Ecological and biological explanation of genotype × environment interaction of common winter wheat (*Triticum aestivum* L.)

Nikolay Tsenov[1]*, Todor Gubatov[1], Ivan Yanchev[2]
[1]Department of Wheat Breeding and Technology, Agronom Breeding Company, 9300 Dobrich, Bulgaria
[2]Department of Plant Science, Faculty of Agronomy, Agricultural University, 4000 Plovdiv, Bulgaria
*E-mail: *nick.tsenov@gmail.com*

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Abstract

Objectives of the study: In a multi environmental field experiment (MET), which included twenty-seven varieties of common wheat, were studied in twelve different environments. The aim of the study is to gather additional information on the influence of meteorological factors related to the locations and the effects of the environment on the components of productivity in their influence on Genotype by Environment interaction (GEI) for grain yield

Experimental approach: A total of nine environmental parameters were analysed as follows: TA-average daily air temperature, Tmax - absolute maximum temperature, Tmin- absolute minimum temperature, GDD (Growing Degree Days) - sum of active temperatures required by plants for growth and development and the SP - sum of precipitation during the growing season. Three of the parameters that differ significantly: average daily air temperature, sum of active temperatures and precipitation are divided into two groups: during the autumn-winter period (from germination to the end of tillering stage (Z10-Z29) - with a suffix (a-autumn) and during the active spring vegetation (from the beginning of the stem elongation stage to full maturity (Z30-Z99), with suffix (s-spring): TAa, TAs; GDDa, GDDs; SPa, SPs. The factor (E) is a combination of the “location” and “season” factors. This approach was adopted in order to be able to specify the data on meteorological factors. The study included quantitative traits related to productivity: GY-grain yield, NPT-number of productive stems per m^2 , NGS-number of grains per spike, TGW-1000 grain weight, WGS -weight of grains per spike (g), NGm - number of grains per m2, EED - date of ear emergence (number of days from 1 January), HI - harvest index and HOS - height of the stem. The interactions between the main factors (G and E) and the effects of meteorological and genetic factors, as co variables were analysed by applying three well known multi-regression models: AMMI, FR, PLS.

Key results: Genotype by Environment interaction for grain yield is very pronounced, with significant principal components reaching in number of PC10. Against the background of this tangible interaction, it was found that the meteorological factors: Tmin, TAa, TAs; GDD, SPa and SPs have a significant effect on the genotype. In turn, the factor “E” interacts with the traits NGm, TGW, EED, WGS and HI, whose shares are included in the overall value of GEI.

Conclusions: The main climatic parameters of the environment - temperature and rainfall, have a serious impact on (G) in its GEI, relative to grain yield. The main factor (E) directly affects important traits, such as TGW, WGS, HI, NGm, whose effects on yield have a significant share in the total GEI.

Key words*:* wheat; genotype x environment; stability; factorial regression; AMMI

INTRODUCTION

The manifestation of the phenotype in real conditions is the result of combining the genetic potential of the variety with the environment, which is expressed through its unique sensitivity to changes in these conditions, known as genotype x environment interaction (GxE or GEI) (de Leon et al., 2016). It occurs when the reaction rates of different varieties are not parallel, I e. they intersect, diverge or merge, with a similar change in environmental conditions (Bustos-Korts, 2017). This whole reaction can be expressed in principle as a result of the main effects of (G), (E) in combination with (GEI), known as GGE (Yan & Rajcan, 2002). In turn, the influence of conditions (E) is a result of soil and ecological characteristics of climate (temperature, precipitation, humidity, solar radiation, carbon dioxide content), widely known as abiotic environmental factors (Roostaei et al., 2021). The grain yield of wheat itself is an integral quantity, which is formed as a result of a combination of a large number of biological factors (quantitative traits, physiological indicators, morphological traits, tolerance to stress), (lo Valvo et al., 2018; Garcia et al., 2019; Senapati et al., 2020). Biotic factors (diseases and pests) also play a role in the whole complex picture of interactions in a real environment (Spanic et al., 2020). When good agricultural practices are applied (fertilization, plant protection, irrigation), it can be assumed that in the area of interactions, from a breeding point of view, mainly environmental and genetic factors remain for analysis.

In studies related to the establishment of GEI, an analysis is made mainly of the influences of the main factors, as well as their interaction on the performance of a given trait (Saltz et al., 2018; Kang, 2020). The establishment of GEI is a prerequisite before a group of varieties can be assessed in specific environmental conditions (van Eeuwijk et al., 2016). The definition of GEI is becoming increasingly important due to global climate change and the growing share of this interaction on productivity (Xiong et al., 2021). The complex picture of the interaction between environmental factors (season and location) and the biological characteristics or properties of plants is a challenge for researchers in their efforts to find approaches to identify the causes (Mohammadi et al., 2020; Roostaei et al., 2021). In his study, Gabriel (1978) formulated the idea that fitting the least squares of a mixed linear (additive) and bilinear (multiplicative) model provides statistical possibilities for the parallel estimation of different groups of covariates. Subsequently, Aastveit & Martens (1986) show that from the covariances between any variables it is possible to derive additional information about the influence of each parameter, causing variation on the GEI. Denis (1988) identified those covariates (factors) that most significantly cause genotype variability by measuring its differential sensitivity to their changes. Thomas et al. (1993) studied six varieties at six locations in Canada and found direct effects on GEI on stem height, winter hardiness and wheat lodging.

Specialized regression models for analysis of the influence of covariant factors, known as: AMMI (Additive main effect and multiplicative interaction analysis, (Gauch, 1988), FR (factorial regression, Denis, 1988) and PLS (Partial least square regression, Aastveit & Martens 1986) became popular after proving their effectiveness for these purposes in a series of field experiments in GEI-related factors by Vargas et al. (1999). Retrospective follow-up of the publications will show the development of knowledge related to the establishment of complex interactions and effects between environmental, genetic and management factors related to GEI.

