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Authors

Arif, Mian Abdur Rehman
Shokat, Sajid
Plieske, Jörg
et al.

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A SNP-based genetic dissection of versatile traits in bread wheat (*Triticum aestivum* L.)

Mian Abdur Rehman Arif[1,*], Sajid Shokat[1], Jörg Plieske[2], Martin Ganal[2], Ulrike Lohwasser[3], Yuriy V. Chesnokov[4], Nataliya V. Kocherina[4], Pawan Kulwal[5], Neeraj Kumar[6], Patrick E. McGuire[7], Mark E. Sorrells[8], Calvin O. Qualset[7] and Andreas Börner[3,*]

[1]*Wheat Breeding Group, Plant Breeding and Genetics Division, Nuclear Institute for Agriculture and Biology (NIAB), Faisalabad, Pakistan,*

[2]*SGS Institut Fresenius GmbH TraitGenetics Section, Am Schwabeplan 1b, Stadt Seeland, OT Gatersleben 06466, Germany,*

[3]*Resources Genetics and Reproduction Group, Leibniz Institute of Plant Genetics and Crop Plant Research, Corrensstr. 3, Seeland, OT Gatersleben 06466, Germany,*

[4]*Laboratory of Ecological Genetics and Plant Breeding, Agrophysical Research Institute, Grazhdanskiy pr. 14, St. Petersburg 195220, Russia,*

[5]*State Level Biotechnology Centre, Mahatma Phule Krishi Vidyapeeth, Rahuri, Ahmednagar, Maharashtra 413 722, India,*

[6]*Department of Plant and Environmental Sciences, Clemson University, 100C Biosystems Research Complex 105 Collings Street, Clemson, SC 29634-0141, USA,*

[7]*Plant Sciences Department, University of California, Mail Stop 3, One Shields Avenue, Davis, CA 95616, USA, and*

[8]*Department of Plant Breeding and Genetics, Cornell University, Ithaca, NY 14853, USA*

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*For correspondence (e-mail boerner@ipk-gatersleben.de; m.a.rehman.arif@gmail.com).

SUMMARY

The continuous increase in global population prompts increased wheat production. Future wheat (*Triticum aestivum* L.) breeding will heavily rely on dissecting molecular and genetic bases of wheat yield and related traits which is possible through the discovery of quantitative trait loci (QTLs) in constructed populations, such as recombinant inbred lines (RILs). Here, we present an evaluation of 92 RILs in a bi-parental RIL mapping population (the International Triticeae Mapping Initiative Mapping Population [ITMI/MP]) using newly generated phenotypic data in 3-year experiments (2015), older phenotypic data (1997–2009), and newly created single nucleotide polymorphism (SNP) marker data based on 92 of the original RILs to search for novel and stable QTLs. Our analyses of more than 15 unique traits observed in multiple experiments included analyses of 46 traits in three environments in the USA, 69 traits in eight environments in Germany, 149 traits in 10 environments in Russia, and 28 traits in four environments in India (292 traits in 25 environments) with 7584 SNPs (292 × 7584 = 2 214 528 data points). A total of 874 QTLs were detected with limit of detection (LOD) scores of 2.01–3.0 and 432 QTLs were detected with LOD > 3.0. Moreover, 769 QTLs could be assigned to 183 clusters based on the common markers and relative proximity of related QTLs, indicating gene-rich regions throughout the A, B, and D genomes of common wheat. This upgraded genotype–phenotype information of ITMI/MP can assist breeders and geneticists who can make crosses with suitable RILs to improve or investigate traits of interest.

Keywords: wheat, single nucleotide polymorphisms, genetic mapping, grain yield, agronomic traits, candidate genes.

INTRODUCTION

Global food security concerns make wheat (*Triticum aestivum* L.) the most important food crop of the world (Curtis and Halford, 2014). Its cultivated area has grown at a rate of 1.18% annually from 2007 to 2016. Since the need for food in developing countries will increase by 60% before 2050 (Curtis, 2002), future wheat breeding will heavily rely on dissecting the molecular and genetic bases of wheat grain yield and related traits, which remains a challenge due to the polygenic nature of traits, the strong influence of the environment, the complex relationships among traits contributing to yield, and the polyploid nature of wheat itself (Li et al., 2015; Wu et al., 2012).

The development of linkage maps and subsequent phenotyping of the targeted populations, however, has made possible the discovery of quantitative trait loci (QTLs) through the use of molecular genetic mapping techniques (Börner et al., 2002). A prerequisite to genetic mapping is the generation of populations (McCough and Doerge, 1995; Paterson, 1996) such as F_2, backcrosses, recombinant inbred lines (RILs), or doubled haploids (DHs). Among them, RILs require several plant generations to develop but they are nearly homozygous or 'true-breeding' lines that can be multiplied and reproduced with little or no genetic changes occurring (Collard et al., 2005). This allows conducting replicated trials across different locations/environments and years, thus, representing 'eternal' resources for QTL mapping. In addition, the population may be shared among research institutes for either linkage analysis (Paterson, 1996; Young, 1994) or genetic mapping of quantitative traits.

A bi-parental RIL mapping population known as the International Triticeae Mapping Initiative Mapping Population (ITMI/MP) was used in this investigation to detect and map QTLs for more than 15 traits that were repeatedly observed in 25 multi-country field trials. ITMI was established in the early 1990s to facilitate and coordinate the development of genomic maps of wheat. ITMI/MP was developed and used worldwide for joint mapping of restriction fragment length polymorphisms and/or microsatellite markers (Nelson et al., 1995a,b,c). The first simple sequence repeat-based genetic map of wheat was created using this population (Röder et al., 1998) and since then, many additional microsatellites have been mapped. ITMI/MP has been used extensively for genetic studies for a wide range of traits, for example, to identify and map loci linked to (i) seed traits such as kernel hardness (Sourdille et al., 1996), seed dormancy (Lohwasser et al., 2005), and longevity (Agacka-Mołdoch et al., 2016; Arif et al., 2012); (ii) resistance to diseases and pests such as tan spot (Faris et al., 1997; Friesen and Faris, 2004), Karnal bunt (Nelson et al., 1998), Fusarium head blight (Anderson, 1998), *Septoria tritici* blotch (Simón et al., 2004), greenbug (Weng et al., 2005), and rust diseases (Kumar et al., 2013); (iii) tolerance to excess copper stress (Balint et al., 2007); (iv) environmental stresses, such as osmotic stress (Landjeva et al., 2008); (v) end-use quality (Nelson et al., 2006); and (vi) many agronomic traits (Börner et al., 2002; Chesnokov et al., 2013; Kumar et al., 2007).

In any QTL mapping study, proper genome coverage is a prerequisite to fully uncover the genetic makeup of any given character in a mapping population or germplasm collection. This is evident from a recent report where an increased genome coverage from 2134 (spring wheat) and 840 (winter wheat) Diversity Arrays Technology markers (Arif et al., 2012, 2017) to 9804 and 11 139 single nucleotide polymorphisms (SNPs), respectively, led to the identification of 13 potentially novel QTLs for seed longevity (Arif and Börner, 2020). Hence, it is possible to deepen our insight into trait architecture by increasing the number of markers. This study, therefore, was initiated to enhance our understanding of the genetic architecture of yield and other agronomic traits and disease resistance in ITMI/MP, one of the most highly investigated bi-parental mapping populations. Phenotypic data from 92 ITMI/MP RILS obtained from field trials in Germany, India, Russia, and the USA (Börner et al., 2002; Chesnokov et al., 2013; Kumar et al., 2007) were examined with newly created SNP marker data to search for potential novel and/or stable QTLs, to search for possible candidate genes located around the detected QTLs, and to examine genetic aspects of trait associations.

