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Drought resistance of introgressive spring common wheat lines with genetic material of tall wheatgrass

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Background. To breed drought-resistant cultivars of common wheat[1] (*Triticum aestivum* L.), it is important to use the gene pools of its relatives, including tall wheatgrass *Thinopyrum ponticum* (Podpěra) Z.-W. Liu & R.- C. Wang (= *Agropyron elongatum* (Host) Beauv.).

Materials and methods. The introgressive lines of spring common wheat with *T. ponticum* genetic material and standard cultivars were studied in the field in the southern forest-steppe of Western Siberia using generally recognized methods. The ecological plasticity of cultivars and introgressive lines by grain yield and yield components was calculated according to the method of S. A. Eberhart and W. A. Russell. During the research period, there was a prolonged drought in 2012, and irregular short severe droughts occurred in 2013, 2014, and 2017.

Results. An analysis of the ecological plasticity of standard cultivars adapted to the regional conditions showed that cv. 'Pamyati Azieva' corresponded to the extensive type, and cvs. 'Duet', and 'Erythrospermum 59' corresponded to the intensive type. Under drought conditions, the grain yield of cv. 'Pamyati Azieva' was determined by the stable development of productive tiller number, seed number and grain yield per main ear, but plasticity in 1000 grain weight was observed. Cvs. 'Duet' and 'Erythrospermum 59' showed ecological plasticity due to the adaptive development of two or three yield components. Introgressive lines exceeded the standard cultivars in grain yield (1.1–2.2 times) in dry seasons. Five lines were similar to cv. 'Pamyati Azieva' in plasticity and stability, and under drought conditions they demonstrated high and stable development of three or four yield components. The intensive lines formed their yield due to the compensatory development of three yield components in different combinations.

Conclusion. Introgressive lines with *T. ponticum* genetic material are valuable for breeding spring common wheat cultivars with various drought-adaptation mechanisms.

Keywords: *Triticum aestivum*, *Thinopyrum ponticum*, breeding material, abiotic factors, ecological plasticity

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[1] При публикации статьи редакцией журнала было учтено настойчивое требование автора на изменение ряда терминов и определений, принятых в журнале: bread wheat исправлено везде на common wheat; Omsk Province исправлено на Omsk Oblast; environmental plasticity исправлено на ecological plasticity; life pattern исправлено на life style; growing season исправлено на vegetation period; standard reference исправлено на standard; yield structure components, или yield components исправлено на yield traits. /When publishing this article, the editors of the Journal took into account the author's insistent intent to change a number of terms and definitions adopted in the Journal: *bread wheat* was replaced everywhere with *common wheat*; *Omsk Province* was changed to *Omsk Oblast*; *environmental plasticity* to *ecological plasticity*; *life pattern* to *life style*; *growing season* to *vegetation period*; *standard reference* to *standard*; *yield structure components*, or *yield components* to *yield traits*.

Научная статья
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Устойчивость к засухе интрогрессивных линий яровой мягкой пшеницы с генетическим материалом пырея удлиненного

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Актуальность. Для создания засухоустойчивых сортов мягкой пшеницы (*Triticum aestivum* L.) актуально использование генофондов родственных злаков, включая пырей удлиненный *Thinopyrum ponticum* (Podpěra) Z.-W. Liu & R.-C. Wang (= *Agropyron elongatum* (Host) P. Beauv.).
Материалы и методы. Интрогрессивные линии яровой мягкой пшеницы с генетическим материалом *T. ponticum* и сорта-стандарты были изучены в полевых условиях в южной лесостепи Западной Сибири (г. Омск) по стандартным методам. Расчет показателей экологической пластичности образцов по продуктивности и элементам структуры урожая был проведен по методике S. A. Eberhart and W. A. Russell. В период исследований в регионе были отмечены длительная засуха в 2012 г., а также нерегулярные жесткие засухи в 2013, 2014 и 2017 г.
Результаты. Анализ экологической пластичности адаптированных к условиям региона стандартов показал, что сорт ‘Памяти Азиева’ соответствовал экстенсивному типу, а сорта ‘Дуэт’ и ‘Эритроспермум 59’ – интенсивному. В условиях засухи продуктивность сорта ‘Памяти Азиева’ определялась стабильным формированием числа продуктивных стеблей, числа зерен и массы зерна главного колоса, но отмечена пластичность по массе 1000 зерен. Сорта ‘Дуэт’ и ‘Эритроспермум 59’ проявили экологическую пластичность за счет усиления развития двух-трех элементов структуры урожая. Интрогрессивные линии в засушливые годы превосходили сорта-стандарты по продуктивности в 1,1–2,2 раза. Пять линий были схожи с сортом ‘Памяти Азиева’ по показателям пластичности и стабильности. В условиях засухи у них отмечено высокое и стабильное формирование трех или четырех элементов структуры урожая. Остальные линии интенсивного типа формировали урожай за счет компенсаторного развития трех элементов структуры урожая (в разных сочетаниях) при наступлении благоприятных условий.
Заключение. Интрогрессивные линии с генетическим материалом *T. ponticum* перспективны для создания резистентных к засухе сортов яровой мягкой пшеницы с различными адаптационными механизмами.

Ключевые слова: *Triticum aestivum*, *Thinopyrum ponticum*, селекционный материал, абиотические факторы, экологическая пластичность

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Introduction

Common wheat *Triticum aestivum* L. is one of the most important cereals that provide nutrition to the world's population. Due to the consumption of products related to the use of its grain, humanity receives ~ 20% of the necessary calories. In connection with the projected growth of the population, it is necessary to increase wheat grain production to 900 million tons by 2050 (Baker et al., 2020). One of the approaches to solve this problem is to reduce crop losses by using cultivars resistant to abiotic and biotic stresses. Climate change unfavorably affects the crop production in different world regions, with drought and high temperatures having the worst effect (Kosová et al., 2014). About 1/3 of the world's 200 million hectares of wheat crops suffer from unstable humidity, especially in the warm regions most favorable for agriculture (Goncharov, 2021).

Drought-resistant plants are considered to be able to survive a water scarcity and overheating for short or long periods, as well as to form a sufficiently high productivity (Turner, 1986). Drought resistance is broadly defined as the ability of a variety to form a higher yield compared to others under conditions of moisture deficiency (Lepekhov, 2014). Stress factors cause the greatest damage to plants during critical periods of development: germination, tillering, flowering, and grain filling (Passioura, 2007; Kosová et al., 2014). The resistance can be achieved in various ways: by avoiding stress, by forming a good root system, by compensatory organ development, by activation of physiological mechanisms (accumulation of osmolites, proteins, etc.) (Sallam et al., 2019). High water-retaining capacity makes it possible to maintain the cell and tissue hydration, which affects the height, area of the photosynthetic apparatus, pollen viability, and grain yield (Passioura, 2007; David, 2012). Since resistance to moisture deficiency is formed due to a set of mechanisms, the trait is controlled by polygenic systems and manifests itself quantitatively. More than 800 QTLs are involved in the control of various drought resistance mechanisms and are localized on most wheat chromosomes (Sallam et al., 2019). The conditions of plant development and stress rhythms in the regions differ significantly, therefore, the set of protective mechanisms should correspond to them (Kosová et al., 2014). Direct assessment in the field makes it possible to define integral drought resistance (Lepekhov, 2014).

