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Yield Phenotypic Plasticity and Stability in Semidwarf Winter Wheat (*Triticum aestivum* L.) Cultivars

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ABSTRACT

Based on the analysis of yield variation observed for nine semidwarf wheat cultivars tested in sixty three yield trials that covered diverse environmental conditions, we consider that, for better description of cultivar response to environments, phenotypic plasticity should include, along with the slope of Finlay-Wilkinson regression, a parameter describing the position of the regression line. The minimum yield predicted by regression at the lowest observed trial average proved to be preferable, as it has more biological sense than the regression intercept, which imply the existence of negative yields, and is more reliable than the observed minimum yield, which is based on results of only one trial. The analyzed cultivars showed large variations in these two components of plasticity, which were not correlated with one another.

Yield stability, as described by the coefficient of variation was not correlated with regression slope but was significantly correlated with the minimum predicted yield.

Cultivar FDL Columna combined a high regression slope with high minimum predicted yield and lower than average coefficient of variation, while cultivar FDL Consecvent had lower regression slope, combined with good minimum yield and the best yield stability. Both these cultivars had top rankings across the entire range of recorded yield levels, while other cultivars ranked at the top only at high yield levels (Ursita), or at lower yield levels (Glosa).

Keywords: wheat, yield, variation, plasticity, stability.

INTRODUCTION

The availability of resources and of conditions that determine plant performance is extremely variable, and climate change amplifies this variation. Plants respond to the variation in environments through environmentally induced shifts in phenotype (**phenotypic plasticity**). Understanding this plastic response "is crucial for predicting and managing the effects of climate change on native species as well as crop plants" (Nicotra et al., 2010).

Bradshaw (1965) defined *phenotypic plasticity* as "the amount by which the expressions of individual characteristics of a genotype are changed by different environments" and showed that "the plasticity of a character is an independent property of that character and is under its own specific genetic control". Kusmec et al. (2018) defined phenotypic plasticity as "the ability of a single genotype to produce different phenotypes in different environments", and Grogan et al. (2016) showed that "phenotypic plasticity describes the range of phenotypes produced by a single genotype in different environments".

Environments are characterized both by predictable sequences of change in environmental variables such as photoperiod and seasonal temperature, but also by random variation in level and timing of optimal, suboptimal, or extreme temperatures, in nutrient availability, in disease pressure, etc. Phenotypic plasticity describes the way plants respond to all these changes.

Although plasticity has been originally described for natural plant populations in a small number of environments, the concept has also been applied to crop performance over multiple environments.

Two approaches have been used to quantify phenotypic plasticity:

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- Sadras et al. (2009), Grogan et al. (2016), Adams et al. (2025) and others used the stability parameter described by Finlay and Wilkinson (1963) as the linear regression coefficient of the genotype mean in each environment on the overall mean for each environment, and
- Dingemanse et al. (2010) used the ratio of the variance of the trait for each cultivar to the overall phenotypic variance of all tested cultivars.

On the other hand, **yield stability** is a desirable trait for any crop, and balancing genome stability and phenotypic plasticity should be an important breeding objective (Jaligot and Rival, 2015). Many methods have been proposed for quantifying yield stability (Wricke, 1962; Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Shukla, 1972; and others).

Lin et al. (1986) compared ten stability statistics and categorized them into four groups and three types. Cheshkova et al., (2020) analyzed seventeen stability statistics and categorized them into five groups. They concluded that choosing the most appropriate method depends “on whether the breeding is to be based primarily on yield, primarily on stability, or simultaneously on yield and yield stability.

Mustăţea et al. (2009) studied the yield stability of fourteen Romanian wheat cultivars, along with the historical check Bezostaya 1, tested in fifty-two environments during the period 2002-2007, but phenotypic plasticity of Romanian wheat cultivars has not been so far object of an analysis.

In this paper we analyzed yield variation of nine semidwarf wheat cultivars from the point of view of phenotypical plasticity and yield stability, trying to understand the differences between cultivars, and to identify the best cultivars and the most useful approach for breeding resilient high yielding cultivars.

