily decrease when maximum dry matter in achieved; therefore, the logistic curve could adequately describe the pattern of grain filling (YIN *et al*., 2003; YIN *et al.,* 2009). In the logistic as well as the RICHARDS, GOMPERTZ and WEIBULL functions, however, an actual weight equal to w_{max} cannot be predicted because these function have the line $w=w_{max}$ as their upper asymptote while the time goes to infinity (YIN *et al*., 2003). That means that, according to these functions, the length of grain filling period is infinite.

Table 1. Stepwise regression for fitting an appropriate polynomial model to grain filling data for the winter wheat variety Prima in the growing seasons 2002/03-2006/07

Growing season		Term						
		x	x^2	x^3	x^4	x^5	x^6	R^2
	2002/03	*§						0,9654*
		*	*					0,9864*
		n§§	*	*				0,9974*
		*	*	*	*			0,9995*
		$y = 2.785 – 0.082x + 7.5E\text{-}4x^2 - 1E\text{-}0.6x^3 + 5E\text{-}10x^4$						
	2003/04	*						0,9746*
		*	*					0,9785*
		*	*	*				0,9986*
		*	*	*	*			0,9992*
		n	n	n	*	*		0,9994*
		$y = 1.737 – 0.024x + 8E\text{-}05x^2 + 3E\text{-}07x^3 - 6E\text{-}10x^4 + 3E\text{-}13x^5$						
	2004/05	*						0,9461*
		*	*					0,9766*
		n	*	*				0,9905*
		*	*	*	*			0,9976*
		$y = 4.705 – 0.100x + 5.59E\text{-}4x^2 – 7E\text{-}07x^3 + 2E\text{-}10x^4$						
	2005/06	*						0,9645*
		*	*					0,9764*
		n	*	*				0,9968*
		*	*	*	*			0,9986*
		n	n	n	*	*		0,9993*
		*	*	*	*	*	*	0,9996*
		$y =-1.12+0.68x-6.9E\text{-}4x^2-3.4E\text{-}6x^3-6.2E\text{-}9x^4+4.9E\text{-}12x^5-1.5E\text{-}15x^6$						
	2006/07	*						0,9685*
		*	*					0,9908*
		*	*	*				0,9982*
		*	*	*	*			0,9993*
		$y = 0.911 – 0.018x + 2.58E\text{-}4x^2 – 3E\text{-}0.7x^3 + 1E\text{-}10x^4$						

§- significant at α=0.05 level, §§ - non-significant

To fit the grain filling process, a segmented terminate function is needed that predicts a smooth transition to the maximum weight and zero slope at the end of the filling period (YIN *et al*., 2003). The zero point at the end is provided by cubic polynomials and from cubic equation it is possible to explicitly predict the actual weight that is equal to w_{max}. Analyzing the data for rice, EGLI (2004) showed that a cubic polynomial fitted better grain filling than the logistic and Gompertz curves.

Table 2. Stepwise regression for fitting an appropriate polynomial model to grain filling data for the winter wheat variety Pobeda in the growing seasons 2002/03-2006/07

Growing season		Term							
		x	x^2	x^3	x^4	x^5	x^6	x^7	R^2
	2002/03	*							0.9735*
		*	*						0.9874*
		n	*	*					0.9985*
		*	*	*	*				0.9993*
		n	n	n	n	*			0.9995*
		$y = 0.347 + 09.1E\text{-}4x + 1.2E\text{-}04x^2 + 5E\text{-}07x^3 - 1E\text{-}09x^4 + 7E\text{-}13x^5$							
	2003/04	*							0.9798*
		*	n						0.9802*
		*	*	*					0.9987*
		$y = 2.984 – 0.059x + 3.22E\text{-}4x^2 - 2E\text{-}07x^3$							
	204/05	*							0.9629*
		*	*						0.9716*
		*	*	*					0.9965*
		*	*	*	*				0.9983*
		n	n	*	*	*			0.9982*
		*	*	*	n	n	*		0.9995*
		$y =-4.8+0.13x-0.001x^2+4.18E\text{-}6x^3-6.28E\text{-}9x^4+4.21E\text{-}12x^5-1.1E\text{-}15x^6$							
	2005/06	*							0.9723*
		*	*						0.9809*
		n	*	*					0.9976*
		*	*	*	*				0.9987*
		n	n	n	*	*			0.9995*
		$y = 1.281 - 3E\text{-}05x + 2E\text{-}05x^2 + 6E\text{-}07x^3 - 1E\text{-}09x^4 + 6E\text{-}13x^5$							
	2006/07	*							0.9513*
		*	*						0.9776*
		n	*	*					0.9937*
		*	*	*	*				0.9981*
		n	n	*	*	*			0.9989*
		n	n	*	*	*	*		0.9992*
		n	n	n	n	*	*	*	0.9994*
		$y =1.1-0.03x+0.001x^2-2E\text{-}6x^3+7E\text{-}9x^4-1.1E\text{-}11x^5+7.9E\text{-}15x^6-2.2E\text{-}18x^7$							