To increase yields, it is important to use drought-resistant cultivars adapted to the changing climate. Distant hybridization is considered one of the promising directions to increase the stress resistance of wheat (Kosová et al., 2014, Ceoloni et al., 2014). Tall wheatgrass *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang (= *Agropyron elongatum* (Host) P. Beauv., $2 = 10x = 70$, $\mathrm{JJJJJJJ^{s}J^{s}J^{s}J^{s}}$ or $\mathrm{E^{e}E^{e}E^{b}E^{b}E^{x}E^{x}StStStSt}$) is a valuable source of genes (Zhang et al., 1996; Chen et al., 1998). *T. ponticum* was mainly used as a source of disease resistance. As a result, the resistance genes controlling leaf and stem rusts, powdery mildew, *Fusarium* head blight, and viral diseases were transferred to the wheat gene pool (Salina et al., 2015; Baker et al., 2020). *T. ponticum* also showed resistance to abiotic factors such as water logging, salinity, and extreme temperatures (Taeb et al., 1993; Colmer et al., 2006; Ceoloni et al., 2014). The *T. ponticum* genetic material was used for breeding hardy winter common and durum wheat cultivars as well as those resistant to unstable moisture conditions. Spring common and durum wheat cultivars bearing translocation 7DL-7Ai (with known *Lr19*/*Sr25*-genes) produced high yields in the areas with unstable humidity: the Volga region, Omsk Oblast, and Italy (Upelniek et al., 2012; Sibikeev, Druzhin, 2015; Kuzmanović et al., 2018; Belan et al., 2021).

Western Siberia is one of the leading agricultural regions of Russia, which provides about 13% of the wheat grain yield (Goncharov, 2021). The main wheat crops are located in the south, where the temperature regime is favorable for growing high-quality grain, but regular rain deficiency leads to large crop losses. In the steppe and forest-steppe zones of Omsk Oblast, droughts were observed in 15 years out of the last 45 years (Belan et al., 2021).

The original introgressive lines of spring common wheat with the genetic material of *T. ponticum* were breed at Omsk State Agrarian University (Omsk SAU, Omsk). The lines were resistant to stem and foliar fungal diseases; they ensured high crop yield and grain quality (Plotnikova et al., 2016, 2019). Due to the tendency for increasing abiotic stress pressure, the research of the lines under drought conditions and the study of their agronomic characters were carried out.

The aim of the research was to study the ecological plasticity of introgressive spring common wheat lines with the genetic material of *T. ponticum* under drought conditions, as well as to identify yield traits that ensure adaptation to stress in Western Siberia.

Materials and methods

Fourteen introgressive lines (ILs) of spring common wheat *Triticum aestivum* (var. lutescens) with the genetic material of *Thinopyrum ponticum*, originated at Omsk SAU were used for the experiments (Table 1). The parent form was the accession of *T. ponticum* obtained from the Main Botanical Garden of the Russian Academy of Sciences (Moscow) under the name "Tall Wheatgrass – *Agropyron elongatum* (Host) P. Beauv.". At the first step of distant hybridization, the interspecific hybrid (*Triticum durum* × *Thinopyrum ponticum*) was produced, and then the Wheat–Wheatgrass Hybrids (WWHs) [(*Triticum durum* × *Thinopyrum ponticum*) × *Triticum aestivum* cv. Pyrotrix 28] were obtained. The spring forms were selected among the self-pollinated WWHs progenies. WWHs were included in the crosses with disease-susceptible spring common wheat cultivars bred in Omsk Oblast (Plotnikova et al., 2011). In the breeding process, individual plants resistant to leaf and stem rusts (introgression marker), with a shortened vegetation period and good yield, were selected (Plotnikova et al., 2014, 2016). Spring common wheat cvs. 'Pamyati Azieva' (medium-early), 'Duet' (medium-ripening), 'Erythrospermum 59', and 'Serebristaya' (medium-late) (since 2017) were used as standard references.

The research was carried out in field conditions in the southern forest-steppe of Western Siberia (Omsk). The samples were sown in the second ten days of May. In 2012–2014 and 2017, the lines were sown in 4 rows with the 40 seeds/m sowing density. In 2017 and 2018, the best lines were studied in trial plots (triplicated 10 m^2 plots), 500 seeds/m^2 sowing density). Phenological phases were determined according to Zadok's scale (Koishybaev, 2018). Harvesting was carried out in the third ten days of August as the plants matured. Yield structure components were determined in the sheaves according to standard methods.

Statistical analysis included the calculation of the mean and standard errors of the mean ($M \pm SEM$), coefficients of variation V (%), and correlation r. For the calculation, the STATISTICA v. 6.0 software (StatSoft, Inc., USA), and Microsoft Office Excel 2010 were used. Calculation of the ecological plasticity of grain yield and yield structure components was carried out for the 2012–2014 and 2017 seasons using the

Table 1. Origin of introgressive spring common wheat lines with genetic material of *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang

Таблица 1. Происхождение интрогрессивных линий яровой мягкой пшеницы с генетическим материалом *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang

Introgressive line, No.	Origin
5	S_5 [WWH × B_3 Chernyava 13]
6, 10, 11, 31	S_5 [WWH × B_4 Chernyava 13]
364, 374	S_5 [WWH × B_5 Chernyava 13]
12	S_5 [(WWH × B_2 Chernyava 13) × B_2 Niva 2]
15	S_5 [(WWH × Lutescens 444) × B_3 Chernyava 13]
17	S_5 [(WWH × B_3 Lutescens 444) × Chernyava 13]
20	S_5 [(WWH × Niva 2) × B_3 Golubkovskaya]
37, 359	S_5 [(WWH × B_3 Lutescens 444) × Chernyava 13]
375	S_5 [(WWH × Niva 2) × B_4 Golubkovskaya]

Note: WWH – Wheat-Wheatgrass Hybrid; B – backcross; S – self-pollination

Примечание: WWH – пшенично-пырейных гибрид; B – беккросс; S – самоопыление

Eberhart–Russell method (1966). For assessment of adaptability, the regressive coefficient b_i (= coefficients of ecological plasticity) was determined; for stability, the mean squared deviation σ_d^2 (deviation of actual from potential traits), and for the estimation of environment, the index of environmental conditions I_j.