MATERIAL AND METHODS

We used yield data obtained for nine winter wheat cultivars in sixty-three yield trials conducted countrywide during the period 2021-2024, on 5 or 10 m^2 plots in three replications. The trials were conducted with the crop management recommended for each environment, including the recommended Nitrogen fertilization, which varied from 82 to 143 kg N/ha.

The testing sites included: the Agricultural Research and Development Station (ARDS) Valu lui Traian (44º16’ N, 28º51’E), National Agriculture Research and Development Institute (NARDI) Fundulea (44°30`N, 26°51`E), ARDS Teleorman (44°07’N, 25°45’E), ARDS Mărculeşti (44°25′N, 27°29′E), ARDS Brăila (45°16′N, 27°57′E), ARDS Piteşti (44º81’N, 24 º86’E), Craiova University - Agricultural Research Station Caracal (44º11’N, 24º37’E), ARDS Șimnic (44°20′N, 23°49′E), ARDS Lovrin (45°57’N, 20°46’E), ARDS Oradea (47°02’N, 21°54’E), ARDS Livada (47°52’N, 23°08’E), ARDS Turda (46º58’ N, 23º78’E), Research and Development Station for Cattle Breeding (RDSCB) Târgu-Mureş (46°32’N, 24°33’E), ARDS Secuieni (46ºN, 26º 86’E), and ARDS Perieni (46°18′N, 27°37′E).

These testing sites covered a large diversity of soils, from chernozem to luvisol with pH from 5.02 to 7.6, and humus content from 1.71 to 3.6%.

Weather conditions during the period 2021-2024 at all sites reflected present climate changes and were diverse, as illustrated by rainfall, which varied from 211.2 to 613.8 mm/year.

Cultivars included in our study were semidwarfs released from the National Agricultural Research and Development Institute Fundulea during 2005-2025 (Glosa, FDL Miranda, Otilia, Pitar, Voinic, Ursita, FDL Abund, FDL Consecvent and FDL Columna).

We quantified phenotypic plasticity using the linear regression coefficient of the genotype mean in each environment on the overall mean for each environment (according to Finlay and Wilkinson, 1963), and the ratio of the variance of the trait for each cultivar to the overall phenotypic variance of the all tested cultivars (according to Dingemanse et al., 2010).

We analyzed the correlations between the regression slope and parameters that describe the position of the regression line, such as the regression intercept, the minimum yield observed in any of the trials and the minimum yield predicted by regression at the lowest recorded average trial yield.

To characterize yield stability we used four statistics that illustrate different definitions of stability, belonging to different groups as described by Lin et al. (1986). These statistics included:

- The phenotypic standard deviation (s_i) of cultivar *i* yields across the *j* environments $[s_i = \sqrt{\sum (xi_j - x_{i.})^2/(q-1)}]$, and the coefficient of variation $(s\% = s_i / x_{i.} * 100)$, representing Group A;
- Wricke's ecovalence $[W_i^2 = \sum (x_{ij} - x_{i.} - x_{.j} + x_{..})^2]$, representing Group B;
- The coefficient of determination (R^2), a deviation parameter provided by the "regression analysis" tool in the Excel software, which is very closely correlated (r=-0.98***) with the deviations from regression after Eberhart and Russel (1966), as representing Group D.

In the above formulas xi_j is the yield of cultivar *i* in the environment *j;* $x_{i.}$ is the yield of cultivar *i* averaged over all environments, $x_{.j}$ is the average yield of all cultivars in environment *j*, and $x_{..}$ is the average yield of all cultivars over all environments.

We did not analyze as stability statistics the methods included by Lin et al. (1986) in the Group C, which includes the Finlay-Wilkinson regression, as they describe more the responsiveness to environments than the stability. In fact, the Finlay-Wilkinson regression slope was accepted by many researchers as a measure of phenotypic plasticity.

In addition, we also used the variance of ranks, one of the non-parametric stability statistics proposed by Huehn (1990).

We used Pearson's correlation coefficients to analyze the relationship between phenotypic plasticity and the stability parameters.