RESULTS

US experiments

Among the 16 traits evaluated in three US environments, viz. Tulelake-2015–2017 (Tlk15, Tlk16, and Tlk17), values for heading (Hd), test weight (Tw), yield (Yd), seeds per spike (Sps), fertile spikelets per spike (F_spklt), and sterile spikelets per spike (S_spklt) were higher for Opata85 (in two or more environments), whereas trait values for other traits including days to maturity (DMT), grain filling duration (GFD), Ht (height), lodging (Ld), non-threshability index (NT_Ind), spike length (Sl), seed weight per spike (Swps), thousand kernel weight (Tkw), seeds per spikelet (Sespklt), and spike density (Dens) were higher for synthetic parent (M6).

Range and mean $\pm$ standard error (SE) of traits measured in RILs alongside their parents are provided in Table 1, whereas the frequency distributions for Tlk15, Tlk16, and Tlk17 in the form of overlaid histograms are provided in Figure 1(a–p). Among RILs, three traits, viz. Hd, Sps, and Swps (mean values of 64.35 $\pm$ 0.27, 48.9 $\pm$ 0.55, and 2.89 $\pm$ 0.03, respectively), had the highest values in Tlk15. Likewise, NT_Ind, Tw, and Dens (mean values of 7.09 $\pm$ 0.65, 59.40 $\pm$ 1.93, and 5.93 $\pm$ 0.05, respectively) had the highest values in Tlk17. The other nine traits, viz. DMT (mean = 109.22 $\pm$ 0.2), GFD (mean = 64.78 $\pm$ 0.29), Ht (mean = 109.76 $\pm$ 0.64), Ld (mean = 67.91 $\pm$ 5.76), Yd (mean = 5802.82 $\pm$ 86.27), Sl (mean = 105.25 $\pm$ 0.66), F_spklt (mean = 17.73 $\pm$ 0.23), Tkw (mean = 46.74 $\pm$ 0.41), and Sespklt (mean = 2.74 $\pm$ 0.02), were highest in Tlk16, and S_spklt was the same in Tlk16 and Tlk17 (means of 0.71 $\pm$ 0.05 and 0.71 $\pm$ 0.04, respectively). A three-way analysis of varince (ANOVA) revealed significant genotypic differences for all traits except Hd at $P < 0.001$. Year or environment had a significant impact on Hd, DMT, GFD, Ld, Tw, Yd, NT_Ind, Sps, Swps, Tkw, and Sespklt at $P < 0.001$, whereas Ht, Sl, F_spklt, S_spklt, and Dens remained uninfluenced by the environment. The year $\times$ genotype (Y $\times$ G) interaction was significant for Tw and NT_Ind at $P < 0.001$. Likewise, the Y $\times$ G interaction was

Table 1 Analysis of variance, mean, and standard errors of ITMI populations evaluated for yield and yield-related traits over 3 years in US environments

	Environment														
	Tlk15				Tlk16				Tlk17				*P*-value		
Trait	M6	Opata85	Range	Mean	M6	Opata85	Range	Mean	M6	Opata85	Range	Mean	P_Y	P_G	$P_Y * _G$
Heading (Hd)	61.25	63.16	56–82	64.35 ± 0.27	41.5	45.33	29–57	44.35 ± 0.3	59	58.85	54–76	60.1 ± 0.24	***	NS	NS
Days to maturity (DMT)	NA	NA	NA	NA	109.5	108	97–120	109.22 ± 0.2	109	101.5	99–124	103.9 ± 0.29	***	***	NS
Grain filling duration (GFD)	NA	NA	NA	NA	68	62.66	51–82	64.78 ± 0.29	50	42.66	33–58	43.92 ± 0.28	***	***	NS
Height (Ht)	104.75	92.83	65–129	102.37 ± 0.63	107.5	102.83	70–135	109.76 ± 0.64	104.5	86.8	68–123	101.63 ± 0.57	NS	***	NS
Lodging (Ld)	72.5	0.83	0–100	53.37 ± 2.65	77.5	63.33	0–100	67.91 ± 5.76	42.5	0	0–100	34.29 ± 2.24	***	***	**,**
Test weight (Tw)	55.45	59.9	47.4–61.9	56.51 ± 0.17	56.5	60.9	50–62.4	58.19 ± 0.15	57.9	59.9	56.4–66.4	59.4 ± 1.93	***	***	***
Yield (Yd)	3518.75	5111.83	885–6639	3772.82 ± 64.89	5462	8264	1773–9316	5802.82 ± 86.27	5094.3	6245.5	2430–7567	5619.8 ± 73.17	***	***	NS
Non-threshability index (NT_Ind)	5.735	0	0–41.1	5.52 ± 0.56	2.1	0.3	0.1–57.4	4.05 ± 0.43	5.63	0.23	0.1–46	7.09 ± 0.65	***	***	***
Spike length (Sl)	101.5	93.66	74–135.5	102.96 ± 0.65	110.25	93.08	55–134.5	105.25 ± 0.66	105.88	90.5	73.5–133	103.35 ± 0.66	NS	***	NS
Fertile spikelets per spike (F_spklt)	13.5	18.16	12.5–22.5	16.96 ± 0.11	17.625	17.25	13.5–27.5	17.73 ± 0.23	16.13	16.67	13.5–21.5	16.89 ± 0.11	NS	***	NS
Sterile spikelets per spike (S_spklt)	0.75	0.91	0–2	0.61 ± 0.04	0.875	1.16	0–10.5	0.71 ± 0.05	1	0.75	0–2.5	0.71 ± 0.04	NS	***	NS
Seeds per spike (Sps)	41.25	54.91	24–73	48.9 ± 0.55	48.25	46.25	32.5–68.5	48.19 ± 0.51	40.63	45.91	24–67	45.6 ± 0.45	***	***	**,**
Seed weight per spike (Swps)	2.145	1.9	1.44–4.28	2.89 ± 0.03	2.27	1.87	1.42–3.5	2.23 ± 0.03	1.96	1.87	1.2–2.9	2.11 ± 0.02	***	***	**,**
Thousand kernel weight (Tkw)	52.33	34.5	21.8–57.8	42.82 ± 0.43	47.73	40.84	24–63.5	46.74 ± 0.41	50.58	37.08	31.95–58.65	46.35 ± 0.33	***	***	NS
Seeds per spikelet (Sespklt)	3.05	3.02	0.82–3.41	2.08 ± 0.03	2.71	2.69	1.814–3.81	2.74 ± 0.02	2.49	2.75	1.7–3.7	2.7 ± 0.02	***	***	*,*
Spike density (Dens)	7.43	4.92	3.86–8.7	5.9 ± 0.05	6.016	5.08	3.01–7.8	5.8 ± 0.04	6.3	5.23	3.98–7.8	5.93 ± 0.05	NS	***	*,*

ITMI, International Triticeae Mapping Initiative; NS, non-significant; P_Y, *P*-value of the year effect; P_G, *P*-value of the genotype effect; $P_Y * G$, *P*-value of the interaction of genotypes by year.
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

