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ALLELIC VARIATION AT THE *PPD-A1* LOCUS AND ITS ASSOCIATIONS WITH HEADING TIME AND WINTER WHEAT (*TRITICUM AESTIVUM* L.) AGRONOMIC TRAITS IN THE NORTHERN BLACK SEA REGION

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Aim. The identification of *Ppd-1*-alleles in winter bread wheat varieties of various origin, including the ones of Ukrainian plant breeding and recombinant-inbred lines Orenburgskaya 48//Cappelle Desprez/2B Chinese Spring, and the evaluation of the effects of allele *Ppd-A1_del303*, including the interaction with different alleles of gene *Ppd-B1*, by the duration of the period before heading and the related agronomically valuable traits. **Methods**. DNA extraction, allele-specific PCR, agarose and polyacrylamide gel electrophoresis, phenological observations, evaluation of frost resistance in seedlings, and analysis of morphobiological traits and elements of yield structure. Statistical analysis of the obtained data was carried out in Microsoft Excel. The significance of the difference between samples was assessed by Fisher's F test. A difference of $p < 0.05$ was considered statistically significant for all indicators. **Results.** The marking of 30 varieties of different origin and 64 recombinant-inbred lines of Orenburgskaya 48//Cappelle Desprez/2B Chinese Spring winter bread wheat was carried out to identify the alleles of the *Ppd-A1* gene. The polymorphism of varieties and populations of recombinant-inbred lines in the northern Black Sea region (Odesa) was evaluated for ten traits: frost resistance of plants in the seedling phase, winter hardiness, duration of the period before heading, plant height, grain number per spike, grain weight per spike, thousand grain weight, number of productive tillers per unit area, harvest index and grain yield. The comparison of the lines evaluation data in terms of agronomic traits and the results of the genotypes identification allowed us to identify the influence of *Ppd-A1* gene alleles and various combinations of the alleles of *Ppd-A1* and *Ppd-B1* genes on these traits. **Conclusions.** A higher prevalence of the *Ppd-A1_del303* allele was found both among varieties and recombinant-inbred lines. The genetic differences by the *Ppd-A1* gene (*Ppd-A1_del303* or *Ppd-A1b*) are significantly related only to frost resistance of seedlings in the absence of significant differences in other traits. The interaction between *Ppd-A1b* and *Ppd-B1c* alleles contributed to the acceleration of early maturity and the formation of the highest indicators of grain weight per spike, thousand grain weight, harvest index, and grain yield. The replacement of the *Ppd-A1b* allele with *Ppd-A1_del303* led to a decrease in the effect of the dominant *Ppd-B1c* allele on accelerating heading and negatively affected the grain weight per spike, thousand grain weight, harvest index and grain yield compared to the *Ppd-A1b Ppd-B1c* genotype.

Key words: winter bread wheat, photoperiod, *Ppd-1* genes, heading, yield.

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INTRODUCTION

Wheat (*Triticum aestivum* L.) and other related cereal species in the moderate zone are adapted to cultivation in different agroclimatic regions. One of the critical factors impacting its ability to adapt is the variability in the heading time, which is directly related to the formation of grain yield and its components (Tsenov et al, 2020). The impact of heading time as an adaptation factor largely depends on regional climate conditions, including photoperiod (Worland et al, 1998; Dyck et al, 2004). Bread wheat is a long-day plant, and usually, wheat varieties grown in northern regions are sensitive to photoperiod, but in southerly latitudes, the need is for the varieties insensitive to photoperiod, which may head under short-day conditions.

The sensitivity of wheat to day duration (photoperiod) is conditioned, first and foremost, by the orthologous series of Photoperiod-1 genes (*Ppd*-1) (Snape et al, 2001), located on 2A (*Ppd-A1*), 2B (*Ppd-B1*) and 2D chromosomes (*Ppd-D1*) (Scarth and Law, 1984). The plants with dominant *Ppd-1* alleles show early heading under both reduced and prolonged day duration. The presence of photoperiod-sensitive alleles inhibits heading considerably, especially in shorter day conditions (Kumar et al, 2012). It is believed that the *Ppd-D1a* gene has the greatest effect on the heading time as compared to *Ppd-B1a* and especially *Ppd-A1a* (Amo et al, 2022), but in some cases, the effect of *Ppd-B1a* alleles (Nishida et al, 2013) or *Ppd-A1a* (Bentley et al, 2013) equals to that of *Ppd-D1a*.

