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THE IMPORTANCE OF PHYSIOLOGICAL TRAITS IN WHEAT BREEDING UNDER IRRIGATION AND DROUGHT STRESS

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The correlation analysis and the path coefficient analysis were applied to wheat data set with the objective to determine the effect of five physiological traits (early vigour, early maturity, leaf senescence, flag leaf area and total biomass per plant) on grain yield under irrigation and drought stress conditions. The data set consisted of 100 divergent genotypes tested in four-year field trials. Highly significant correlations were found between grain yield, early vigour and total biomass per plant in both treatments. A

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highly negative correlation was detected between grain yield and days to flowering, as well as, between grain yield and leaf senescence in both treatments. The path analysis revealed a highly significant direct effect of days to anthesis and total biomass per plant on grain yield. Early vigour, leaf senescence and the flag leaf area had a significant indirect effect on grain yield via days to anthesis and total biomass per plant. Early vigour, early maturity and leaf senescence were found to be suitable for wheat breeding under different moisture regimes. These traits can be evaluated quickly and easily, and thus they can be used for the evaluation of large populations.

Key words: correlation analysis, grain yield, path analysis, physiological traits, wheat

INTRODUCTION

The improvement of tolerance to drought has been a principal goal of the majority of breeding programmes for a long time, as a water deficit in certain stages of wheat growth is common for many wheat growing regions of the world (MOUSTAFA et al., 1996). In regions where drought conditions happen less frequently and where wet years predominate, such as most of Europe, improving yield under water-limited conditions can usually be achieved by selecting for more productivity under optimum conditions. This strategy is typified by the traditional approach of CIMMYT with its emphasis on selecting for high yield under optimum conditions (RAJARAM et al., 1996). QUARRIE et al. (1999) consider that wheat breeding for solely yielding potential in Serbia is not the best approach to improving yield under conditions of drought, regarding the existing climatic changes and production conditions (weed infestation, poor mineral nutrition). It is obvious that besides the yield it is necessary to include some other (adapted) traits related to good resistance to drought into wheat breeding for drought conditions. Over the years, many physiological, morphological, and developmental traits have been suggested to be useful in improving drought tolerance (LUDLOW and MUCHOW, 1990; QUARRIE et al., 1999; WRIGHT and RACHAPUTI, 2004). As the development of varieties is an extremely pragmatic work and implies working with a great number of plants (DENČIĆ et al., 2001) breeders (together with physiologists) have found out several indirect parameters of resistance to drought (early vigour, leaf temperature, leaf rolling and yellowing, biomass) that prove themselves to be very reliable. Phenological traits, i.e. pheno-phases of the growth and development, have the greatest impact on the adaptation of plants to the existing environment all with the aim of achieving a maximum productivity (PASSIOURA, 1996; RICHARDS, 1996). Selection for one trait can reduce a chance for a successful selection for some other trait, due to a competitive relationship towards the same source of nutrients. However, the combination of traits that in various ways contribute to the improvement of yields can result in a maximum gain of each trait individually (QUARRIE et al., 1999).

The objectives of the current study were to: i) establish the correlations between yield and physiological traits; and ii) determine the direct and indirect effects of physiological traits on grain yield in bread wheat grown under irrigated and drought conditions in order to find out a suitable trait that could be used for the yield improvement under both conditions.

MATERIALS AND METHODS

Field experiments were conducted during the 1997/98, 1998/99, 1999/00, and 2000/01 growing seasons at the Centre for Agricultural and Technological Research, Zaječar, Serbia. The experimental material consisted of 100 wheat cultivars and landraces of a worldwide origin, chosen on the basis of their differences in yields and the performance of several physiological traits under irrigated and drought stress conditions. The genotypes were grown in three treatments: fully irrigated plots (IP), rainfed plots (RP) and a rain-out plot shelter (drought plots-DP). The IP and DP results are presented in this study.

