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QTL mapping for germination of seeds obtained from previous wheat generation under drought

Research Article

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Abstract: The QTLs controlling germination and early seedling growth were mapped using seeds acquired from mapping population and parental lines of Chinese Spring and SQ1 grown under water-limited conditions, severe drought (SDr) and well-watered plants (C). Germination ability was determined by performing a standard germination test based on the quantification of the germination percentage (GP24) of seeds incubated for 24 h at 25°C in the dark. Early seedling growth was evaluated on the basis of the length of the root and leaf at the 6th day of the experiment. QTLs were identified by composite interval mapping method using Windows QTLCartographer 2.5 software. For the traits studied, a total of thirty eight additive QTLs were identified. Seventeen QTLs were mapped in C on chromosomes: 1A, 2A, 7A, 1B, 2B, 3B, 4B, 5B, 6B, 7B, 2D, 3D, 4D and 6D, while twenty one QTLs were identified in SDr on chromosomes: 1A, 2A, 5A, 2B, 3B, 4B, 5B, 6B, 7B, 3D, 5D and 6D. Most of the QTLs for GP and early leaf growth parameters were clustered on chromosome 4B (associated with the *Rht-B1* marker) both in C and SDr plants. The results indicate the complex and polygenic nature of germination.

Keywords: *Germination • Leaf • Root • Quantitative trait loci • Triticum aestivum L.*

Abbreviations:

QTL – quantitative trait loci,
DH – double haploid,
C – control (well-watering),
SDr – severe drought.

1. Introduction

Periodic water deficit is one of the major factors that limits the yield of cultivated plants, particularly spring crops, which do not benefit from the winter reserves of water in the soil [1,2]. Drought is one of the environmental factors affecting the life cycle of plants, which can lead to irreversible damage to the plant's functioning or even to its death [3]. It is also one of the major problems in agriculture, which struggles with insufficient resistance of plants to adverse environmental conditions.

The germinability of seeds can be one of the earliest indicators to assess seed viability [4]. It is a parameter of the sowing value of seeds, serving to determine the potential of germination [5]. There are many factors which may lead to adverse structural and metabolic changes in seeds, resulting in either the low-level or absence of activation of the seed embryo, causing poor growth of seedlings or even complete inhibition of growth. The process of germination is extremely complex and subject to the effects of many physiological factors [6]. The germination potential is a quantitative trait, probably controlled polygenically [7,8] that is also affected by external factors. Therefore, measurable results can be expected from quantitative

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trait loci (QTL) analysis, based on phenotypic data [9]. The inheritance of traits associated with the process of germination and growth of a seedling has been studied in wheat [10], *Brassica* ssp. [7], rice [11], barley [12], and sunflower [13]. The length of the coleoptile of wheat seedlings is an important adaptation to unfavorable conditions in the initial stages of embryo development and markedly affects the yield obtained [14-16]. This trait shows high heritability and low susceptibility to environmental changes [15]. Several QTLs were detected in various populations tested for the length of coleoptile in different environmental conditions [15,17]. Studies aimed at investigating the indices of germination and seedling growth, as well as the genetic background of these phenomena, were performed by analyzing SSR markers [18]. The genetic background (QTL) for tolerance of germinating kernels of rice to flooding was also studied [19], as well as the effect of extreme temperatures on the germination potential in *M. truncatula* [20]. Moreover, QTLs for seed germination in tomato were sought in plants under cold stress and salt stress [21]. Correlations were also investigated between nitrogen metabolism and germination efficiency in maize, measured at physiological and genetic levels [22]. However, there have been no reports on the germination of seeds obtained from the previous generation treated with drought stress, or optimally watered, in connection with the search for QTLs influencing drought resistance.

The objective of the experiments was to investigate the consequent effect of severe drought stress and optimum watering on germination, growth and weight of seedlings from grains obtained from the previous generation of parental forms and lines of CSDH populations, in connection with the search for QTLs associated with drought resistance.