At present, a complete nucleotide sequence has been determined for each of three *Ppd-1* genes of bread wheat (Beales et al, 2007; Guo et al, 2010; Diaz et al, 2012). As for *Ppd-1* genes, some sensitive (recessive) and insensitive (dominant) alleles were detected, the occurrence of which was conditioned by different mutations of their older forms (Bentley et al, 2013). At the same time, little is known about the impact on heading time and other traits of wheat and the spreading of photoperiod-sensitive and insensitive *Ppd-A1* alleles in the varieties from different countries or regions contrary to *Ppd-B1* and *Ppd-D1* genes, which are associated mainly with variability in terms of photoperiodic sensitivity (Langer et al, 2014). Nishida et al (2013) described a dominant allele *Ppd-A1a.1* in *T. aestivum*, the marker of the presence of which in bread wheat varieties is the deletion of 1085 bp in the promoter. The alleles of *Ppd-A1a,* insensitive to day duration, were first found in durum wheat (Wilhelm et al, 2009). The variety GS-100 is remarkable for the deletion of 1027 bp (*Ppd-A1a.2*), and the variety GS-105 – for the deletion of 1117 bp (*Ppd-A1a.3*). A reliable effect of dominant *Ppd-A1a* gene alleles on the heading time (Seki et al, 2013; Grogan et al, 2016; Royo et al, 2016), plant height, grain number per spike, thousand grain weight, protein content in grain, harvest index and crop performance was determined (Whittal et al, 2018; Arjona et al, 2019; Achilli et al, 2022). At the same time, the dominant alleles of *Ppd-A1* gene did not spread much in the gene fund of bread wheat. Only 2–15 % of bread wheat varieties from different regions of the world are carriers of the dominant alleles of *Ppd-A1a* gene (Seki et al, 2013; Grogan et al, 2016; Whittal et al, 2018; Alipour and Abdi, 2021; He et al, 2023). However, Ma et al (2022) noted a much higher frequency of the dominant allele of *Ppd-A1a.1* (32.9 %) in the varieties of the eastern US regions. In spring and winter varieties of bread wheat in Ukraine (over 420 samples), the marker fragment was found in size of 452 bp (Chebotar et al, 2019; Balashova and Fait, 2021; Fait and Balashova, 2022), which demonstrated the absence of deletions in the promoter and the correspondence of the genotype to the recessive allele of *Ppd-A1* (Wilhelm et al, 2009; Nishida et al, 2013).

At the same time, it was determined that along with the wild type (*Ppd-A1b* allele), the *Ppd-A1* gene also has mutations that do not lead to qualitative changes in expression but impact the formation of non-functional *Ppd*-proteins. For instance, a deletion of 303 bp was found in the Cappelle-Desprez variety, which covers the area of intron 5 and exons 5, 6 (Beales et al, 2007), indicated by us in this article as *Ppd-A1_del303* allele. The information about the spreading of this allele in winter bread wheat is limited to collections GEDIFLUX and Watkins (Shaw et al, 2013) and the collection of modern varieties of winter wheat in Europe (Makhoul et al, 2024). In the latter case, there is a more than fourfold decrease in the frequency of *Ppd-A1_del303* allele (haplotypes PpdA1-Hap2 + Hap3, as per the authors) in modern varieties in the breeding process for the last 50 years. As per Royo et al (2020) *Ppd-A1_del303* allele is present only in 20 % of the local varieties of durum wheat from 13 countries of the Mediterranean region and in none of the modern commercial varieties. The information about the impact of *Ppd-A1_del303* allele on the heading time is contradictory (Shaw et al, 2013; Royo et al, 2020), and the data on other traits are rather limited (Makhoul et al, 2024).

At present, the information about the spreading of recessive alleles of the *Ppd-A1* locus in bread wheat varieties in Ukraine is absent, and their impact on the development rates before to heading and the traits related thereto, have not been evaluated yet. The natural multiple allelism determines the variability of *Ppd-A1* genotypes, which allows the development of varieties that are more adapted to the cultivation in certain climate conditions. Yet, their creation requires a preliminary study on the urgency of a specific genotype, which is impossible without determining the carriers of specific alleles and their different combinations.

The aim of this publication is the identification of *Ppd-1* alleles in winter bread wheat of various origin, including the ones of Ukrainian plant breeding and recombinant-inbred lines Orenburgskaya 48//Capelle Desprez/2B Chinese Spring, and the evaluation of the effects of *Ppd-A1_del303* allele including the interaction with different gene alleles, in terms of the period prior to heading and the related agronomically valuable traits.

MATERIALS AND METHODS

The initial material of the study was 30 varieties of winter bread wheat of different geographic origin, including 21 varieties from Ukraine, two from Germany, Kazakhstan, France each, and one variety from Russia, Slovakia, and Finland each, as well as 64 recombinant-inbred lines (RIL) $F_{2:9}$ obtained by cross-breeding Orenburgskaya 48 and Cappelle Desprez/2B Chinese Spring line recombinantly replaced along chromosome 2B, previously created by us.

The identification of genotypes of 30 varieties of different geographic origin, variety Orenburgskaya 48 and replaced line Cappelle Desprez /2B Chinese Spring, and 64 RIL, created on their basis by alleles of the *Ppd-A1* gene, involved the application of PCR (**Table 1**), developed based on DNA polymorphism in the promoter zone of the locus.

To label *Ppd-A1,* we used the PCR test, which determined the absence of mutations in the promoter, which was notable for the recessive state. A marker was a fragment of 452 bp (Wilhelm et al, 2009). To detect the presence of the deletion of 303 bp in exons 5, 6 of the *Ppd-A1* gene, we used the PCR test, recommended by Takenaka, Kawahara (2012). The presence of allele, labeled by us as *Ppd-A1_del303,* was determined by the PCR-fragment of 220 bp, and in this case, the control was the Capelle-Desprez variety with this mutation.

DNAs were extracted from seedlings or grain using the CTAB-buffer. The amplification was conducted using Tertsik device (DNA-technology, Russia). The conditions of the PCR were as follows: denaturation – 94 °C for 2 min, then 20 s; annealing – 60 °C for 30 s; elongation – 72 °C for 50 s for 35 cycles; the final elongation – 72 °C for 3 min. The reaction buffer for the PCR contained 50 mM KCl; 20 mM tris-HCl, pH 8.4; 2.0 mM $MgCl_2$; 0.01 % Tween-20; 0.15 mM of each dNTP; 5 pM of each primer, 20 ng of DNA and 1 unit of *Taq*-polymerase. The amount of reaction mixture equaled 20 µl. The amplification products were fractioned in 10 % polyacrylamide gel, and their visualization in PAAG was conducted by staining with 0.012 M $AgNO_3$. The molecular weight of the amplification products was determined using markers pUC19/MspI.