Weather conditions (according to Omsk Weather Station) varied significantly during the period of research (Table 2). The driest and hottest season was 2012, when the sum of rainfall was two times smaller, and the sum of positive temperatures was 266°C higher than the mean multiannual ones. Low amount of precipitation was also observed in 2014 and 2017 (1.5 times lower than the normal), when the sum of positive temperatures exceeded the mean multiannual one by 42°C and 101°C, respectively. The 2013 season was close to normal in terms of precipitation, but its effective temperatures were lower (–79°C). The most humid season was 2018, when the precipitation was 1.3 times higher, and temperatures were 320°C lower than the mean multiannual rates. For detailed description of weather conditions, the ten-day and growing-season hydrothermal coefficients (HTC – the indicator of moisture content for the territory) were calculated.

Results

The breeding of cultivars with *T. ponticum* genetic material is a complex and prolonged process. The material obtained by distant hybridization is often characterized by low yield and a number of negative properties. Such effects may be induced by an incomplete compensation of cultural loci with alien fragments or a close linkage between the genes that determine valuable and undesirable traits (Salina et al., 2015). *T. ponticum* is characterized by a perennial life style and fine grain (Upelniek et al., 2012). The initial generations of spring WWHs had a long vegetation period (up to 130 days), low yield, and small grains (Plotnikova, 2014). After backcrossing and individual selection, improved ILs resistant to foliar and stem diseases were originated. Among the 390 ILs studied, fourteen were selected with a high average grain yield in 2012–2017 (Table 3).

In 2012–2014 and 2017, precipitation and temperatures were distributed extremely unevenly, as shown by a comparison with the average multiannual and ten days HTC (see Table 2). In these years, a spring/early summer drought typical for the region was observed, as confirmed by the low ten-day HTC in the period from the second ten days of May to the second ten days of June. In addition, low rainfall at high temperatures occurred during the tillering in 2013 and 2014, the period from the first node to stem elongation in 2013, 2014 and 2017, from heading to anthesis in 2012, and from milk ripeness to wax ripeness in 2012 and 2017. In all years, except for 2014, a significant amount of precipitation fell in the third ten days of August, which increased the HTC for the vegetation period, but did not significantly affect grain yield. The most unfavorable season for the yield was 2014, when the spring-early summer drought coincided with low soil moisture reserves (the index of environmental conditions was $I_j = -0.38$, and average grain yield was 0.98 g/plant) (see Table 3). In 2012, despite the low amount of precipitation and high temperatures, the index of environmental conditions was close to zero ($I_j = 0.06$). This was probably due to the fact that scant rains fell during critical period of plant development. The most favorable was 2013, when the negative effect of the spring-early summer drought was compensated by heavy rainfall in July and August (average grain yield: 1,92 g/plant, $I_j = 0.56$). In general, in the seasons with unstable precipitation, environmental conditions had the main impact on grain yield (87.5%), the genotype determined 6.2%, and the genotype × environment interaction determined 6,3% of the total variation. In those seasons, standard reference cultivars developed within 83–88 days, and ILs within 81–97 days. The ILs were distributed into four groups of ripeness: medium-early, medium-ripening, medium-late, and late-ripening (see Table 3).

During the research, cv. 'Pamyati Azieva' demonstrated the lowest variability in grain yield (variation coefficient $V = 20\%$). The assessment of its adaptability by the Eberhard–Russell method showed that the coefficients of ecological plasticity and stability were low ($b_i = 0.07$ and $\sigma_d^2 = 0.16$, respectively), and its regression line was directed almost

Table 2. Weather conditions in the forest-steppe zone of Western Siberia (Omsk, 2012–2014, 2017, and 2018)
Таблица 2. Метеорологические условия в лесостепной зоне Западной Сибири (Омск, 2012–2014, 2017 и 2018 г.)

Month, weather parameter	Ten-day period	Phenological phases (Zadok's scale)	Mean multiannual			2012			2013			2014			2017			2018		
			Rainfall, mm	Temperature, °C*	HTC	Rainfall, mm	Temperature, °C*	HTC	Rainfall, mm	Temperature, °C*	HTC	Rainfall, mm	Temperature, °C*	HTC	Rainfall, mm	Temperature, °C*	HTC	Rainfall, mm	Temperature, °C*	HTC
May	II	Germination ph.0	10	12.1	4.8	8	13.5	2.3	13	7.8	–	2	15	0.4	8	12.8	2.9	10	6.7	–
	III	Emergence ph.10	14	14.0	3.5	3	16.3	0.5	9	13	3.0	19	10.5	3.8	11	15.5	2.0	37	10.3	123
June	I	Leaves Tillering ph.11-30	14	16.1	2.3	14	20.3	1.4	5	13.7	1.4	3	12.8	1.1	29	17	4.1	8	16.9	1,2
	II	First node Stem elongation ph. 30-36	17	18.3	2.0	16	19.8	1.6	8	16.9	1.2	5	20.4	0.5	1	21.8	0.1	5	16.6	0,8
	III		22	18.9	2.5	17	21.4	1.5	0	19.4	0.0	7	18.2	0.9	1	20.1	0.1	49	18.2	6,0
July	I		21	19.8	2.1	2	20.1	0.2	24	16.6	3.6	20	19.2	2.2	11	18.1	1.4	0	21.2	0,0
	II	Flag leaf Heading Anthesis ph. 37-65	21	19.7	2.2	5	25.6	0.3	54	19.3	5.8	17	15.4	3.1	32	17	4.6	5	21.8	0,4
	III	Milk ripe ph. 66-80	25	18.8	2.8	1	22,8	0.1	21	21.1	1.9	19	14.8	4.0	27	20.2	2.6	40	16.7	6,0
August	I		20	17.8	2.6	19	19.8	1.9	36	19.4	3.8	16	19.4	1.7	10	19.7	1.0	10	17.8	1,3
	II	Wax ripe Full ripe ph. 81-91	16	16.9	2.3	7	19.6	0.7	1	17.7	0.1	22	19.7	2.3	0	14.5	0.0	18	16.9	2,6
	III		17	14.6	3.7	23	14.4	5.2	23	14.2	5.5	5	18.4	0.6	4	20.2	0.4	34	13.7	9,2
Sum of rainfalls, mm**	–	–	197	–	–	115	–	–	194	–	–	135	–	–	134	–	–	216	–	–
HTC **		–	–	–	2.56	–	–	1.11	–	–	2.7	–	–	1.8	–	–	1.54	–	–	3,1
Sum of active temperatures, °C**	–	–	–	1870	–	–	2136	–	–	1791	–	–	1828	–	–	1969	–	–	1550	–

Note: * – average for ten days; ** – for the period 'second ten days of May – the third ten days of August; HTC – hydrothermal coefficient

Примечание: * – среднедекадная; ** – период «II декада мая – III декада августа»; НТС – гидротермический коэффициент

Table 3. **Grain yield, ecological plasticity, and stability of spring common wheat cultivars and introgressive lines with *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang genetic material** (Omsk, 2012–2014, and 2017)

Таблица 3. **Масса зерна с растения, экологическая пластичность и стабильность сортов и линий яровой мягкой пшеницы с генетическим материалом *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang** (Омск, 2012–2014, 2017 г.)