2. Experimental Procedures

2.1 Plant material

The mapping population consisted of 90 doubled haploid lines (CSDH) generated from the cross between hexaploid wheat (*Triticum aestivum* L.) genotypes Chinese Spring (CS) and SQ1 [23]. The genetic map was additionally saturated with DArT markers (http://www.triticarte.com.au) as previously reported [24]. The seeds for the study were collected from plants subjected to severe drought (SDr), or optimally watered plants (C) as described by [25]. The parental forms differ in tolerance to drought and present diverse physiological responses and yields. These characteristics were previously confirmed in earlier studies [23,25,26].

The seeds of controls and of plants subjected to severe drought were placed on Petri dishes of 60 mm diameter, lined with moistened absorbent paper. Six seeds were placed on each dish and replicated 3 times for each of the CSDH lines and the parental form. The absorbent paper in each dish was moistened with 1.3 ml of distilled water. The seeds were kept for 4 days in an air-conditioned *in vitro* chamber, at a temperature of 25ºC, in darkness. During seed germination a constant level of moisture in the absorbent paper was maintained by the addition of distilled water when needed. The germination potential of grains was evaluated after the 1st, 2nd and 3rd day. On the 5th day, the plants were placed in a room at a temperature of 25ºC and natural light. On the 6th day, the length of the first leaf, the length of the longest root, the fresh and dry weight of leaves and roots were measured for 5 plants/per Petri dish. The dry weight of leaves and roots was determined after drying for 24 h at 60ºC.

2.2 Statistical analysis of the results and QTL analyses

The data obtained in the experiment were analyzed in Microsoft Excel 2007 for Windows XP. Based on the mean values for each of the traits investigated, the basic characteristics were evaluated, such as mean, minimum (min.) and maximum value (max.) as well as distribution parameters (skewness and kurtosis). The text was edited using Microsoft Word 2010 software. Phenotypic data analyses were used to locate QTLs in 90 lines of the CSDH population by composite interval mapping (CIM), performed with Windows QTLCartographer 2.5 software [27]. A QTL locus was identified in a region designated by the maximum LOD score, and declared significant if it exceeded a critical value, determined by 1000 permutations (typically LOD>3.3). However, as this criterion generated relatively few significant results, QTLs with maximum LOD scores ranging from 2.0 to 3.3 were also included.

3. Results

3.1 Phenotypic variation, identification of QTLs

The results concerning observations of studied traits are presented in Tables 1 and 2. In Table 1 the mean values of the traits for the parental lines and the mapping population are shown, together with the symbol of the QTL assigned to each of the traits. The QTLs identified and located are described in Table 2. The differences in the germination capacity of CS and SQ1 grains obtained from the previous generation of parental forms of plants (genotypes), subjected to severe drought (SDr) and

Trait	Locus Symbol	Treatment	Parental Line		CSDH Population					
			CS	SQ1	Mean	SD	Min.	Max.	Skewness	Kurtosis
Germination ability after 24 h [%]	*GP24*	C	77.78	72.22	67.67	22.36	11.11	100.00	-0.49	-0.34
		SDr	83.33	88.89	89.75	15.50	33.33	100.00	-1.96	3.45
Germination ability after 48 h [%]	*GP48*	C	100.00	100.00	96.96	5.78	72.22	100.00	-2.25	5.04
		SDr	100.00	100.00	99.05	2.66	88.89	100.00	-2.88	7.57
Germination ability after 72 h [%]	*GP72*	C	100.00	100.00	99.27	2.17	86.67	100.00	-3.34	12.90
		SDr	100.00	100.00	99.53	1.76	88.89	100.00	-4.00	17.07
Leaf lenght [mm]	*Lfl*	C	131.93	118.40	118.66	18.54	75.00	160.53	-0.16	-0.46
		SDr	156.07	122.73	123.71	20.06	80.80	161.60	-0.14	-0.69
Root lenght [mm]	*Rl*	C	108.73	106.33	109.92	15.71	67.40	145.60	-0.22	0.21
		SDr	110.53	99.80	98.77	19.34	55.40	150.93	0.34	0.21
Leaf dry weight [mg]	*LfDW*	C	8.13	8.47	6.97	1.35	3.40	9.80	-0.46	-0.02
		SDr	7.80	7.60	6.48	1.30	2.87	9.87	-0.23	-0.02
Root dry weight [mg]	*RDW*	C	5.33	5.93	4.54	1.04	1.53	7.60	-0.10	0.83
		SDr	2.93	5.00	3.93	0.87	1.90	6.00	0.00	-0.25