The seeds of the investigated varieties of winter wheat were sown in autumn (on October 6, 2021, September 30, 2022, and October 11, 2023) on the field with one-row plots of 1.25 m, 25 plants in a row, with the nutrient area of 5 × 30 sq.cm. Each variety was considered as a separate repeat. To determine the duration of the period before heading, the heading of individual plants was registered at the time of the appearance of the main head from the flag leaf sheath. The calendar date of May 1 was used as a starting point.

Our previous study determined *Ppd-B1* genotypes and defined the phenotypic evaluation by the complex of traits of the population of 64 recombinant-inbred lines F_9 from the cross-breeding of Orenburgskaya 48// Cappelle Desprez/2B Chinese Spring (Fait et al, 2017), and these data on genotyping by locus *Ppd-B1* and phenotyping of the population by the complex of traits were used in this work. The seeds of RIL and parents were sown in autumn for three years (on October 22, 12, and 4, respectively) on areas of 3 sq.m., 500 grains per one sq.m. The experiment had three repeats.

The winter hardiness was determined in the field by counting the plants in the phase of three leaves in au-

Table 1. The primers for PCR analysis and the size of amplification fragments to label alleles *Ppd-A1b* and *Ppd-A1_del303*

Gene	Primer	Sequence of primers	Size of fragment, bp
Ppd-A1b	durum_Ag5del_F2	tgtcacccatgcactctgtt	452 bp
	durum_Ag5del_R2	ctggctccaagaggaaacac	
Ppd-A1_del303	303 bp_del_F2	cttacatctgtgagaagtatctgcatc	220 bp
	303 bp_del_R3	cagatcagcagctcgaacaattac	

tumn and in spring, the plants survivors after the renewal of vegetation. During vegetation in the field, we registered the heading date visually if 75 % of plants with spike were present in the plot and then transformed it (from the date of May 1) into the duration of the period before the heading (DPH). Prior to collecting yield, we counted the number of productive tillers per area unit (NPT). While harvesting, the grain yield (GY) of the land plot was determined. After collecting the grain from 30 plants from each line (10 from one repeat), we measured the plant height (PH), counted the grain number per spike (GNS), and determined the grain number per spike (GWS), the thousand grain weight (TGW), the weight of the grain in a plant, the weight of straw and chaff of the plant to calculate the harvest index (HI) which is the ratio between the weight of the grain per plant and the total weight of the grain, straw, and chaff per plant.

The frost resistance of RIL seedlings (stage 09: “Seedlings” according to the BBCH scale) was evaluated at –12 °C twice, using the RIL seeds of different years of cultivation. The seeds of the lines (75 seeds of each line 25 per one repeat) were grown in the rolls of filtration paper of 7 × 19 cm at room temperature. Five-day-old seedlings were subjected to the first phase of northering at +2 °C and 24 h illumination with the intensity of 10 klx for 29 days. The second phase of northering was conducted without illumination at –6 °C for 3 days. Then the temperature was gradually decreased by 2 °C/h to the temperature of frosting. Plants were frosted at –12 °C for 24 h. After frosting, the temperature was gradually increased by 2 °C/h to complete defrosting of seedlings. The seedlings were cut at the height of 5–6 cm from the upper end of the roll and grown for 15 days at the natural day duration and the temperature of +10–12 °C with subsequent counting of live and perished plants. The percentage of live plants after frosting was accepted as the frost resistance criterion.

All the abovementioned indices were compared against the data of the PCR analysis of the lines by the alleles at *Ppd-A1* and *Ppd-B1* loci. The statistical processing of the obtained data was conducted by common methods of the analysis of variance and correlation analysis using Microsoft Excel package 2007. While comparing two or more samplings, Fisher’s F test was used to evaluate the significance of the “genotype” factor for the variation of traits. The reliability of the difference between the mean values was determined using the least significant difference (LSD). The differences at the values of $p < 0.05$ were considered significant.

The meteorological conditions during the period of the study covered the entire spectrum of possible unfavorable environmental factors common for the Steppe of Ukraine. It ensured the objective evaluation of the initial material regarding the average adaptation to these conditions and allowed for the differentiation of the varieties and RIL of winter wheat by the complex of economically valuable traits by different alleles of *Ppd-1* genes.

RESULTS

The frequency of alleles of Ppd-A1 gene. The identification of allelic differences among 30 varieties of different geographic origin, variety Orenburgskaya 48 and replaced line Cappelle Desprez/2B Chinese Spring, and 64 RIL, created on their basis by the gene of photoperiodic sensitivity *Ppd-A1*, involved the application of allele-specific molecular markers.

11 out of 30 varieties in the total sampling were carriers of allele *Ppd-A1b* and 19 – *Ppd-A1_del303* (**Fig. 1**). Among 21 varieties of Ukrainian breeding, 38.1 % had allele *Ppd-A1b* and, thus, 61.9 % – allele *Ppd-A1_del303* in their genotype. Taking into consideration the preliminary identification of varieties by dominant alleles of genes *Ppd-D1a*, *Ppd-B1a* and *Ppd-B1c* (Fait VI, Balashova IA, 2022), the genotypes of varieties Alia, Dykanka, Doridna, Zapashna, Maira, Oriyka, Radyslavka, Statna, Fermerka, Tsarychanka, Velta may be labelled as *Ppd-D1a Ppd-B1b Ppd-A1b*; Hordovyta, Zoloto Ukrayiny, Istyna odeska, Koliada, Ladyzhynka, Malanka, Pryvablyva, Rozkishna, Kharkivska 105 – *Ppd-D1a Ppd-B1b Ppd-A1_del303*; Smila, Vesnianka, Ekspromt, Polianka – *Ppd-D1a Ppd-B1c Ppd-A1_del303.* The varieties Alinea, KWS Emil, Severnaya zorya, Cappele-Desprez, KWS Ronin, Vakka were identified as the ones with the recessive allele *Ppd-A1_del303* in their genotype.