Vargas et al. (2001) analysed a database of two field experiments with wheat, which examined three groups of factors: quantitative traits, environmental parameters, and agricultural practices. Both experiments are over a sufficiently long period (7-10) of research and include 14 quantitative characteristics, 4 meteorological parameters and 4 groups of agricultural practices: tillage (2 levels), basic fertilization with manure (2 levels), nitrogen nutrition (3 levels) and predecessors (2 levels). The regression models used and compared (AMMI, FR and PLS) are effective in determining the influence of each factor or combination of factors on GEI. This publication provides a wealth of information on new statistical models. Their use provides real opportunities, by including additional factors of different nature (environmental, genetic and agronomic), to enrich the knowledge of the complex picture of GEI.

Haji & Hunt (1999) found a significant influence on the yield of environmental factors: the minimum and average temperatures in winter and the amount of rainfall during the grain filling in a study of eighteen varieties of winter wheat in different seasons.

Yan & Hunt (2001) for seven seasons in Canada studied a large number of varieties (10-33), in terms of variation of 10 quantitative traits (including disease resistance) against the background of basic ecological parameters: temperature (average, minimum and maximum) and the amount of precipitation. Biological factors: stem height and early maturity and environmental factors: low temperature in winter and high temperature during ripening have a significant share in the impact on GEI.

Reynolds et al. (2002) investigated the role of physiological processes on the yield of common, durum wheat and triticale grown under optimal conditions for six consecutive seasons. The data analysis was performed using the two multi-regression models FR and PLS. The growth and development of the three crops is associated with the main environmental parameters: minimum and maximum temperatures, precipitation, the amount of active temperatures and solar radiation. An analysis of the influence of these environmental factors on yield and quantitative traits directly related to it: TBM, NPT, NGS, TGW and NGm during five stages of growth and development of the studied cereals. Detailed regression analysis proves that about 80% of the magnitude and five of the six traits are influenced by the effects of environmental parameters. They are relatively weakest on the NGS trait (63%). Very detailed information is provided on the impact of each ecological parameter on each trait, in each stage of growth and development of the cereal plant. At the level of the trait, the ranking (rank) of the ecological factors is made, according to their influence on it during the whole vegetation period. The most critical from the point of view of ecological influence is the stage of ear formation, followed by the stage of grain filling, and the strongest is the influence of the average temperature.

Brancourt-Hulmel & Lecomte (2003) studied in France 13 varieties of wheat in 7 environments by analysing, using the AMMI and BIAREG (FR) models, the influence of environmental and genetic factors on GEI. It was found that the yield of wheat grain is mainly influenced by two components, which are formed for two different periods: the number of grains per square meter and 1000 grain weight. Their performance is directly dependent on the variation of temperature, water deficit, and solar radiation, resistance to powdery mildew and resistance to lodging.

Voltas et al. (2005) examined 21 wheat genotypes in Spain for the influence of four environmental parameters (TT-thermal time, DI-drought index, on 5 quantitative traits and scores for tolerance to three diseases. In winter wheat, a strong negative effect of GDD (TT), minimum temperature and tolerance to lodging down directly on the genotype in GEI was found. The maximum temperature after flowering in combination with genetic susceptibility to powdery mildew (score) and the index of drought resistance before flowering, have a strong negative effect on GEI, alone and in combination with each other. The three most stable varieties of each group (winter and spring) wheat are most strongly influenced by the individual effects of TT, Tmin, DI, as well as from the combined effects of lodging x TT, tolerance to PM x DI. Based on these results, they present a scheme for the combination of conditions in which stable varieties would realize to the maximum their genetic potential for grain yield.

Verhulst et al. (2011) attempt to establish the complex nature of management x environment interaction. They analyse the impact of five tillage options in combination with the six main environmental parameters (temperature: minimum and maximum, relative humidity, precipitation, evapotranspiration and solar radiation) on yield variation and two main traits: grain size and number of grains per m^2. These parameters were measured during different stages of wheat development. The interaction between the conditions and options for tillage has a share of 20% (yield and number of grains per m^2) and about 40% at a 1000 grain weight. The share of environmental parameters in GEI in all three traits exceeds 90%. In grain yield, the share of the minimum temperature is the strongest (22%), followed by solar radiation (18%) during flowering and the relative humidity during the ear emergence period (16%). The remaining parameters have a share of about 8-10%, each mainly in the vegetative stages of growth.

Sanchez-Garcia et al. (2012) studied 27 genotypes in eight different environmental conditions (combination of four locations with 2 seasons), which analysed the influence of basic ecological parameters in two vegetation periods: from sowing to heading (Z 55) and from heading to ripening (Z 90). The application of the AMMI and FR models provides definite information on the presence of combined effects between genotype, environment and part of the ecological variants. Three of the studied meteorological parameters: Tmin, GDD, RHmax (relative humidity) interact with both the genotype and the environment, and their individual shares vary from 4 to 16%. Only the RHmax parameter has an effect during the period (Z 90), while the other two parameters have a significant effect during the period up to heading. The mentioned effects affect approximately similarly the studied main components of productivity: NPT, NGS and TGW.

Crossa et al. (2015) present a statistical methodological development in which examples with different levels of GEI complexity are selected. It thus illustrates how to analyse and interpret GEI and how the components of the interaction can be separated by comparisons with biological interpretations. Researchers are offered a professional explanation of how to use interaction information outside of standard statistical tests. Simple SAS codes are provided to perform standard interaction contrasts and determine interaction covariances.