To obtain a clearer understanding of yield stability and the adaptation of the analyzed cultivars to different levels of environmental conditions favorability, we grouped the yield trials according to the trial average yield, from less than 4000 kg ha^{-1} to more than 9000 kg ha^{-1} and established the ranking of the cultivars for each group.

RESULTS AND DISCUSSION

The large diversity of environmental conditions present in the analyzed yield trials was reflected in the yield range from 2217 to 11961 kg ha^{-1}. Environments were the main source of variation, but cultivars and interaction between cultivars and environments were also significant sources of variation (Table 1).

Table 1. Source of variation contribution to the total sum of squares from ANOVA for the sixty-three yield trials with wheat cultivars

Source of Variation	Percent contribution	p value
Environments (site-years)	81.2	<0.0001
Cultivars	2.9	<0.0001
Cultivars*Environments	7.9	<0.0001
Residual	8.0	
Total	100.0	

The percent contribution of each variation source was calculated using ANOVA sum of squares (SS) as: Percent contribution = [SS (source)/SS (total)] × 100.

The range of plasticity for yield measured by the regression slope was 0.94 to 1.08, while the variance ratio varied from 0.94 to 1.21. As the two measures of plasticity were strongly correlated (R^2=0.89), we only used for further analysis the regression slope according to the Finlay-Wilkinson approach, which has the advantage of better illustrating the yield variation, "of being computationally simple, applicable to unbalanced datasets (within reason), and requiring nothing more than yield data" (Adams et al., 2025).

We selected six cultivars for graphical presentation of regression results, as examples of different responses to environment (different combinations of regression slopes and regression line positions) across Romania (Figures 1 and 2). Regressions of cultivars FDL Columna, FDL Abund and FDL Miranda had similar slopes, but were positioned differently (Figure 1). On the other hand, cultivars FDL Consecvent, Ursita and Pitar had different regression slopes, as seen in Figure 2.

Obviously, to describe the cultivar responsiveness to environments, and therefore the phenotypic plasticity, one should consider both the regression slope and the position of the regression line. This agrees with Adams et al. (2025) who stated that "along with the regression slope, the practical picture of variety performance is not complete without taking the regression intercept into account".

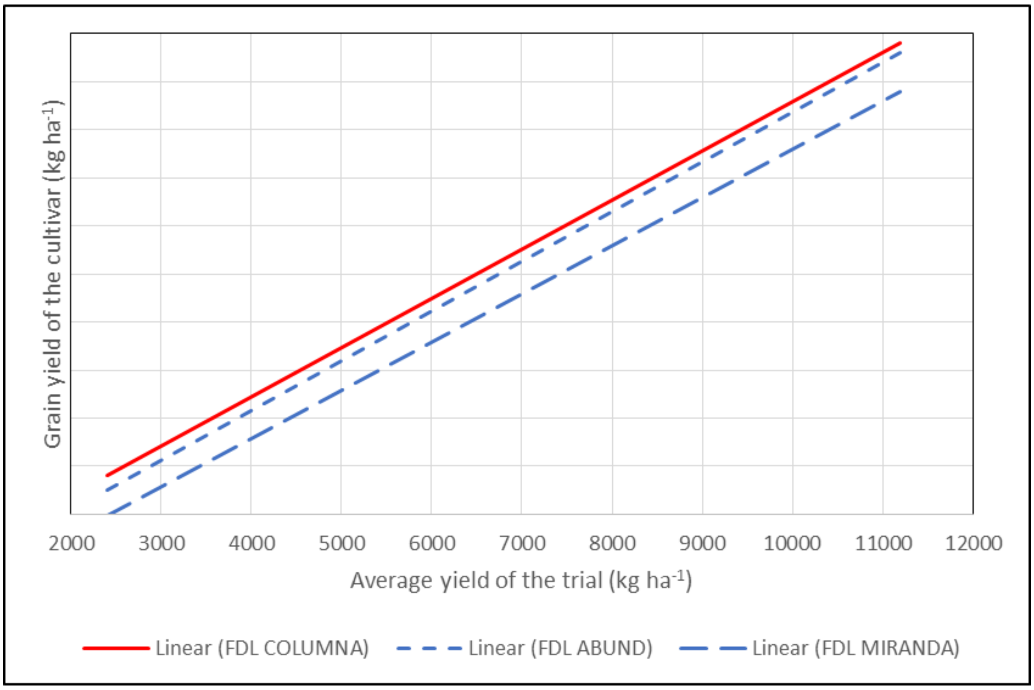

Figure 1. Regressions of FDL Columna, FDL Abund and FDL Miranda yields on the average yield of the trial