The parental genotypes of RIL of Orenburgskaya 48 variety and the replaced line Cappelle Desprez/2BChinese Spring are carriers of different recessive alleles of gene *Ppd-A1*. In the replaced line Cappelle Desprez/2B Chinese Spring, we identified allele *Ppd-A1_del303*. Orenburgskaya 48 variety is a carrier of a “classic” recessive allele *Ppd-A1b*. By the presence or absence of some alleles of *Ppd-A1* gene, the recombinant-inbred lines F_9 (RIL) may be divided into two groups. *Ppd-A1b* allele was detected in 15 lines, similarly to Orenburgskaya 48 variety. The other 49 lines, similar to the other parent – the replaced line Cappelle Desprez/2B Chinese Spring, are carriers of allele *Ppd-A1_del303*.

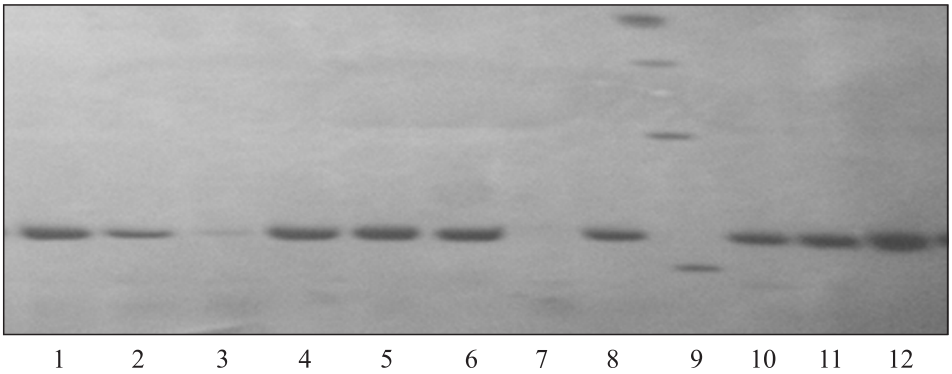

Fig. 1. Detecting allele *Ppd-A1_del303* in Ukrainian winter wheat varieties: 1 – Hordovyta, 2 – Zoloto Ukrainy, 3 – Dykanka, 4 – Istyna odeska, 5 – Koliada, 6 – Ladyzhynka, 7 – Doridna, 8 – Capelle-Desprez (control), 9 – molecular weight marker pUC19/MspI, 10 – Ekspromt, 11– Polianka, 12 – Smila

Previously, we conducted a marker analysis of parents and 64 RILs by the alleles of *Ppd-B1* gene (Fayt et al, 2017). The presence of a mutant allele *Ppd-B1c* was found in the replaced line Capelle-Desprez/2B Chinese Spring and 39 RILs; in Orenburgskaya 48 and 22 RILs a recessive allele *Ppd-B1b* was detected, and three lines were polymorphic by alleles of the *Ppd-B1* gene. According to the results of the identification of alleles of two *Ppd-1* genes, the genotype of Orenburgskaya 48 variety may be labeled as *Ppd-A1b Ppd-B1b*, and that of the replaced line Cappelle-Desprez/2B Chinese Spring – *Ppd-A1_del303 Ppd-B1c*. In the population of RILs, four theoretically possible genotypes were defined with different combinations of alleles of parental components, which may be obtained for random recombination of alleles of two *Ppd-1* loci. *Ppd*-genotype, identical to that of the parental replaced line Cappelle-Desprez/2B Chinese Spring, is inherent to most RILs, namely, 30 lines. The combination of alleles *Ppd-A1_del303 Ppd-B1b* and *Ppd-A1b Ppd-B1c* is inherent to 16 and nine recombinant-inbred lines, respectively. The last group, composed of six lines, is notable for the combination of alleles *Ppd-A1b* and *Ppd-B1b*. These combinations provide for the evaluation of the effects of the interaction between dominant and recessive alleles of the genes of the orthologous series *Ppd-1* under different conditions by the duration of the period before heading and the other related traits.

The effects of Ppd-A1 alleles on the time of heading of the varieties. The year of cultivation had a considerable impact on the heading date (F = 78.24; $F_{0,05}$ = = 3.10). The conditions in 2022 and 2023 did not differ considerably (F = 3.45; $F_{0.05}$ = 4.01), and the ranks of varieties by the duration of the period to heading in the mentioned two years mostly coincided (r = 0.94). The conditions of 2024 differed considerably from those in 2022 (F = 81.41; $F_{0.05}$ = 4.01), and in 2023 (F = 109.79; $F_{0.05}$ = 4.01). The ranks of heading for the varieties in 2024 somewhat differed from both previous years (r = 0.85 as compared to 2022 and 2023). The comparison of the duration of the period to heading among 30 winter varieties demonstrated a wide genetic diversity of the investigated set by the mentioned trait in conditions of each year of the study. The varieties which are carriers of different dominant and recessive alleles of *Ppd-1* genes were heading in 2022 on average on day 17.4 ± ± 0.56, with the variation range of 13 days (May 12–25), and in 2023 – on day 18.8 ± 0.51, with the variation range of 12 days (May 14–26). Earlier renewal of vegetation in 2024 promoted earlier, by 10–11 days, heading of the plants as compared to two previous years. On average, in the experiment, the heading was noted on day 7.2 ± 0.98, but the variation by the heading date was 21 days (May 2–22).