Table 1. Mean values (%, mm, mg) of studied traits of parental and doubled haploid lines (CSDH) and standard deviation (SD), minimum (min.), maximum (max.), skewness and kurtosis for CSDH line previous generation treated under severe drought stress subjects (SDr) and control (C) and the symbols of their loci.

well-watered plants (C), were detected as early as after 24 hours. Therefore, the germination capacity after this time was selected for QTL analyses. The differences were observed in relation to both the treatment (SDr and C) and genotype (CS and SQ1).

A decrease in the germination capacity between SDr and C treatments was ca. 3-fold higher in the cultivar CS than in SQ1 (Table 1). At the same time, in CS, after 6 days of further growth of seedlings in natural light conditions – an increase in the leaves length in SDr was over 15% higher compared with C, while in SQ1 it was higher by only 3.5%. No statistically significant differences were found in the root lengths and in the fresh weight of leaves in relation to the treatment. In both CS and SQ1, the SDr caused an increase in the fresh weight of roots by about 20%. After drying the plants, it was found that in SDr, a slight decrease occurred (by ca. 6%) in the dry weight of leaves in the cultivar CS, whereas the dry weight of roots increased by about 30% compared to the cultivar SQ1.

A comparison between CS and SQ1 revealed that under SDr, the germination capacity was more than 10% lower than in C plants. At the same time, in the cultivar CS, an increase was noted in the length of both aerial parts and roots by 21 and 10%, respectively. The dry weight of leaves was comparable, whereas the dry weight of roots in plants germinating after the SDr treatment was higher by over 40% in SQ1 compared to CS (Table 1).

On the basis of the traits presented in Table 1 (except for the germination capacity after 48 and 72 h), thirty eight QTLs with LOD from 2.0 to 16.3 were identified using composite interval mapping (CIM) (Table 2). Among many *loci* identified by the CIM method, a total of twenty one QTLs were confirmed for the plants obtained from the previous generation treated with SDr, and seventeen QTLs for the C plants. The lowest number of QTLs associated with the leaf length was detected in both C and SDr plants. Among the quantitative traits examined, the parameters pertaining to the length of the root were distinguished as traits with the higher numbers of *loci*.

3.2 *Loci* determining germination ability after 24 h [*GP 24*]

Genome scan identified two *loci* in C plants, located on chromosomes 1B and 4B. LOD values of these loci were 4.2 and 6.5 and their contribution to trait phenotypic variation amounted to 12.3% and 20.7% for 1B and 4B, respectively (Table 2). In SDr plants, single QTLs were located on chromosomes 5A, 3B, 4B, and two QTLs on chromosome 6B. The highest LOD score (4.2) was calculated for *QGP24.csdh*-6B-1 *locus*, and it represented 14.1% of the variability of the trait examined. The analysis of the additive effects of CS allele indicated that this allele reduces the germination capacity after 24 h in all *loci* except for *QGP24PDS.csdh*-6B-2.