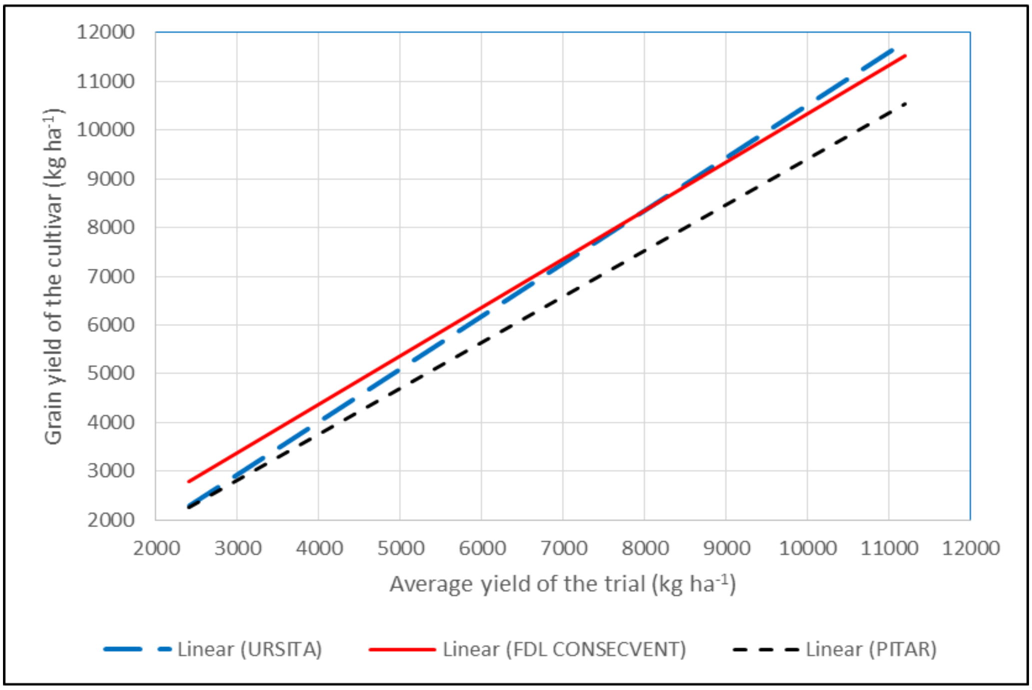

Figure 2. Regressions of FDL Consecvent, Ursita and Pitar yields on the average yield of the trial

In the context of recent climate changes, cultivar performance in unfavorable conditions is of particular interest. For this purpose, many researchers have used the intercept of the regression line (Grogan et al., 2016; Adams et al., 2025). However, the intercept is an extrapolation beyond the recorded range of variation, and this implies the existence of negative yields, which is biological nonsense. Therefore, we analyzed two alternatives to the intercept, namely the lowest observed yield, and the minimum yield predicted by regression corresponding to the lowest trial average yield. These are presented in Table 2, along with the intercept and the cultivar yield averaged over all site-years.