Cultivar, line	Vegetation period, days^a	Grain yield, g/plant						Coefficient of ecological plasticity, b_i	Stability, σ_d^2
		2012	2013	2014	2017	Average	V, %		
Medium-early									
Pamyati Azieva	83 ± 6	1.08	1.01	0.77	1.36	1.06 ± 0.11	20.0	0.07	0.16
364	82 ± 5	1.80*	1.17*	1.16*	2.15*	1.57 ± 0.21	27.2	0.49	0.22
374	81 ± 5	1.87*	1.75*	1.53*	1.66*	1.70 ± 0.06	7.3	0.87	0.03
$SSD_{0,05}$	–	0.20	0.11	0.09	0,27	–	–	–	–
Medium-ripening									
Duet	86 ± 7	1.08	2.96	1.06	1.02	1.53 ± 0.41	54.1	2.08	0.25
17	86 ± 6	1.45*	2.57	0.97	1.53*	1.63 ± 0.29	36.3	1.52	0.08
359	85 ± 8	1.50*	2.14	0.88	1.24*	1.44 ± 0.23	32.4	1.27	0.01
375	84 ± 6	1.51*	1.40	0.61	2.22*	1.44 ± 0.29	40.1	0.70	0.31
$SSD_{0,05}$	–	0.21	0.15	0.21	0.22	–	–	–	–
Medium-late									
Erythrospermum 59	88 ± 7	1.04	2.84	0.84	1.23	1.49 ± 0.40	53.2	2.00	0.22
11	88 ± 5	1.10	2.15	0.88	1.49*	1.41 ± 0.24	34.3	1.19	0.05
15	87 ± 6	1.47*	1.94	1.26*	1.09	1.44 ± 0.16	22.1	0.84	0.02
$SSD_{0,05}$	–	0.19	0.17	0.18	0.16	–	–	–	–
Late-ripening									
10	89 ± 8	1.51	2.03*	0.90	1.20	1.41 ± 0.21	30.0	1.16	0.01
12	89 ± 9	2.14*	1.53	0.77	1.20	1.41 ± 0.25	35.2	0.55	0.11
20	89 ± 7	2.99*	2.14	1.50*	1.57*	2.05 ± 0.30	29.3	1.90	0.74
31	91 ± 7	1.95*	1.18	1.48*	2.44*	1.76 ± 0.24	27.1	1.41	0.98
37	90 ± 8	1.96*	1.80	0.93	1.51*	1.55 ± 0.20	25.2	1.24	0.42
5	96 ± 9	1.04	1.73	0.79	1.77*	1.33 ± 0.21	32.0	1.87	0.59
6	97 ± 9	1.10	1.53	1.45*	2.10*	1.55 ± 0.18	23.2	1.57	1.08
$SSD_{0,05}$	–	0.19	0.17	0.13	0.16	–	–	–	–
I_j		0.06	0.56	–0.38	–0.24	–	–	–	–

Note: ^{a} average for 2012–2014, and 2017; V – coefficient of variation; I_j – index of environmental conditions; * – significantly exceeded the standard ($p \le 0.05$)

Примечание: ^{a} среднее за 2012–2014 и 2017 г.; V – коэффициент вариации; I_j – индекс условий среды; * – достоверное превышение стандарта ($p \le 0,05$)

horizontally (see Table 3, Figure 1, track 1). According the Eberhart–Russell model, such indicators correspond to an extensive cultivar, unable to significantly increase grain yield under favorable conditions, but weakly reduce it under stresses. Cvs. ‘Duet’ and ‘Erythrospermum 59’ showed high variability (V = 53–54%), mainly affected by intense precipitation in July 2013. The coefficients of ecological plasticity for these cultivars were $b_i > 1$, while stability was low (b_i = 2.00–2.08, σ_d^2 = 0.22–0.25), and their regression lines were positioned obliquely (Figure 1, tracks 4, 8). Such parameters demonstrate ecological plasticity under favorable conditions and are typical for intensive cultivars. At the same time, low stability indicates the ability to maintain yield under stress. Such features are considered the most valuable for crop cultivation.

The variability of the ILs in grain yield was lower than that of cvs. ‘Duet’ and ‘Erythrospermum 59’ (7–40%). A signifi-