Vargas et al. (2015) describe in detail the analysis of two field experiments related to technological practises and one breeding experiment grown in different environmental conditions. The aim is to demonstrate how to properly apply statistical analyses directly related to the study of the interaction of technology x E (Exp. 1 and 2), as well as to the evaluation and decomposition of the effects of GEI (Exp. 3). The authors provide valuable information on all possible details when applying the main regression models AMMI, FR and PLS, as well as for proper analysis of the results.

Mohammadi et al. (2015) studied 25 durum wheat genotypes in 21 different environmental conditions (combination of seven locations with three seasons) and analysed four quantitative traits and grain yield, as well as seven ecological parameters, during different vegetation periods of the crop. Against the background of the extremely strong influence of the environment (82%) they try to group the varieties in the locations, according to the size of the grain yield. Temperature and precipitation have a markedly strong effect on all traits and through them on the magnitude of GEI. Two of the traits: number of days to heading and number of days to full maturity, have a positive effect, and stem height and weight of 1000 grains have a negative effect on GEI.

Mohammadi et al. (2020) conducted a detailed analysis of 20 durum wheat varieties in order to gather additional information on the interaction of environmental and genetic factors on GEI. As a result of the parallel use of the three statistical models (AMMI, FR and PLS), they found a high share of environmental and climatic factors on the GEI for grain yield. The effects of environmental factors: temperature, rainfall and relative humidity and genetic factors: date of emergence, stem height and weight of 1000 grains, largely determine the stability of varieties. The authors discuss the possibilities for breeding of wheat in connection with the established patterns.

Cooper et al. (2021) review all aspects related to the complex multi-layered nature of genotype x environment x management (G × E × M) interactions. They believe that this type of analysis will make an important contribution to maximizing productivity by skilfully adapting the technology to properly manage the G x M interaction. Climate change further complicates the picture of the interaction. This is the reason to consider the existing possibilities for predicting their combined effects. They believe that by changing the genetics (G), according to the collected objective information about the effect of environmental factors (E) on it, would facilitate the efforts of adequate management (M), through various technological solutions, in specific good studied environmental conditions.

Scientific reports published in the last year show that research on the influence of the main groups of factors described above: environmental variables (temperature, precipitation, humidity, sunshine) (Hilmarsson et al., 2021), biological or physiological traits and genotype-related traits (quantitative traits, early maturity, stem height, biomass) (Katsenios et al., 2021) and agronomic practices such as fertilization, irrigation (Ebadi et al., 2020; Ljubičić et al., 2021) continue to accumulate valuable information on all possible aspects of the GEI.

There is a complete lack of information about the conditions in Bulgaria related to such issues. Studies in wheat are mainly related to the assessment of genotype performance and stability, but not to the influence of external factors on the mechanism of genotype x environment interactions (Tsenov & Atanasova, 2015; Desheva & Deshev, 2021; Dimitrov et al., 2021). This is the reason why an attempt was made on the basis of previously collected data on common wheat to establish an already strong and complex GEI.

The main purpose of this study is to determine whether ecological factors and quantitative traits have effects on genotype x environment interactions (GEI) with respect to grain yield**.** The main tasks that arise from the goal are: *i*) to determine the magnitude and nature of the effects on yield under the genotype by environment interaction in regional trails on common wheat, *ii*) to study the contribution of meteorological factors and components of productivity in this G x E interaction and *iii*) to analyse the role of quantitative traits on the change in yield through their impact on that interaction.

MATERIALS AND METHODS

Plant material and experimental design

Twenty-seven varieties (27) of winter common wheat, created in the last few years by the Agronom breeding company, are the subject of research. The group of varieties was studied in four locations of the country for three consecutive years (Table 1).

Each environment (E) is a combination of the conditions of the location and the year. The reason for adopting this approach to analysis is the established significant differences between the years, in each of one of the locations (Table 2). A similar approach is applied in cases where strong season-

Table 1. General information on the levels of the main factors - Location, Season of testing and Environments in the multi environmental field trails (MET)

Subregion of Bulgaria, Location, District	Coordinates		Altitude	Season	Environment Designation
	North	East			
North East				2016	D16
Paskalevo	43^{0}38’47”	27^{0}48’40”	248	2017	D17
Dobrich District				2018	D18
Central North				2016	S16
Svistov	43^{0}36’30”	25^{0}30’02”	110	2017	S17
V.Tarnovo District				2018	S18
South East				2016	R16
Radnevo	42^{0}17’25”	25^{0}58’26”	140	2017	R17
Stara Zagora District				2018	R18
Central South				2016	P16
Plovdiv, Agri. University	42^{0}08’13”	24^{0}48’22”	155	2017	P17
Plovdiv District				2018	P18

Table 2. Meteorological characteristics in twelve test environments (Location-Year) in the study

	Ecological variables										
Environment	TAmin	TAmax	TA	TAa	TAs	SP	SPa	SPs	GDD	GDDa	GDDs
S16	-9.3	27.4	7.9	3.0	17.5	323	182	141	2514	504	1010
S17	-9.3	27.4	7.9	7.6	22.7	323	122	92	2514	1420	1708
S18	-7.6	29.4	8.4	3.5	18.3	441	257	184	2302	637	1665
D16	-4.7	20.3	9.7	6.0	14.7	374	215	160	2058	710	1348
D17	-0.1	29.1	9.7	6.4	15.8	187	121	67	2763	1226	1538
D18	-3.5	25.9	8.3	4.6	15.6	502	273	229	2347	906	1442
P16	-20.8	34.7	9.7	5.5	16.6	520	331	189	2592	656	937
P17	-9.6	39.2	10.0	8.0	20.7	315	215	242	2973	1504	1984
P18	-9.5	35.4	9.0	5.0	17.5	324	403	133	2771	1066	1706
R16	-13.2	37.0	0.1	6.0	12.5	436	295	141	2161	895	1265
R17	-9.6	39.2	10.1	7.3	15.5	173	191	124	2973	1512	1758
R18	-18.8	34.6	0.3	5.0	18.0	536	150	173	2603	896	1707

TAmax - absolute maximum temperature, TAmin - absolute minimum temperature, TA - average daily air temperature during the whole growing period, TAa - average daily air temperature in autumn subperiod, TAs-average daily air temperature in spring subperiod, GDD-Growing Degree Days during the whole growing period, GDDa -Growing Degree Days in the autumn subperiod, GDDs -Growing Degree Days in the spring subperiod, SP - sum of precipitation during the whole growing period, SPa - sum of precipitation during the autumn subperiod, SPs - sum of precipitation during the spring subperiod al variations are found within the study locations (Brancourt-Hulmel & Lecomte, 2003: Sanchez-Garcia et al., 2012).

