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A NOVEL INTEGRATIVE APPROACH TO STUDY THE DYNAMICS OF AN INCREASE IN COMMON SPRING WHEAT ADAPTIVITY AND HOMEOSTATICITY (on the example of breeding programs in the Northern Trans-Ural)

V.V. NOVOKHATIN[1], T.V. SHELOMENTSEVA[1], V.A. DRAGAVTSEV[2] ✉

[1]*Federal Research Center of the Tyumen Scientific Center SB RAS,* 86, ul. Malygina, PO Box 1230, Tyumen, 625000 Russia, e-mail sciensec@ikz.ru;
[2]*Agrophysical Research Institute*, 14, Grazhdanskii prosp., St. Petersburg, 195220 Russia, e-mail dravial@mail.ru (✉ corresponding author)
ORCID:
Novokhatin V.V. orcid.ogr/0000-0002-2191-0420
Dragavtsev V.A. orcid.ogr/0000-0002-0934-020X
Shelomentseva T.V. orcid.ogr/0000-0003-4855-6182
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Abstract

Though there are a number of evolutionary theories of living nature, no approach is available to quantify changes occurring during long-term breeding programs. By N.I. Vavilov, selection is evolution directed by the man's will. Here, we suggest and used a novel method for studying shifts in statistical genetic parameters which have occurred in sets of varieties of soft spring wheat (*Triticum aestivum* L.) over an approximately 80-year period. During 8 years (in 2005-2012), 23 varieties of soft spring wheat zoned in the period from the 1930s were investigated in the conditions of the northern forest-steppe of Western Siberia (experimental field of the Research Institute of Agriculture of the Northern Trans-Urals, Tyumen, 57°09'N, 65°32'E). All of them were successfully cultivated in the Northern Trans-Urals in various years. The effects of genotype by environment interaction changing the crop ranks by year of testing were measured. The average yield of the varieties zoned in the 1940s was 20.2 c/ha (a reference point). These varieties showed a pronounced plasticity and homeostaticity of grain production. The regression lines for yields vs. ecological years (from bad to favorable conditions) were flat with a 31°-39° inclination. Milturum 321, the first zoned variety for the region is stable for grain yields (S^2d_i = 3.5). During 1950-1970s, Saratov varieties and the late-maturing variety of Siberian selection Milturum 553 have been zoned in the Northern Trans-Urals. The average yield of the group is 23.4 c/ha. The regression lines were above the lines of the first group and had similar inclination. Saratov varieties showed yield homeostaticity similarly to the varieties of the first group but lodging at yields above 20-25 c/ha. In 1970-1990s, the varieties resistant to lodging became widespread. Their yields in testing averaged 29.1 c/ha (+44 % to the reference point), the regression lines inclination reached 39°-47° indicating a decrease in yield homeostaticity. These varieties more strongly responded to a better or adverse environments compared to the varieties of the first and second groups. Strela and Tyumenskaja 80 varieties of local selection are quite stable in terms of yields (S^2d_i = 4.8-6.1). Currently used medium-ripe intensive varieties capable of producing grain yields of 34.3 c/ha on average (+70.0 % to the reference point) strongly responded to changes in environments, which followed from the inclination of the regression lines (50°-54°, b_i = 1.21-1.40). Plasticity and crop homeostaticity are characteristic of the Chernyava 13 variety showing a flat regression line (29°, b_i = 0.56). The most stable crop performance was characteristic of the varieties Lutescens 70 and Icar (S^2d_i = 8.7 and S^2d_i = 8.6, respectively). Modern zoned early-ripening varieties are less productive than the varieties of the previous group (x = 31.1 c/ha), with flat regression lines (37°-38°). The Tulunskaya 12 and Novosibirskaya 15 varieties are unstable in terms of yields (S^2d_i = 26.6 and S^2d_i = 29.0, respectively). The Novosibirskaya 29 variety is more productive (33.3 c/ha) and similar to the medium-ripe varieties from the previous group in terms of plasticity and stability. The assessment of a genotype response to environments affecting crop plasticity and stability (and homeostaticity) evaluates different characteristics of crop adaptability. So this allows us to investigate varieties under changing environments, to assess the effectiveness of their use in the Northern Trans-Urals environment, and to optimize breeding programs. High-yielding varieties with a well-pronounced adaptability should be involved in breeding.

Keywords: variety, yield, genotype by environment interaction, limiting factors, plasticity, homeoctaticity, stability, statistical genetic parameters

Currently, there are about 40 breeding centers in Russia, each of which has a long history of creating zoned varieties and preparing variety changes, leading to an increase in gross grain yields in cultivation zones. According to N.I. Vavilov, selection is evolution controlled by the human will [1]. For the processes occurring in nature, various evolutionary theories have been proposed and discussed, e.g., Lamarckism [2], Darwinism [3], synthetic [4] and epigenetic [5] theories. However, for the quantitative description of the changes observed in any national breeding center during the implementation of long-term breeding programs, no single methodological approach has been proposed.

N.I. Vavilov [1] emphasized the importance of adapting a species and variety to specific environmental conditions and noted that the behavior of varieties and species is not the same both in different agro-climatic zones and in one zone depending on the conditions of the year. The increase in wheat yield is associated with the ability of varieties to compensate for the effects of limiting environmental factors that reduce productivity [6-8], that is, with the degree of severity of the adaptive properties of varieties [9-11].

Ecological testing is an effective way to assess both adaptability [12, 13] and cultivar plasticity (and yield homeostaticity) [14]. The extent of the adaptability of varieties is provided by the ability to withstand the action of limiting environmental factors [15-19] due to genetic and physiological systems of adaptability (GPSA) [20]. The plasticity of a variety and the maintenance of its yield over the years depend on the number of GPSAs in the genome [9, 21-23].