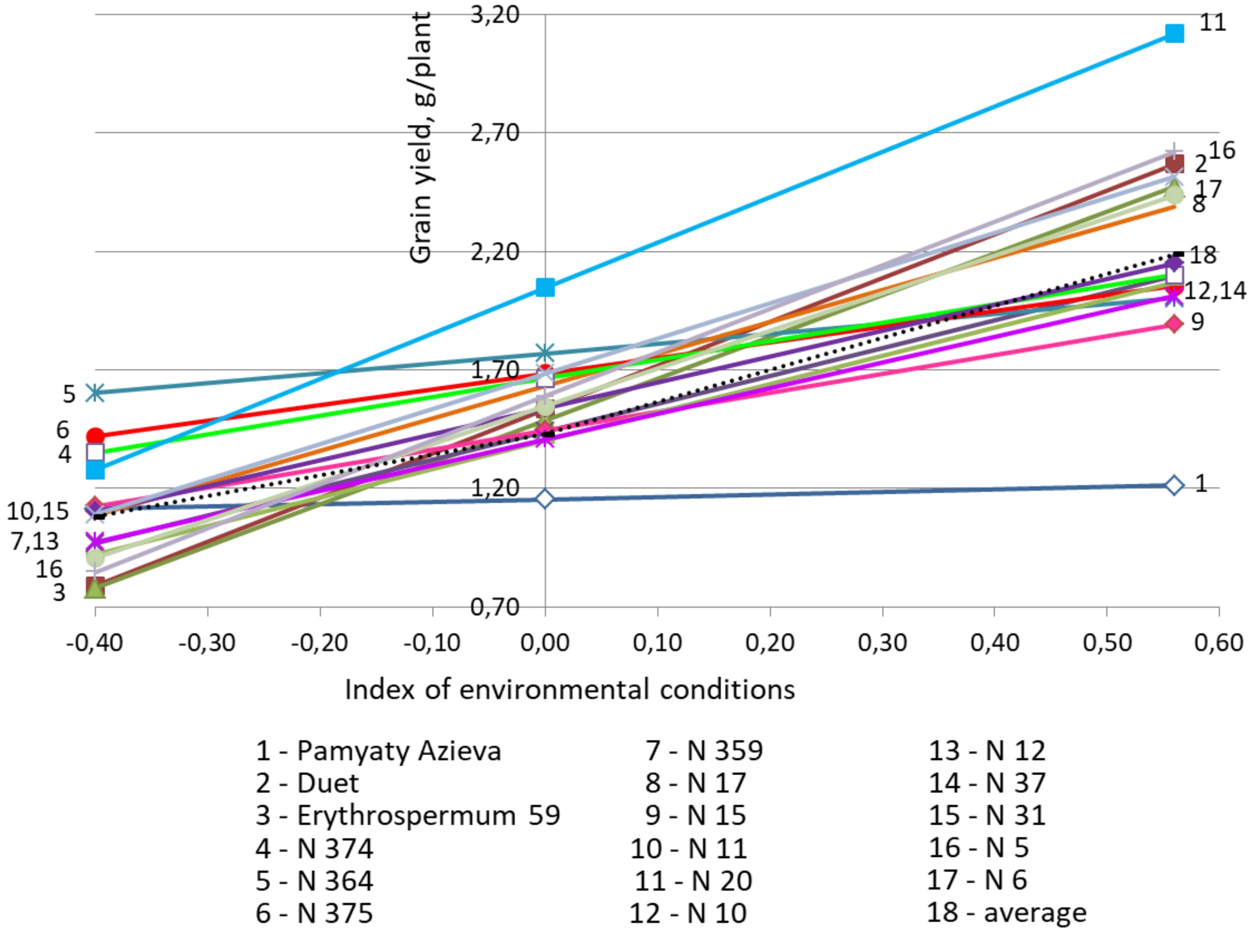

Fig. 1. **Regressive lines of grain yield per plant of spring common wheat cultivars and introgressive lines with genetic material of *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang** (Omsk, 2012–2014, and 2017)**:**
1 – 'Pamyati Azieva'; **2** – No. 374; **3** – No. 364; **4** – 'Duet'; **5** – No. 375; **6** – No. 359; **7** – No. 17; **8** – 'Erythrospermum 59'; **9** – No. 15; **10** – No. 11; **11** – No. 10; **12** – No. 12; **13** – No. 20; **14** – No. 37; **15** – No. 31; **16** – No. 5; **17** – No. 6; **18** – average

Рис. 1. **Линии регрессии массы зерна с растений сортов и линий яровой мягкой пшеницы с генетическим материалом *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang** (Омск, 2012–2014 и 2017 г.)**:**
1 – 'Памяти Азиева'; **2** – № 374; **3** – № 364; **4** – 'Дуэт'; **5** – № 375; **6** – № 359; **7** – № 17; **8** – 'Эритроспермум 59'; **9** – № 15; **10** – № 11; **11** – № 10; **12** – № 12; **13** – № 20; **14** – № 37; **15** – № 31; **16** – № 5; **17** – № 6; **18** – среднее

cant part of them exceeded the standards in 2012, 2014, and 2017, but had lower yield in a more favorable 2013. The exception was the medium-early ILs Nos. 364 and 374, which exceeded cv. 'Pamyati Azieva' in all seasons.

According to the coefficients of ecological plasticity, the ILs were divided into three groups. The first group (Nos. 364, 374, 375, 12, and 15) had significantly higher grain yields than the standards under unfavorable conditions but low plasticity (weak response to improving conditions) and stability (b_i = 0.49–0.87; σ_d^2 = 0.02–0.31), and their regressive lines were positioned at a small angle to the horizontal axis (see Figure 1, tracks 2, 3, 5, 9, 12). The second group included the ILs (Nos. 359, 17, 11, and 10), which had indicators similar to the intensive cvs. 'Duet' and 'Erythrospermum 59' (b_i = 1,16-1,52; σ_d^2 = 0.01–0.08) (see Figure 1, tracks 6, 7, 10, 11). The third group included late maturing ILs (Nos. 20, 37, 31, 5, 6) that combined high plasticity (b_i = 1.24–1.90) with large deviations from potential yields (σ_d^2 = 0.42–1.08) (see Figure 1, tracks 13, 14, 15, 16, 17). The late-ripening ILs Nos. 20 and 31 exceeded all standards in yield under unfavorable conditions (1.5–2.5 times).

A correlation analysis was carried out to determine the traits that significantly impacted the grain yield of cultivars and ILs under stress conditions. The closest linkage was identified between grain yield and the number of productive tiller number, seed number per main ear, and main ear grain yield (r = 0.55–0.75) (Table 4). The linkage between the number of main ear spikelets and 1000 grain weight was much weaker (0.26–0.43 and 0.20–0.37, respectively). The low correlation of grain yield with 1000 grain weight can be explained by the negative influence of foliar and stem diseases, which were maximally developed in August and reduced grain filling (Plotnikova, 2016, 2019; Belan et al., 2021). The analysis of yield trait data showed that most ILs (except for Nos. 374 and 5) had productive tiller number higher than that of the cultivars (Table 5). Previously, it was shown that a large number of tillers (up to 8) is typical for WWHs, but when breeding the tillering was reduced (Plotnikova et al., 2014). The regularities for other traits were not established.

To determine the effect of droughts on the development of the most significant yield traits of the ILs, ecological plasticity and stability coefficients were calculated. The greatest polymorphism in the plasticity of the ILs was noted in their productive tiller number and 1000 grain weight (see Table 5, Figure 2, a, d). As for seed number and grain yield per main ear, the ILs were divided into two groups (see Figure 2, b, c). The

Table 4. **Correlation coefficients (*r*) between grain yield per plant and yield traits of spring common wheat cultivars and introgressive lines with genetic material of *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang** (Omsk, 2012–2014, and 2017)

Таблица 4. **Коэффициенты корреляции между массой зерна с растения и элементами структуры урожая сортов и линий яровой мягкой пшеницы с генетическим материалом *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang** (Омск, 2012–2014 и 2017 г.)

Yield traits	Years			
	2012	2013	2014	2017
Total tiller number, No.	0.56*	0.56*	0.43*	0.55*
Productive tiller number, No.	0.61*	0.66*	0.55*	0.58*
Spikelet number per ear, No.	0.26	0.42*	0.31	0.43*
Seed number per ear, No.	0.60*	0.59*	0.64*	0.53*
Main ear grain weight, g	0.58*	0.59*	0.75*	0.64*
1000 grain weight, g	0.37*	0.23	0.27	0.20

* – significant ($p \leq 0.05$)
* – достоверно ($p \leq 0,05$)

Table 5. **Ecological plasticity of spring common wheat cultivars and introgressive lines with genetic material of *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang by yield traits** (Omsk, 2012–2014, and 2017)

Таблица 5. **Экологическая пластичность сортов и линий яровой мягкой пшеницы с генетическим материалом *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang по элементам структуры урожая** (Омск, 2012–2014 и 2017 г.)