At every location, the field experiment was set up in a randomized block of 3 replications at the size of the experimental plot of 10 m^2 (12 rows, 8 m in length, and 10,5 cm. between rows). The planting density of the plants is the standard for the country of 500 germinating seeds per m^2. The experiment was fertilized with 15 kg ha^{-1} N (active substance), twice before sowing and in phase (Z29) by Zadoks et al. (1974) and 12 kg ha^{-1} P (active substance): once before sowing. In order to prevent side effects from diseases and pests, plant protection was applied during the active vegetation. It includes a single application of herbicide and insecticide, as well as fungicide treatment, twice in phases (Z33) and (Z51). The data collected from each plot include quantitative traits related to productivity: GY-grain yield (t ha^{-1}), NPT - number of productive tillers per m^2, NGS-number of grains per spike, TGW -1000 grain weight (g), WGS-grain weight per spike (g), NGm^2-number of grains per m^2 and EED-date of ear emergence (as number of days from 1 January), HI - harvest index and HOS - height of stem (cm).

Experimental conditions

Important for the growth and development of wheat meteorological parameters were measured in each place with the help of a mobile meteorological station (Table 2). A total of 11 parameters were analysed as follows: TA-average daily air temperature, TAmax-average maximum temperature, TAmin-average minimum temperature, GDD-Growing Degree Days (the sum of active temperatures that plants need to grow and develop) (Russelle et al., 1984) and SP-sum of precipitation during the growing season. Three of the parameters that differ significantly by sub seasons: average daily air temperature, growing degree-days and rainfalls (precipitation) quantity are divided into two more groups: values during the autumn-winter period - with designation (a-autumn) and values during the active spring vegetation - with designation (s-spring) – as follows (TAa, TAs; GDDa, GDDs; SPa, SPs). The autumn-winter period lasts from sowing to the end of the tillering stage (Z0-Z29). The spring vegetation period is from the beginning of the stem elongation to ripening stage (Z30-Z99).

Statistical analyses

AMMI model

The statistical method for estimating variance, call AMMI (Additive main effect and multiplicative interaction analysis, (Gauch, 1988) is a model that combines the capabilities of variance analysis (ANOVA) with principal component analysis (PCA), identifies GEI as a source but cannot clearly identify all components of the interaction. Principle Component Analysis (PCA) fails to distinguish the reliable main effects of the genotype of those from the environment. Linear Regression (LR) effectively analyses the interaction only when the data match of the specificity of the regression model and takes into account a small part of the sum of the interaction of the squares (Zobel et al., 1988).The AMMI model separates the additional from the multifactor variance coordinate axes, which explain in more detail the model of interaction and the assessment performed with the help of least squares principle (van Eeuwijk et al., 1996; Gauch, 2006). By applying an additional test in it (Gollob, 1968), the reliable number of principal components (PCA) is determined by the ratio of the mean squares of the data axis and the error of experience. (Pacheco et al., 2015). The results of the AMMI analysis can be represented graphically in the form of a bipolar graph (biplot), in which the results of genotypes and environments of the first two or three main components (PCA) are presented as vectors in space. This is the reason why this model is widely used in research on similar topics

Factorial regression (FR)

The factorial regression (FR) model provides opportunities to include different covariates in explaining the causes of genotype environment interactions (Crosa et al. 1996). By using the differential sensitivity of the genotype to external changes, it provides opportunities to determine those co variations (factors) that most significantly cause the variability of the genotype. Any hypothesis about the influence of external variables on GEI can be tested statistically, which is an exceptional advantage of the model (Denis, 1988). Like any linear model, FR becomes unusable when the number of variables increases because multicollinearity between them increases. In these cases, the Partial least square regression (PLS) model would be significantly more applicable. These basic regularities in the use of regression models have been revealed in a series of multifactor field experiments by Vargas et al. (2001).

Partial least square regression (PLS)

Partial Least Squares regression (PLS) is a model that allows the inclusion of external variables (environmental or genotypic) as part of the GEI (Pacheco et al., 2015). They provide a high degree of collinearity between variables, thus determining which of these external variables affect the interaction (Vargas et al. 1998). Existing covariances between any variables allow additional information to be derived on the impact of each parameter causing variation on GEI (Aastveit & Martens (1986).

All analyses related to the regression models were performed with the GEA-R program (Pacheco *et al.* 2015). The FR model has been applied to meteorological parameters and quantitative characteristics separately in order to avoid the multicollinearity that accumulates when using a large number of covariables. All variables and genotype-related variables are included in the calculation of the PLS model at the same time. This is done in order to directly compare all possible effects on GEI, as well as to determine their direct influences related to the specific environments and genotypes grown in them. The correlations between the individual meteorological parameters and the quantitative characteristics were calculated using the Statgraphic XVIII software. With its help, a graphical representation of the PLS coefficients between them was made.