The influence of environmental factors on varieties is accompanied by microevolutionary processes (artificial and natural selection) [24, 25], shifts in the intensity of recombinogenesis [26], the appearance of provocative backgrounds in different years [27-30], which determine the specific selection effects [31-33]. As a result, high-yielding varieties appear that are highly adapted to average local weather and climatic conditions for years, with homeostatic yields over a number of years, which is one of the main reasons for the long-term industrial cultivation of the variety [34]. The adaptability characteristics of a variety include its ecological plasticity [21, 35], which reflects the degree of responsiveness (yield increase) to the weakening of the inhibitory effect of the limiting environmental factor [22, 23]. The adaptability of the variety is due to its stability [17, 36, 37[, which allows combination of high yields with their minimum decrease under adverse conditions [38-41]. Statistical methods are used to assess the adaptability and stability of varieties [42-44). Methods have been developed for quantitative assessment of the functional plasticity of the genome in varieties and genotype-environment interaction through variances [22, 45], through the multidirectional effects of genotypic factors and the vector of environmental influence on the manifestation of productivity traits (in two-dimensional coordinate systems-traits), the contributions to the yield of each of seven genetic-physiological systems — HPS [46]. Indicators of plasticity and yield stability of a variety are interconnected [38, 47] and are integral component properties of adaptability [38]. Yield homeostasis (in breeding terms, variety plasticity) is an important characteristic of varieties [9, 48, 49].

Plants during the growing season are affected by different (in terms of the number and intensity of exposure) abiotic and biotic factors. Together with GPSA, they determine the features of the genotype–environment interaction (GEI) [18, 34]. The nature of the effects of such an interaction is complex [50-52]. Varietal differences in terms of genotype–environment interaction are quite significant [51, 53], which characterizes their modification capabilities [14, 54], expressed through the effects of GEI [34, 55]. The evaluation of the latter gives an idea of the plasticity and stability of varieties [56-58]. A change in environmental conditions leads to a change in the limiting environmental factors (lim-factors) that determine yields [9, 59]. The change in productivity ranks in a set of varieties (in different years at one ecological point or in one year, but at different points) is due to the variability of GEI effects that determine yield [60]. Management of the effects of GEI (agrotechnological or genetic breeding activities) is a significant reserve for increasing yields [20, 61], which is confirmed by studies conducted in the Northern Trans-Urals [62]. Here, in the formation of the yield of spring wheat, varietal characteristics account for 25.2-29.0%, and in the old varieties cultivated here for GEI this indicator is 14.8%, for the variety factor 11.5%, and in modern varieties the first indicator increases to 19.3%, the second one decreases to 5% [62]. Increasing environmental sustainability [15, 40, 63] is an important factor in "bringing" adaptive systems to ensure yields, which is the real contribution of breeding to increasing crop production [64, 65] and increasing wheat yields [66-70].

In our work, we propose an approach that seems to us optimal for quantitative assessment of the results of wheat breeding in the historical aspect (on the example of the Tyumen breeding center).

The purpose of our study is to describe the dynamics of changes in the plasticity and adaptability of varieties created and released in the Northern Trans-Urals, from the 1930s to the present.

Materials and methods. The main set of 23 varieties of soft spring wheat (*Triticum aestivum* L.) include 19 varieties of different years of breeding at the Tyumen breeding center and 4 varieties from other breeding regions which have been registered for use in the Northern Trans-Urals. After equalizing sowing and reproduction, the varieties were grouped by the years of cultivation and for 8 years (2005-2012) and studied in the conditions of the northern forest-steppe of Western Siberia (experimental field of the Research Institute of Agriculture of the Northern Trans-Urals, Tyumen, 57 09' N, 65 32' E). The soil of the plot is dark gray forest, the predecessor is black fertilized fallow ($N_{30}P_{45}K_{30}$ kg a.i./ha), plot area is 10 m^2, repetition is 4-fold, plot placement is randomized, the seeding rate is 650 viable seeds per 1 m^2. Seeds were obtained at the Siberian Research Institute of Plant Growing and Breeding (Krasnoobsk settlement, Novosibirsk Province). Sowing was carried out at the optimal time for the region using a seeder SKS-6-10 (Russia). Yield records and observations were carried out according to the standard method ("Methodology of the State Variety Testing of Agricultural Crops", Moscow, 1989). Vegetation conditions for the years of testing differed in temperature and precipitation.

For statistical processing of the experimental data, analysis of variance [62, 71] was used, LSD_{05} and correlation coefficients were calculated. The response effect index (RE) of varieties on environmental conditions was calculated according to our proposed formula [72], plasticity (b_i values), stability (S^2d_i values) and environmental index (Ii) were calculated according to S.A. Eberhart and W.F. Russell [22] using the R.A. Urazalieva et al. [73], homeostaticity was determined by V.V. Khangildin [74].

Results. During the observation period, 2007 and 2008 were dry years, despite significant precipitation during the growing season (349 and 294 mm at a rate of 243 mm, by months the precipitation had a shower character). HTC values for the season were 1.50 and 1.84 (wet). However, the I-II decades of each month were dry (HTC of 0.30-0.56 and 0.15-0.67). The year 2009 turned out to be dry, with a deficit of precipitation during the growing season of 62 mm (–26%) at close to average long-term values of the hydrothermal coefficient (HTC = 0.96, dry).

July (HTC = 0.13) and the second half of August (HTC = 0.26) were very dry. The year 2012 was especially dry, when only 98 mm of precipitation fell during the growing season (44% of the norm of 243 mm). Under elevated active temperatures (> 10 °C), their sum amounted to 2210 °C with precipitation of 315 mm (or +20% to the norm), while on average HTC = 0.44 (dry). July turned out to be very dry (HTC = 0.11-0.13). During these years, the ear was formed small, and the grain was low-grade. 2005, 2010 and 2011 were average in terms of climatic conditions, when precipitation during the growing season was less than the norm (213, 210 and 225 mm), and the sums of active temperatures were slightly above the norm (+168 °C, +190 °C, +68 °C). The HTC values for the years were 1.04, 1.06 and 1.18 (weakly humid). Quite wet (349 mm of precipitation) and cool (–382 °C) was 2006 (HTC = 2.21, humid). In general, it should be noted that the spring-early summer type of drought (Siberian type) manifests itself in all years.