Cultivar, line	Productive tiller number			Seed number/ main ear			Grain weight/ main ear			1000 grain weight		
	average, pcs.*	b_i	σ_d^2	average pcs.	b_i	σ_d^2	average, g*	b_i	σ_d^2	average, g*	b_i	σ_d^2
Medium-early												
Pamyati Azieva	1.53 ± 0.08	0.46	0.23	20.8 ± 1.2	0.37	27.8	0.90 ± 0.06	1.12	0.03	40.4 ± 4.1	0.08	65.0
364	2.12 ± 0.10	0.88	0,37	23.8 ± 1.3	0.87	69.2	1.06 ± 0.05	2.38	0.15	41.8 ± 3.9	0.28	68.2
374	1.65 ± 0.08	0.78	0.35	25.1 ± 1.4	0.18	7.5	0.78 ± 0.04	0.12	0.30	39.4 ± 2.8	0.71	55.6
Medium-ripening												
Duet	1.98 ± 0.11	0.19	0.81	24.3 ± 3.1	1.41	5.3	0.91 ± 0.13	1.82	0.03	40.9 ± 4.8	1.47	14.5
17	2.12 ± 0.11	0.68	0.15	21.8 ± 1.2	0.92	6.0	0.91 ± 0.05	0.83	0.01	41.3 ± 2.8	0.13	41.3
359	2.22 ± 0.11	0.81	0.12	19.8 ± 3.1	1.15	34.8	0.87 ± 0.16	1.69	0.04	38.8 ± 3.5	1.21	16.6
375	2.50 ± 0.36	1.57	0.15	19.7 ± 4.1	0.79	51.3	0.80 ± 0.16	1.66	0.10	39.0 ± 6.9	0.13	60.9
Medium-late												
Erythrospermum 59	1.83 ± 0.11	0.17	0.98	22.6 ± 3.1	1.14	32.7	0.88 ± 0.13	1.54	0.13	38.3 ± 2.2	0.77	10.4
11	2.29 ± 0.19	1.16	0.24	20.9 ± 4.4	1.41	28.6	0.82 ± 0.12	2.45	0.03	37.4 ± 3.9	0.76	24.9
15	2.16 ± 1.20	0.24	0.14	25.9 ± 2.5	0.17	30.2	0.85 ± 0.09	1.16	0.02	35.7 ± 4.3	0.64	28.8
Late-ripening												
10	2.50 ± 0.16	1.60	0.08	22.8 ± 2.5	1.27	16.8	0.85 ± 0.03	1.27	0.01	36.6 ± 2.8	0.23	19.4
12	2.26 ± 0.10	0.65	0.22	21.6 ± 1.2	0.24	28.9	0.88 ± 0.03	0.29	0.19	35.8 ± 1.5	0.87	15.4
20	3.00 ± 0.55	2.48	0.76	24.2 ± 5.2	0.10	51.5	1.05 ± 0.09	1.19	0.16	37.4 ± 3.3	1.37	14.6
31	2.21 ± 0.45	2.40	4.55	22.6 ± 5.2	2.00	61.5	0.95 ± 0.07	0.78	0.21	40.5 ± 8.9	4.37	73.1
37	2.00 ± 0.48	2.28	3.48	19.7 ± 5.8	1.99	48.3	0.78 ± 0.06	0.74	0.17	35.0 ± 7.1	3.56	52.0

Table 5. The end
Таблица 5. Окончание

Cultivar, line	Productive tiller number			Seed number/ main ear			Grain weight/ main ear			1000 grain weight		
	average, pcs.*	b_i	σ_d^2	average pcs.	b_i	σ_d^2	average, g*	b_i	σ_d^2	average, g*	b_i	σ_d^2
Late-ripening												
5	1.78 ± 0.25	2.21	3.12	21.2 ± 6.1	2.27	69.7	0.92 ± 0.08	0.93	0.14	41.5 ± 8.5	4.37	71.2
6	2.40 ± 0.46	3.02	4.74	23.4 ± 4.0	2.35	86.1	0.96 ± 0.06	0.86	0.44	38.3 ± 8.0	4.17	64.8
Average	2.06 ± 0.43	–	–	20.8 ± 3.6	–	–	0.81 ± 0,17	–	–	35.8 ± 7.2	–	–

Note: ^{a} average for 2012–2014, and 2017; b_i – coefficient of ecological plasticity; σ_d^2 – stability

Примечание: ^{a} среднее за 2012–2014 и 2017 г.; b_i – коэффициент экологической пластичности; σ_d^2 – стабильность

