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CROP PRODUCTION

Ecological Variability, Stability, and Plasticity of Winter Rye on Grain Quality Features

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Abstract—Results of studying the correlation dependence and ecological variability of grain quality features of 18 varieties of winter rye grown in 2014–2019 in a wide range of the weather factors are presented. The following features were studied: the water extract viscosity (WEV), the falling number (FN), the amilogram height (AH), shape stability of hearth bread (H/D), starch gelatinization temperature (T, °C), quality of pan bread's crumb, bread volume, grain nature, weight of 1000 grains, and the content of protein and starch in grain. Coefficient of an ecological variation (*CVe*), phenotypical stability (SF), ecological plasticity b_i, and coefficient of heritability H^2 were calculated for each feature. It is shown that the level of quality of toppling and square loaf from rye was authentically defined by the amilogram height, falling number, temperature of starch gelatinization, and viscosity of water extract (r = 0.48–0.83). Amilogram height and falling number most strongly varied under the influence of weather conditions of the year. The Alfa variety with high FN and high-viscosity population GK-494HV had the best baking qualities. Low-viscosity population GK-614LV was steadily distinguished from the worst varieties. It is shown that the high potential of WEV is an important feature improving the baking properties of rye grain. The adaptive potential of GK-494HV and GK-614LV populations was compared. It resulted in a tenfold divergent selection on the basis of WEV. It is established that repeated divergent selection on WEV correlatively changed many features defining baking properties of rye grain. The trend towards decrease in ecological and phenotypical stability of the main (closely correlating) features of grain quality with a simultaneous increase in their ecological plasticity was a typical feature of the selection performed. At the same time, the ecological variation of features at minus selection increased stronger than at plus selection.

Keywords: winter rye, variety, feature, ecological variation, correlation, phenotypical stability, ecological plasticity, baking qualities

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INTRODUCTION

It is known that the baking qualities of rye depend on the state of the carbohydrate-amylase complex of the grain [1]. Rye flour differs from wheat flour in its relatively high carbohydrate content, relatively low starch gelatinization temperature, and high activity of amylolytic enzymes. For this reason, rye grain with a low swelling capacity of starch, which is not able to bind all the moisture of the dough and reduces its baking qualities, is formed in some years. It is also important that lactic acid fermentation (not alcoholic one as in wheat) dominates in rye when kneading the dough. The proteins of this crop dissolve easily in sour dough and do not form a coherent gluten complex [2].

The main biochemical components of rye grain are starch, proteins, and pentosans (nonstarch saccharides). The carcass-forming role in rye bread is played by pentosans, the content of which is 7–10%, which is much higher than that in other cereals [3]. Approximately 40% of the total amount of pentosans in rye flour is water-soluble. They are distinguished by their high water-holding capacity, which is decisive for their suitability for baking. When flour is mixed with water, they quickly swell, bind water, and form a dough. If there are few pentosans, then rye flour has a low water absorption capacity and a low viscosity of the dough, which, with a high activity of alpha-amylase, does not have sufficient strength to maintain its shape during proofing and baking bread [4].

The role of pentosans in baking has not been clarified for a long time, and varietal differences in their content have not been studied. Data have appeared only in recent years that the baking, feed, and technological qualities of grain strongly depend on the level of pentosans, especially their water-soluble fraction [5–8]. The quantitative content of water-soluble pentosans is most often estimated indirectly by measuring the relative viscosity of an aqueous extract of grain meal using high-precision viscometers [9]. Studies have shown that the WEV, along with the falling number, is an important component of the bakery rye formula and should be used in breeding [10].

At the same time, the quality of rye grain depends not only on its biochemical structure but also on many environmental factors, and their negative consequences can be overcome only by creating ecologically sustainable varieties and hybrids [11]. Therefore, it is important to take into account not only the degree of phenotypic manifestation of features in created varieties but also the nature of their adaptive reactions in various environmental conditions [12]. The created varieties can differ in the amplitude of adaptability, that is, have a relatively "wide" or "narrow" ecological plasticity. The concept of "adaptability" means the ability of a variety to provide high and sustainable productivity in varying environmental conditions [13]. Environmentally sustainable varieties can grow relatively normally in a wide range of environmental factors. Rye varieties with a high homeostasis of features that determine baking qualities are of particular interest. Meanwhile, the adaptive reactions of this category of features in rye have hardly been studied, which does not allow us to reliably evaluate the range of influencing environmental factors and to identify genotypes with a high potential for adaptability. Although rye varieties are characterized by higher ecological resistance than its hybrids [14], the adaptive potential of varieties must be improved, since environmental stress can negatively affect the expression of quality features. All this predetermines the relevance of the ecological-adaptive orientation of breeding in relation to the conditions of a particular region.