Contrasting conditions, while observing the principle of a single difference, allowed us to give an objective assessment of all the studied varieties.

According to the “Catalogue of varieties of agricultural crops created by scientists of Siberia and included in the State Register of the Russian Federation (zoned) in 1929-2008” (Novosibirsk, 2009, v. 4, issue 1), in 1924, the State Variety Testing Network under the People’s Commissariat of the RSFSR has been established. On the territory of the Northern Trans-Urals (Tyumen region) since 1929, 29 varieties of soft spring wheat have been cultivated (with 10-15-20-year periods, successively covering six variety changes) (“State variety book of the inspection of variety testing in the Tyumen region”, 2001; “Catalog of zoned varieties of agricultural crops in Siberia, 1997 and 2009”).

In the first breeding varieties, zoned in the Northern Trans-Urals (group I) and cultivated from the 1930s to the 1950s, the grain yield averaged 20.2 c/ha (we took it as the base for further assessments) (Table 1). The potential yield of these varieties did not exceed 32.4-34.1 q/ha. They reacted strongly to dry conditions, which turned out to be more characteristic of the Cesium 111 variety. In wet and average years, these varieties lodging strongly.

1. Grain yield (c/ha) **of soft spring wheat (*Triticum aestivum* L.) varieties grouped by the periods of cultivation in Western Siberia over the years of observation** (trial fields of the Research Institute of Agriculture of Northern Trans-Urals, Tyumen, 57°09' N, 65°32' E)

Variety	2005	2006	2007	2008	2009	2010	2011	2012	Average
Group I (1930-1950)									
Lutescense 956	21.8	17.3	17.6	16.5	29.7	32.4	17.3	15.2	21.0
Cezium 111	18.2	9.6	10.4	16.2	22.0	34.1	19.4	14.7	18.1
Milturum 321	24.4	22.0	12.8	15.3	27.4	33.6	23.2	13.7	21.6
x	21.5	16.3	13.6	16.0	26.4	33.4	20.0	14.5	20.2
Group II (1951-1970)									
Lutescense 758	26.2	18.3	18.2	16.0	28.5	37.7	26.3	17.7	23.8
Milturum 553	29.7	25.9	14.4	15.1	29.5	43.3	16.5	13.5	23.5
Saratovskaya 29	28.1	19.1	18.7	17.9	31.2	37.3	26.7	19.9	24.9
Skala	22.4	29.7	20.4	20.2	29.7	40.5	36.8	18.1	27.2
x	26.6	23.3	17.9	17.3	29.7	39.7	26.6	17.3	24.9
Group III (1971-1990)									
Strela	28.8	27.3	21.1	24.6	34.5	45.8	34.3	20.0	29.6
Novosibirskaya 67	19.3	16.1	13.3	17.1	31.7	35.3	31.2	14.5	22.3
Rang	33.3	37.1	28.8	19.4	36.6	39.1	35.6	19.2	31.2
Tyumenskaya 80	34.5	35.5	30.5	22.7	41.2	49.4	44.6	23.1	35.2
x	29.0	29.0	23.4	21.0	36.0	42.4	36.4	19.2	29.6
Group IV (1991-2012)									
Omskaya 20	35.3	42.3	23.3	21.7	38.3	48.9	37.9	18.7	33.3
Lutescense 70	32.9	35.9	22.8	23.7	42.4	55.1	41.3	28.2	35.3
.Il’inskaya	34.5	40.5	29.9	22.7	38.4	58.0	37.6	22.8	35.6
AVIADa	35.3	27.9	28.8	19.5	41.5	50.5	50.0	19.6	34.2
Chernyava 13	34.3	34.6	26.0	30.1	41.7	34.9	44.0	28.1	34.2

Continued Table 1

Ikar	32.5	28.8	16.8	22.5	40.3	50.0	45.3	20.1	32.0
SKENT 3	28.8	33.7	22.1	18.2	36.6	44.9	49.7	21.6	32.0
Riks	47.0	38.7	18.0	28.2	38.3	57.6	46.3	30.1	38.0
x	35.1	35.3	23.5	23.3	39.7	50.0	44.0	23.7	34.3
Group V (1991-2012)									
Tulunskaya 12	29.3	38.9	17.1	22.7	31.7	37.6	42.3	17.7	29.7
Novosibirskaya 15	27.9	39.3	23.5	29.1	39.2	38.8	31.1	15.1	30.5
Iren'	35.5	30.7	27.3	23.7	32.5	39.1	40.5	19.7	31.1
Novosibirskaya 29	33.6	35.3	25.8	21.9	45.0	46.3	42.3	16.5	33.3
x	31.6	36.1	23.4	24.4	37.1	40.5	39.1	17.3	31.2
Average	30.7	30.3	21.3	21.2	35.7	43.1	35.9	19.6	29.7
LSD_{05}	1.8	1.9	1.5	1.6	2.2	2.5	2.2	1.5	1.9

N o t e. Groups I-IV — mid-ripening varieties originated from Tyumen Breeding Center (except for Omskaya 20 variety); group V — early-ripening varieties originated from other regions; 10 m^2 plots, 4-fold repetition.

In the 1950s-1970s, varieties of the semi-intensive type were cultivated, of which the Milturum 553 variety is late-ripening, Skala is medium-early. The average yield for this group was 24.9 c/ha, which is 20% higher than that of the varieties of the previous group (see Table 1).