Trait	Treatment	QTL	Marker	Peak [cM]	LOD	R^2	Add
GP 24	C	*QGP24PC.csdh-1B**	wPt-6425	79.1	4.2	12.3	-7.823
		*QGP24PC.csdh-4B**	m62p64.4	74	6.5	20.7	-10.276
	SDr	*QGP24PDS.csdh-5A*	wPt-797581	31.7	2.2	7.0	-4.194
		*QGP24PDS.csdh-3B**	wPt-732049	19.4	3.3	10.6	-5.278
		QGP24PDS.csdh-4B	psp3163	57.1	2.3	7.0	-4.252
		QGP24PDS.csdh-6B-1	psr167	2.0	2.5	8.3	-4.898
		*QGP24PDS.csdh-6B-2**	wPt-2000	75.2	4.2	14.1	6.040
LfL	C	*QLflength PC.csdh-4B**	Rht-B1	66.2	8.5	26.9	10.107
		QLflength PC.csdh-3D	psr1203.2	207.9	3.2	8.7	-5.708
	SDr	*QLflength PDS.csdh-4B-1*	tPt-5519	35.5	3.0	5.9	-5.715
		*QLflength PDS.csdh-4B-2**	Rht-B1	65.2	16.3	46.1	15.630
		QLflength PDS.csdh-3D	psr1203.2	207.9	3.3	6.5	-5.471
LfDW	C	*QLfDWPC.csdh-1A*	wPt-5577	122.1	2.1	6.4	-0.361
		*QLfDWPC.csdh-4B**	Rht-B1	65.2	8.2	29.1	0.771
		QLfDWPC.csdh-5B	gwm271	121.6	2.1	6.4	-0.358
	SDr	*QLfDWPDS.csdh-2A*	m92p78.10	55.2	3.3	9.6	0.431
		*QLfDWPDS.csdh-4B**	wPt-733745	76.4	7.0	22.4	0.652
		QLfDW PDS.csdh-6B-1	wPt-6247	60.7	2.5	7.1	0.494
		*QLfDWPDS.csdh-6B-2**	wPt-5461	83	3.8	10.9	-0.624
RL	C	*QRlengthPC.csdh-1A*	wPt-5577	122.1	2.9	8.9	-4.817
		QRlengthPC.csdh-2A	m87p78.3	35.3	2.0	7.9	4.430
		QRlengthPC.csdh-2B	m87p78.5YT	94.6	2.6	7.3	4.308
		QRlengthPC.csdh-7B	wPt-4140	245.8	2.4	7.4	4.456
		*QRlengthPC.csdh-2D**	wPt-665102	203.7	3.8	12.1	5.595
		QRlengthPC.csdh-4D	psp3103	30.0	2.2	10.3	5.685
	SDr	*QRlengthPDS.csdh-1A**	wPt-664972	89.7	6.7	24.0	-9.573
		*QRlengthPDS.csdh-5B-1**	wPt-1951	51.9	3.5	10.5	6.426
		QRlengthPDS.csdh-5B-2	m60p64.3	174.2	2.1	6.5	5.220
		QRlengthPDS.csdh-7B	wPt-0137	103.4	2.3	6.8	5.490
		*QRLengthPDS.csdh-5D**	gwm174	137	3.6	12.9	-7.261
RDW	C	*QRDWPC.csdh-7A*	wmc488b	150.7	2.2	7.7	0.3110
		QRDWPC.csdh-3B	wmc418	119.5	2.4	8.3	0.3201
		QRDWPC.csdh-6B	gwm608.3	139.1	2.3	8.0	-0.324
		QRDWPC.csdh-6D	wPt-734218	161.6	2.1	2.1	0.297
	SDr	*QRDWPDS.csdh-2B**	wPt-3755	141.3	4.2	13.4	-0.341
		QRDWPDS.csdh-5B	wPt-1548	99.0	2.2	6.6	0.2374
		QRDWPDS.csdh-5D	gwm174	134.0	2.5	9.5	-0.295
		*QRDWPDS.csdh-6D**	gwm469	26.6	3.7	11.8	0.325

Table 2. Identification and localization of QTLs, that control: germination (GP), leaf length (LfL), root length (RL), and dry weight of leaves (LfDW) and roots (RDW) using the algorithm of CIM and the characteristics of the basic parameters of the QTL. * QTLs significant at 1000 permutations.