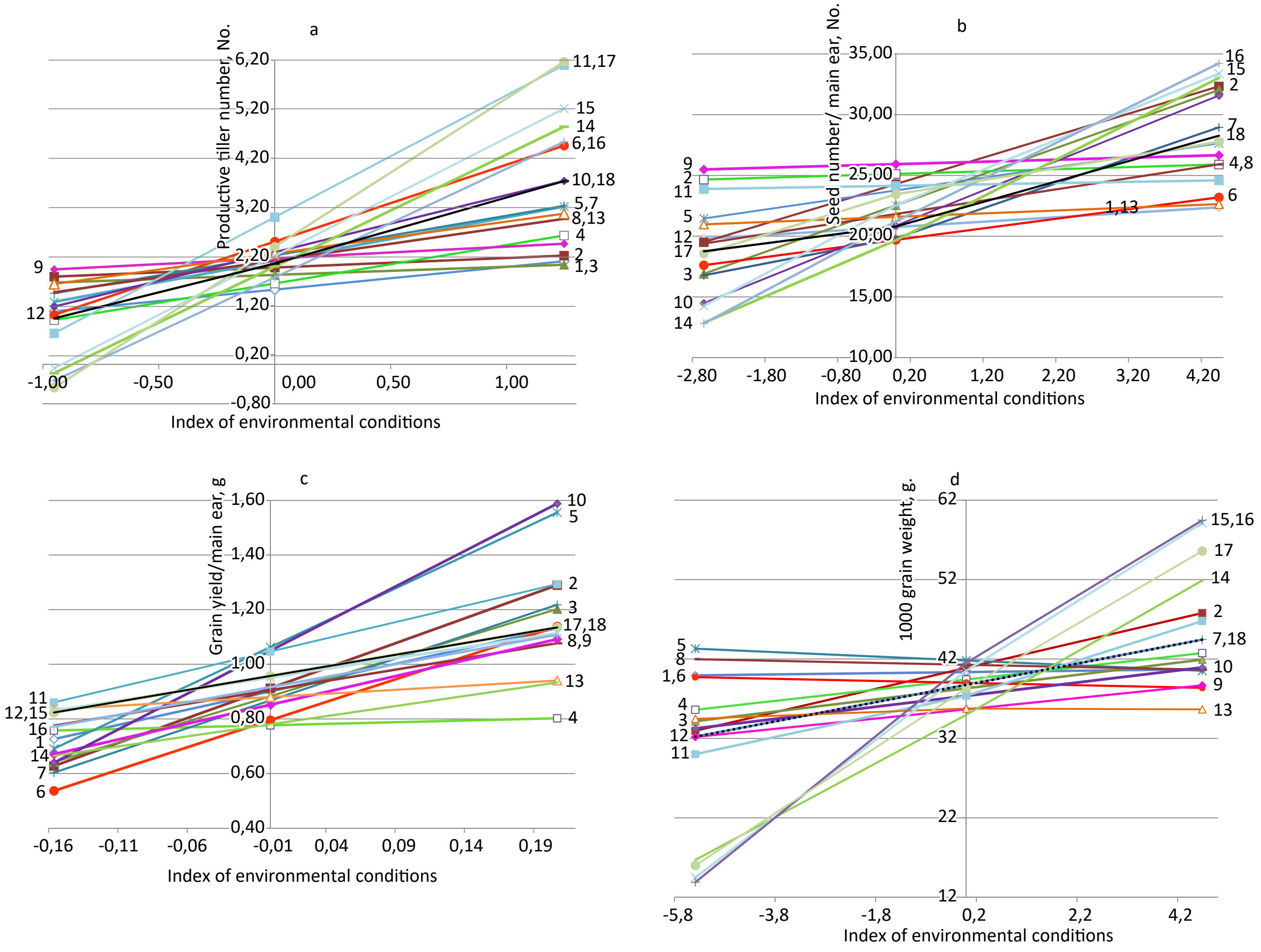

Fig. 2. **Regression lines of yield traits of spring common wheat cultivars and introgressive lines with genetic material of *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang** (Omsk, 2012–2014, and 2017): ***a*** – productive tiller number, pcs.; ***b*** – seed number per main ear, pcs.; ***c*** – grain yield per main ear, g; ***d*** – 1000 grain weight, g; **1** – 'Pamyati Azieva'; 2 – 'Duet'; **3** – 'Erythrospermum 59'; **4** – No. 374; **5** – No. 364; **6** – No. 375; **7** – No. 359; **8** – No. 17; **9** – No. 15; **10** – No. 11; **11** – No. 20; **12** – No. 10; **13** – No. 12; **14** – No. 37; **15** – No. 31; **16** – No. 5; **17** – No. 6; **18** – average

Рис. 2. **Линии регрессии сортов и линий яровой мягкой пшеницы с генетическим материалом *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang по элементам структуры урожая** (Омск, 2012–2014 и 2017 г.): ***a*** – число продуктивных стеблей, шт.; ***b*** – число зерен главного колоса, шт.; ***c*** – масса зерна главного колоса, г; ***d*** – масса 1000 зерен, г; **1** – 'Памяти Азиева'; 2 – 'Дуэт'; **3** – 'Эритроспермум 59'; **4** – № 374; **5** – № 364; **6** – № 375; **7** – № 359; **8** – № 17; **9** – № 15; **10** – № 11; **11** – № 20; **12** – № 10; **13** – № 12; **14** – № 37; **15** – № 31; **16** – № 5; **17** – № 6; **18** – среднее extensive cv. 'Pamyati Azieva' and the ILs Nos. 364 and 15 showed plasticity of the grain weight per main ear ($b_i = 1.12$, 2.38 and 1.16, respectively), but as for other yield traits (productive tiller number, seed number per main ear, and 1000 grain weight), plasticity was lower ($b_i < 1$). Lines Nos. 374 and 12 showed low plasticity and good stability of all four yield components. This indicates that the cv. 'Pamyati Azieva' and the listed lines formed most yield traits in a stable manner, despite the stress conditions. The intensive cultivars showed high ecological plasticity of several yield traits. Cv. 'Erythrospermum 59' showed the plasticity of seed number and grain yield per main ear, and cv. 'Duet' of three traits (additionally 1000 grain weight). The intensive ILs showed adaptive variability through three yield components in different combinations. The greatest plasticity of productive tiller number, seed number per main ear, and 1000 grain weight was noticed in the late-ripening group.

The best eight lines were further studied in 2017 and 2018 in plot trials. The 2018 season differed from the previous ones by regular heavy precipitation (HTC = 3.1). Under favorable conditions of 2018, the ILs significantly increased tiller density, as well as grain yield per plant by 3-4 yield traits. All lines, both extensive and intensive, significantly exceeded the standards in grain yield m^{-2} for two years (Table 6). The highest yield was formed by ILs Nos. 364 and 374 (medium-early), 17 and 375 (medium-ripening), and 20 and 31 (medium-late). These results show that the selected lines are able to form high yields under various moisture conditions.

Discussion

Water deficit significantly limits the plant's potential productivity and decreases the crop yield. The breeding of drought-resistant cultivars for Southwest Siberia is extremely difficult, since the rhythms of droughts are unstable. Spring-early summer droughts are typical for the region. They coincide with the phases of germination, tillering, and early tiller development for spring common wheat. In the Altai region, spring-early summer droughts resulted in the loss of up to 34% of durum wheat crop yield, and the durable drought in 2012 caused losses of up to 78% (Ereshchenko, Khlebova, 2017). In Omsk Oblast, a severe drought in 2012 led to the loss of 50% of the wheat crop, and after shorter droughts, losses reached 20% (Belan et al., 2021).

Cvs. 'Pamyati Azieva', 'Duet', and 'Erythrospermum 59' have been cultivated in Omsk Oblast for a long time and used as standards. They were included in the State Register for Selection Achievements of the Russian Federation in 2000, 2004, and 1994, respectively (https://reestr.gossortrf.ru). According to the set of field resistance indices under drought conditions, cvs. 'Pamyati Azieva' and 'Duet' were among the best cultivars of the South Ural and West Siberian breeding (Vasilevsky, 2019).

The introgressive lines with genetic material of *T. ponticum* originated at Omsk SAU were analyzed from the point of view of adaptability to drought for the first time. Under contrasting humid conditions, cv. 'Pamyati Azieva', as well as two ILs, were characterized by a stable development of the majority of yield traits, with the exception of the main ear grain weight, which showed low plasticity. In this regard, it is possible to assume that there are similar adaptive mechanisms both in the cultivar and ILs. Three ILs from different maturity groups exceeded the standards in unfavorable seasons and stably formed all studied yield traits. But the high productivity of IL No. 374 was provided by a large seed number per ear, and that of Nos. 17 and 12 by an increased productive tiller number. The stable development of plant organs under stressful conditions is considered a manifestation of tolerance to drought (Sallam et al., 2019).