RESULTS

Grain yield shows a significant change in the different experimental conditions, which is expressed by as many as ten reliably, confirmed main components of variation (Table 3). The predominant part of this variation (86.19%) is due to the growing conditions. The share of the genotype is insignificantly low only 3.12%, which is much lower than that reported in similar studies in barley and durum wheat (Wardofa et al., 2019; Mohammadi et al., 2021). The combined interaction between genotype and environments shows a share of 10.69%, which is also lower than studies in wheat recently (Aktas, 2020; Naik et al., 2022). The number of proven main components is ten (PC10) and their values show a significant predominance of the nonlinear (sum of PC2 - PC10=65.0%) type of variation over the linear one (PC1=32.39%). These results undoubtedly show the complex nature of GEI, although its share of the total variation is only about 10%. Similar results were reported by Ljubičić et al. (2021) with the difference that only two main components of variation have been identified (PC1 and PC2).

Six of the eleven meteorological (ecological) parameters have a significant interaction with the genotype factor (Table 4). Their shares were statistically confirmed by applying the criterion of (Akaike, 1974). The interaction that the selected parameters have on the genotype is similar in magnitude. It can be divided into three groups: with the largest share of influence - TAmin (12.8%) and SPa (12.7%), with a medium share - TAa (10.9%), GDD (9.5%) SPs (10.0%), and TAs, whose share is relatively the lowest one: 8.0%. All other five parameters remain out of the range of statistically significant effects, the shares of which in the GEI range from 6.6% (SP) to 8.6% (TA) (Table 3).

Surprisingly, the TAmax parameter, whose share is 11.3%, dropped out of this group, but according to the accepted selection criterion, it did not move into the group of proven parameters. The situation is similar with the GDDa parameter (9.5%). The probable explanation for this “discrepancy” according to the numerical values of the shares is due to the relatively small differences between the values of the listed parameters in the environments studied (Table 2).

Five of the total number of nine quantitative traits studied, including grain yield, are significantly influenced by environmental conditions (Table 5). This influence as a share is relatively low and varies from 2.8% (Env x WGS) to 7.2% (Env x NGm). For the other three traits, the share of interactions is of the order of about 5% (Env x GY, Env x TGW and Env x HI). The low values of the interaction of the genotype with the individual meteorological parameters explain about ¼ of the whole interaction.

The strongest influence of the environment is on NGm, which is an integral index between the two main components of productivity - NPT and NGS, which did not pass the reliability test (AIC). These two traits, as well as the EED and HOS traits, are not affected by the conditions in this experiment. The probable reasons are the small differences between the studied varieties precisely on these grounds. On

Table 3. ANOVA by Site regression analysis (SREG) for G x E effects*

Source	Sum Sq.	Porcent	Porcenac	*df*	F value	Prob F
Environment	1970.87	86.19	86.19	*11*	1692.29	*0.0000*
Genotype	71.34	3.12	89.31	*26*	25.92	*0.0000*
Genotype x Environment	244.49	10.69	100.00	*286*	8.07	*0.0000*
PC1	102.30	32.39	32.39	*36*	27.02	*0.0000*
PC2	44.41	14.06	46.45	*34*	12.42	*0.0000*
PC3	41.09	13.01	59.46	*32*	12.21	*0.0000*
PC4	31.38	9.94	69.40	*30*	9.95	*0.0000*
PC5	26.62	8.43	77.83	*28*	9.04	*0.0000*
PC6	19.73	6.25	84.07	*26*	7.22	*0.0000*
PC7	13.73	4.35	88.42	*24*	5.44	*0.0000*
PC8	10.65	3.37	91.80	*22*	4.60	*0.0000*
PC9	10.23	3.24	95.03	*20*	4.87	*0.0000*
PC10	7.17	2.27	97.30	*18*	3.79	*0.0000*
Residuals	34.30	3.21		324		

* Gollob's test for determining the number of multiplicative terms (Gollob, 1968). Porcent-percent of the total variability explain, Porcenac -percent of the total variability explain accumulative, Prob F - value of significance of the test ($p<0.001$)

Table 4. Factor regression model steps for meteorological variables according to the Akaike information criterion (AIC)

Effect name	Sum Sq	Df	F-value	AIC*	Pr>F	%GxE *
Gen x TAmin	22.241	26	2.540	1267.9	0.0000	12.8
Gen x TAa	24.841	26	3.440	1174.8	0.0000	10.9
Gen x TAs	34.796	26	3.203	1346.6	0.0000	8.0
Gen x GDD	25.496	26	2.508	1325.5	0.0000	10.5
Gen x SPa	18.788	26	2.291	1242.3	0.0000	12.7
Gen x SPs	24.873	26	2.637	1297.2	0.0000	10.0

*AIC selected model=506.4 (Akaike, 1974)

Table 5. Steps of the regression factor model for genotypic variables according to the Akaike information criterion (AIC)

Effect name	Sum Sq	Df	F-value	AIC*	Pr>F	%GxE *
Env x NGm	23.514	11	5.014	1346.5	0.0000	7.2
Env x TGW	11.562	11	2.640	1321.3	0.0027	4.0
Env x GY	7.797	11	1.809	1310.4	0.0028	5.1
Env x HI	11.553	11	1.888	1268.8	0.0388	4.9
Env x WGS	6.943	11	1.793	1295.4	0.0424	2.8

*AIC selected model =1285.3

the other hand, the WGS, which is in fact an index between the NGS and TGW traits, showed a low, but significant share of the interaction of 2.8%.

The application of the PLS model allows to extract as extensive information as possible, which is related to the direction and magnitude of the influences of the individual main factors (genotype and environment) and covariates (biological and meteorological) in the whole picture of GEI interaction (Figure 1). The effect that each of the meteorological parameters has on the grain yield is different in direction and magnitude. From the point of view of the values of the first two main components, four zones of influence are clearly distinguished.