With the intensification of the farming system (1971-1990), associated with the development of the Tyumen energy complex of the USSR, intensive mid-ripening varieties Strela, Novosibirskaya 67, Rang, Tyumenskaya 80 (group III) became widespread in the region. Their average yield in our test was 29.6 c/ha which is 46% higher than in group I. The best yield values (45.8, 35.3, 39.1, and 49.4 c/ha, respectively) were recorded in 2010. In all years of study, the yield of Novosibirskaya 67 variety was lower than that of other varieties in the group. This is especially evident in dry conditions (2007, 2008 and 2012), which significantly affect productivity [23, 33, 37]. Varieties Novosibirskaya 67 (var. *albidum*) and Tyumenskaya 80 (var. *lutescens*) were characterized by a strong germination of grain in the ear during the pre-harvest period in humid conditions (in 2007, 2010 and 2011, from 46, 54 and up to 86%, respectively). Varieties Rang and Tyumenskaya 80 showed resistance to lodging. In the Rang variety, in cool, wet years (2005, 2006), the growing season was extended. Due to the revealed too strong reaction of the varieties of this group to the pronounced lim-factors of the environment (see Table 1), the physical indicators and technological properties of the grain are reduced.

In the 1990s, the use of mineral fertilizers decreased by more than 3 times, from 87 to 22-24 kg a.i. per ha). From 2005 to the present, over the Tyumen region, mineral fertilizers have been applied in an amount of 32 to 35 kg a.i. per ha which is clearly not enough. Despite this, due to the introduction of new, more productive varieties (mainly of local selection, group IV), the yield in that period increased from 17-18 to 22-24 c/ha. In our tests, the average yield in the group over the years of study was the highest, 34.3 c/ha (+70% to the value in group I). As in other programs [25, 66-70], the increase in this group was due to selection work.

The mid-early group in our study was represented by four varieties of foreign selection cultivated in the region. Their productivity potential turned out to be somewhat lower than that of varieties from group IV, and the reaction to drought conditions, which were most severe in 2012, was more pronounced (see Table 1).

The distribution of the studied genotypes by ranks (by years) and the sum of ranks (Table 2) reflects both the similarity of agroclimatic conditions in the years of research and the pronounced differences that manifested themselves in the dry years of 2007, 2008, and 2012. It should be noted that drought (especially under the conditions of ongoing climate aridization) is considered as the main abiotic stress and a risk factor for yield losses in wheat cultivation [6, 17, 33].

2. Rank distribution of soft spring wheat (*Triticum aestivum* L.) varieties grouped by periods of cultivation in Western Siberia over the years of observation on grain yields (trial fields of the Research Institute of Agriculture of Northern Trans-Urals, Tyumen, 57°09' N, 65°32' E)

Variety	2005	2006	2007	2008	2009	2010	2011	2012	Sum	Ranking
Group I (1930-1950)										
Lutescense 956	16	21	16	16	14	22	21	17	143	19
Cezium 111	18	23	22	17	18	20	20	19	157	21
Milturum 321	14	18	21	19	17	21	19	20	149	20
Group II (1951-1970)										
Lutescense 758	13	20	14	18	16	15	18	15	129	16
Milturum 553	9	17	19	20	15	11	22	21	184	17
Saratovskaya 29	11	19	13	14	13	17	17	9	113	15
Skala	15	13	12	10	14	12	12	14	102	14
Group III (1971-1990)										
Strela	10	16	11	4	11	9	14	8	83	12
Novosibirskaya 67	17	22	20	15	13	18	15	19	139	18
Rang	7	6	3	12	10	13	13	12	76	10
Tyumenskaya 80	5	8	1	6	5	6	5	4	40	2
Group IV (1991-2012)										
Omskaya 20	4	1	8	9	9	7	10	13	61	6
Lutescense 70	8	7	9	5	2	3	8	2	44	3
.Il'inskaya	5	2	2	6	8	1	11	5	40	2
AVIADa	3	15	3	11	4	4	1	11	52	4
Chernyava 13	6	10	5	1	3	19	6	3	53	5
Ikar	9	14	18	7	6	5	4	7	70	8
SKENT 3	10	11	10	13	10	10	2	6	72	9
Riks	1	5	15	3	9	2	3	1	39	1
Group V (1991-2012)										
Tulunskaya 12	10	4	17	6	13	16	7	15	88	13
Novosibirskaya 15	12	3	7	2	7	14	16	18	79	11
Iren'	2	12	4	5	12	13	9	10	67	7
Novosibirskaya 29	6	9	6	8	1	8	7	16	61	6

Note. Groups I-IV — mid-ripening varieties originated from Tyumen Breeding Center (except for Omskaya 20 variety); group V — early-ripening varieties originated from other regions.

In 2007 and 2008, the first growing season was dry, which is typical for the region. In 2012, the entire growing season was characterized by a lack of moisture, when only 93 mm of precipitation fell at a rate of 243 mm. The most favorable year was 2010. Despite the apparent climatic differences, the general trend in the rank distribution of varieties over the years has a fairly significant similarity, with the exception of some genotypes. Thus, in the dry year of 2012, the Saratovskaya 29 variety showed a higher ranking mark compared to previous years, while the Omskaya 20 variety, on the contrary, decreased. It was shown that varieties of the early ripening group react sharply to climatic changes. Varieties of groups I, II and Novosibirskaya 67 occupied low places in the rank distribution in all the years of observations. A smaller sum of ranks and high places in the ranking indicate a pronounced plasticity of genotypes, which is typical for most varieties of groups III and IV, as well as for early ripe varieties Iren and Novosibirskaya 29. This is due to a rather strong share (up to 20%) of the influence of GEI on their yield formation which has been previously reported [46] and discussed in a number of other studies [50-52, 55, 60].

The rank correlation of genotypes by years of research (Table 3) was significant ($R_{05} \geq 0.413$). It should be taken into account that if $r = 1$, GEI = 0. This indicates rather high differences in GPSA, determining productivity traits [2, 16-19]) which affect yield formation under conditions of the ecological zone. An analysis of the correlation coefficients over the years of observation shows that in dry years, the formation of yields is controlled by other sets of gene products. This is due to less pronounced associations ($r = 0.447$-0.480) with the best years in terms of productivity. The same is true for favorable years, when the correlation coefficients increased (up to $r = 0.716$). Given this circumstance, a breeding strategy should be planned aimed at creating productive varieties of spring wheat with a pronounced plasticity of yield formation.