Peak - position of the peak of the QTL in centiMorgans LOD – Log 10 of the likelihood odds ratio
R^2(%) - % of phenotypic variance explained by the QTL Add - additive effect of the Chinese Spring allele

3.3 *Loci* determining the length of the leaves and dry weight – [*LfL, LfDW*]

The QTLs for the leaf length (LfL) and its dry weight (LfDW) were identified on chromosomes 1A, 2A, 4B, 5B, 6B and 3D. Significant *loci* affecting the length of the leaves and dry weight were recorded for all traits in the region of chromosome 4B, close to the marker *Rht-B1-4B*, in both plants subjected to SDr and in C plants. These *loci* were characterized by LOD values ranging from 6.8 to 16.3, and controlled 23.1-46.1% of the variability of the examined trait. The QTL for the leaf length (R^2 at ca. 7) was located on chromosome 3D in C and SDr plants. QTL for dry weight (*QLfFWPC.csdh-1A*) was mapped in C plants on chromosome 1A, with a low value of LOD=2.1, and controlled 6.4% of the variability of the trait. Another dry weight *locus* was detected on chromosome 5B, with similar values as the latter *locus* on chromosome 1A. Three additional *loci* were identified in SDr plants on chromosomes 2A (*QLfDWPDS.csdh-2A*) and 6B (*QLfDWPDS.csdh-26B-1* and *QLfDWPDS.csdh-6B-2*). Corresponding LOD scores of these loci were 3.3, 2.5, and 3.8, and these QTLs controlled 9.6, 7.1, and 10.9% of the trait variability, respectively (Table 2).

3.4 *Loci* determining the length and dry weight of roots – [*RL, RDW*]

In C plants, the QTLs associated with root length and its dry weight were identified on chromosomes 1A, 2A, 7A, 2B, 3B, 6B, 7B, 2D, 4D and 6D, while in SDr plants they were found on chromosomes 1A, 2B, 5B, 7B, 5D, and 6D.

Particular QTLs explained the variability of root parameters ranging from 6.5% (LOD=2.1) to 24.0% (LOD=6.7) (Table 2). The largest amount of phenotypic variation in the length of the root (24.0%) was explained by *QRL.csdh*-1A, located on chromosome 1A in SDr plants, while in C plants a contribution of *QRLh.csdh*-1A *locus* located on chromosome 1A was also observed, which explained 8.9% of the variability. Among *loci* identified in C plants, *locus QRLPC.csdh*-2D on chromosome 2D had the highest *LOD* score (3.8), and controlled 12.1% of the variability of the trait. On the other hand, *loci* found in SDr plants impacting the root length were characterized by low LOD values of about 2.0-2.5. The most significant *loci* in SDr plants were identified on chromosomes 5B and 5D (*QRL.csdh*-5B-1 and *QRL.csdh*-5D). They were characterized by respective LOD values of 3.5 and 3.6, and controlled 10.5% and 12.9% of the variability of the trait. Furthermore, the most significant QTLs in SDr plants for the dry root weight were located on chromosomes 2B and 6D. These *loci* were characterized by respective LOD scores of 4.2 and 3.7, and explained 13.4% and 11.8% of the trait variability (Table 2). In the experiments conducted in the current study, statistically most significant groups of QTLs for the traits examined were identified in the region of chromosome 4B (mostly near *RHT-B1* marker). They were associated with GP, leaf length and dry weight parameters in SDr as well as in C plants (Figure 1).