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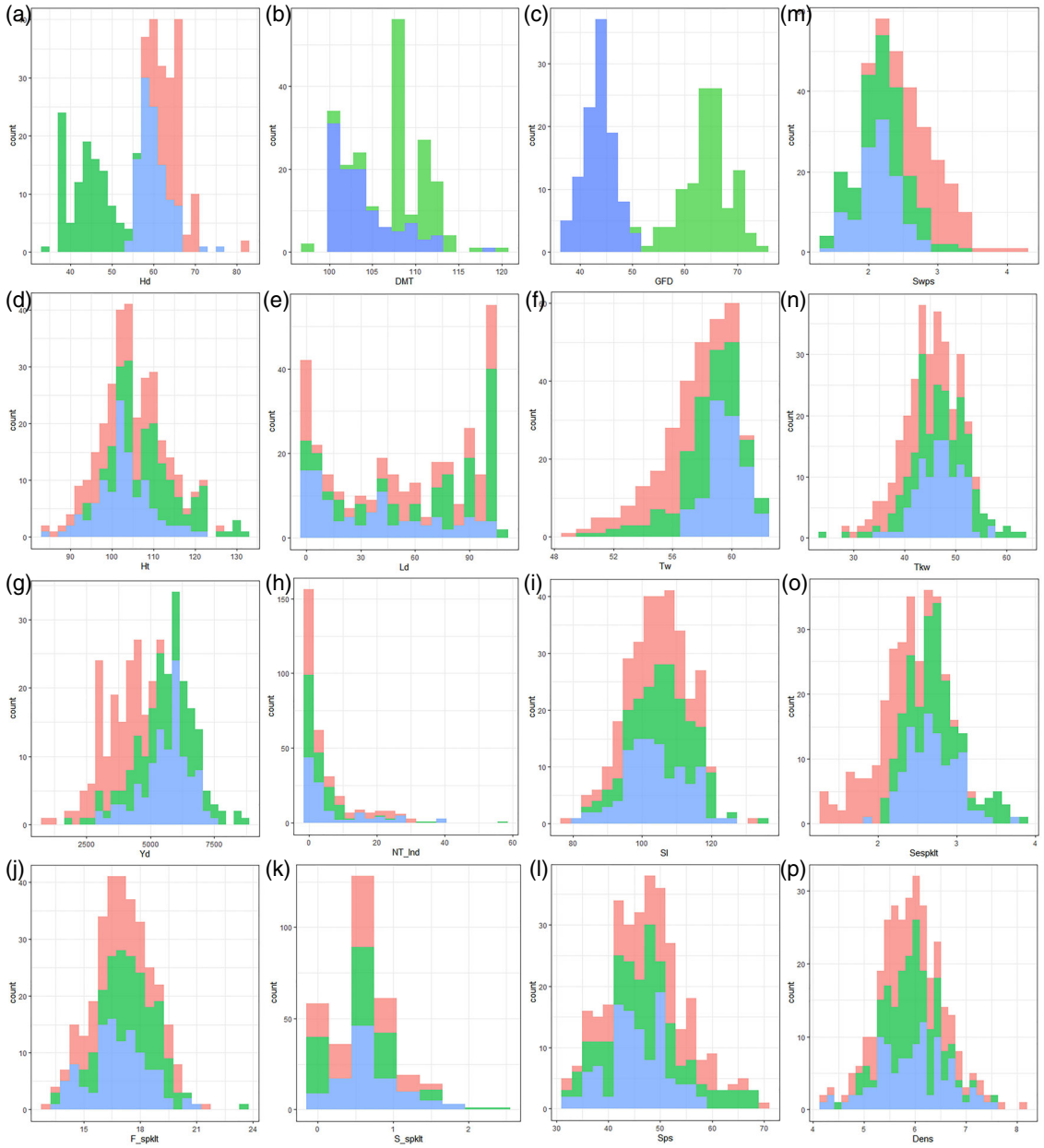

Figure 1. Frequency distribution in the form of stacked histograms of (a) heading time (Hd), (b) days to maturity (DMT), (c) grain filling duration (GFD), (d) height (Ht), (e) lodging (Ld), (f) test weight (Tw), (g) yield (Yd), (h) non-threshability index (NT_Ind), (i) spike length (SI), (j) fertile spikelets per spike (F_spklt), (k) sterile spikelets (Sr_spklt), (l) seeds per spike (Sps), (m) seed weight per spike (Swps), (n) thousand kernel weight (Tkw), (o) seeds per spikelet (Seed_spklt), and (p) spike density (Dens) in Tlk15 (red), Tlk16 (green), and Tlk17 (blue) environments.

significant for Ld, Sps, and Swps at $P < 0.01$ and for Sespklt and Dens at $P < 0.05$. This interaction, however, was insignificant for Hd, DMT, GFD, Ht, Yd, SI, Tkw, F_spklt, and S_spklt (Table 1).

The highest correlation among the same traits in different environments was observed for NT_Ind (r^2 = 0.62–0.79), followed by Dens (r^2 = 0.52–0.78) and Ht (r^2 = 0.66–0.74), whereas the lowest correlation was observed for Swps (r^2 = 0.17–0.26), followed by S_spklt (r^2 = 0.21–0.24). GFD was not correlated at all, and Yd (r^2 = 0.39–0.41) and Tw (r^2 = 0.44–0.57) showed moderate correlations. Correlation coefficients between different traits of the same experiment indicated that spike-related traits (SI, Sps, Swps, Tkw, Seed_spklt, and Dens) were generally strongly positively correlated, except Tkw and Sps, Tkw and F_spklt, and F_spklt and Dens, which were moderately negatively correlated with each other (Table S1; Figure S1). Interestingly, SI was also moderately negatively correlated with both Yd and Tw. Tw, however, was positively correlated only with GFD and Yd (Table 2).

Table 2 Correlation among same traits measured in different environments in US experiments

Trait	Tlk15 and Tlk16	Tlk15 and Tlk17	Tlk16 and Tlk17
Heading (Hd)	0.43**	0.57**	0.57**
Days to maturity (DMT)	0.56**	NA	NA
Grain filling duration (GFD)	–	NA	NA
Height (Ht)	0.66**	0.74**	0.7**
Lodging (Ld)	–	0.47**	0.16*
Test weight (Tw)	0.57**	0.44**	0.44**
Yield (Yd)	0.39**	0.41**	0.39**
Non-threshability index (NT_Ind)	0.62**	0.79**	0.72**
Spike length (Sl)	0.56**	0.68**	0.51**
Fertile spikelets per spike (F_spklt)	0.54**	0.7*	0.47**
Sterile spikelets per spike (S_spklt)	0.24**	0.21*	–
Seeds per spike (Sps)	0.46**	0.47**	0.41**
Seed weight per spike (Swps)	0.17*	0.2*	0.26**
Thousand kernel weight (Tkw)	0.44**	0.53**	0.43**
Seeds per spikelet (Sespklt)	0.16*	0.21*	0.74**
Spike density (Dens)	0.57**	0.78**	0.52**

–: no correlation.
NA, not applicable.
*$P < 0.05$.
**$P < 0.01$.