The purpose of our research was to study the environmental sustainability, stability, and plasticity of various features that directly or indirectly determine the baking qualities of winter rye as well as their comparative assessment by various parameters of adaptability in order to optimize the selection of this crop to improve the baking qualities of grain.

MATERIAL AND METHODS

The initial material included 18 varieties of winter rye (Alfa, Voskhod 1, Valdai, Tatyana, Moskovskaya 12, Moskovskaya 15, Moskovskaya 18, Krona, Population 11, ZhZ-760, GK-984, GK-796, GK-2701, GK-2731, GK-785, GK-985, GK-494HV, GK-614LV), which were field tested in 2014–2019 on plots of 15 m^2 in four replicates. The baking qualities of grain were evaluated by laboratory test baking of hearth and pan bread from wholemeal flour [15]. Grain quality was assessed by 11 characteristics: weight of 1000 grains (g), nature (g/L), protein and starch content (%), water extract viscosity (WEV), falling number (FN), amylogram height (AH), starch gelatinization temperature (T, °C), shape stability of hearth bread (H/D), volumetric yield of pan bread (cm^3), and crumb quality (point). The content of raw protein and starch was determined on an IR-6250 infrared spectrophotometer, the falling number was determined on a Hagberg-Perten device, the amylogram height and starch gelatinization temperature were determined on a Brabender amylograph, the relative viscosity of the water extract of grain meal was determined in centipoise (cP) on a VT5L viscometer (Germany). The coefficients of ecological (*CVe*) and genotypic (*CVg*) variation were calculated. The components of dispersions and the coefficients of heritability H^2 were calculated according to the guidelines of A.V. Smiryaev et al. [16].

The weather conditions varied considerably over the years of study. The most favorable conditions for the formation of high-quality grain were formed in 2017, when the crops did not lay down until harvesting, and the filling and maturation of grain took place in warm and dry weather. This contributed to the formation of a relatively large grain with a high amylogram and low activity of amylolytic enzymes. The weather conditions in 2014 and 2019 turned out to be very unfavorable, when frequent rains in the form of heavy downpours fell on the period of mass flowering of winter rye, which caused early lodging of crops and the formation of shrunken grain in the ear. At the same time, lodging was of a root character and was retained until harvesting, which negatively affected the weight of 1000 grains and the value of the falling number, and a visible germination of grain in the ear was noted in some varieties.

The coefficient of ecological variation *CVe* expressed as a percentage was calculated to assess the ecological stability of the feature. The lower its value is, the higher is the ecological stability of the feature. The stability factor *SF* proposed by D. Lewis [17] was also calculated to assess the ability of a genotype to create a narrow (or wide) range of phenotypes under changing environmental conditions. At $SF = 1$, the variety is ideally stable in terms of the phenotype, since it does not change features when grown in different environments. At $SF > 1$, the phenotype is unstable, and when this indicator is higher its phenotypic instability is greater. The ecological plasticity of the varieties was assessed by S.A. Eberhart and W.A. Russell [18], calculating the linear regression coefficient b_i as a measure of genotype responsiveness to changing conditions. When this coefficient is higher, the specific increment (or decrease) in the value of the feature under the influence of an external factor and its plasticity, which is achieved by reducing the phenotypic stability, is higher. A low reaction rate ($b_i < 1$) indicates a high buffering capacity of the feature under various environmental conditions.