3. Rank correlation of soft spring wheat (*Triticum aestivum* L.) varieties grouped by periods of cultivation in Western Siberia over the years of observation on grain yields (trial fields of the Research Institute of Agriculture of Northern Trans-Urals, Tyumen, 57°09' N, 65°32' E)

Year	2005	2006	2007	2008	2009	2010	2011	2012	Year
2005		0.6550*	0.6808*	0.5810*	0.6293*	0.7034*	0.6821*	0.6262*	2005
2006	0.6550*		0.6043*	0.7044*	0.5685*	0.5740*	0.5340*	0.4469*	2006
2007	0.6808*	0.6043*		0.5696*	0.6773*	0.4805*	0.5026*	0.5130*	2007
2008	0.5810*	0.7044*	0.5696*		0.6920*	0.4765*	0.6301*	0.6585*	2008
2009	0.6293*	0.5685*	0.6773*	0.6920*		0.6158*	0.7160*	0.5941*	2009
2010	0.7034*	0.5740*	0.4805*	0.4765*	0.6158*		0.6383*	0.6127*	2010
2011	0.6821*	0.5340*	0.5026*	0.6301*	0.7160*	0.6383*		0.7042*	2011
2012	0.6262*	0.4469*	0.5130*	0.6585*	0.5941*	0.6127*	0.7042*		2012

* Reliably higher than the significance level ($R_{05} \geq 0.413$).

4. Effects of response (RE) **to environment conditions in soft spring wheat (*Triticum aestivum* L.) varieties grouped by periods of cultivation in Western Siberia over the years of observation** (trial fields of the Research Institute of Agriculture of Northern Trans-Urals, Tyumen, 57°09' N, 65°32' E)

Variety	2005	2006	2007	2008	2009	2010	2011	2012
Group I (1930-1950)								
Lutescense 956	–0.12	–4.25	5.04	3.95	2.77	–1.96	–9.87	4.42
Cezium 111	–0.81	–9.01	0.75	6.56	–2.02	2.65	–4.86	6.73
Milturum 321	2.36	–0.17	-0.38	2.13	–0.15	–1.38	–4.59	2.20
Group II (1951-1970)								
Lutescense 758	2.88	–6.05	2.84	0.65	–1.23	0.54	–3.67	4.02
Milturum 553	5.28	1.85	–0.66	0.05	0.12	6.44	–13.17	0.12
Saratovskaya 29	2.31	–6.32	2.27	1.48	0.40	–0.93	–4.34	5.15
Skala	–5.75	1.37	1.61	1.42	–3.46	–0.09	3.40	0.99
Group III (1971-1990)								
Strela	1.21	5.38	6.07	–3.32	–0.30	–5.43	–1.74	–1.85
Novosibirskaya 67	–1.68	–2.81	–0.02	3.49	–0.99	2.88	–1.43	0.56
Rang	–3.94	–6.77	2.22	3.23	3.45	–0.38	2.71	2.30
Tyumenskaya 80	–1.63	–0.26	3.73	–4.06	0.06	0.83	3.22	–1.99
Group IV (1991-2012)								
Omskaya 20	1.07	8.44	–1.57	–3.16	–0.94	2.23	–1.58	–4.49
Lutescense 70	–3.32	0.05	–4.06	–3.15	1.17	6.53	–0.17	3.02
.Il'inskaya	–1.98	4.39	2.67	–4.41	–4.09	9.08	–4.13	–2.64
AVIADa	0.19	–6.84	3.05	–6.24	1.38	2.95	9.64	4.17
Chernyava 13	–0.84	–0.47	0.22	4.33	1.55	–12.68	3.61	4.00
Ikar	–0.47	–3.80	–6.81	–1.10	2.32	4.59	7.08	–1.83
SKENT 3	–4.08	1.19	–1.42	–5.31	–1.29	–0.42	11.57	–0.24
Riks	8.04	0.12	–11.59	–1.38	–5.66	6.21	2.10	2.19
Group V (1991-2012)								
Tulunskaya 12	–1.29	8.68	–4.13	1.48	–3.90	–5.43	6.46	–1.85
Novosibirskaya 15	–3.53	8.24	1.43	7.04	2.76	–5.07	–5.58	–5.29
Iren'	3.45	–0.98	4.61	1.02	–4.56	–3.39	3.20	–1.84
Novosibirskaya 29	–0.67	1.40	0.89	–3.00	5.72	–0.41	2.78	–6.73
Ii	+0.93	+0.56	–8.43	–8.44	+5.94	+13.37	+6.18	–10.11

Note. Groups I-IV — mid-ripening varieties originated from Tyumen Breeding Center (except for Omskaya 20 variety); group V — early-ripening varieties originated from other regions. Ii — index of environment conditions.

The response of varieties to climatic conditions is well reflected in the index of environmental conditions Ii (Table 4), which was high in the favorable year 2010 (+13.37) and good in 2009 and 2011 (+5.94 and +6.18). In 2007, 2008 and 2012 this index took negative values. Determination of yields by lim-factors is well reflected in the effects of the response (RE) of varieties to environmental conditions [72], which have a pronounced year-to-year ranking and are largely genotypically determined. Extensive (group I) and semi-intensive (group II) varieties due to lodging showed negative reaction effects in wet years and well-pronounced positive ones in dry years (see Table 4).

In intensive varieties from group III, the response effects on the yield formation of are less contrasting. At the same time, in the Rang variety, in years when cool temperatures are combined with sufficient moisture during the grain formation phase, the growing season is extended, which leads to the production of low-grade grain. During these years, lodging in the Strela variety and grain germination in the spike in the Novosibirskaya 67 and Tyumenskaya 80 varieties reduced the yield to the level of that of the Rang variety in dry conditions (RE = –1.85 to –1.99 and –3.32 to –4.06).