German dataset

Taken together, data of 69 traits collected across eight environments from Germany exhibited a wide range of variation (Table S2) for quantitative traits, viz. Sl, Hd, flowering time (Flt), Swps, Ht, and thousand kernel weight (Tkw). Performance of three common traits (Sl, Swps, and Tkw) indicated that the population performed better in the Hohenthurm-1999 (HFS99) environment, where mean Sl and Tkw were highest (means of 10.79 $\pm$ 2.23 and 50.07 $\pm$ 3.52, respectively). Swps was highest (mean = 3.56 $\pm$ 1.70) in the Silstedt-1999 (SFS99) environment. Range and mean $\pm$ SE of the traits are provided in Table S2. Other details of these data are given in (Chesnokov et al., 2013).

Russian dataset

Although altogether data of 149 traits from 10 different environments were used, only five traits (Flt, Ht, Sl, Sps, and Tkw) were common to all environments (Table S3). Among common traits, the lowest and highest Flt values were observed in the Mikhnevo-2005 (Moscow District) (Mo05) and Mikhnevo-2008 (Mo08) environments, respectively (means of 24.06 $\pm$ 0.58 and 67.9 $\pm$ 1.86, respectively). Sl (mean = 41.44 $\pm$ 1.14) and Sps (mean = 9.52 $\pm$ 0.18) were highest in the Pushkin-2009 (suburb of St. Petersburg) (Pu09) environment. Likewise, Tkw was highest in the Pushkin-2005 (Pu05) environment (mean = 54.19 $\pm$ 0.55). Further details of these data are available elsewhere (Chesnokov et al., 2013).

Indian dataset

Phenotypic distributions of the seven traits (Table S4) recorded in the Indian environments indicate that the RILs performed better in Meerut-2001 (M01) as compared to the Meeut-2002 (M02), Pantnagar-2002 (P02), and Ludhiana-2002 (L02) environments since biological yield (BY), grain yield (Yd), and fertile spikelets per spike (F_spklt) were highest (means of 50.1 $\pm$ 1.59, 12.63 $\pm$ 0.48, and 20.64 $\pm$ 0.3, respectively) in M01. Sl, tillers per plant (TPP), and Sps were highest (means of 11.61 $\pm$ 0.16, 10.41 $\pm$ 0.3, and 48.01 $\pm$ 0.88) in M02, whereas the harvest index (HI) was highest (mean = 30.84 $\pm$ 0.86) in the L02 environment. Other details are available in (Kumar et al., 2007).

Genetic map and characteristics

The genetic map created from the ITMI/MP with the 20K array is comprised of 7584 SNP mapped markers (Figures S2a,b and S3) covering a distance of 7743.56 cM (Table S5) with an average density of 1.02 SNPs/cM. The number of SNPs mapped to each chromosome ranged between 25 (chromosome 4D) and 763 (chromosome 2B), resulting in different chromosome lengths. For example, the shortest and longest chromosomes were chromosomes 1A (216.3 cM) and 7A (739.86 cM), respectively (Figure 2). On the other hand, the densest chromosome was chromosome 2B (0.46 SNPs/cM), whereas the least dense was chromosome 4D (10.17 SNPs/cM). Among homoeologous groups, group 2 chromosomes were covered the most, with 1366 SNPs encompassing a distance of 1150.2 cM (0.84 SNP/cM), whereas the lowest number of SNPs (619) were mapped to group 4 chromosomes, covering a distance of 1239.7 cM (2.00 SNPs/cM). From a genomic point of view, 3858 SNPs (50.87%) were mapped to the B genome at an average density of 0.63 SNPs/cM, making it the densest genome covered. The number of SNPs mapped to the A genome was 3010 (39.68%), at a density of 1.02 SNP/cM. The D genome was sparsely covered (716 SNPs [9.44%]), at an SNP density of 3.09 SNP/cM).

QTL identification

QTL analysis of 46 traits recorded across three environments in the USA, 69 traits across eight environments in Germany, 149 traits across 10 environments in Russia, and 28 traits across four environments in India (a total of 292 traits in 25 environments) with 7584 SNPs (292 $\times$ 7584 = 2 214 528 data points) revealed a total of 874 QTLs, where 442 QTLs had a limit of detection (LOD) of $2 < LOD \leq 3$, and 432 QTLs had an LOD of >3 (Figure S5; Tables S6 and S7). In terms of environments, a total of 119 (83 with $2 < LOD \leq 3$ and 36 with $LOD > 3$), 247 (138 with $2 < LOD \leq 3$ and 109 with $LOD > 3$), 432 (216 with $2 < LOD \leq 3$ and 216 with $LOD > 3$), and 76 (34 with $2 < LOD \leq 3$ and 42 with $LOD > 3$) QTLs were detected in the USA, Germany, Russia, and India, respectively. No

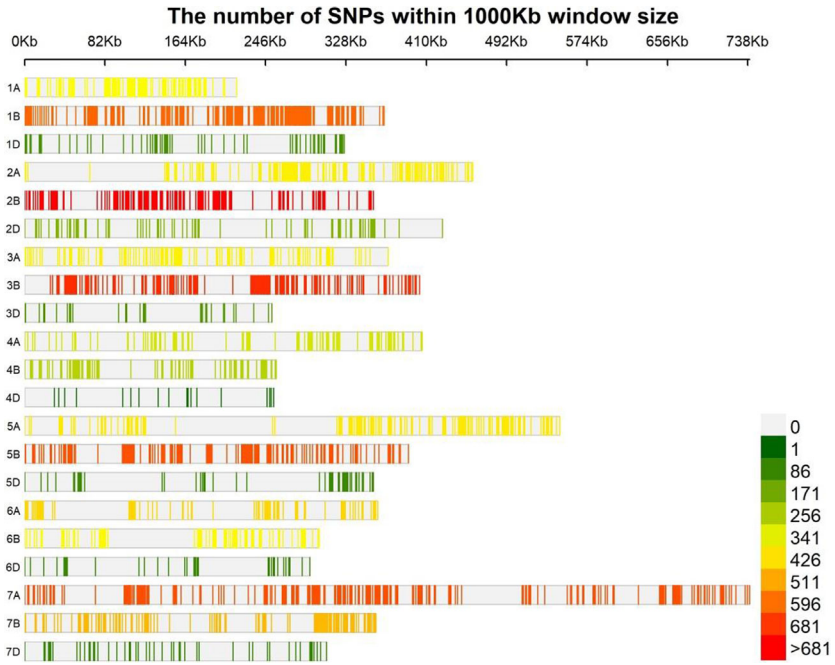

Figure 2. Density of single nucleotide polymorphisms (SNPs) per chromosome mapped in the International Triticeae Mapping Initiative (ITMI) mapping population.

QTLs, however, could be detected for five traits in the USA (F_spklt_Tlk16, GFD_Tlk17, Ht_Tlk15, Swps_Tlk16, and Tw_Tlk17), two traits in Germany (Flt_HFS98 and Gc_GFS98), 17 traits in Russia (Awn_M09, Awn_P09, Awn_S09, Hd_S09, Ht_M06, Gc_P09, GMSp_M07, GMSp_P09, KC_P09, Lwax_P07, Lwax_S09, Sespklt_M09, Sespklt_P09, Sespklt_S09, F_Spklt_M07, Pdl_M08, and Sl_P09), and three traits in India (Sps_M01, Sl_P02, and TPP_L02).