In the total sampling, without the consideration of differences by genes *Ppd-D1* and *Ppd-B1*, the varieties-carriers of alternative alleles of the *Ppd-A1* gene: *Ppd-A1b* or *Ppd-A1_del303* did not differ much by the duration of the period prior to heading regardless of the year of study (**Fig. 2**). The limitation of genetic diversity by genes *Ppd-D1* and *Ppd-B1* (*Ppd-D1a Ppd-B1b* genotype) did not impact the differences between varieties with different recessive alleles of the *Ppd-A1* gene (the data are not presented).

The field evaluation of the population of recombinant-inbred lines. In the field conditions near the city of Odesa (46.48° nort.lat. 30.74° east.long.), the recombinant-inbred F_9 lines Orenburgskaya 48//Cappelle Desprez/2B Chinese Spring differed considerably by several economically valuable traits (**Table 2**). There was a significant impact of the year of the study and the line genotype, as well as their interaction on the

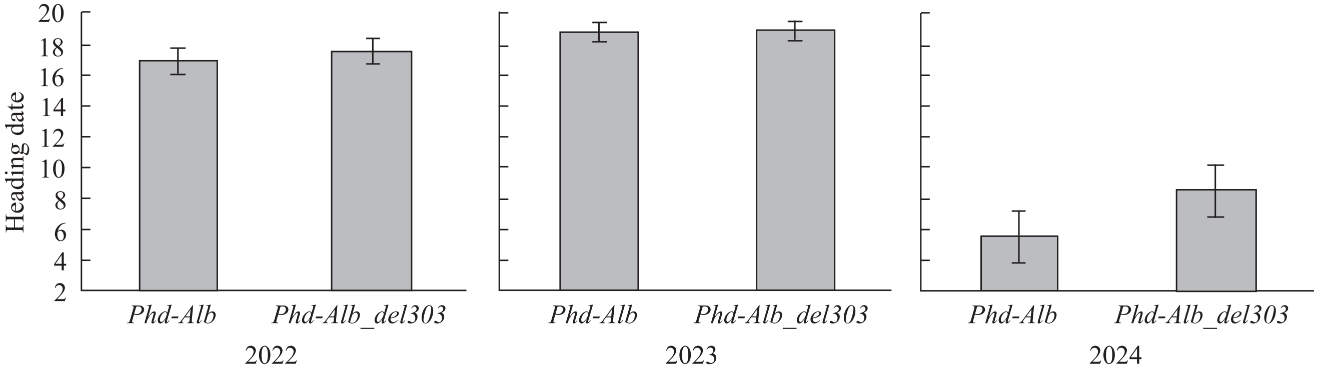

Fig. 2. The duration of the period to heading in carriers of different alleles of the *Ppd-A1* gene in 2022, 2023, and 2024, days

manifestation of all the traits under investigation. Low variation of the trait was notable for PH, TGW, GNS, and NPT (7–9 %), medium variation (11–15 %) – for GY, HI, GWS, DPH, and winter hardiness, and high variation (34 %) – for frost resistance.

Due to the favorable conditions for the growth and development of winter wheat plants during the wintering period, the level of winter hardiness of the population of recombinant-inbred lines was generally quite high (79 % of living plants). At the same time, the resistance to adverse wintering factors of more winter-hardy lines exceeded that of less winter-hardy lines almost three times (from 34 to 94 %). The frost resistance of the population at the stage of seedlings was quite low (12 % of live plants), varying from 4 to 68 % in individual lines. The difference in the duration of the period before heading between early and late heading lines was nine days (from 6 to 13 days in different years), and the difference in plant height between taller and shorter lines was 36 cm (32–45 cm in different years). The number of grains per spike varied from 22 to 32, and the grain weight per spike of more productive lines exceeded that of less productive ones by 0.43 g. The thousand-grain weight in the whole population of RIL in all years of study was relatively low and equaled 32.6 ± 0.34 with a variation between lines from 25.8 to 37.8 g. The difference between the extreme variants by the trait 'number of productive tillers' (NPT) ranged from 338 to 509 it./sq.m. The grain yield (GY) of the more productive lines reached 0.411 kg/

Table 2. The main statistics for economically valuable traits of recombinant-inbred lines Orenburgskaya 48//Cappelle Desprez/2B Chinese Spring in the field conditions

Trait*	$\overline{x}^{**}$	S_x^{**}	CV, % **	max**	min**	F_g 1	F_y 2	Fg_{xy} 3
Frost, %	12	0.05	34	68	4	26.25	13.64	3.54
Winter, %	79	0.04	15	94	34	6.67	98.97	3.71
DPH, days	15.9	0.27	13	20	11	35.2	4776.30	4.30
PH, cm	109	0.91	7	125	89	13.6	1668.50	2.40
GNS, it.	26	0.30	9	32	22	3.27	465.44	1.37
GWS, g	0.93	0.01	12	1.15	0.72	3.61	593.16	1.25
TGW, g	32.6	0.32	8	37.8	25.8	12.7	282.70	1.70
HI	0.49	0.01	12	0.54	0.37	2.01	242.45	1.24
NPT, it./sq.m.	430	5.04	9	509	338	2.45	360.32	1.26
GY, kg/sq.m.	0.332	0.00	11	0.411	0.244	3.40	22.02	1.93