In modern intensive varieties, the reaction effects were more pronounced and more contrasting over the years. This is explained by the fact that in the proportion of genotypic variability that determines the formation of their yield (24.3%), four-fifths (19.3%) falls on the genotype-environment interaction [46]. In this group, cv. Chernyava 13 responded less than others to dry conditions (2007, 2008, 2012), showing positive RE values in these years (see Table 4). In favorable years (2010), a strongly pronounced negative effect was observed (RE = –12.68) due to lodging, which also manifests itself in 2005 and 2006, good climatic conditions (RE = –0.84, RE = –0.47). The remaining varieties of this group responded with negative RE values to dry conditions, which is typical for this ecotype.

Early maturing varieties from group V showed negative RE of varying degree under favorable conditions, which is due to the low potential of these varieties, and negative RE values in dry years (for example, in 2012) which was determined by the biological features of varieties in group V.

The response effects revealed over a rather long period of time (by years) demonstrate their good manifestation in most varieties in IV and some varieties in V groups. This indicates a pronounced adaptability of such varieties to the conditions of the Northern Trans-Urals and serves as a model characteristic for newly created varieties of soft spring wheat. In addition to the above, we present an assessment of the entire set of studied varieties in terms of the ecological variability of their yield in terms of its maximum (max) and minimum (min) values, the scatter range R, stability S^2d_i, plasticity b_i, and homeostaticity Hom [22, 74].

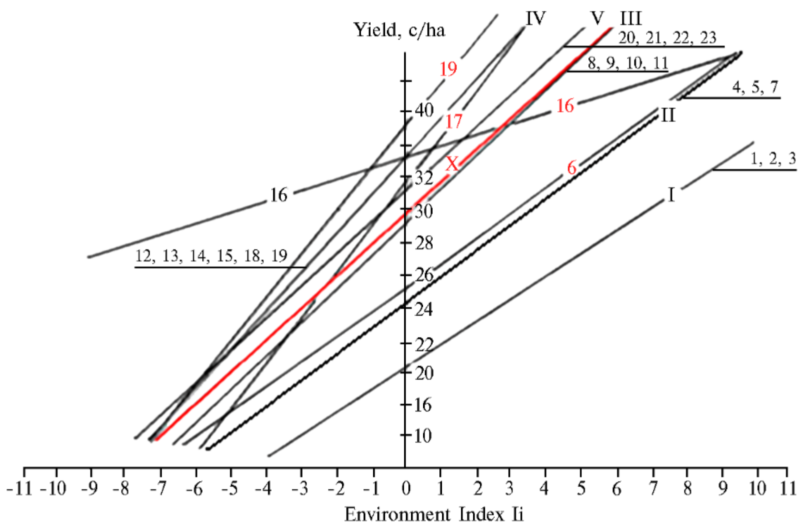
5. Ecological yield variability in soft spring wheat (*Triticum aestivum* L.) varieties grouped by periods of cultivation in Western Siberia over the years of observation (trial fields of the Research Institute of Agriculture of Northern Trans-Urals, Tyumen, 57°09' N, 65°32' E, 2005-2012)

Variety	x, c/ha	Lim, c/ha		R, c/ha	S^2d_i	b_i	Hom
		min	max				
Group I (1930-1950 гоы)							
Cezium 111	18.1	9.6	34.1	24.8	22.2	0.71	0.26
Milturum 321	21.6	12.8	33.6	20.8	3.4	0.83	0.94
Lutescense 956	21.0	15.3	32.4	17.1	16.0	0.61	0.42
x	20.2					0.72	
Group II (1951-1970)							
Lutescense 758	23.8	16.0	37.7	21.7	9.6	0.81	0.61
Milturum 553	23.5	13.5	43.3	29.8	35.4	1.03	0.42
Saratovskaya 29	24.9	17.9	37.3	19.4	19.9	0.76	0.74
Skala	27.2	18.1	40.5	22.4	8.9	0.92	0.93
x	24.9					0.86	
Group III (1971-1990)							
Strela	29.6	20.0	45.8	25.8	4.8	0.97	1.50
Novosibirskaya 67	22.3	13.3	35.3	22.0	11.7	0.96	0.51
Rang	31.2	20.9	46.3	26.3	14.2	0.83	0.98
Tyumenskaya 80	35.2	22.7	49.4	26.7	6.1	1.11	1.90
x	29.6					0.97	

			Group IV (1991-2012)				
Omskaya 20	33.3	18.7	48.9	30.2	13.0	1.21	1.16
Lutescense 70	35.3	23.7	55.1	31.4	8.7	1.24	1.60
Il'inskaya	35.6	22.7	58.0	35.3	19.7	1.24	0.93
AVIADa	34.2	19.5	50.5	31.0	22.3	1.35	0.96
Chernyava 13	34.2	26.0	44.0	18.0	16.6	0.56	1.08
Ikar	32.0	16.8	50.0	33.2	8.6	1.40	1.31
SKENT 3	32.0	18.2	49.7	31.5	22.6	1.23	0.81
Riks	38.0	18.0	57.6	39.6	33.0	1.32	0.95
x	34.3					1.28	
			Group V (1991-2012)				
Tulunskaya 12	29.7	17.1	42.3	25.2	26.6	0.98	0.65
Novosibirskaya 15	30.5	15.1	39.2	24.1	29.0	0.79	0.65
Iren'	31.1	19.7	40.5	20.8	10.3	0.78	1.14
Novosibirskaya 29	33.3	16.5	46.3	29.8	9.1	1.26	1.40
x	31.2					0.95	
Average	29.7						
LSD_{05}	2.2						

N o t e. Groups I-IV — mid-ripening varieties originated from Tyumen Breeding Center (except for Omskaya 20 variety); group V — early-ripening varieties originated from other regions; max means maximum, min means minimum values, R means a scatter range, S^2d_i is a stability parameter, b_i assesse plasticity, and Hom means homeostaticity.