We divided the multiple traits into seven parts to reduce complexity. These included traits related to (i) awns, coloration, and waxiness (awn color [Awnc], Awn, Gc, Wax, Lwax, Swax, and kernel color [KC]), (ii) the flag leaf (Ler, Flp, Fll, and Flw), (iii) plant development and maturity (Hd, Flt, DMT, and GFD), (iv) height (Ht, Pdl, and Ld), (v) spikes and seeds in spikes (Sl, Sps, Swps, Sespklt, F_spklt, S_spklt, GMSp, Dens, and NT_Ind), (vi) yield and related traits (Yd, Tw, BY, Tkw, Hl, and TPP), and (vii) disease resistance (Pm, Lr, Yr, and Fhs).

Awns, coloration, and waxiness (Awn, Awnc, Gc, KC, Wax, Lwax, and Swax). For Awn, we discovered a total of five QTLs (including two QTLs with LOD > 3.0), whereas a total of 25 Awnc QTLs were detected (including 15 QTLs with LOD > 3.0) (Table S6). Altogether the phenotypic variance explained (PVE) by these QTLs ranged between 8–15% and 5.4–53% for Awn and Awnc QTLs, respectively. A total of 31 (including 24 QTLs with LOD > 3.0; PVE = 6–69%) and 15 QTLs (including seven QTLs with LOD > 3.0, PVE = 6–26%) were discovered for Gc and KC, respectively. Wax was controlled by 19 QTLs (including 13 QTLs with LOD > 3.0; PVE = 5.6–91.6%). Lwax was controlled by 16 QTLs (including 13 QTLs with LOD > 3.0; PVE = 6–24.5%), and Swax was controlled by 17 QTLs (including 12 QTLs with LOD > 3.0; PVE = 5.6–70.5%).

Flag leaf traits (Ler, Flp, Fll, and Flw). For Ler, we detected 11 QTLs (including three QTLs with LOD > 3.0; PVE = 6–15.7%) whereas Fll, Flp, and Flw were controlled by 15 (including two QTLs with LOD > 3.0; PVE = 6–15.8%), 16 (including 10 QTLs with LOD > 3.0; PVE = 6–27.3%), and 21 QTLs (including 12 QTLs with LOD > 3.0, PVE = 5.7–34.8%), respectively.

Plant development and maturity (Hd, Flt, DMT, and GFD). A total of 51 (including 32 QTLs with LOD > 3.0; PVE = 5–30%) and 58 QTLs (including 32 QTLs with LOD > 3.0; PVE = 5–51%) were discovered for Hd and Flt, respectively, whereas five QTLs were discovered for DMT (including one QTL with LOD > 3.0; PVE = 6–17%). There was also one QTL discovered for GFD (LOD = 2.49; PVE = 12%). These QTLs resided on 18 wheat chromosomes where most of them were localized to particular locations across each chromosome. These include four QTLs on chromosome 1A (109–115 cM), three QTLs on 2A (182–199 cM), 11 QTLs on 2D (74–91 cM), four QTLs on 3A (331–368 cM), four QTLs on 4A (256–307 cM), four

(38–89 cM) and 11 QTLs (497–509 cM) on 5A, four (111–130 cM) and six QTLs (349–372 cM) on 5B, 12 QTLs (216–226 cM) on 5D, three QTLs (250–264 cM) on 6D, four QTLs (0–30 cM) on 7B, and seven QTLs (17–29 cM) on 7D.

Traits related to height (Ht, Pdl, and Ld). A total of 118 QTLs were detected on all 21 wheat chromosomes for Ht (65 QTLs including 32 QTLs with LOD > 3.0), Pdl (30 QTLs including 10 QTLs with LOD > 3.0), and Ld (23 QTLs including eight QTLs with LOD > 3.0). The PVE was 5–31%, 6–21%, and 5–19% for Ht, Pdl, and Ld, respectively. There were at least four chromosomes (3A, 4A, 5A, and 5B) that carried four to five Ht QTLs, whereas chromosome 4B carried as many as 10 Ht QTLs detected in all the three environments in which Ht was recorded.

Spike-related traits (Sl, Sps, Swps, Sespklt, F_spklt, S_spklt, GMSp, Dens, and NT_Ind). There were 90 QTLs discovered for Sl where 45 QTLs had an LOD of >3.0 that explained 6–30% of the phenotypic variation (PV). The 44 QTLs discovered for Sps (including 19 QTLs with LOD > 3.0) explained 6–27% of the PV. In addition, 40 QTLs (including 17 QTLs with LOD > 3.0) for Swps were responsible for 6–30% of the PV. A total of 14 QTLs (including four QTLs with LOD > 3.0) were discovered for Sespklt that explained 5–26% of the PV. F_spklt and S_spklt were controlled by 39 (including 17 QTLs with LOD > 3.0; PVE = 6–35%) and three QTLs (LOD = 2.21–2.30; PVE = 10–11%), respectively. Furthermore, 26 QTLs were discovered for NT_Ind, among which 11 had an LOD of >3.0 explaining altogether 5–29% of the PV.

Yield and related traits (Yd, Tw, BY, TPP, Tkw, and HI). Yd was controlled by a total of 20 QTLs (including nine QTLs with LOD > 3.0; PVE = 5–36%) whereas BY was controlled by a total of eight (including two QTLs with LOD > 3.0; PVE = 7–19%) QTLs. In addition, 43 QTLs were discovered for Tkw (including 10 QTLs with LOD > 3.0; PVE = 7–22%). For TPP, we discovered seven QTLs where five QTLs had LOD > 3.0 explaining 7–19% of the PV. In addition, a total of seven (including six QTLs with LOD > 3.0; PVE = 8–46%) and two QTLs (including one QTL with LOD > 3.0, PVE = 10–15%) were discovered for HI and Tw, respectively.

Disease resistance traits (Pm, Lr, Yr, and Fhs). We discovered a total of 83 QTLs linked to various diseases. Among them, the highest number of QTLs was discovered for Pm (52 QTLs including 32 QTLs with LOD > 3.0) that explained 6–24% of the PV, followed by Lr (19 QTLs including seven QTLs with LOD > 3.0) responsible for 5–23.5% of the PV. Furthermore, seven (including five QTLs with LOD > 3.0) and five QTLs (including four QTLs with LOD > 3.0) were discovered for Yr and Fhs, respectively, where the total PVE was 5–73% (Yr) and 6–16% (Fhs).

QTL distribution and novelty

Considering all the QTLs, the highest and lowest numbers were detected on chromosomes 2D (100 QTLs with 72 QTLs with LOD > 3) and 4D (12 QTLs with three QTLs with LOD > 3), respectively. Among homoeologous groups, the highest numbers of QTLs were located on group 5 chromosomes (199 QTLs with 92 QTLs with LOD > 3), followed by group 2 (186 QTLs with 113 QTLs with LOD > 3). A total of 142 QTLs were detected on group 7 chromosomes including 60 QTLs with LOD > 3. This was followed by group 4 chromosomes (103 QTLs with 47 QTLs with LOD > 3.0) and group 3 chromosomes (85 QTLs with 26 QTLs with LOD > 3.0). Finally, the lowest numbers of QTLs were observed on group 1 (81 QTLs with 46 QTLs with LOD > 3.0) and group 6 chromosomes (78 QTLs with 34 QTLs with LOD > 3.0). From a genomic perspective, the highest number of QTLs were detected on the A-genome (358 QTLs with 189 QTLs with LOD > 3.0), followed by the D-genome (266 QTLs with 145 QTLs with LOD > 3.0), and the lowest number of QTLs were detected on the B-genome (250 QTLs with 98 QTLs with LOD > 3.0) (Table S8).