The first zone in which both components have positive values (top-right), only two parameters (TAmin) and (TA) have any influence. As already mentioned, neither of these two parameters affects GEI, and TAmin is reliable. In this zone the D1, D18 and S16, S18 are situated. It is located in the grain yield point (GY), as well as those of EED, WGS, NGS. Two of the analysed quantitative traits GY and WGS significantly affect the varieties in their reaction to environmental conditions. Varieties whose points are in this zone should be most strongly influenced by the change in TAmin in the environments already indicated. These are the varieties marked: 7, 9, 11, 12, 14, 18, and 22.

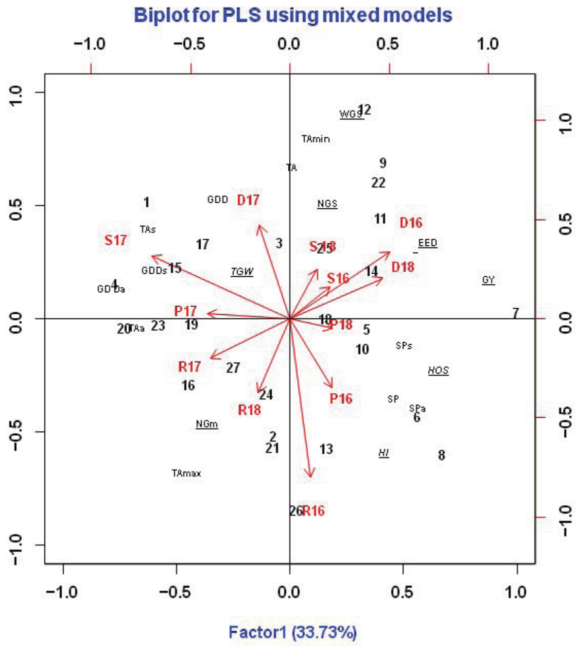

Figure 1. Biplot of the first and second PLS factors, representing X-loadings for 27 wheat varieties and Y-loadings in 12 environments, accompanied by X-loadings of 11 meteorological and 9 genotypic co-variables

The second zone, in which PC1 has positive and PC2 has negative values (bottom right), is characterized by a proven strong influence of the three precipitation parameters (SP, SPa and SPs). It is natural that the amount of precipitation is an important factor for the conditions P16, P18, R18, which differ compared to other environments with larger anomalies of these amounts (Table 2). In this zone is located the points of the HI and the HOS, the values of which should be related to the amount of precipitation in the mentioned environments. Six of the varieties: 5, 6, 8, 10, 13, 26 are related to the influence of precipitation part, by changing mainly the HI and TGW characteristics.

The third zone (top-left), with negative values of PC1 and positive values of PC2, includes several parameters: TAs, GDD, GDDa, GDDs and respectively the trait TGW. Here, in the conditions of environments D17, S17, P17, the sum of active temperatures throughout the growing season (GDD) is the reason for a proven change in GEI in varieties: 1, 3, 4, 15 and 17. The weight per 1000 grains is clearly influenced by the sum of the active temperatures (GDD), as its share on the interaction with the conditions amounts to 4% (Table 5).

The fourth zone, in which both components are negative, the parameters TAmax and TA are located. The first has no significant effect, while the second (TA) causes a change of about 11% (Table 4). The only representative of the quantitative traits is NGm, and its effect on GEI is actually the strongest of all trait studies (7.2%). These two groups of influence can be attributed mainly to varieties 2, 16, 19, 20, 21, 23, 24 and 27, under the conditions of R17 and R18.

The mutual location of the parameters and traits in relation to the locations and varieties is a unique representation of several layers of data (Figure 1). They are extremely useful for direct assessment of the performance of each variety at each location. The localization of the varieties can be related to the influence of ecological parameters on each of them, through the studied traits. Such a discussion is not the purpose of this study.

Several of the analysed environmental parameters have a significant impact on yield (Table 6). The amount of precipitation during the autumn pe-

Table 6. Correlationships between the two main principal components (IPC1 and IPC2) of the AMMI model with the environmental and genotypic variables

Environmental Covariables	GY (r)	PC1	PC2	Genotypic Covariables	GY (r)	PC1	PC2
TAmin	-0.04	-0.27	0.90***	NPT	0.33	-0.22	0.87**
TAmax	-0.56**	-0.12	-0.86**	TGW	0.11	0.23	-0.84**
TA	-0.21	-0.28	0.96***	NGS	0.24	-0.83**	0.51*
TAa	-0.61**	-0.72**	-0.45*	WGS	0.36*	0.91***	-0.24
TAs	-0.47*	-0.68**	0.04	NGm	0.41*	0.50*	0.98***
SP	0.34	0.65**	-0.41*	EED	0.25	-0.58*	-0.56*
SPa	0.41*	0.69**	-0.07	HI	0.75**	0.33	-0.77**
SPs	0.22	0.38	-0.03	HOS	0.13	-0.27	0.33
GDD	-0.12	-0.54**	0.58*				
GDDa	-0.64**	-0.86***	-0.26				
GDDs	-0.47*	-0.72**	-0.07				

*, **, *** - significant at 5%, 1% and 0.1%, respectively

riod SPa has a proven positive effect on the yield (r = 0.41 *). The influence of the other precipitation-related parameters (SP and SPs) on it is also positive, but they have not been proven to be high. The correlations between yield and TAmin (r = -0.04), TA (r = -0.21) and GDD (r = -0.12) are unreliable. A total of six parameters have a marked negative impact on yield: TAmax (r = -0.56 **), the average daily air temperature during the two sub periods, TAa (r = -0.61 **) and TAs (r = -0.47 *), as well as and the sums of the active temperatures during the two studied sub periods: GDDa (r = -0.64 **) and GDDs (r = -0.47 *). These effects on yield, in addition to being diametrically opposed, are related to the two main components of variation of the principal component analysis. Each positive correlation coefficient (r) is mainly related to a positive correlation to PC1, and the negative correlation coefficient is related to a negative correlation, with the specification that not all values are statistically significant. In three of the parameters, opposite values of the correlations between PC1 and PC2 were found: TAmin, SP and GDD. These results show the complex nature of the influence of environmental parameters on yield variation due to GEI. The different directions of correlations with the main components are an indication for a partial explanation of the linear and nonlinear type of influence on GEI.