Table 2. Regression slope (b) and parameters describing the position of the regression line in nine wheat cultivars

Cultivar	b	Regression intercept (a)	Lowest observed yield (kg/ha)	Predicted minimum yield (kg/ha)	Average yield (kg/ha)
Ursita	1.083	-314	2411	2295	7348
FDL Abund	1.037	2	2261	2499	7335
FDL Columna	1.027	321	2620	2794	7583
FDL Miranda	1.006	-465	2217	1958	6650
FDL Consecvent	0.995	378	2521	2775	7420
Voinic	0.979	102	2658	2460	7024
Otilia	0.970	-1	2394	2336	6861
Glosa	0.961	-18	2305	2298	6782
Pitar	0.942	-4	2193	2265	6657

Cultivars Ursita, FDL Abund, FDL Columna and FDL Miranda had regression slopes higher than one, but contrasting intercepts, from -465 in FDL Miranda to +321 kg ha^{-1} in FDL Columna. Similar differences between these two cultivars were observed for the lowest observed yields (from 2217 to 2620 kg ha^{-1}) and for the minimum predicted yields (from 1958 to 2794 kg ha^{-1}). Highest yields in unfavorable conditions were recorded in cultivars FDL Columna and FDL Consecvent, which differed in the regression slope, suggesting lack of correlation and possibilities of combining the two traits.

Indeed, the regression slope was correlated with the average yield, but not with the parameters describing the cultivar performance in the most unfavorable environments (Table 3). The minimum yield predicted by regression at the lowest trial average yield was very closely correlated with the intercept and also significantly correlated with the observed minimum yield.

Table 3. Correlation between regression slope (b) and parameters describing the position of the regression line

	Slope (b)	*Intercept (a)*	Lowest observed yield	Minimum yield predicted by regression
Regression slope (b)	1			
Regression intercept (a)	-0.25	1		
Observed minimum yield	0.29	0.62	1	
Minimum yield predicted by regression	0.15	***0.92***	**0.70**	1
Average yield	**0.68**	0.54	**0.76**	***0.82***

Coefficients written in **bold** are significant at P<0.05.
Coefficients written in ***bold italic*** are significant at P<0.01.

Figure 3 illustrates the fact that, for the analyzed cultivars and the environmental range included in our study, no correlation was observed between the regression slope and the minimum predicted yield. Cultivar FDL Columna combined elevated levels of responsiveness to favorable environments with high yields in the worse conditions. This contradicts the statement of Sadras et al. (2009) who, based on data from very diverse environments in Mexico, concluded that “high yield plasticity was an undesirable trait as it was associated with low yield in low-yielding environments”, but agrees with Grogan et al. (2016) who found that “plasticity was not associated with an yield penalty under suboptimal conditions”.