With a lower yield (20.2 c/ha) in extensive varieties (group I) compared to other genotypes, its minimum values (9.6-15.3 c/ha) occur in dry years and maximum (32.4-34.1 c/ha) in years with high moisture supply (at R = 17.1-24.5 c/ha) (Table 5). Among them, the most stable in terms of yield was the old Siberian variety Milturum 321 (S^2d_i = 3.4), the source material for which was selected at the beginning of the 20th century in the Trans-Urals by N.L. Skalozubov, the first agronomist of the Tobolsk province. Low yield stability was noted in the Lutescens 956 variety and especially in the Cesium 111 variety, S^2d_i = 16.0 and S^2d_i = 22.2, respectively). The pronounced plasticity of the latter (b_i = 0.61 and b_i = 0.71) should be noted (see Table 5), which is well reflected by regression lines with a gentle slope (31°-35°) (Fig.).



Plasticity of soft spring wheat (*Triticum aestivum* L.) varieties grouped by periods of cultivation in Western Siberia over the years of observation: group I (1930-1950), group II (1951-1970), group III (1971-1990), group IV (1991-2012) — mid-season varieties from the Tyumen breeding center; group V (1991-2012) — early-ripening varieties from other regions. Group I: 1 — Cezium 111, 2 — Milturum 321, 3 — Lutescense 956; group II: 4 — Lutescense 758, 5 — Milturum 553, 6 — Saratovskaya 29, 7 — Skala; group III: 8 — Strela, 9 — Novosibirskaya 67, 10 — Rang, 11 — Tyumenskaya 80; group IV: 12 — Omskaya 20, 13 — Lutescense 70, 14 — Il'inskaya, 15 — AVIADa, 16 — Chernyava 13, 17 — Ikar, 18 — SKENT 3, 19 — Riks; group V: 20 — Tulunskaya 12, 21 — Novosibirskaya 15, 22 —

Iren’, 23 — Novosibirskaya 29. Trial fields of the Research Institute of Agriculture of Northern Trans-Urals (Tyumen, 57°09' N, 65°32' E, 2005-2012), The average regression line is marked in red.

In variety Milturum 321, at b_i = 0.83, the regression line is steeper, with a slope of 39°, therefore, it responds more strongly to changes in environmental conditions. The foregoing is well interpreted through the indexes of environmental conditions Ii (see Table 4, Fig.). The index of homeostasis (Hom), reflecting the adaptability of the variety to varying external conditions, was higher in the variety Milturum 321 (Hom = 0.94), lower in the variety Lutescens 956 (Hom = 0.42) and very low in the variety Cesium 111 (Hom = 0.26). This indicates their insufficient adaptability to the agro-climatic conditions of the Northern Trans-Urals and serves as one of the explanations for the fact that not a single variety was created with the participation of the Cesium 111 variety using classical breeding methods. We used the yield and variability of these varieties as basic indicators for further evaluation and interpretation of test results.

In semi-intensive varieties cultivated in 1950-1970 (group II), the average yield was 24.9 c/ha with higher limit values than in group I. The R values in most varieties from group II remained within the limits for the genotypes described above. The exception was the late-ripening variety Milturum 553 with a high maximum yield value (43.3 c/ha) with R = 29.8 c/ha. The variety Milturum 553 had a low yield stability (S^2d_i = 35.4) and a lower homeostatic index (Hom = 0.42), which indicates the inefficiency of its cultivation in the region. The remaining varieties of this group, Lutescens 758, Saratovskaya 29 and Skala showed a certain stability in yield formation (S^2d_i of 8.9, 9.9, and 19.9) and plasticity (b_i of 0.76, 0.81, and 0.92). The regression lines reflecting plasticity (see Fig.) run higher than for the Milturum 553 variety, and at a less steep slope (37-39° vs. 45° for the Milturum 553 variety) and cross the y-axis higher (at 24.9 c/ha). Therefore, these varieties respond to improved cultivation conditions, but at yields above 25 c/ha, they are prone to lodging. Variety Skala turned out to be quite resistant to lodging and well adapted to local conditions (Hom = 0.93), due to which it was cultivated in the West Siberian region for many years.