All studied quantitative traits have a direct positive effect on grain yield. The correlations between GY and the traits WGS (r = 0.36 *), NGm (r = 0.41 *) and HI (r = 0.75 **) have been proven to be high and significant. For both traits, the WGS and NGm indices showed positive correlations with both principal components (PC1, PC2), with the exception of WGS, versus PC2 (-0.24). For NGS and EED, correlations with PC1, are high and negative r = -0.83 ** and r = -0.58, respectively. In the second of these traits EED, as well as in TGW and HI, correlations with PC2 are negative (r = -0.56 *, r = -0.84 **, r = -0.77 **). In NPT all correlations are positive, but only the one with PC2 is reliable (r = 0.87 **). In the case of stem height, all correlations have low and unproven values. A positive change in the WGS leads to a positive change in yield (PC1 = 0.91 ***, PC2 = -0.24) and vice versa. The situation is similar with the trait HI (PC1 = 0.33, PC2 = -0.77 **), whose changes cause adequate changes in grain yield direction. A change in the NGm characteristic can lead to a change in yield in a different direction, because both components have a strong positive correlation (PC1 = 0.50 *, PC2 = 0.98 ***). Probably this is related to the performance of the trait that most strongly determines the values of NGm: NGS. The change in its values could cause a different change in grain yield, because the correlation between it and the two components is diametrically opposed (PC1 = -0.83 **, PC2 = 0.51 *). Environmental conditions, which are to some extent subject to ecological parameters, cause complex and contradictory changes in the quantitative characteristics of grain production. Among them, there are compensatory mechanisms in which an increase in values in some causes an inevitable decrease in others (Tsenov et al., 2021). There is multicollinearity between them, which is the reason why the correlations with the yield have reliable but low values. All these changes, especially in combination with the effects of environmental conditions, cause the strong genotype x environment interaction observed here. Diverse changes in the characteristics create a huge dispersion of data. Precisely due to the compensatory biological mechanisms of the components of productivity, the most successful value of the yield is determined by the integral indices: WGS and NGm.

The specific influence of environmental factors on the quantitative traits is given in Figure 2. It graphically presents the regression coefficients of influence between the parameters and traits for which a reliable interaction with Genotype or Environments has been established (Tables 4 and 5). Each of the environmental parameters has some influence on the selected quantitative characteristics. At the 1000 grain weight, all environmental parameters have a pronounced negative effect, being the strongest of TAs and negligible of TAmin. In the case of HI, the stronger negative effects of TAmin, TA and SPs predominate, against the background of the positive effects on it from: TAs, SPa and GDD. In fact, this trait is the most controversial, as a change in terms of the direct effects of environmental factors on it.

In WGS, the positive effects of TAmin, TA, TAs, and GDD predominate, against the background of the negative effects of SPa, SPs, which as sum are significantly weaker than the positive ones. In the case of NGm, the two parameters TAmin, TAs, have a negative effect, and GDD, SPa and SPs - a positive effect. The TA parameter generally has no effect on it.

DISCUSSION

The variation in yield as a result of the studied factors in this experiment is huge (Table 3). The share of genotype in the yield variance in this study is very low (3.12%), and when interacting with environmental conditions it reaches about 14%. The GEI interaction is strongly non-linear due to the fact that the first principal component has a value of about 1/3 (32.39%). The rest of it covers as many as 10 main principal components that are statistically significant. The characteristics found here for the influence of genotype, environment and GEI are very similar to a number of other studies in wheat (Chamurliyski et al., 2015; Mohammadi et al., 2020; Aberkane et al., 2021). Another group of studies (Desheva & Deshev (2021; Dimitrov et al., 2022) reported a relatively strong share of "Genotype" in

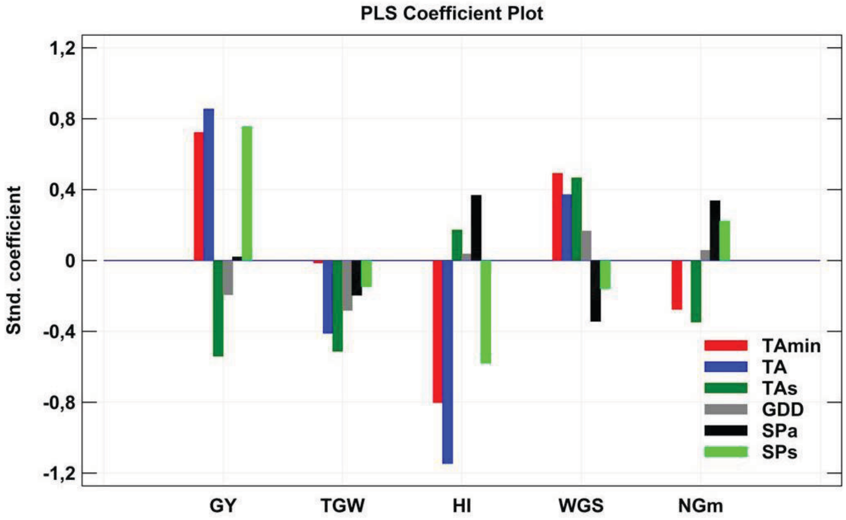

Figure 2. Partial Least Square regression (PLS) coefficients of the proven effective ecological variables onto the grain yield and genotypic quantitative characteristics

variation (30-40%), with the proviso that in them only the conditions of the year are factor (E). Similarly, strong and varied yield variations (> 5 major PCA components) have been reported in a number of similar studies (Mohammadi *et al.,* 2020; Verma et al., 2021; Pour-Aboughadareh et al., 2022). The numbers of varieties or the contrasting conditions of the seasons between the study locations are probably the reason for that strong variation.