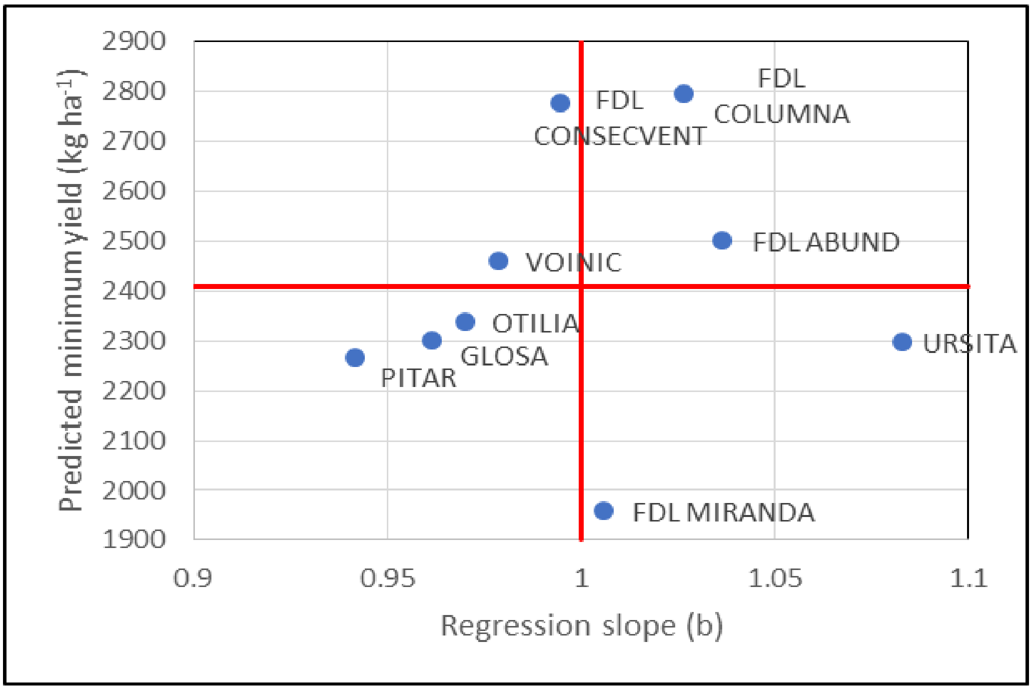

Figure 3. Relationship between phenotypic plasticity (b) and the predicted minimum yield

The wheat cultivars showed a large variation of the analyzed stability parameters (Table 4).

Table 4. Regression slope and stability parameters of nine wheat cultivars

Cultivar	b	R^2	Standard deviation	s%	Rank variance	Ecovalence
Ursita	1.083	0.94	*2013*	27.39	4.79	16023223
FDL Abund	1.037	0.91	1965	26.79	5.37	23012184
FDL Columna	1.027	*0.87*	1987	26.21	4.34	*32442836*
FDL Miranda	1.006	*0.87*	1940	*29.17*	*5.67*	29238732
FDL Consecvent	0.995	0.90	1889	**25.47**	5.54	21508918
Voinic	0.979	**0.96**	1803	25.67	4.59	**8571710**
Otilia	0.970	0.94	1800	26.24	**4.11**	11353476
Glosa	0.961	0.92	1808	26.65	4.41	16528984
Pitar	0.942	0.92	**1767**	26.54	4.53	15442493

Values considered to be the best are written in **bold.**
Values considered to be the worst are written in *italic.*

The regression slope was closely correlated with the standard deviation of yields but was not correlated with the other analyzed stability parameters (Table 5). As expected, the standard deviation of yields was correlated with the average yield, as was the regression slope. The share of variation explained by the relationship between individual cultivar yields and the average yield of the trial (R^2) showed a remarkably close negative correlation with the cultivar contribution to the interaction variance (ecovalence). The coefficient of variation (s%) showed significant negative correlation with the minimum predicted yield, being the stability parameter that reflected better the performance in unfavorable conditions.

Table 5. Correlation between yield phenotypic plasticity (b) and stability of nine wheat cultivars

	b	R^2	Standard deviation	s%	Rank variance	Ecovalence
b	1					
R^2	-0.19	1				
Standard deviation	***0.94***	-0.51	1			
s%	0.30	-0.38	0.39	1		
Rank variance	0.32	-0.44	0.43	0.42	1	
Ecovalence	0.38	***-0.98***	**0.67**	0.41	0.45	1
Average yield	**0.68**	-0.23	**0.68**	-0.41	0.11	0.35
Minimum predicted yield	0.15	-0.16	0.18	**-0.79**	-0.10	0.18

Coefficients written in **bold** are significant at $P<0.05$.
Coefficients written in ***bold italics*** are significant at $P<0.01$.

Figure 4 illustrates the lack of correlation between the regression slope (b) and the stability measured by the coefficient of variation (s%). Cultivar FDL Columna showed a rare combination of regression slopes higher than one and lower than average coefficient of variation. Figure 5, which illustrates the relationship between the regression slope and stability measured by the variance of ranks, offers a similar picture, showing the same outstanding combination of high plasticity and stability of cultivar FDL Columna.