Note: * Frost. – frost resistance of plants in the phase of seedlings at –12 °C, Winter. – winter hardiness, DPH – duration of period before heading (starting since May 1), PH – plant height, GNS – number of grains per spikelet, GWS – grain weight per spike, TGW – thousand grain weight, NPT – number of productive tillers, HI – harvest index, GY – grain yield; $\overline{x}^{**}$ – mean arithmetic for the trait, S_x – standard error, CV – coefficient of variation, max – maximal value of the index, min – minimal value of the index; 1 – F_g – impact of the genotype factor, $F_{0.05}$ = 1.32 at df1 = 63 and df2 = 192; 2 – F_y – impact of the year factor, $F_{0.05}$ = 2.99 at df1 = 2 and df2 = 192; 3 – F_{gxy} – impact of the interaction of year and genotype factors, $F_{0.05}$ = 1.22 at df1 = 126 and df2 = 192.

sq.m. and exceeded that of the less productive lines by 0.167 kg/sq.m. The proportion of grain in total aboveground biomass (HI) in some lines ranged from 0.37 to 0.54.

Effect of Ppd-A1 and Ppd-B1 gene alleles on phenotypic traits of RIL. Genetic differences between the groups of recombinant-inbred lines with the presence of one or another allele of the *Ppd-A1* gene for most of the studied traits in the field experiment were not significant (**Table 3**). Thus, when comparing groups of lines by recessive alleles of the *Ppd-A1* gene, significant differences were noted only in the frost resistance of seedlings. In both experiments, the lines carrying the *Ppd_A1del303* allele were characterized by significantly higher frost resistance. At the same time, there was a tendency to a decreased duration of the period before heading, higher winter hardiness, thousand grain weight, number of productive tillers per unit of the area, and yield in genotypes with the *Ppd-A1b* allele compared to those with *Ppd-A1_del303*.

As compared to the *Ppd-A1* gene, the most significant impact of RIL differences by some traits was made by the allelic differences in the *Ppd-B1* gene (Fayt et al, 2017). The presence of *Ppd-B1c* allele in the RIL genotype promoted the reduction of DPH by 2.7 days. The lines of genotype *Ppd-B1c* were notable for a larger grain weight per spike (per 0.10 g) and the thousand-grain weight (by 2.6 g), and a higher harvest index (by 0.05) as compared to *Ppd-B1b*-genotypes. The grain yield of RIL which are carriers of allele *Ppd-B1c* was 0.342 kg/sq.m. and exceeded that for the lines with allele *Ppd-B1b* by 0.035 kg/sq.m.

Different combinations of alleles of *Ppd-A1* and *Ppd-B1* genes had a considerable impact on the differences between genotypes in the field conditions of Odesa by the duration of the period before heading, the grain weight per spike and the thousand grain weight, the harvest index, and grain yield (**Table 4**). The decisive factor for the formation of most traits was the presence of the four-copy allele *Ppd-B1c* or one-copy allele *Ppd-B1b* in the genotype of the line. For instance, regardless of some recessive alleles of the *Ppd-A1* gene, the genotypes with the *Ppd-B1b* allele started heading almost simultaneously and 2.5–3.5 days later than those with allele *Ppd-B1c*. There was a tendency toward the reduction in DPH in the lines-carriers of the *Ppd-A1b* gene as compared to such carriers of the mutant allele *Ppd-A1_del303* during the interaction with allele *Ppd-B1c*. The allelic differences by these two genes conditioned 3.5 days (or 38.9 %) of differences in terms of DPH as compared to 9 days of differences for the population of RIL of Orenburgskaya 48//Cappelle Desprez/2B Chinese Spring by this trait in the field conditions of Ukrainian Steppe.

The combination of alleles *Ppd-A1b Ppd-B1c* promoted the formation of higher grain yield and its main constituents: grain weight per spike, thousand grain weight, and harvest index. The replacement of allele *Ppd-A1b* in this genotype with the alternative *Ppd-A1_del303* (genotype *Ppd-A1_del303 Ppd-B1c*) led to a significant decrease in the yield due to a reliable

Table 3. The average values of winder hardiness, frost resistance (% of living plants), and economically valuable traits for RIL groups of Orenburgskaya 48//Cappelle Desprez/2BChinese Spring – carriers of different alleles of the *Ppd-A1* and *Ppd-B1* genes

Traits [1]	*Ppd_A1del303*	*Ppd-A1b*	F[2]	*Ppd-B1c*	*Ppd-B1b*	F[3]
Frost, %	14	7	4.02 *	14	9	2.43
Winter, %	78	81	0.59	80.1	75.4	2.52
DPH, days	16.0	15.7	0.23	15.0	17.7	92.30 *
PH, cm	110	108	0.52	110	108	1.09
GNS, it.	26.4	26.5	0.02	26.7	26.0	1.87
GWS, g	0.93	0.93	0.00	0.96	0.86	23.53 *
TGW, g	32.6	32.8	0.10	33.5	30.9	43.64 *
NPT, it./sq.m.	426	445	2.70	426	439	2.14
HI	0.49	0.50	0.52	0.51	0.46	11.29 *
GY, kg/sq.m.	0.330	0.339	0.65	0.342	0.307	19.57 *

Note: [1] Frost. – frost resistance of plants in the phase of seedlings at –12 °C, Winter. – winter hardiness, DPH – duration of the period before heading (starting since May 1), PH – plant height, GNS – number of grains per spike, GWS – grain weight per spikelet, TGW – thousand grain weight, NPT – number of productive tillers, HI – harvest index, GY – grain yield; [2] F = 3.89 at $P \leq 0.05$; [3] F = 3.84 at $P \leq 0.05$