This study identified multifarious QTLs, which were crowded in the form of two to many QTLs at certain locations on wheat chromosomes making clusters. We assigned the 769 QTLs to 183 clusters (Table S7) based on the common markers and the relative proximity of related QTLs to each other on the wheat chromosomes, where the number of clusters varied from three (chromosome 4D) to 19 (chromosome 7A) on an individual chromosome (Figure S4). The other 105 QTLs were regarded as solitary QTLs because they did not share SNPs or closeness with other loci.

Comparing the present study with (Börner et al., 2002), 174 QTLs (70.44% of the total) in German environments were novel, that is, not detected by the authors, where 89 QTLs had $2 < \text{LOD} \leq 3$ and 85 QTLs had an LOD of >3 (Figure S5). Among the QTLs detected in Russian environments, 357 QTLs (82.63% of the total) were not reported earlier (Chesnokov et al., 2013) but the remaining 76 were common. However, 128 of the 357 unreported QTLs had $2 < \text{LOD} \leq 2.5$ and were hence not reported in (Chesnokov et al., 2013), so the novel QTLs account for $(76 + 128)/432 \times 100\% = 47.22\%$. Of the total QTLs detected in Indian environments, 44 QTLs (57.89%) are potentially novel (Table S6).

DISCUSSION

To meet the impending demand to feed the world, the yield potential of wheat must be enhanced by manipulating QTLs/genes controlling traits contributing to yield.

Grain yield is controlled by large numbers of QTLs/genes with low heritability (Akram et al., 2020) and high genotype × environment interactions. To dissect these complex traits, the phenotypic evaluation of a wide range of traits in diverse environments can lead to an inside view of their genetic control. In addition, high-density genetic maps and phenotypic data can serve as resources to identify the genetic loci controlling traits contributing to yield. In the present study, we genetically dissected a large number of traits (292 traits) evaluated in four countries and three continents over a period of 20 years using ITMI/MP, which was genotyped with 7584 high-quality SNPs.

Phenotypic variation

The RILs performed differently for all the traits investigated in different environments. A continuous variation and transgressive segregation were evident (Figure 1a–p; Table 1). Moreover, genotypes differed significantly for all the traits except Hd, whereas environment significantly influenced all traits except Ht, Sl, F_spklt, S_spklt, and Dens. Moreover, the genotype × environment interaction was significant for Ld, Tw, NT_Ind, Sps, Swps, Sespklt, and Dens, evidencing that these traits and the environments to which they are exposed strongly interplay. The same trend was witnessed in German (Börner et al., 2002), Russian (Chesnokov et al., 2013), and Indian (Kumar et al., 2007) datasets. This variation and segregation were the key to the identification of 874 QTLs linked to the 266 traits investigated in 25 different environments, implying that the genetic basis of most of the important traits in this population is complicated.

In the US experiments, RILs performed better at Tlk16 than Tlk15 and Tlk17, as nine traits (DMT, GFD, Ht, Ld, Yd, Sl, F_spktl, Tkw, and Sespklt) were highest in Tlk16. This superior performance of Tlk16 over both Tlk15 and Tlk17 could be attributed to prolonged DMT and GFD (Hd in Tlk16 > Hd in Tlk15 and Tlk17), beside other advantages, as there was ample time for important constituents to move, be part of the grains, and add to the final yield (Arif et al., 2020; Bennett et al., 2012). Final yield was positively correlated with Tw and Tkw (R^2 = 0.47 and 0.18, respectively) and negatively correlated with Hd, DMT, NT_Ind, Sl, and F_spklt (R^2 = −0.33, −0.21, −0.36, −0.19, and −0.14, respectively), indicating a complex control of yield (Table S1).

Awns, coloration, and waxiness (Awn, Awnc, Gc, KC, Wax, Lwax, and Swax). QTLs linked to Awnc have been reported to be located on group 1 chromosomes in addition to chromosomes 2D, 5D, and 7D (Börner et al., 2002), whereas new QTLs were detected on chromosomes 2A, 3B, 4A, 5A (three QTLs), 6D, 7A (three QTLs), and 7B. Likewise, QTLs linked to awn color have been reported to be located only on chromosome 6B by Chesnokov et al. (2013), whereas in addition to 6B, we discovered five other awn color QTLs (detected in different environments) on chromosomes 3B (three), 2A (one), and 4A (one). Three complementary genes (*Bla1*, *Bla2*, and *Bla3*) on chromosomes 1AS, 1BS, and 1DS are known to control awn color (Panin and Netsvetaev, 1986), whereas four variants were detected for awn color in Turkish germplasm (Sönmezoğlu et al., 2012). In addition, Sheoran et al. (2019) have reported chromosome 1B as a site for Awnc QTLs. However, we conclude that awn color may be influenced by more loci than previously reported.

QTLs linked to Gc on the distal part of the short arm of chromosome 1D have been reported earlier (Börner et al., 2002; Chesnokov et al., 2013). We, however, identified a cluster (cluster C-1D.6) located on the distal part of the long arm of chromosome 1D that carried seven Gc QTLs detected in as many environments. Moreover, only chromosome 3B has been reported to carry a Gc QTL (Chesnokov et al., 2013). It is well known that Gc is controlled by a set of three genes, viz. *Rg-A1*, *Rg-B1*, and *Rg-D1*, located on homoeologous group 1 chromosomes (Khlestkina et al., 2006), but the inheritance of the trait seems to be more complex. QTLs were described on chromosomes 2D and 6B and group 5 chromosomes (Börner et al., 2002). In our study, QTLs for Gc have been detected on chromosomes 3D, 4A, and 5A in different environments. More recently, chromosomes 4B and 5A have been reported to carry Gc QTLs (Sheoran et al., 2019).

For waxiness, ITMI/MP has been investigated earlier by Nelson et al. (1995a) and Börner et al. (2002), who reported three QTLs on chromosome 1DS and four QTLs on chromosome 2D, whereas Chesnokov et al. (2013) reported chromosome 2D to be the main site of Wax QTLs. With the new genetic data, we have detected two major clusters carrying QTLs in both German and Russian (for Wax, Lwax, and Swax) environments on chromosomes 1D (C-1D.6 carrying five QTLs) and 2D (C-2D.1 carrying 17 QTLs), respectively. According to Nelson et al. (1995a), the ITMI/MP population is segregating for the gene $W2^{l}$ located on chromosome 2DS. Hence, the C-2D.1 QTLs (Table S7) could represent that gene. Wax QTLs have been reported on chromosomes 1B, 2A, 5A, and 5B (Wang et al., 2019). In addition to the above stated QTLs, chromosomes 1B, 2A, 2B, 5A, 5B, 6B, and 7B also carried multiple QTLs for Wax, Lwax, and Swax in various environments in our investigation. A more complex inheritance was already indicated by Wang et al. (2019).