The rain-out shelter was pitched on the plots at the end of the winter period when the majority of genotypes were at the tillering stage. The drought plot was provided with a 1-m deep ditch around the edge to prevent rain from seeping into the plot. The irrigated plots were watered manually when water in the top 75 cm of soil had declined to less than 55% of field capacity, i.e. 21% of soil moisture. The average yield reduction due to the drought treatment in the sheltered plots was 36.6% (23.2, 20.8, 45.2, and 57.2% in 1998, 1999, 2000, and 2001, respectively).

Plants were scored for the following traits: early vigour (EV), days to flowering (DTF), leaf senescence (LS), flag leaf area (FLA), total biomass per plant (TBP) and grain yield (GY). Early vigour was assessed visually at the 6-7-leaf stage (1 to 5, with 5 being the best). Leaf senescence was assessed visually at the anthesis (1 to 5, with 1 being the best). The date of anthesis (anthers exerted from the spikelets) for each genotype was recorded when 50% of the ears were at this stage, calculated as the days from the first of April. The flag leaf areas (leaf width x leaf length x 0.75) (cm²) were measured on 20 randomly selected main stems at the anthesis. Total biomass per plant (g) and grain yield (t ha⁻¹) were measured after harvesting plots at maturity.

Descriptive statistics parameters, mean values and the coefficient of variation (CV) were determined for the studied traits. The analysis of variance (ANOVA) for a randomised complete block design with combined data from the four seasons was performed for each variant. The broad-sense heritability was estimated according to the results of the analysis of variance as the ratio of the total genetic variance to the total phenotypic variance. Genotypic and phenotypic correlations were determined according to the method developed by KWON and TORRIE (1964). Partitioning the correlation coefficient into direct and indirect effects on the tissue culture traits was done through the path analysis technique (LI, 1975).

RESULTS AND DISCUSSION

Table 1 presents mean squares in the analysis of variance, average values and coefficients of variation of analysed traits in 100 wheat genotypes over cropping treatments. The analysis of variance for yield and five physiological traits revealed that the differences among genotypes were highly significant (P<0.01) for all the traits in both treatments. The rather similar variability was obtained for each trait in both treatments, except for LS (43.3% and 23.2% in IP and DP, respectively). The coefficient of variation (CV) ranged from 10.3% (DTF) to 43.3% (LS) and from 10.5 (EV) to 23.8 (GY) in the IP and the DP treatment, respectively. It seems that a high level of phenotypic variation was accumulated for the selected traits among analysed wheat genotypes. Except EV all traits showed significant difference (P < 0.05) in a mean value between the IP and the DP variant. The average reduction for TBP, GY and FLA due to the drought treatment in the sheltered plots was 38.1%, 36.6% and 24.0%, respectively. On the average, all genotypes had anthesis date six days earlier in DP than in IP. Drought stress increased LS at the anthesis by 88% on the average for all genotypes. The absence of difference in means of EV between the two treatments can be reasonably explained by the fact that its evaluation was done in the period when there were no effects of drought yet on plants in DP.

Table 1. Mean squares for genotype (MS), arithmetic mean and coefficient of variation (CV) of 100 wheat genotypes for the yield and physiological traits (averaged across four years)

Trait	Irrigation			Drought stress		
	MS	Mean [†]	CV (%)	MS	Mean [†]	CV (%)
EV	1.40**	3.7 ^a	11.5	1.13**	3.6 ^a	10.5
DTF	165.66**	50^{a}	10.3	201.28**	44 ^b	10.8
LS	0.62**	0.9 ^b	43.3	0.95**	1.7 ^a	23.2
FLA	103.37**	30.4 ^a	16.8	51.91**	23.1 ^b	1.7
TBP	10.82**	7.57^{a}	15.4	5.60**	4.69 ^b	17.8

** Significantly different at P < 0.01

† Values in the same row followed by the same letter are not significantly different at the 0.05 probability level