Table 1. Genotypic (*CVg*) and ecological (*CVe*) variation of grain quality features in winter rye (based on average data for 2014–2019)

Feature	Range of variation (minmax) by factors of influence variety/year	Coefficient of variation *CVg*/*CVe*, %	Variety		Year	
			best	worst	best	worst
Falling number, s	129–219/	13.2/	Alfa	GK–614LV	–	–
	81–263	38.8	–	–	2017	2019
Amylogram height, u.a.	142–268/	12.8/	GK–494HV	GK–614LV	–	–
	136–356	38.0	–	–	2017	2019
Water extract viscosity, cP	2.7–10.7/	35.2/	GK–494HV	GK–614LV	–	–
	4.2–5.8	13.5	-	-	2014	2018
H/D	0.18–0.31/	12.8/	GK–494HV	GK–614LV	–	–
	0.18–0.29	16.1	–	–	2019	2017
Gelatinization temperature	57.6–63.2/	2.1/	Alfa	GK–614LV	–	–
	57.0–63.0	5.7	–	–	2017	2019
Crumb quality, score	2.9–4.2/	9.3/	Alfa	GK–614LV	–	–
	2.5–4.1	18.9	–	–	2014	2019
Pan bread volume, cm	276–311/	3.2/	Mos–12	Krona	–	–
	278–320	5.5	–	–	2017	2019
Grain nature, g/L	677–728/	1.8/	Mos–15	GK–614LV	–	–
	695–729	2.9	–	–	2017	2019
Weight of 1000 grains, g	29.6–34.2/	3.9/	GK–984	GK–614LV	–	–
	29.8–35.2	6.6	–	–	2017	2019
Protein content	11.4–13.5/	4.6/	GK–614HB	GK–796	–	–
	11.1–12.8	5.1	–	–	2015	2018
Starch content	52.5–56.2/	2.1/	GK–984	GK–614LV	–	–
	52.1–58.3	4.6	–	–	2014	2015

RESULTS AND DISCUSSION

The genotype of the variety and the weather conditions of the year were the main factors influencing the expression of quality features in our experiments (Table 1). They were the most pronounced in the fall number and the height of the amylogram. Under the influence of the variety genotype, these features varied at the level of 12.8–13.2% and 38.0–38.8% under the influence of the conditions of the year. That is, the environmental variation was three times higher than the genotypic one.

In terms of WEV, the intervarietal variation prevailed almost threefold over the ecological one (35.2 and 13.5%, respectively), which is explained by the inclusion in the studied set of unique varieties GK-494HV and GK-614LV, selected for high and low values of the feature. As for other features, the weakest (3–7%) of both types of variation were manifested in the nature of the grain, the mass of 1000 grains, the temperature of starch gelatinization, the volume of pan bread, and the protein and starch content in the grain. Nevertheless, the influence of the environmental factor also exceeded the influence of the genotype of the variety. The variation in the form stability of hearth bread (H/D) and the quality of the crumb of the pan bread was average, but the influence of the ecological factor over the genotypic factor was predominant.

The best and worst varieties were identified for almost every quality feature. The majority of them reflected different facets of their quality characteristics, so different varieties fell into the category of "best" or "worst." Alfa, obtained by multiple selection for a high falling number, and GK-494HV, selected for high WEV, were the best varieties more often than others. In all the years of testing, the Alfa variety surpassed other varieties not only in the falling number but also in the starch gelatinization temperature and the quality of the crumb of the pan bread.

The population of GK-614LV, selected for a low WEV, stood out steadily among the worst varieties. Small grain, low nature, low starch content, low FN and WEV are its characteristic features. Together, these features contribute to the slow process of starch hydrolysis, which takes place at a relatively low gelatinization temperature. As a result, a lot of dextrins and little intact starch remain in the dough, which is why the bread turns out to be very fuzzy, with a large-porous, sticky, and crumbling crumb.

However, not the Alfa variety but the high-viscosity population GK-494VV was the best in terms of amylogram height and shape stability of hearth bread. Due to its high WEV, this variety with a falling number lower than that of Alfa (by 13s) had the highest amylogram (268 u.a.) and was the leader in terms of form stability of hearth bread (H/D = 0.31). Consequently, a high WEV contributes to the improvement of the baking properties of rye grain. It is known that the WEV feature closely correlates ($r = 0.97$) with the content of water-extractable pentosans [19].