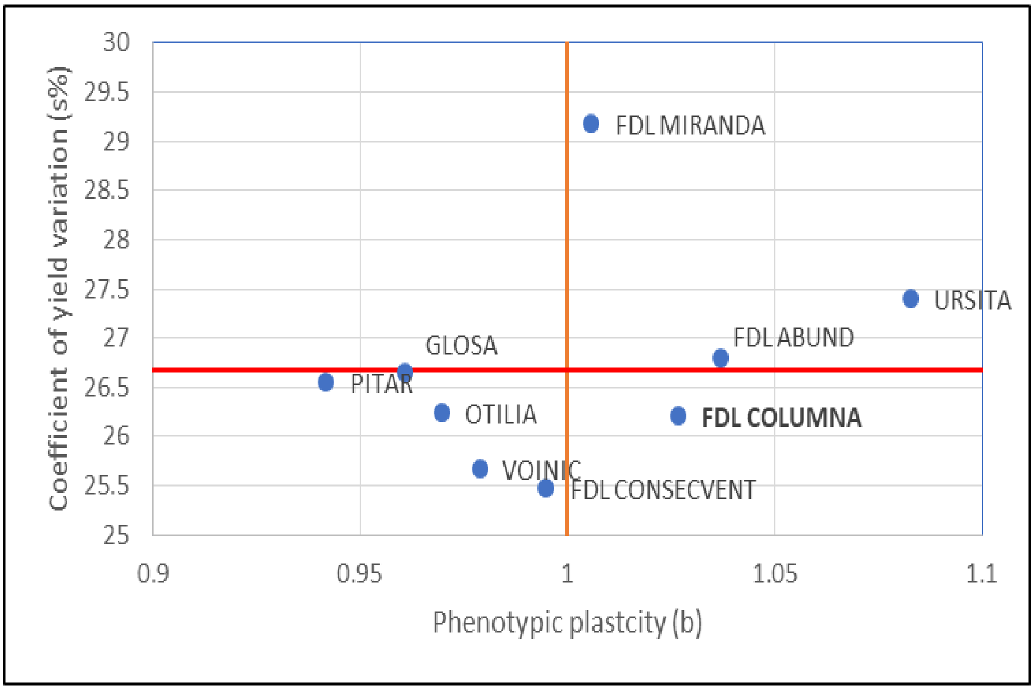

Figure 4. Relationship between yield phenotypic plasticity and stability, measured by the coefficient of variation

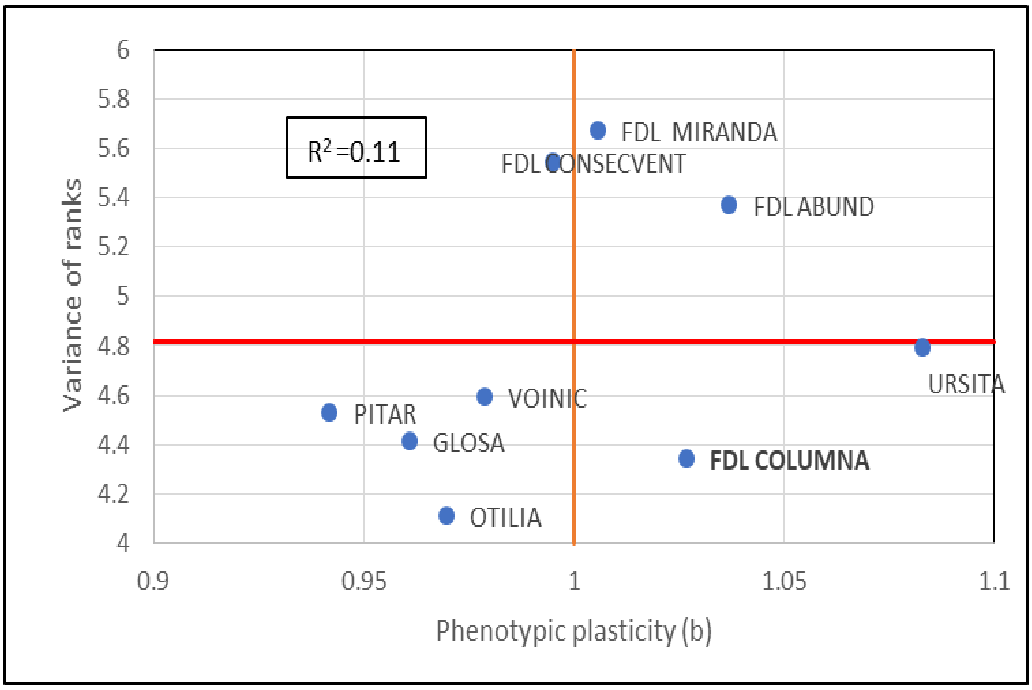

Figure 5. Relationship between yield phenotypic plasticity and stability measured by the variance of ranks

More information about cultivar stability can be obtained by analyzing their ranking at various yield levels (Table 6). The yield stability of FDL Columna in the analyzed trials is confirmed by its top ranking at average trial yields from less than 4000 kg ha^{-1} to 9000 kg ha^{-1}. In contrast, Ursita showed large rank variation, being placed in the eight position in unfavorable conditions and on the top two positions at average yields over 8000 kg ha^{-1}, while Glosa had better ranking at low yields than at high yields.