The magnitude of heritability was, in general, similar under irrigation and drought stress conditions, except for LS (Table 2). This is in agreement with statements made by SIMMONDS (1991) that convincing proofs showing that the trait heritability was generally lower in stress environments were not presented. The heritability estimate in IP for DTF was 97.1%, followed by GY (83.1%), FLA (75.1%), TBP (69.8%), EV (41.9%) and LS (16.0%). In DP the highest heritability of 97.4% was exhibited by DTF, followed by GY (80.8%), FLA (77.6%), TBP (66.2), EV (32.5%) while the lowest heritability (31.3%) was observed for LS. Hence, under both environments the broadsense heritability for TBP, FLA, GY and DTF was moderate to high, whereas for EV and LS was low.

The heritability of the most important trait GY was rather high (over 80%) indicating that genetic factors had a higher influence than the environment on the expression of this trait, what is in agreement with KASHIF and KHALIQ, 2004; UL-HAQ *et al.*, 2008. Nevertheless, heritability estimates for grain yield of several other authors (UDDIN *et al.*, 1992; JEDYNSKI, 2001) were intermediate or low. The difference in findings may be due to various reasons including the genetic material used and the environmental conditions.

It is generally considered that the heritability of physiological traits is lower than the heritability of morphological traits, which was only partially confirmed by obtained results. KASHIF and KHALIQ (2004), i.e. FATEHI *et al.* (2008) also obtained a high heritability for FLA (61.2%), i.e. TBP (75.0%), respectively. The reasons for the lower heritability of EV and LS should be sought out in a great participation of the experimental error in the total phenotypic variability. PREMACHANDRA and SHIMADA (1988) point out to a need to improve the accuracy of measuring physiological parameters. However, BLUM (1988) emphasises that due to different reason a clear proof on the importance of certain physiological traits is hard to establish under field conditions, but the major problem is not so much their measurement but the evaluation of yields under stress conditions. Anyway, the same author underlines that it should not lead to discouragement in the application of physiological parameters in breeding programmes, as it is reasonable to sacrifice a part of the experimental preciseness in order to test a great number of genotypes.

The information of correlations among traits can be of a great use to breeders, as it points out to the traits to which selection should be directed in order to increase the yield under certain environmental conditions. Genetic correlations point to the cohesion of traits after variations, due to environmental effects, are eliminated and they are the basis for the indirect selection (VAN GINKEL *et al.*, 1998). Genotypic and phenotypic correlations between the yield and physiological traits under study are presented in Table 2.

Trait –	Irrigation			Drought stress		
	r _g	$r_{\rm f}$	h²(%)	r _g	r _f	h²(%)
EV	0.395**	0.295**	41.9	0.627**	0.276**	32.5
DTF	-0.423**	-0.404**	97.1	-0.399**	-0.364**	97.4
LS	-0.493**	-0.037	16.0	-0.547**	-0.292**	31.3
FLA	0.039	0.103	75.1	0.071	0.132	77.6
TBP	0.377**	0.465**	69.8	0.543**	0.614**	66.2
GY	/	/	83.1	/	/	80.8

Table 2. Heritability (h²) and *genotypic (r_g) and phenotypic (r_g) correlation coefficients between yield and physiological traits in 100 wheat genotypes (averaged across four years)*

** indicates significance at the P < 0.01

A significant and positive genotypic and phenotypic correlation with the yield in both treatments was observed for EV and TBP (P < 0.01). The genotypic and phenotypic correlations between GY and DTF was negative and significant (P < 0.01) in both treatments. The genetic correlation between LS and GY in IP was negative and significant ($r_g = -0.493^{**}$), while the phenotypic correlation was also negative, but insignificant ($r_f = -$ 0.037). In DP, both genotypic ($r_g = -0.547^{**}$) and phenotypic ($r_f = -0.292^{**}$) correlations between GY and LS were negative and significant. GY and FLA showed positive, but insignificant genotypic and phenotypic associations in IP and DP treatments.