Genotype as a factor in GEI is influenced by several environmental parameters (Table 4). Four of them are related to temperature (TAmin, TAa, TAs, GDD), and another two to the sum of precipitation (SPa and SPs). The effects of each of them have a share of about 10% (TAs = 8.0% - TAmin = 12.8%) which in sum is approximately 65% of the genotype variation. Individual indicators of temperature and rainfall during different periods are quite natural to have an effect on the genotype factor. The main question that is always on the agenda is: what is the magnitude and direction of this impact. All publications, in which TAmin has been analysed, report a proven effect on genotype (Yan & Hunt, 2001; Verhulst et al., 2011; Mohammadi et al., 2020). Voltas et al. (2005) and Sanchez-Garcia et al. (2012) found the most stable varieties of the studied group are most strongly influenced by active temperatures (GDD), compared to other environmental factors. According to the research of Mohammadi et al. (2015) and Cooper et al. (2021), the role of precipitation is decisive for changes in the genotype and magnitude of its grain yield. All major environmental parameters, such as temperature, precipitation, and solar radiation, influence grain formation in the critical stages of wheat development (Reynolds et al., 2002; Brancourt-Hulmel & Lecomte 2003).

Grain yield as a trait is naturally the most studied, and in various studies it is associated with the change of a different set of traits, which according to the authors are decisive for it: a 1000 grain weight and number of grains per m^2 (Reynolds et al., 2002; Verhulst et al., 2011), date of emergence and stem height (Yan & Hunt, 2001; Mohammadi et al., 2015). Five of the 9 traits analysed here are significantly influenced to some extent by environmental conditions (Table 5). NGm is the trait on which the conditions have the highest share of 7.2%. The performance of that trait determines to a very strong extent the size of grain yield (Reynolds et al., 2002; Brancourt-Hulmel & Lecomte 2003; Verhulst et al., 2011). The share of change of the other traits is about 5%, for each one, and for the WGS this share is only 2.8%. The sum of all identified effects on yield is about 25%, which is a serious influence on the part of the studied traits.

The direct influence of quantitative traits on yield as well as the nature of their correlations through the main components of PCA is different (Table 6). The TGW, WGS and HI have the most serious positive impact on yield, both directly and through interaction with environmental conditions. The positive correlation with PC1 and/or simultaneously the negative correlation with PC2 indicates that the direction of change of each of them causes a change in yield in the same direction. In this respect, the effects of WGS and HI are the most serious. The change in NGm, which has the strongest share on yield (7.2%), can have both positive and negative effects on it. The change in the EED character has an ambiguous effect on yield (correlations with PC1 and PC2 are negative). This is a signal for a specific, according to conditions performance of the trait, leading to a different impact on yield. These complex relationships between the two traits have been described in detail in a previous study (Tsenov et al., 2021). Changes in NPT and NGS values may cause opposite changes in grain yield due to their negative correlations with PC1 and significantly high positive correlations with PC2. In this study, the height of the stem is a trait, the change of which according to the conditions does not have a significant effect on grain yield. The regularities established here with regard to precisely these characters are largely analogous to those in the studies of Reynolds et al. (2002) and Sanchez-Garcia et al. (2012).

Environmental factors that have been shown to be effective for genotype yield also affect some of the studied traits (Figure 2). This reveals the complex picture of the combined impact of environmental and genetic factors on grain yield, as an integral quantitative character. A change in temperature can cause a positive (NGm) or negative effect on the traits (WGS and HI). The sum of the active temperatures has a positive effect on almost all the presented traits, except for TGW. The amount of precipitation during the autumn period has a negative effect on TGW, WGS, and positively on NGm. The sum of precipitations during the spring active period has a positive effect only on NGm, while on other traits has a negative effect. A similar multi-layered interpretation of the possible link between ecological and genetic parameters was made by Reynolds et al. (2002). They found that the average temperature during the different stages (vegetative and generative) affected all the traits discussed here. This has become an additional motive for the data to be analysed in a similar way to their research.

The regularities discussed in detail outline a really complex picture of the mutual influences between environmental, genetic and basic factors (E, G) in wheat cultivation. Undoubtedly, in case of strong changes in the parameters determining the appearance of the environment (E), the changes that occur in the individual traits are different in value and direction in order to be able to predict the level of yield. The complex interactions between the groups of covariates still give some picture of the influences such as magnitude and direction. This picture (Figure 1) gives a clear idea of the relationships between the parameters in the specific field trail. Additional useful information on the performance (stability) of specific varieties at these locations and their zoning could be derived from it. This was deliberately not discussed due to the intention to show the possibilities for gathering additional information on the GEI concerning the types of interactions involved. The regularities revealed here are accepted as an additional opportunity in the future to make this analysis routine for any field trail related to the study of the peculiarities of GEI. The accumulated knowledge of the established patterns is also important for the assessment of specific varieties in terms of yield stability or other quantitative characteristics.

CONCLUSIONS

Climatic parameters, TA, TAmin, TAmax, GDD SPa and SPs have a serious influence on the genotype in their GEI in terms of grain yield.

Environmental conditions, in turn, have a direct and significant strong impact GY and on five of the studied quantitative traits (TGW, WGS, HI, NGm), changes in which largely determine the magnitude and variability of yield in the studied environments.

The application of the three popular regression models (AMMI, FR and PLS) provides additional information on the complex interactions of the main factors directly or indirectly influencing the two classical basic factors (E) and (G) and their combination (GGE). Their efficiency and accessibility through software products is a prerequisite for future research on increasingly complex combinations of factors, recently referred to as G x E x M (Management).

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