KC is a complex trait in wheat, which is controlled by several genes with additive effects; many QTLs have been reported on chromosomes 3A and 7A (Parker et al., 1998), 3B, 4B, 5B, and 7A (Mares and Campbell, 2001), 1B, 4A, 4B, 6A, 7A, and 7B (Zhang et al., 2008), 1B and 7A (Zhang et al., 2009), and 2A, 3B, 5A, and 7A (Blanco et al., 2011). The homoeologous group 7 chromosomes account for up

to 50% of the PV in KC (Elouafi et al., 2001), whereas the QTLs on chromosomes 5B and 3B were responsible for 12–20% of the PV (Blanco et al., 2011; Mares and Campbell, 2001). Our results, therefore, match with those of (Blanco et al., 2011; Mares and Campbell, 2001; Zhang et al., 2008) for QTLs discovered on chromosomes 2A, 3B, 4A, and 5A. However, we did not detect the major locus reported on group 7 chromosomes as reported earlier (Elouafi et al., 2001), possibly because it was detected in durum wheat. Likewise, 3D and 6D QTLs remained undetected in aforementioned studies. Nevertheless, in addition to the 3B locus (Chesnokov et al., 2013), we detected several loci linked to KC here.

Flag leaf traits (Ler, Flp, Fll, and Flw). The uppermost three leaves and especially the flag leaf are recognized as primary sources of the photo-assimilates accumulated in the kernels (Foyer, 1987; Hirota et al., 1990; Li et al., 1998). Others reported that an estimated 50% of the total photosynthetic activity and 41–43% of the carbohydrates needed for grain filling are provided by the flag leaf (Hengyong and Junshi, 1995; Sharma et al., 2003). The amount of incident light that the leaf receives depends on leaf erectness or the flag leaf angle (Fla) (Liu et al., 2018b). Moreover, a certain plant architecture (erect leaves) may help the plants to escape diseases (Börner et al., 2002). Therefore, the morphology of the flag leaf (Fla, Fll, Flw, and erectness) may also be targeted to modify plant architecture to enhance yield by capturing more sunlight or increasing disease resistance in cereal crops (Sakamoto et al., 2006; Xue et al., 2008).

We discovered flag leaf trait QTLs on all wheat chromosomes except chromosomes 1A and 4D. On the contrary, only two major (2AS and 2DL) and two minor QTLs (5DS and 6AL) were reported before (Börner et al., 2002). Likewise, chromosomes 2A, 3A, and 3D, group 5 chromosomes, and chromosomes 6A and 6B have been reported to harbor Flp, Flw, and Fll QTLs (Chesnokov et al., 2013). Important chromosomes could be group 5 chromosomes that carried 20 flag leaf QTLs in total (nine for Flw, five for Fll, three for Flp, and three for Ler), among which 12 remained unreported by Börner et al. (2002) and Chesnokov et al. (2013). Chromosomes 5A and 5B have been reported to carry multi-environmental QTLs linked to Fla, Flw, and Fll (Wu et al., 2016) corroborating our findings. In addition, chromosome 3D carried five (four novel QTLs) and chromosome 7D carried four QTLs detected in different environments, which is an indication of the quantitative inheritance of these traits.

Plant development and maturity (Hd, Flt, DMT, and GFD). Of the 40 QTLs linked to Flt and Hd in German environments, nine have been reported earlier on chromosomes 2B, 2D, and 7D (Börner et al., 2002). Likewise, 12 of the 53 QTLs on chromosomes 5A and 5D in Russian environments have been reported by Chesnokov et al. (2013). It is well known that chromosome 5A carries the *VRN-A1* gene at approximately 90 cM (Chen et al., 2010); hence, the same gene can be suggested to be located at the site of chromosome 5A (38–89 cM) QTLs. Likewise, chromosome 5B carries the *VRN-B1* gene between 100 and 104 cM (Milec et al., 2012). The other QTLs on chromosome 2D are near to *EPS* QTLs (Lombardo et al., 2019). Moreover, a homoeology could also be suggested for the 60% of the total QTLs discovered on group 2 (25 QTLs) and group 5 chromosomes (44 QTLs). The other minor or inconsistent QTLs suggest that there is a wide variety of flowering time genes present in the ITMI/MP.

Traits related to height (Ht, Pdl, and Ld). Ht is an important consideration in the development of wheat varieties, and all 21 chromosomes carry genes that control plant height in wheat (Börner et al., 1996; Snape et al., 1977). Up to now, 24 reduced height (*Rht*) genes (*Rht1*–*Rht24*) are catalogued in wheat (McIntosh et al., 2017; Mo, 2018), where *Rht8* on chromosome arm 2DS has been extensively explored (Gasperini et al., 2012; Korzun et al., 1998). We could locate only two QTLs to chromosome 2DL, whereas the ones reported by (Börner et al., 2002) on chromosome 2DS could not be detected. Likewise, the so-called green revolution semidwarfing genes *Rht-B1* and *Rht-D1* are located on chromosomes 4BS and 4DS, respectively (Mo, 2018), and our nine QTLs on chromosomes 4B could correspond to the abovementioned *Rht-B1* gene. Börner et al. (2002) failed to detect any QTLs on chromosomes 4B and 5B because of poor marker coverage on chromosome 4B, and chromosome 5B remained completely unmapped hitherto.

As compared to the two QTLs of Pdl on chromosome 6A detected earlier (Börner et al., 2002), we detected five highly significant QTLs on chromosomes 3D, 4B, 6A, 7A, and 7B and seven significant loci on chromosomes 2B, 4B, 4D, and 5B, as well as two QTLs on chromosomes 5D and 6A, with the newly created marker data. The positions of 6A QTLs match those reported by Börner et al. (2002). Of the 18 QTLs linked to Pdl in Russian environments, only two have been reported by Chesnokov et al. (2013), providing evidence that a wide variety of genes control Pdl in wheat. Thirteen of the 30 Pdl QTLs were discovered on chromosomes 5A (five QTLs), 4A, and 5B (four QTLs each) that are known to carry height and flowering time genes (Börner et al., 2002). Moreover, 10 (one QTL each on chromosomes 2B, 3A, 3D, and 4B and two QTLs each on chromosomes 5A, 5B, and 6A) of the 30 Pdl QTLs overlapped with Ht QTLs.

Displacement of stems from their upright position is termed as lodging (Keller et al., 1999; Verma et al., 2005), which may account for a reduction in final yield of 4–20% (Briggs et al., 1999) or in some cases up to 30–40% (Easson

et al., 1993). With regard to Ld, 12 QTLs on six chromosomes and 11 QTLs on nine chromosomes were discovered in two German and three US environments. Common chromosomes to both environments were chromosomes 2A, 2D, 5A, 5B, and 5D and chromosome 5B. Our Ld QTLs were mostly independent of Ht (except on chromosome 6A). On the contrary, Verma et al. (2005) found a strong correlation between Ld and Ht. Ld QTLs on chromosomes 1B, 2A, 2D, 4A, 5B, and 7B, with peak positions at 32, 2, 100, 10, 128, and 64 cM, respectively, have been reported before (Keller et al., 1999). The two QTLs for Ld reported by Börner et al. (2002) were located on chromosomes 2D (at 31–54 cM) and 6A (at 85–90 cM). We have located three QTLs between 41 and 100 cM in both German and US environments, which is in line with the results by Börner et al. (2002). To add to it, consistent QTLs for Ld have been reported on chromosomes 4D, 6D, and 7D (Verma et al., 2005), confirming our results.