The expression of quality features was significantly influenced by the weather conditions of the year. The best grain of rye for baking was formed in 2017 and the worst was in 2019. According to our observations, this differentiation is caused not only by the amount of precipitation but also by the nature, degree, and duration of crop lodging caused by them. At the same time, not all studied features reacted unambiguously. The exceptions included three features: WEV and protein and starch content in grain. Their high expression was achieved in relatively dry years (2014, 2015, and 2018) when warm and dry weather prevailed during grain loading and there was no heavy lodging.

Phenotypic correlations between various features of grain quality are presented in Table 2. As can be seen, the main cluster of closely correlated features that determine the quality of hearth and pan bread included the falling number, starch gelatinization temperature, amylogram height, WEV, and grain nature. Reliable correlation coefficients between them are $r =$ 0.48–0.83. The relationship between the falling number and the starch gelatinization temperature was especially strong. These features are almost directly related to each other. The same can be said about the conjugation of the falling number with the amylogram height. The high correlation of these features is explained by their similar response to changes in weather conditions during the period of grain loading and ripening [20].

It is important to note that the quality of pan bread's crumb was most accurately determined by the falling number ($r = 0.71$). Analyzing this relationship, we find that the amylogram height, the starch gelatinization temperature, and the content of water-soluble pentosans make a positive contribution to the quality of pan bread's crumb. The quality potential of hearth bread is determined by three features: the amylogram height ($r = 0.53$), WEV ($r = 0.68$), and the falling number ($r = 0.58$). The last two features closely correlated with each other ($r = 0.59$). Therefore, an objective forecast of the baking properties of hearth bread is better achieved not by one but by two features.

The most indifferent features included the volume of pan bread and the mass of 1000 grains. None of them significantly correlated with other quality features. Their ambiguous reaction to changing weather conditions of the year could be the reason. In this regard, one can indirectly estimate the content of water-soluble pentosans in the grain by the value of the WEV feature. The peculiarity is that, when kneading rye dough, the key role in its viscosity is played not by proteins but by water-soluble pentosans, which protect starch from destruction by amylases. In dry years, there are more such pentosans in rye grain. The falling number and peak amylogram have higher values, resulting in bread with elastic and fine-pored crumb but with a lower volumetric yield. In wet years, the content of water-soluble pentosans in grain is low, their water-retention capacity and protective role decrease, and the fall number and height of the amylogram are also low. Against the background of the combined effect of these characteristics, pan bread has a higher volume. This circumstance explains why the volumetric yield of pan bread does not correlate with other quality attributes.

The protein content in the grain had a negative effect on the grain nature ($r = -0.64$) and the amylogram height ($r = -0.53$). The high water solubility of proteins, which were not able to form an springy and elastic crumb could be the reason. Against this background, the role of starch in baking increases, since its content positively correlated with the nature of the grain ($r = 0.59$). Starch is the main component of swelling, which, together with pentosans, absorbs water when kneading the dough and participates in the formation of bread crumb.

It should be noted that there is no significant correlation between WEV and AH ($r = 0.39$). This can be explained by various factors influencing the expression of these features: the potential of WEV depends mainly on the amount of water-soluble pentosans, and the amylogram height depends on the amount and quality of starch. These components of swelling do not adequately respond to changing weather conditions, which is confirmed by different coefficients of ecological variation (*CVe* = 38.0% for HA and 13.5% for WEV). The slight synchronicity of the variation of the features became the reason for the weak correlation between them.

The decomposition of the total variance of the studied features into ecologically and genotypically determined components is of interest. If a feature has a strong ecological dependence, then it is characterized by high phenotypic variation and a strong interaction of the genotype with the weather conditions of the year. This can be judged by the value of the coefficient of heritability H^2, which indirectly reflects the level of adaptive ability of the genotype (Table 3). In our experiments, the H^2 heritability coefficients turned out to be highly reliable for all studied features

Table 2. Correlation coefficients (r) between various features of grain quality in winter rye (on average for 2014–2019, $n = 18$)