Intensive mid-season varieties of group III (1971-1990) gave good average yields over the years (29.6-35.2 c/ha). The exception was the variety Novosibirskaya 67 with the average yield over the years of 22.3 c/ha. Its limiting values, as well as the homeostatic index (Hom = 0.51) were close to those of a number of varieties from group II, which refers the variety Novosibirskaya 67 to genotypes less adapted to the conditions of the zone. The grain of variety Novosibirskaya 67 (var. *albidum*) germinates in the ear in autumn in humid conditions. All this influenced the removal of the variety from zoning in the Northern Trans-Urals. Strela and Tyumenskaya 80 varieties (S^2d_i = 4.8 and S^2d_i = 6.1) were the most stable varieties created in the Trans-Urals in terms of yield. They turned out to be well adapted to the conditions of the zone (Hom = 1.50 and Hom = 1.90). Variety Rang in terms of ecological variability of yield was identical to varieties Strela and Tyumenskaya 80, but, unlike them, it was less homeostatic (Hom = 0.98). The narrow-local variety Rang, due to its high resistance to lodging, was cultivated only in the conditions of the northern forest-steppe of the Tyumen region under intensive farming with the use of mineral fertilizers at high doses (100-120 kg a.i./ha). With their decrease, the yield of the Rang variety drops sharply. According to the plasticity in varieties Rang, Strela and Tyumenskaya 80 (b_i = 0.83, b_i = 0.97 and b_i = 1.11), it can be seen that these varieties quite noticeably respond to changes in environmental conditions. Their regression lines had a steeper slope (39°, 42° and 47°). When the environmental conditions improved, the productivity of these varieties increased adequately, and when the environmental conditions worsened, they similarly reduced it. This is well demonstrated by the averaged regression line, which crosses the y-axis at 29.6 c/ha, being significantly higher than for the previous two groups (see Fig.). Along with the practical significance, the genotypes of this group are widely used in hybridization. Thus, the Strela, Novosibirskaya 67 and Rang varieties, among 15 genotypes, were included in the regional Interdepartmental DIAS program (study of the genetics of spring wheat productivity traits in Western Siberia, 1973-1984) [34] with a wide ecological scope (in eight zones of Siberia). A large-scale hybridological analysis (Heyman diallel analysis) followed by hybrids' and parental forms' testing at eight geographical sites, made it possible to study the genetics of quantitative traits of varieties in the ecological gradient. These genotypes show good variety-forming ability. With their participation, a number of released and registered varieties were created under this program: DIAS-2, Lutescens 70, Altaiskaya 88, Altaiskaya 92, Altai prostor, Kazakhstanskaya early ripening, Kazakhstanskaya 17, Baganskaya 93, Kantegirskaya 89 [34]. In Krasnoufimsk, the spring wheat variety Gornouralskaya was created (allowed for the regional cultivation in 2009), in Tyumen — the varieties Riks, Tyumenskaya 29, Grenada (allowed for the regional cultivation in 2011, 2014, 2018) [34] and the variety Atlanta 1, which has been under State variety testing since 2018. Mid-season intensive varieties cultivated since the late 1990s, the Omskaya 20, Lutescens 70, Chernyava 13, AVIAD, Ikar, SKENT 3 and Riks have increased their yields (x = 34.3 c/ha, i.e., +14.1 c/ha, or +70% to the baseline which was significantly higher vs. the previous group with +4.7 c/ha). The minimum yield in dry conditions remained at the same level as that of varieties from group III well adapted to local conditions. Their maximum yield was significantly higher than that of the compared varieties (48.9-58.0 c/ha), due to which the dispersion index also increased significantly (R = 30.2-39.6 c/ha), which associated with high GEI levels [46]. From the indicated set, the varieties Lutescens 70 and Ikar widely distributed in the Trans-Urals (S^2d_i = 8.7, S^2d_i = 8.6) were distinguished by the stability of crop formation. Variety Chernyava 13 with a good average yield (34.2 c/ha) showed a rather high minimum yield (26.0 c/ha), which indicates its good drought resistance. The maximum yields of the Chernyava 13 variety are significantly less than those of other varieties (44.0 c/ha), which is due to the tendency to lodging. Because of this, the yield value dispersion in this variety is almost 2 times less than that of others (R = 18.0 c/ha). Cultivar Chernyava 13 was distinguished by plasticity (b_i = 0.56), its regression line had a small slope angle (29°) and crossed the y-axis at a high mark (34.2 c/ha) (see Fig.). Consequently, variety Chernyava 13 responds less than other varieties to the deterioration of environmental conditions. All other varieties from group IV had high rates of ecological plasticity (b_i = 1.21-1.40). In graphical form, this was reflected by regression lines with slopes of 50°-54°. This characterizes a strong response to improved conditions for growing varieties and indicates their intensity.

Modern early-ripening varieties Tulunskaya 12, Novosibirskaya 15, Iren', Novosibirskaya 31 (group V) turned out to be less productive than cultivated mid-ripening ones (x = 31.2 c/ha, or –3.1 c/ha compared to mid-ripening varieties). In early ripe varieties, a lower maximum yield (39.2-42.3 c/ha) and a smaller R = 20.8-25.2 c/ha were noted. Varieties Tulunskaya 12 and Novosibirskaya 15 were unstable in terms of yield formation (S^2d_i = 26.6 and S^2d_i = 29.0). The regression lines for varieties Novosibirskaya 15 and Iren' were flatter with slope angles of 37°-38° (b_i = 0.79-0.78) (see Fig.), which indicates a more pronounced homeostatic yield in these varieties compared to variety Tulunskaya 12 (b_i = 0.98), in which the regression line is rather steep (slope angle 44°) and close to the average for the experiment. Cultivar Novosibirskaya 29 in terms of yield (x = 33.3 c/ha), its R = 29.8 c/ha, values of plasticity, stability and homeostaticity parameters (b_i = 1.26,

S^2d_i = 9.1 and Hom = 1.40) was similar to the intensive mid-ripening varieties Lutescens 70 and Ikar, widespread in the Trans-Urals and adapted to local conditions. The low homeostasis index, which we found in the varieties Tulunskaya 12 and Novosibirskaya 15 (Hom = 0.65), indicates their low adaptation to the conditions of the zone due to poor drought resistance in the early summer period, rapid growth, accelerated passage of the tillering phase, and the tendency to preharvest germination of grain in the ear.

Our findings confirm the conclusions of many breeders that varieties with high potential productivity under favorable conditions are more likely to respond to its decline in unfavorable conditions than less productive varieties [13].

So, based on an 8-year study of five groups of soft spring wheat varieties that have been used in the Northern Trans-Urals over an 80-year period, we have proposed an approach to quantitatively describe the changes that occur during long-term selection. Monitoring is based on several important characteristics of varieties. i.e., yield variation over the years of testing; effects of response to environmental conditions, changing the ranks of yields over the years; parameters of variety plasticity (yield homeostaticity); relationship between maturity and productivity. The variability of yield over years for one variety and the change in yield ranks over the years observed between varieties (effects of response to environmental conditions) largely depend on the adaptive genetic systems of each variety which ensure yield, when the limiting environmental factors vary from year to year or between geographical locations. The information obtained by the proposed method makes it possible to predict the behavior of varieties in changing environmental conditions and indicates the optimal directions for selection. Varieties adapted to local conditions with high contributions of adaptability systems and response effects to the formation of yield should be used as the starting material in breeding work.

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