In the DP variant, the highest coefficient of genetic correlation was recorded between GY and EV ($r_{g=}0.627^{**}$), while the highest coefficient of phenotypic correlation was registered between GY and TBP ($r_{g} = 0.614^{**}$). QUARRIE et al. (1999) state that the rapid early plant growth rate is important for several reasons, and especially because of soil evaporation and the increase of competitiveness of wheat crops against weeds. A greater early vigour provides more efficient water utilisation and the increase of wheat crop yields under the conditions of the Mediterranean-type climate (REBETZKE et al., 1999). Indirectly, early vigour is attributed to a better developed and deeper root system (RICHARDS, 1991), what is very important knowing that the direct measurement of the root is hard and impractical. VAN GINKEL et al. (1998) also obtained a positive and significant genetic correlation of wheat biomass and yields under the conditions of drought and irrigation. The increase of biomass under conditions of drought is essential as the translocation of assimilates from vegetative parts into grain significantly contributes to vield (PHELOUNG and SIDDIQUE, 1991). Leaf senescence (LS) showed a significant and negative influence on yield. It is known that drought affects early and rapid leaf yellowing. For a long time, postponed leaf yellowing has been considered a desirable trait in breeding of small grains under conditions of drought and heat stress (THOMAS and SMART, 1993). The early maturity, expressed over the days to flowering (DTF) was negatively correlated with GY in the DP variant, which means that short-season genotypes had higher yields. In spite of the fact that a longer growing season means higher yields (BLUM, 1993), early maturity genotypes are more desirable under our climatic conditions, as their shorter growing period provides the avoidance of drought and high temperatures during pollination and grain filling when the adverse consequences are the greatest. Unlike other authors (UDDIN et al., 1992; VAN GINKEL et al., 1998) we obtained a negative correlation of DTF with GY even in the IP variant. This can be explained by the increase in the number of tropical days during the wheat maturation when temperatures could be close to 40° C (DODIG *et al.*, 2002). During tropical days, the soil temperature at the depth of 5 cm is higher by $4-5^{\circ}$ C than the air temperature, while air relative humidity decreases below 20% in the afternoon hours. Plants, even if irrigated, can suffer from heat stress, which will result in lower yields, because rates of the photosynthesis decrease are high at temperatures above 35°C (ALKHATIB and PAULSEN, 1992). A positive but not significant correlation between FLA and GY was also reported by KASHIF and KHALIQ (2004).

The correlation coefficient measures the mutual association between a pair of variables independent of other variables to be considered. Therefore, when more than two variables are involved, the correlations per se do not give the complete information of their relationships. The path coefficient analysis is particularly useful for the study of the cause and the effect relationship, because it simultaneously considers several variables in data set to obtain the coefficients (FAKOREDE and OPEKE 1985). The direct and indirect effects of physiological traits on GY in IP and DP treatments are shown in Table 3.

The path correlation analysis revealed that TBP (0.847^{**}) and DTF (-0.627^{**}) had the highest positive and negative direct effect (P < 0.01) on GY in DP. Both, the

correlation and the path analyses indicated that TBP (positive direction) and DTF (negative direction) were significantly associated with GY. Others have also established the importance of total biomass for the yield increase in wheat (REYNOLDS *et al*, 2007), especially under drought stress conditions (WHAN *et al.*, 1991; QUARRIE *et al.*, 1999). A higher biomass production under drought stress conditions, particularly during grain filling period, would have an advantage because the translocation of assimilates from the vegetative parts of a plant to seeds contribute significantly to yield (PHELOUNG and SIDDIQUE 1991).