Feature	Amilogram height	Gelatinization temperature	Water extract viscosity	H/D	Crumb quality	Grain naturea	Pan bread volume	Weight of 1000 grains	Protein content	Starch content
Falling number	0.72**	0.83**	0.59**	0.58*	0.71**	0.19	–0.20	0.05	–0.08	–0.09
Amilogram height	–	0.70**	0.39	0.53*	0.53*	0.62**	0.05	0.03	–0.53*	0.33
Gelatinization temperature		–	0.25	0.41	0.65**	0.54*	–0.05	0.15	–0.22	0.13
Water extract viscosity			–	0.68**	0.48*	–0.25	–0.12	–0.04	0.19	–0.40
H/D				–	0.41	0.08	–0.45	0.11	–0.33	–0.14
Crumb quality					–	0.24	–0.14	0.20	–0.09	0.01
Grain naturea						–	0.33	0.22	0.18	0.02
Pan bread volume							–	0.31	–0.64**	0.59**
Weight of 1000 grains								–	–0.25	0.22
Protein content									–	–0.62**

*, ** Coefficients are reliable at 5 and 1% significance level, respectively.

Table 3. Dispersion components and heritability coefficients (H^2) of various grain quality traits of winter rye

Feature	Dispersion			H^2	F_{fact}
	phenotypic $F_{fact.}$ (σ^2_{ph})	environmental (σ^2_e)	genotypic (σ^2_g)		
Falling number	10950	4562	1140	0.20	2.40
Amilogram height	22058	9520	2090	0.18	2.32
Gelatinization temperature	135.3	15.1	20.0	0.57	8.96
Water extract viscosity	57.7	0.64	9.51	0.93	90.10
H/D	0.018	0.0037	0.0024	0.39	4.86
Crumb quality	2.36	0.64	0.29	0.31	3.69
Pan bread volume	2775	793	309	0.28	3.50
Grain nature	10293	654	1606	0.71	15.7
Weight of 1000 grains	39.0	6.7	5.4	0.45	5.82
Protein content	9.7	0.60	1.51	0.72	16.4
Starch content	1047	11.2	172.6	0.94	93.5

F_{tabl} = 2.15 at 5% significance level.

(F_{fact} = 2.32–93.5 with F_{tab} = 2.15), but there were differences between them. The highest share of genotypic variance in the total phenotypic variance was noted for the content of starch, protein, WEV, and grain nature (H^2 = 0.71–0.94). The lower share was noted for the falling number and the amylogram height (H^2 = 0.18–0.20), which should be expected due to their large ecological variation (Table 1).

It is also important to assess the ecological stability of varieties in terms of quality. The adaptability parameters *CVe*, *SF*, and b_i used by us illuminate different facets of the ecological buffering capacity of varieties and positively correlate with each other. In our experiments, these correlations were r = 0.77–0.98 (between *CVe* and *SF*), r = 0.58–0.95 (between *CVe* and b_i), and r = 0.62–0.91 (between *SF* and b_i). The relationship is as follows: when the *CVe* and *SF* parameters are smaller, the ecological stability and phenotypic stability of the feature are higher and its responsiveness to changing weather conditions of the year is lower, which is estimated by the b_i parameter. It is necessary to know not only the range of adaptive reactions of varieties during cultivation in various environmental conditions but also their dependence on the phenotypic expression of the feature. In our experiments, the parameters *CVe*, *SF*, and b_i ambiguously correlated with the mean value of the feature. Significantly negative correlation manifested only between the *CVe* coefficient and three features: the falling number (r = –0.48), the quality of the crumb of the pan bread (r = –0.74), and the starch content in the grain (r = –0.57). This means that selection for a high manifestation of these features will help reduce their ecological variation. The phenotypic stability index *SF* correlated negatively with the studied features in most cases, but a significant relationship was noted only for the nature of the grain (r = –0.50) and starch content (r = –0.48), which is natural since the features are closely coupled with each other (r = 0.59, Table 2). The coefficient of ecological plasticity b_i positively correlated with the expression of the studied features in the majority of cases. That is, the responsiveness of varieties to changing weather conditions of the year increased, which does not coincide with the task of selection for ecological stability. The reason for this lies in the genetic determinism of the reaction rate, the manifestation of which strongly depends on the interaction of genotype and environment [21]. Therefore, it is reasonably believed that the preference in breeding for adaptability should be given to varieties with a narrow rather than a wide reaction rate [22].