Table 4. The average values of winder hardiness, frost resistance (% of living plants), and economically valuable traits for RIL genotypes of Orenburgskaya 48//Cappelle Desprez/2BChinese Spring with different combinations of alleles of the *Ppd-A1* and *Ppd-B1* genes

Trait *	*Ppd-A1b* *Ppd-B1b*	*Ppd-A1_del303* *Ppd-B1b*	*Ppd-A1b* *Ppd-B1c*	*Ppd-A1_del303* *Ppd-B1c*	F**	$LSD_{0.05}$
Frost, %	6.0	9.8	8.0	15.6	1.93	
Winter, %	80.7	71.7	81.0	80.3	1.59	
DPH, days	17.8	17.7	14.3	15.2	14.40	0.6
PH, cm	110	107	107	111	1.11	
GNS, it.	26	26	27	26	0.53	
GWS, g	0.85	0.88	0.98	0.95	4.02	0.04
TGW, g	31.3	30.9	33.8	33.4	5.49	0.9
HI	0.44	0.47	0.54	0.50	4.41	0.03
NPT, it./sq.m.	440	437	448	421	1.40	
GY, kg/sq.m.	0.309	0.307	0.359	0.338	6.17	0.013

Note: * Frost. – frost resistance of plants in the phase of seedlings at –12 °C, Winter. – winter hardiness, DPH – duration of the period before heading (starting since May 1), PH – plant height, NGS – number of grains per spike, GWS – grain weight per spikelet, TGW – thousand grain weight, NPT – number of productive tillers, HI – harvest index, GY – grain yield; ** F=2.77 at $P \leq 0.05$.

decrease in the harvest index and an insignificant decrease in the indices of the weight of grain per spike and thousand grain weight. The genotypes with allele *Ppd-B1b* together with any allele of the *Ppd-A1* gene were greatly inferior to the carriers of alleles *Ppd-A1b Ppd-B1c* or *Ppd-A1_del303 Ppd-B1c* – a smaller grain weight per spike by 0.07–0.13 g, a smaller thousand grain weight by 2.1–2.9 g, a lower harvest index by 0.03–0.10 and, as a result, a lower grain yield by 0.029–0.052 kg/sq.m. One-third (31.1 % or 0.052 from 0.167 kg/sq.m.) of the differences by this trait in the population of RIL was caused by the differences between these two *Ppd-1* genes.

DISCUSSION

We used the diagnostic molecular markers to characterize 30 samples of winter bread wheat of various origin by alleles of the *Ppd-A1* gene. Most of them (19 samples or 63 %) were found to have allele *Ppd-A1_del303*. With the exception of several varieties, mainly from western Europe, this allele was detected in the varieties (21 samples), which were products of the breeding programs of the northern east, center, and south of Ukraine. The frequency of allele *Ppd-A1_del303* among Ukrainian varieties was 69 %, which may partially be related to a rather limited number of varieties in the sampling. At the same time, this value was lower than that for the varieties in Sweden (88 %), but much higher than that for the varieties of the 1920–1930s in France (35 %) and the varieties of the 1940–1980s in Poland (30 %) (Shaw et al, 2013). Among the recombinant-inbred lines, there was a much higher fraction of the carriers of allele *Ppd-A1_del303*.

We did not detect reliable allelic differences in the *Ppd-A1* gene by the heading date in the sampling of varieties or in the population of recombinant-inbred lines in the field conditions. This fact was determined in our previous study (Pogrebnyuk et al, 2023) regarding the impact of allele *Ppd-A1_del303* on the heading date of the recombinant-inbred lines Orenburgskaya 48//Cappelle Desprez/2B Chinese Spring in conditions of a natural day (Odesa, Ukraine) and a day, artificially reduced to 10 h after the previous vernalization for 50 days. The absence of the impact of allele *Ppd-A1_del303* on the heading date of winter bread wheat was noted in the field conditions of Great Britain with the natural day duration and the duration artificially extended to 16 h (Bentley et al, 2013). At the same time, Shaw et al (2013) indicated the difference in the heading date between *Ppd-A1_del303* and *Ppd-A1b* genotypes on days 1–4 while cultivating spring bread wheat in conditions of artificial climate during a natural day and the one extended to 18 h. Later heading date (by 2–4 days) of durum wheat varieties with allele *Ppd-A1_del303* was observed in the field conditions of Spain as compared to such carriers of allele *Ppd-A1b* (Royo et al, 2020). We did not note a considerable effect of allelic differences in the *Ppd-A1* gene on other traits of recombinant-inbred lines either: winter hardiness, plant height, number and weight of grains per spike, thousand grain weight, harvest index and grain yield, which is confirmed by the data of Makhoul et al (2024) regarding the effect of different haplotypes of this gene by the complex of traits in different media. The only observed exception was the higher winter hardiness of seedlings with the *Ppd-A1_del303* gene as compared to the wild-type *Ppd-A1b*. However, the average level of winter hardiness was rather low, so further studies are required in this direction.