* - significant at α=0.05 level, § - nonsignificant

Table 3. Stepwise regression for fitting an appropriate polynomial model to grain filling data for the winter wheat variety Diplomat in the growing seasons 2002/03-2006/07

Growing season		Term					
		x	x^2	x^3	x^4	x^5	R^2
	2002/03	*					0.9773*
		*	n				0.9773*
		*	*	*			0.9981*
		*	*	n	n		0.9981*
		n	n	*	*	*	0.9992*
		$y = -0.341 – 0.038x - 5E\text{-}04x^2 + 3E\text{-}06x^3 - 5E\text{-}09x^4 + 3E\text{-}12x^5$					
	2003/04	*					0.9749
		n	*				0.9891
		*	*	*			0.9984
		n	n	*	*		0.9994
		$y = 1.335 – 0.007x - 9E\text{-}05x^2 + 6E\text{-}07x^3 - 6E\text{-}10x^4$					
	2004/05	*					0.9807*
		*	n				0.9821*
		*	*	*			0.9989*
		*	*	*	n		0.9991*
		n	n	n	*	*	0.9996*
		$y = 0.059 + 0.016x – 1.3E\text{-}04x^2 + 1E\text{-}06x^3 - 2E\text{-}09x^4 + 7E\text{-}13x^5$					
	2005/06	*					0.9878*
		*	n				0.9893*
		*	*	*			0.9987*
		n	n	*	n		0.9987*
		n	n	n	*	*	0.9990*
		$y = 0.208 + 0.025x – 1.9E\text{-}04x^2 + 1E\text{-}06x^3 - 2E\text{-}09x^4 + 7E\text{-}13x^5$					
	2006/07	*					0.9764*
		*	n				0.9766*
		*	*	*			0.9986*
		*	*	n	n		0.9986*
		*	*	*	*	*	0.9997*
		$y = 0.475 + 0.038x – 3.5E\text{-}04x^2 + 1E\text{-}06x^3 - 2E\text{-}09x^4 + 8E\text{-}13x^5$					