It is of great interest to elucidate the possible trend dynamics of the *CVe*, *SF*, and b_i parameters under the influence of targeted selection. For this purpose, we compared the GK-494HV and GK-614LV populations obtained as a result of tenfold selection for high-viscosity (HV) and low-viscosity (LV) genotypes from varieties Alfa and Moskovskaya 12 and subsequent positive assortative crossing of populations from plus and minus selection (Table 4). Multidirectional selection for WEV correlatively influenced many other quality attributes. A characteristic feature of the high-viscosity GK-494HV population was a high falling number, amylogram height, and grain nature. When baked, this population produced a spread-resistant bread with a firm and fine-pored crumb with a lower volumetric yield. The low-viscosity GK-614LV population had the lowest falling number and amylogram height; a relatively small, low-grade, and low-starchy grains; and produced a highly spreading bread with an increased volumetric yield but with a large pore and sticky crumb. As can be seen, breeding for WEV led to

Table 4. Results of a comparative assessment of the technological and baking properties of grain varieties Alfa, Moskovskaya 12, GK-494HV, and GK-614LV (average for 2014–2019)

Variety	WEV, cP	FN, s	AH, u.a.	H/D	Weight of 1000 grains, g	Crumb quality, score	Bread volume, cm	Temperature, °C	Grain nature, g/L	Protein, %	Starch, %
Alfa	4.9	220	266	0.256	32.1	4.2	296	63.2	726	12.0	53.6
Moskovskaya 12	4.8	176	260	0.228	32.2	3.8	312	59.8	720	11.9	55.3
GK-494HV	10.7	206	268	0.315	30.8	3.9	292	60.6	719	11.4	53.7
GK-614LV	2.7	129	142	0.184	30.0	2.8	298	57.6	694	12.6	52.7

a change in other characteristics that were not exposed to direct selection.

A graphical assessment of the GK-494VV and GK-614NV populations in comparison with the original parental form AM-12 (the average value of the *CVe*, *SF*, and b_i parameters for varieties Alfa and Moskovskaya 12) is shown in Fig. 1. The compared populations differed markedly in all parameters. However, these differences were especially clear only in a constellation of closely correlated features: WEV, FN, AH, H/D, and bread crumb quality. For other features, the populations differed slightly. The specificity manifested in the fact that the high-viscosity popula-