Among four genotypes of the carriers of different alleles of *Ppd-A1* and *Ppd-B1* genes, there were considerable differences ($P \leq 0.05$) in terms of the duration of the period before heading, the grain weight per spike and the thousand grain weight, the harvest index and grain yield. A later heading date and lower yield indices were remarkable for the genotypes with allele *Ppd-B1b*, regardless of the presence of allele *Ppd-A1b* or *Ppd-A1_del303*, and early heading date and higher yield indices – the presence of allele *Ppd-B1c*. The positive effect of multicopy *Ppd-B1* genes on the reduction in the period before heading and the increase in the indices of specific yield constituents was reported before (Kiss et al, 2014; Harris et al, 2017; Wu et al, 2021). At the same time, the effect of allele *Ppd-B1c* on the heading date and other traits largely depended on the presence or absence of the line of the mutant allele *Ppd-A1_del303* in the genotype. The genotypes-carriers of allele *Ppd-A1b* or *Ppd-A1_del303* did not differ considerably by any trait during the interaction with allele *Ppd-B1b*. At the same time, while interacting with allele *Ppd-A1b,* the effect of the dominant allele *Ppd-B1c* by the earlier heading date was 3.5 days, and with *Ppd-A1_del303* – only 2.5 days. Thus, the presence of allele *Ppd-A1_del303* in the genotype of the line led to a reduction in the effect of the dominant allele *Ppd-B1c* in terms of accelerating the heading date. A similar situation regarding the heading date, delayed by allele *Ppd-A1b_del303*, during the interaction with dominant allele *Ppd-B1c*, was previously determined for durum wheat (Royo et al, 2020). In this study, we also noted the negative effect of allele P*pd-A1_del303* during the interaction with the dominant allele *Ppd-B1c* on the grain weight per spike, the thousand grain weight, harvest index and grain yield.

CONCLUSIONS

We used the alleles of the *Ppd-A1* gene to identify the genotypes of 30 winter bread wheat of various origin and 64 recombinant-inbred lines F_9 of the crossbreeding combination Orenburgskaya 48//Cappelle Desprez/2B Chinese Spring. Most varieties (19 samples or 63 %) and recombinant-inbred lines (49 lines or 76 %) were found to have allele *Ppd-A1_del303*. No considerable effect of the mutant recessive allele *Ppd-A1_del303* was found regarding the heading date and other economically valuable traits of winter bread wheat plants as compared to the allele *Ppd-A1b* in the field conditions, except for frost resistance of the seedlings, which was considerably higher for the first genotype than for the other one. The combination of alleles *Ppd-A1b* and *Ppd-B1c* promoted the acceleration of early maturity and the formation of the highest indices of the grain weight per spike and thousand grain weight, harvest index and, as a result, grain yield. The replacement of the *Ppd-A1b* allele with *Ppd-A1_del303* led to a decrease in the effect of the dominant *Ppd-B1c* allele on accelerating heading and negatively affected the grain weight per spike, thousand grain weight, harvest index and grain yield compared to the *Ppd-A1b Ppd-B1c* genotype.

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Алельна варіація в локусі *PPD-A1* і її асоціації з часом колосіння та агрономічними ознаками пшениці озимої (*Triticum aestivum* L.) у північному Причорномор᾿ї

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Мета. Ідентифікація *Ppd-1*-алелів у сортів пшениці м'якої озимої різного походження, в тому числі української селекції та рекомбінантно-інбредних ліній Оренбурзька 48//Cappelle Desprez/2B Chinese Spring та оцінка ефектів алеля *Ppd-A1_del303*, в тому числі при взаємодії з різними алелями гена *Ppd-B1*, за тривалістю періоду до колосіння та пов'язаними з нею агрономічно цінними ознаками. **Методи.** Виділення ДНК, алель-специфічна

ПЛР, електрофорез в агарозному та поліакриламідному гелях, фенологічні спостереження, оцінка морозостійкості у паростках, аналіз морфобіологічних ознак та елементів структури врожаю. Статистичний аналіз отриманих даних проводився в Microsoft Excel. Значущість різниці між зразками оцінювалась за критерієм F Фішера. Різниця $p < 0,05$ вважалася статистично достовірною для всіх показників. **Результати.** Проведено маркування 30 сортів різного походження та 64 рекомбінантно-інбредних ліній Оренбурзька 48//Cappelle Desprez/2B Chinese Spring пшениці м'якої озимої для ідентифікації алелів гена *Ppd-A1*. Оцінено поліморфізм сортів та популяції рекомбінантно-інбредних ліній в умовах північного Причорномор'я (м. Одеса) за 10 ознаками: морозостійкість рослин у фазі проростків, зимостійкість, тривалість періоду до колосіння, висота рослини, кількість зерен колоса, маса зерен колоса, маса 1000 зерен, кількість продуктивних пагонів на одиницю площі, індекс урожаю та врожайність зерна. Зіставлення даних оцінювання ліній за агрономічними ознаками з результатами ідентифікації генотипів дало змогу виявити вплив алелів гена *Ppd-A1* та різних комбінацій алелів генів *Ppd-A1* і *Ppd-B1* за вказаними ознаками. **Висновки.** Виявлено більше поширення алеля *Ppd-A1_del303* як серед сортів, так і рекомбінантно-інбредних ліній. Генетичні відмінності за геном *Ppd-A1* (*Ppd-A1_del303* або *Ppd-A1b*) істотно пов'язані лише з морозостійкістю паростків, при відсутності значних відмінностей за іншими ознаками. Взаємодія алелів *Ppd-A1b* і *Ppd-B1c* сприяла пришвидшенню скоростиглості та формуванню найбільших показників маси зерен колосу, маси 1000 зерен, індексу урожаю й урожайності зерна. Заміна алеля *Ppd-A1b* на *Ppd-A1_del303* призводила до зменшення ефекту домінантного алеля *Ppd-B1c* щодо прискорення колосіння та негативно впливала на масу зерна колоса, масу тисячі зерен, індекс урожаю, урожайність порівняно з генотипом *Ppd-A1b Ppd-B1c*.

Ключові слова: пшениця м'яка озима, фотоперіод, *Ppd-1* гени, колосіння, урожай.

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