4. Discussion

Germination, sprouting, and growth of seedlings are prerequisites of efficient cultivation. The germination capacity of grain is determined by standard germination tests. Although relatively low variations were observed in the results, major differences may occur in the quality of grain. Therefore, in order to provide more accurate evaluation, it is recommended to test grain vigour. This includes not only the germination capacity but also the capacity to grow seedlings under various environmental conditions [28,29]. The combination of high grain vigour with the strong growth of a seedling is essential, particularly under conditions that deviate from the optimum. Various studies carried out, *e.g.* by [30] and [8] indicate a positive correlation between the germination capacity and the early vitality of grain. The germination capacity depends closely on the external conditions accompanying the processes of grain setting and filling, grain storage conditions [31-34] as well as grain size [35]. The use of molecular markers in genotypes selection is now widely applied in breeding programs [36,37] but requires prior determination of the main *loci* of genes associated with the desired traits [38-40], which is made possible by QTL analysis. The experiments conducted on wheat grain germinating under osmotic stress or control conditions resulted in mapping different QTLs distributed throughout the genome [10], suggesting a possible role of stress factors in the change of grain vigour. Wild species related to bread wheat show remarkable genetic diversity essential to the improvement of the quality of cultivated plants. The D genome originating from *A. tauschii* is considered a potential donor of traits associated with the vigour of grain, including germination capacity [30,41,42]. The principal regions on D genome associated with grain germination provide a common location for the genes coding for D-type cyclins (1D) and cytochrome 450 genes (P450 gene family), spermitine synthase 1 (SPDSY 1) (7D), and protein synthase gene. The P450 gene family is responsible for a number of physiological changes indispensable to normal functioning of plants [43], while SPDSY 1 is