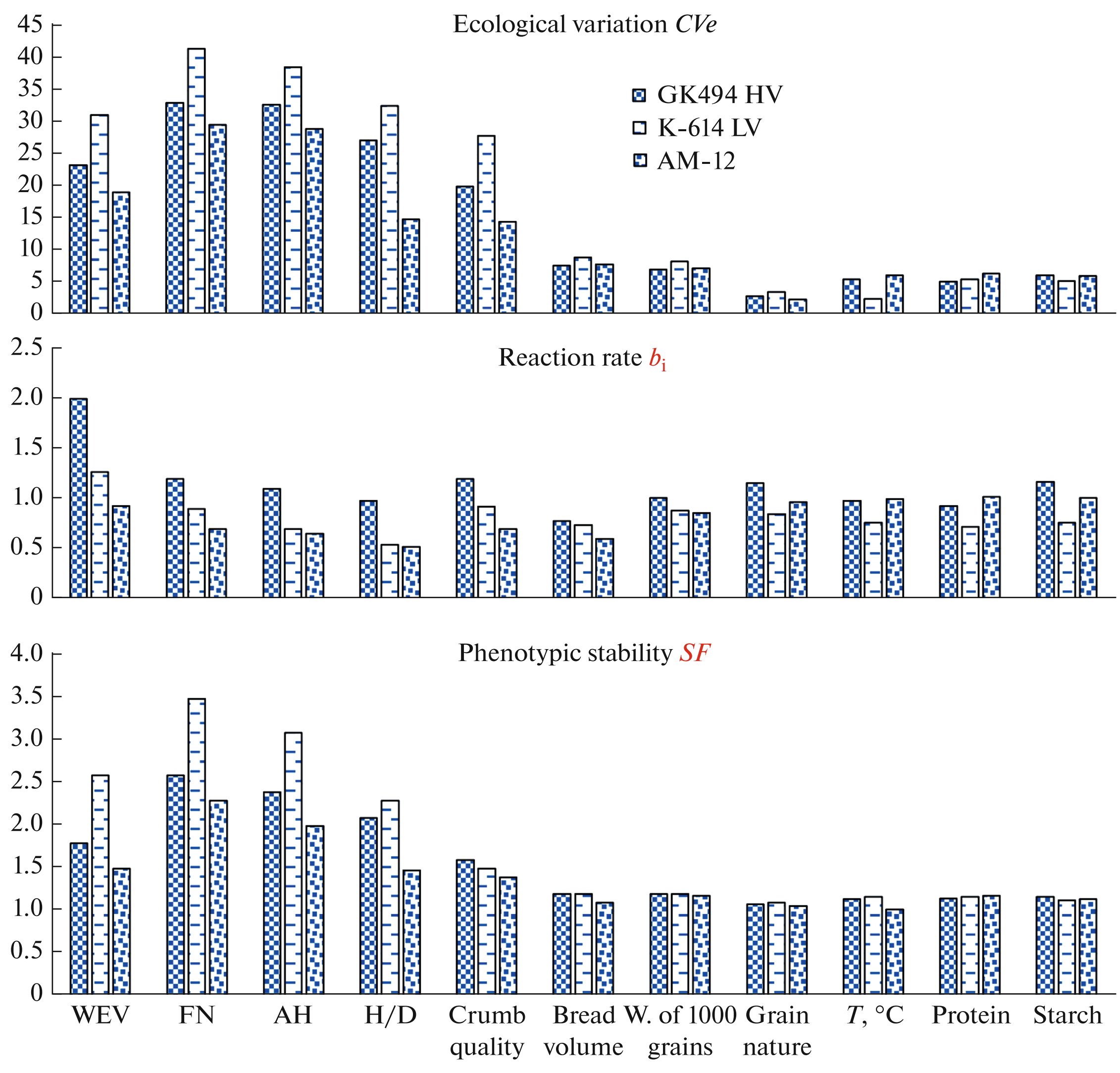

Fig. 1. Comparison of the *CVe*, *SF*, and b_i adaptability parameters in the winter rye populations with contrasting WEV: GK-494HV, GK-614LV, and AM-12.

tion GK-494HV had lower values of the *CVe* and *SF* parameters but higher estimates for the b_i parameter. Relatively high *CVe* and *SF* parameters were noted in the low-viscosity GK-614LV population. However, it had a lower b_i coefficient; that is, it was characterized by a lower reaction rate.

Comparison of these two populations shows that multiple divergent selection for WEV significantly affected the potential of their adaptability. Both populations turned out to be environmentally less stable than the original AM-12 form since they varied and changed their phenotype more strongly under the influence of external conditions. At the same time, the high-viscosity GK-494VV population, against the background of the low-viscosity GK-614LV, had the best baking qualities of grain in years differing in weather conditions. From the breeding point of view, the low *CVe* and *SF* scores typical for the GK-494HV population are of more important adaptive value than the high ecological plasticity (high reaction rate for b_i). The reason is that the property of ecological plasticity can be effectively used only in favorable years. In our experiments, high ecological stability and phenotypic stability of the GK-494HV population were combined with increased responsiveness to changing environmental conditions. This is not always desirable since high plasticity reduces the phenotypic stability of features. Such "straightforward" genotypes may be of interest for breeding in highly specific conditions. This thesis corresponds to the conclusion of A.A. Zhuchenko [12] that a wide reaction rate in the adaptive potential of a variety should not dominate over ecological stability. Varieties with high responsiveness to environmental factors are environmentally unstable. Such genotypes are less valuable in terms of breeding since they show sensitivity not only to favorable but also to unfavorable environmental conditions.

CONCLUSIONS

Thus, multiple selection for high WEV correlatively improved the form stability of hearth bread, the amylogram height, the falling number, and other baking properties of rye grain. A trend towards a decrease in the ecological stability and phenotypic stability of features while increasing their ecological plasticity is a characteristic feature of this selection. With the selection of forms with a low WEV, the ecological stability and stability of the features decreased more than with the plus selection. At the same time, the ecological responsiveness to the difference in environmental factors was more pronounced. Therefore, in order to create rye varieties that are ecologically sustainable in terms of grain quality, the selection vector should be aimed at adapting to such stressful conditions that most often go beyond the biological optimum in a given region. To expedite this assessment, the genotypes to be selected should be tested at different ecological points.

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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