Table 6. Cultivar ranks for yield at various levels of trial average yields

Cultivar	Ranges of trial average yield					Average rank
	<4000	4001-6000	6001-8000	8001-9000	>9000	
FDL Columna	1	1	1	1	2	1.20
FDL Consecvent	2	2	2	4	4	2.80
FDL Abund	5	3	3	3	3	3.40
Ursita	8	4	4	2	1	3.80
Voinic	3	5	5	5	5	4.60
Glosa	4	7	7	6	8	6.40
Otilia	6	6	6	8	7	6.60
FDL Miranda	7	9	9	7	6	7.60
Pitar	9	8	8	9	9	8.60

Analysis of yield variation observed in wheat cultivars tested in diverse environments confirmed the opinion of Adams et al. (2025) that the Finlay-Wilkinson regression slope is not sufficient for a comprehensive description of phenotypic plasticity. Our results suggest that phenotypic plasticity should include, along with the regression slope, the minimum yield predicted by the regression at the lowest observed average yield of the trial. This parameter has more biological sense than the regression intercept, which, being defined as the yield of a particular cultivar when all cultivars average at a particular site equals zero, implies existence of negative yields, and is more reliable than the minimum observed yield, which is based on only one trial.

In our attempt to understand the relationship between phenotypic plasticity and stability, we faced the challenge of choosing the most meaningful stability parameter. Our data suggested that Wricke's ecovalence is in fact a measure of similarity of a particular cultivar response to environments with the average response of all cultivars, implying that this average response is the most desirable, and this might not be true. The coefficient of determination (R^2) and the correlated deviations from regression after Eberhart and Russel (1966), are in fact measures of predictability, quantifying the extent to which the regression explains the observed variation, and not the yield stability. The standard deviations, as well as the variance of yields across the environments, reflect stability, but are too much influenced by the average, as it is obvious that the higher the average is, the larger the variation can be. The coefficient of variation (s%), being the ratio between standard deviation and the average yield, makes the necessary correction and for this reason we consider it the most suitable stability parameter. It proved to be not correlated with the average yield and showed a significant negative correlation with the minimum predicted yield. According to Jalaluddin and Harrison (1993) only *b* and *s%* were repeatable across subsets of environments, and according to Ortiz et al. (2001) *s%* had the highest narrow-sense heritability (h^2=0.522). Mustăţea et al. (2009) also considered that plotting *s%* against average yield can be most useful in identifying cultivars with high and stable yield.

Yield stability quantified by the coefficient of variation was confirmed by cultivar rankings across the range of trial average yields from less than four to more than nine t ha^{-1}. Cultivars FDL Columna and FDL Consecvent had top ranks across all yield levels.

CONCLUSIONS

- Phenotypic plasticity should include the minimum yield predicted by regression at the lowest observed trial average, along with the widely used regression slope.
- The analyzed semidwarf cultivars showed large variations in these two components of plasticity, which were not correlated with one another.
- Yield stability, as described by the coefficient of variation was not correlated with regression slope, but was significantly correlated with the minimum yield predicted by regression.
- Cultivar FDL Columna combined regression slope above one with high minimum predicted yield and lower than average coefficient of variation. Cultivar FDL Consecvent had a regression slope of less than one, combined with good minimum yield and the best yield stability. These characteristics, along with the high average yields, recommend cultivars FDL Columna and FDL Consecvent as potential tools for obtaining high and stable yields in most environents found in Romanian wheat growing farms.

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