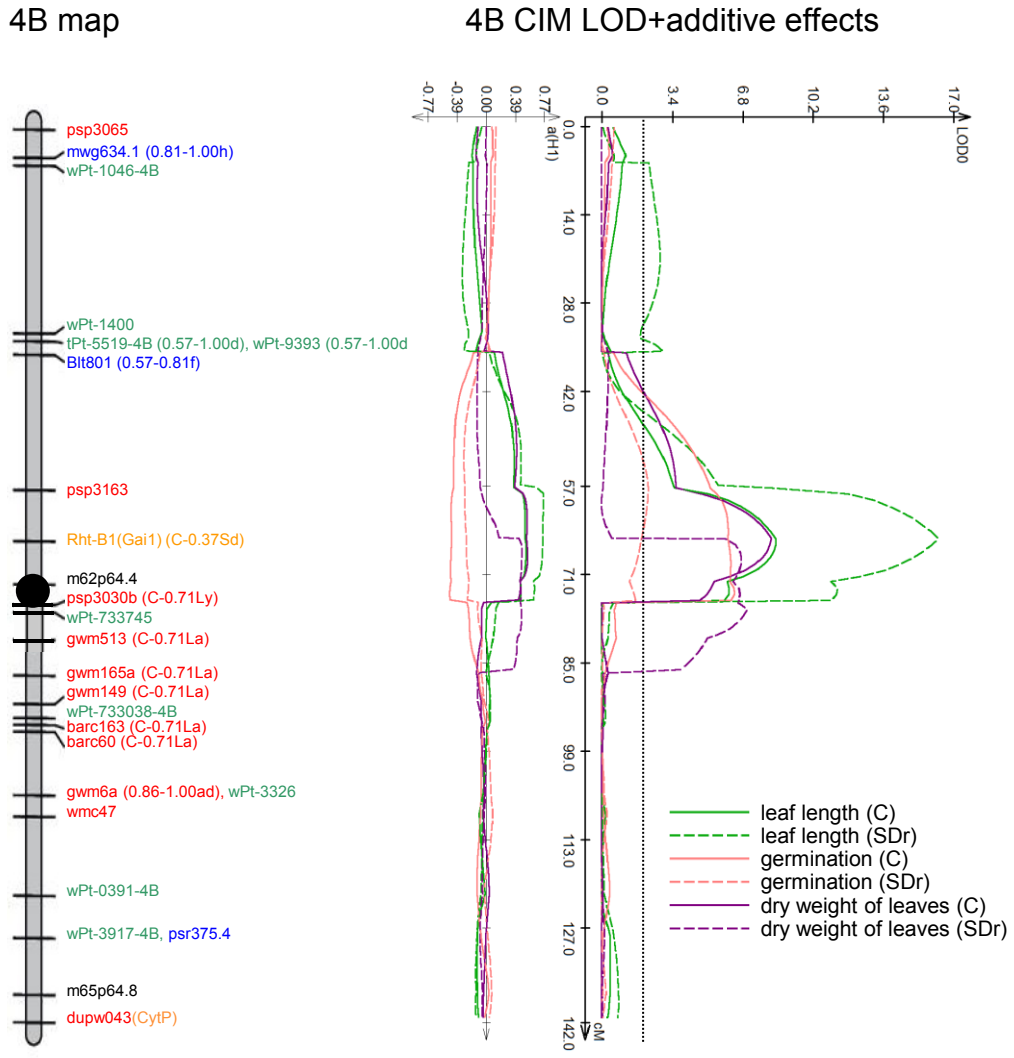

Figure 1. Maps for chromosome 4B, divided into the genetic map (left) and CIM LOD and additive traces for traits (right). On the genetic map marker (left) type is identified by colour: AFLPs - black, RFLPs - blue, SSRs - red, known-function markers - orange, DArTs - green. Explanations for the genetic map are as described previously by Czyczyło-Mysza et al. 2013. The right-hand map shows the CIM LOD output only for those traits giving a LOD maximum approaching 2.0 or more. The dotted black line indicates a LOD score of 2.0. Underneath the LOD traces, the additive effects are shown as fractions of ±1 S.D. Additive effects show the direction of the QTL: positive where the Chinese Spring allele, and negative where the SQ1 allele increased the trait.

essential to the proper development of the embryo [44]. In another study mapping QTLs [45] associated with the grain germination process, the viability of grain and the early seedling development on D genome, 20 QTLs were located on chromosomes 1D, 2D, 4D, 5D, and 7D. Most of the QTLs related to germination *sensu stricto* were located on chromosome 1DS, between *gwm1291* and *gwm337* markers. In our study, only one QTL for leaf length was located, on chromosome 1D in C plants. According to [45], the region on chromosome 7DS associated with the *gwm1002* marker is responsible for the control of the normal development of seedlings, whereas QTLs associated with seed vigour were located on chromosome 5DL (near *gwm960* marker). In their study, the QTLs associated with seed longevity coincided with the QTLs associated with germination and seed vigour, and were present on chromosomes 1D and 5D. However, the QTLs associated with seedling growth were located on chromosomes 4D and 5D. In our study, the QTLs for leaf length in SDr and C plants were located on chromosome 5D whereas no QTLs were mapped on chromosome 7D. Nevertheless, the QTLs identified on chromosomes 1D and 5D were also affecting the leaf length and the length and dry weight of the root. In our

experiment, the most statistically significant QTL groups for the examined traits were identified in both SD and C plants in the region of chromosome 4B (mostly near the *RHT-B1* marker). They were associated with the parameter of germination capacity after 24 h, and with the length and dry weight of the leaf. In our previous studies, many QTLs were identified in this region both under drought stress and control conditions in the same mapping population. These QTLs influenced such parameters as chlorophyll fluorescence, content of photosynthetic pigments, biomass and thousand grain mass [23-25,46 and unpublished data]. In this region of chromosome 4B, several other authors also located QTLs for various agronomic traits in wheat [23,47-50].

In summary, in our study the largest number of QTLs was found in the B genome (23), followed by D (9) and A (7) genomes. No QTLs were detected on chromosomes 3A, 4A, 6A, and 7D. Many of the QTLs identified were found in both C and SDr plants. At this stage of research, the mutual relationships are difficult to determine. The results presented in our study indicate the complex and polygenic nature of germination.

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