The intensive cvs. 'Duet' and 'Erythrospermum 59' under contrasting moisture conditions maintained their grain yield due to a compensatory development of some yield traits when favorable conditions occurred. Intensive ILs showed ecological plasticity in terms of yield traits, which was similar to that of intensive cultivars or caused by other combinations of yield traits. It is possible that the differences in adaptive responses were associated with a different distribution of alien loci controlling drought resistance among the ILs.

It was previously shown that the cultivars characterized by stable morphogenesis in tissue cultures combined high potential productivity with increased drought resistance in Omsk Oblast (Rosseyev et al., 2016). Pollen resistance to low humidity and high temperatures may be of great importance while increasing the seed number per ear (Passioura, 2007; David, 2012). The important role in drought resistance at all stages of development is played by the water-retaining capacity of plants, associated with the accumulation of osmolytes (Kosová et al., 2014; Sallam et al., 2019).

Currently, the synthetic wheat with the D genome from *Aegilops tauschii* Coss. is considered an important source of genes for improving wheat resistance to abiotic factors. The high yield of such synthetics and common wheat cultivars originated on their basis in the dry regions of the world was associated with the intensive development of the root system and leaf apparatus, and the resistance to high temperatures during grain filling. The cultivars made on the basis of synthetics ensured good harvests in the arid regions of Australia, India, and South America (Li et al., 2018). It is of interest to compare our results with the study of synthetics (from the CIMMYT and Kyoto University collections) carried out simultaneously at the Omsk SAU experimental field in 2017. The synthetics surpassed cvs. 'Pamyati Azieva' and 'Serebristaya' in root development, height, leaf size, and 1000 grain weight. However, they were significantly worse than the standards in terms of spike-bearing stem density, productive tiller number, seed number, and grain weight per main ear (Pototskaya et al., 2019). It indicates that the synthetics had lower field seed germination, weaker tillering and seed setting than the standards. As a result, the synthetics were significantly inferior to standards in grain yield m^{-2}. At the same time, the ILs with the genetic material of *Thinopyrum ponticum*, exceeded cvs. 'Pamyati Azieva', 'Duet', and 'Serebristaya' in grain yield (1.1–1.3 times). Obviously, the standard cultivars adapted to the climate of Western Siberia and the ILs have additional or enhanced drought adaptation mechanisms compared to the synthetics. Additional research is needed to understand the complex system of protective mechanisms in cultivars and ILs against drought.

Conclusion

For the first time, the drought resistance of fourteen ILs of spring common wheat with *T. ponticum* genetic material was studied in comparison with cultivars adapted to the conditions of Southwest Siberia. The main part of ILs exceeded the cultivars in productivity (1.1–2.2 times) in dry seasons. Five ILs showed adaptive morphogenesis similar to the extensive cv. 'Pamyati Azieva'. They stably formed the productive tiller number, seed number, and grain weight per main ear, and three ILs also stably formed 1000 grain weight. Nine ILs showed ecological plasticity similar to the intensive cvs. 'Duet' and 'Erythrospermum 59', due to adaptive variability in three

Table 6. Analysis results for yield traits of spring common wheat cultivars and introgressive lines with genetic material of *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang (Omsk, 2017 and 2018)

Таблица 6. Результаты анализа элементов структуры урожая сортов и линий яровой мягкой пшеницы с генетическим материалом *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang (Омск, 2017 и 2018 г.)

Cultivar, line	Vegetation period, days^a	Grain yield, g/m^2		Productive tiller number, pcs./m		Grain yield, g/plant		Productive tiller number, pcs./ plant		Seed number/ main ear, pcs.		Grain weight/ main ear, g		1000 grain weight, g	
		2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018
Medium-early															
Pamyati Azieva	77 ± 3.2	351	485	84	96	1.36	1.55	1.25	1.60	25.4	30.5	1.18	1.13	45.7	35.3
364	76 ± 2.0	627*	670*	100*	123*	2.15*	2.58*	1.35	1.63	32.5*	36.4*	1.67*	1.56*	50,0*	45.6*
374	76 ± 2.2	647*	686*	112*	143*	1.66*	2.53*	1.40*	1.90*	28.1*	40.3*	1.58*	1.83*	41.3*	44.9*
SSD$_{05}$	–	24	35	9	12,5	0.22	0.28	0.13	0.15	2.3	3.3	0.19	0.22	3.2	3.5
Medium-ripening															
Duet	82 ± 3.1	441	557	85	115	1.02	2.44	1.20	1.75	24.3	38.6	0.85	1.73	34.4	43.7
17	81 ± 4.6	678*	658*	106*	123*	1.53*	2.12	1.45*	1.66	21.9	35.4	1.04*	1.65	47.3*	46.8*
375	80 ± 6.5	627*	653*	125*	118	2.22*	2.89*	1.85*	2.50*	26.8*	40.0*	1.26*	2.23*	46.1*	54.8*
SSD$_{05}$	–	36	41	8	6	0.15	0.21	0.17	0.15	1.8	1.3	0.13	0.18	2.9	3.0
Medium-late															
Serebristaya	86 ± 4.1	513	410	125	118	1.40	1.92	1.90	1.72	19.9	35.5	0.82	1.43	39.1	36.8
15	83 ± 3.6	565*	548*	115	159*	1.68*	1.79	1.70	1.75	20.6	28.6	0.94*	1.12	35.7	36.2
20	84 ± 3.2	655*	748*	133	167*	1.57*	2.32*	2.21*	2.33*	31.8*	39.6*	1.22*	1.74*	36.7	42.6*
31	85 ± 4.4	672*	683*	108	138*	2.44*	2.25*	1.70	2.32*	27.9*	41.4*	1.45*	1.85*	52.0*	44.6*
37	84 ± 4.1	581*	626*	118	123	1.51	2.31*	1.85	1.95*	22.4*	32.4*	1.09*	1,69*	48.1*	54.2*
SSD$_{05}$	–	22	26	11	15	0.12	0.19	0.15	0.17	1.4	2.1	0.11	0.12	1.9	2.4

Note: ^{a} – average for 2017–2018; * – significantly exceeded the standard ($p \leq 0.05$)

Примечание: ^{a} – среднее за 2017–2018 гг.; * – достоверное превышение стандарта ($p \leq 0,05$)

grain traits in different combinations. ILs are likely to possess different sets of drought resistance mechanisms. Introgressive lines with the genetic material of *T. ponticum* are of interest for breeding drought-resistant cultivars for rain-deficient areas.

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