* - significant at α=0.05 level, § - nonsignificant

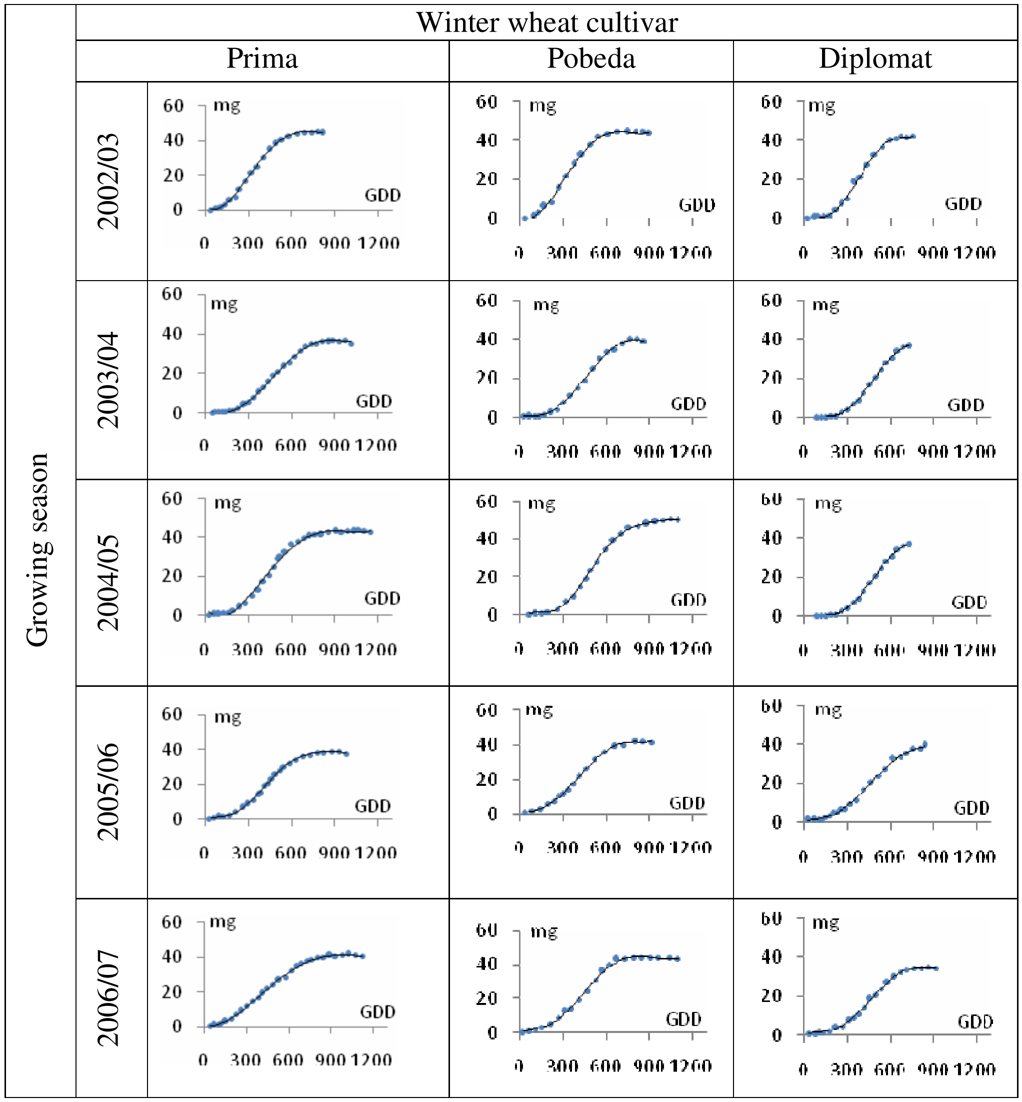

Figure 1. Polynomial regression models that fitted the dry matter accumulation during the grain filling periods of the winter wheat cultivars Prima, Pobeda and Diplomat in the five growing seasons

The cubic curve is symmetrical, presenting the period from anthesis to physiological maturity with the maximum slope, i.e., with the inflection point midway through the growth period, which is not quite true from the biological point. Although the cubic polynomial has obvious disadvantages, it still could be applied for description of the grain filling pattern in the tested winter wheat cultivars.

CONCLUSIONS

The stepwise regression procedure showed that grain filling is a complex biological process and that it is difficult to offer a simple and accurate polynomial equation that fits the data of dry matter changes during grain filling, i.e., from anthesis to maximum weight, in winter wheat. If this procedure is followed, polynomials with high powers, mostly quartic and quintic, should to be used to describe grain filling. Although it has certain disadvantages, the cubic equation could be used to describe the pattern of grain filling in winter wheat.

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ANALIZA VEGETATIVNOG PERIODA I PERIODA NALIVANJA ZRNA KOD OZIME PŠENICE HIJERARHIJSKIM MODELOM VIŠESTRUKE REGRESIJE. II. PERIOD NALIVANJA ZRNA

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I z v o d

Stopa i trajanje akumulacije suve materije u zrnu zavisi od genotipa i uslova gajenja. Cilj ovoga istraživanja bio je da se metodom hijerarhijske višestruke regresije odredi matematički model nalivanja zrna kod tri sorte ozime pšenice. Ovaj metod je pokazao da je nalivanje zrna kompleksan biološki proces, i da je teško odrediti jedinstvenu i odgovarajuću matematičku jednačinu koja bi određivala promenu u sadržaju suve materije u zrnu od cvetanja do postizanja maksimalne mase zrna. Primenom navedenog metoda utvrđeno je da se promena u masi zrna tokom njegovog nalivanja može predstaviti polinomom četvrtog ili petog stepena. Pošto se radi o prilično komplikovanim jednačinama predlaže se primena, kubna jednačina, uprkos njenim određenim nedostacima.

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