Trait	Irrigation						
ITall	EV	DTF	LS	FLA	TBP		
EV	0.141	0.026	0.069	0.034	0.071		
DTF	-0.131	-0.703**	-0.176	-0.272	-0.291		
LS	-0.098	-0.050	-0.200	-0.019	-0.072		
FLA	0.012	0.020	0.005	0.051	0.021		
TBP	0.371	0.304	0.265	0.309	0.735		
Total	0.295**	-0.404**	-0.037	0.103	0.465**		
-]	Drought stress				
EV	-0.006	-0.001	-0.001	-0.002	-0.001		
DTF	-0.131	-0.627**	-0.219	-0.005	-0.221		
LS	-0.015	-0.038	-0.112	-0.020	-0.006		
FLA	-0.005	-0.001	0.002	-0.025	-0.005		
TBP	0.433	0.303	0.038	0.184	0.847**		
Total	0.276**	-0.364**	-0.292**	0.132	0.614**		

Table 3.Direct (diagonal) and indirect effects of the physiological traits on grain yield in wheat

** indicates significance at the P < 0.01

Although genotypic and phenotypic correlations between GY and EV in DP were positive and significant, the path analysis showed an insignificant and slightly negative direct effect of EV on GY (-0.006). Nevertheless, it was found out that EV had a strong indirect effect on GY via TBP (0.433). Although the significance test for the indirect effects cannot be applied, these indirect effects of EV via TBP can be considered significant as they exceed values of corresponding direct effects. Similarly, LS showed a significant influence on GY by the correlation analysis, while the path analysis gave also negative and insignificant direct effect (-0.112). Under drought stress, LS had significant indirect effect on GY via DTF (-0.219) whereas under irrigation via TBP (0.265). The *path* coefficient analysis showed that FLA had no significant direct effect on GY in both DP (-0.025) and IP treatments (0.051). This is in agreement with the correlation analysis. Although direct effect of FLA was not significant it exerted a positive effect on GY through other traits like TBP (0.184) in the DP variant and TBP (0.309) and DTF (-0.272) in the IP variant. SUBDHANI and CHOWDHRY (2000) found that the flag leaf area had no direct effect on grain yield in wheat under irrigation, but under drought stress, a direct effect was positive and significant.

In conclusion, the traits which mostly accounted for high yield under drought stress were early maturity and above all biomass per plant, which produced the consistent direct and indirect effect on grain yield. Traits such as early vigour and prolonged leaf senescence had also positive correlation and an indirect effect on grain yield. Moreover, early vigour, early maturity, prolonged leaf senescence and total biomass per plant had positive correlations with grain yield under irrigation, so that they may be used as suitable selection criteria under a range of moisture conditions. Most importantly, as early vigour, early maturity and leaf senescence can be evaluated quickly and easily, these traits may be used for evaluation of large populations.

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ZNAČAJ FIZIOLOŠKIH SVOJSTAVA U SELEKCIJI PŠENICE U USLOVIMA NAVODNJAVANJA I STRESA SUŠE

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I z v o d

Korelaciona i *path* analiza korišćene su da bi se otkrio utacaj pet fizioloških osobina (rani, vigor, ranostasnost, žućenje listova, površina lista zastavičara i ukupna biomasa po biljci) na prinos pšenice u uslovima navodnjavanja i suše. Ispitivano je 100 različitih genotipova u četvorogodišnjim poljskim ogledima. Značajna i pozitivna korelacija utvrđena je između prinosa, ranog vigora i ukupne biomase u oba tretmana. Između prinosa i broja dana do cvetanja, kao i između prinosa i žućenja listova ustanovljena je značajna negativna korelacija u oba tretmana. *Path* analizom je utvrđeno da je uticaj ranostasnosti i ukupne biomase na prinos bio direktan i značajan. Rani vigor, žućenje listova i površina lista zastavičara su pokazali značajan indirektni uticaj na prinos preko ranostasnosti i ukupne biomase po biljci. Rani vigor, ranostasnost i žućenje listova se mogu smatrati kao pogodni kriterijumi za selekciju u različitim režimima vlažnosti. Ocenjivanje ovih osobina je brzo i lako, pa se mogu koristiti u radu sa velikim brojem populacija

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