Spike-related traits (SI, Sps, Swps, SespkIt, F_spkIt, S_spkIt, GMSp, Dens, and NT_Ind). All wheat chromosomes (except 4D and 6B) carried 89 QTLs of SI (nine in US, 34 in German, 31 in Russian, and 16 in Indian environments), where 11, 10, and nine QTLs have been reported in Chesnokov et al. (2013), Börner et al. (2002), and Kumar et al. (2007) in Russian, German, and Indian environments, respectively. Of particular interest are the seven locations where QTLs from contrasting environments for SI were detected. Among them, the first one is on chromosome 4A, which has been reported to carry clusters of SI QTLs (Börner et al., 2002; Chesnokov et al., 2013; Kumar et al., 2007). Others include chromosome 1A with four QTLs at 265–273 cM, chromosome 2A with four QTLs at 190–197 cM, chromosome 2D with two QTLs at 38–42 cM, chromosome 4B with three QTLs at 29–47 cM, chromosome 5A with two QTLs at 443 cM, and chromosome 6A with five QTLs at 207–234 cM. So far, as many as 350 QTLs have been identified to control SI in many different studies (Cui et al., 2012; Faris et al., 2014; Jantasuriyarat et al., 2004; Liu et al., 2018a; Ma et al., 2007; Xie et al., 2015). Of these, a chromosome 2D locus named *HL1* has been fine-mapped elsewhere (Wu et al., 2014) and a connection with the *Rht8* allele was suggested. More recently, another major QTL (*QSpl.nau-7D*) linked to SI and SpkIt was fine-mapped and designated as *HL2* (Yao et al., 2019). While we detected only two QTLs on chromosome 7D linked to SI, we speculate that the other loci, in particular those detected on chromosomes 2A and 6A, could be exploited to increase SI in future.

The 44 QTLs linked to Sps (eight in US, 24 in Russian, and 12 in Indian environments) were detected on all chromosomes except chromosomes 1D, 3D, 5A, and 6B. None overlapped in contrasting environments, although two QTLs on chromosome 2D and three QTLs on chromosome 5D overlapped in the US and Russian ones. Chromosomes 2D (with five QTLs), 3B, and 6D (each with four QTLs) could be important in future wheat breeding. Chromosome 3B has been identified as a site of Sps in previous studies (Arif et al., 2020). The 40 Swps QTLs were harbored by 16 different chromosomes (1A, 1D, 2A, 2B, 2D, 3A, 3B, 4A, 4B, 5A, 5D, 6A, 6D, 7A, 7B, and 7D), where only chromosomes 4A, 5A, 7A, and 7D carried multi-environmental QTLs. Both Sps and Swps QTLs were more related to each other than to other spike-related traits, with overlapping QTLs on chromosomes 3B, 4A, 4B, 5D, 7A, and 7D.

The 42 QTLs linked to SpkIt (F_spkIt [39 QTLs] and S_spkIt [3 QTLs]) were majorly located on groups 2, 3, 4, 5 and 7 chromosomes. Whereas chromosomes 2D and 4A carried overlapping SpkIt QTLs in Indian and Russian environments, respectively, chromosome 7A carried SpkIt QTLs detected in both Indian and Russian environments which could be used to micro-dissect SpkIt in the future. Ma et al. (2019) have identified a major and stable SpkIt QTL (*QSns.sau-2D*) at the distal part of chromosome 2DS, which mirrors our QTLs on chromosome 2D. Fourteen QTLs for SespkIt were identified on 14 different chromosomes. Eight QTLs linked to GMSp were located on chromosomes 1D, 2D (two QTLs), 4D (two QTLs), 5A, and 7B (two QTLs).

Dens QTLs were detected on chromosomes 1B, 2A, 2B (two QTLs), 2D, 3D (two QTLs), 4B (two QTLs), 5A (two QTLs), 5D, 6A, and 7B (two QTLs). In fact, the two QTLs on chromosomes 4B and 5A were at exactly the same locations (47 cM and 254–256 cM, respectively), indicating the presence of major genes. A recent study reported 24 QTLs related to Dens in eight environments on 12 chromosomes (Liu et al., 2020). More importantly, the QTL on chromosome 4B (*Q. Sd.sicau-4B.1*) detected by Liu et al. (2020) was located at 48–49 cM, whereas our Dens 4B QTLs were approximately 1 cM apart at 47–48.5 cM. Since both Liu et al. (2020) and this study were based on SNPs, we conclude that it is the same QTL and a number of candidate genes (for example *DNA-binding storekeeper protein-related transcriptional regulator*, *zinc finger protein VAR3*, *microsomal glutathione S-transferase 3*, *basic blue protein*, *protein kinase-like protein*, *regulator of Vps4 activity in the MVB pathway protein*, and *AT-rich interactive domain protein*) were proposed. Furthermore, three domestication genes, including *Q* (which controls free-threshing spike and influences plant height, spike density, rachis toughness, and spike emergence time; Faris et al., 2003; Simons et al., 2006; Sormacheva et al., 2015), *compactum* (*C*), (which controls spike density, grain size, grain shape, and grain number per spike; Johnson et al., 2008), and *sphaerococcum* (*S*) (which pleiotropically imparts dense spikes, rigid short culms, straight flag leaves, hemispherical glumes, and small spherical grains; Rao, 1977), are mapped to chromosomes 5A, 2D, and 3D, respectively (Faris et al., 2003; Johnson et al., 2008; Rao, 1977). Our Dens QTLs on chromosomes 5A, 2D, and 3D could

represent the *Q*, *C*, and *S* genes, respectively. Since moderate spike density is the default choice of breeders to breed high-yielding and disease-resistant cultivars (Liu et al., 2020), selection for the locus on chromosome 4B or 5A could be an ideal choice in that scenario.

Our major QTL on chromosome 2DS linked to NT_Ind at 52–62 cM was detected in all environments. The same locus has also been reported previously (Jantasuriyarat et al., 2004), where NT-Ind QTLs co-located with glume tenacity and rachis fragility QTLs and *Tg*, a gene for tenacious glumes, was suggested for this trait (Jantasuriyarat et al., 2004). The major QTL on chromosome 5A could correspond to the *Q* gene discussed above (Jantasuriyarat et al., 2004). A seemingly undiscovered site for minor NT_Ind genes could be chromosome 7A, which carried NT_Ind QTLs in six of the seven environments, particularly at 295–296 and 730–739 cM, which were also independent of other traits. Since modern wheat cultivars have a free-threshing habit as a result of domestication, which might cause yield loss in case of delayed harvest or altered climatic conditions, crossing schemes could be designed to incorporate NT_Ind alleles to reduce the level of threshing in the face of climate change.

Yield and related traits (Yd, Tw, BY, TPP, Tkw, and HI). Yd is a complex quantitative trait controlled by multiple genes and highly influenced by the environment (Li et al., 2018). Collectively, 30 QTLs were detected for yield (BY [8], Yd [20], and Tw [two]), corroborating the findings of Li et al. (2018). Interestingly, chromosomes 2A, 2D, 5A, 5D, and 7A carried yield QTLs detected in both US and Indian environments. In particular, on chromosome 2D, four different QTLs overlapped at 73– 87 cM (Tables S7 and S8). Likewise, Yd and Tw QTLs on chromosome 5A were at the same location (500–501 cM) and three BY and one Yd QTL resided at 277–283 cM on chromosome 6A. Moreover, 15 of the abovementioned 30 QTLs were linked with spike-related traits (Sps, SI, Spklt, and F_spklt), most notably on chromosomes 1A, 3B, 6D, 7A, and 7B, whereas those on chromosomes 2D, 5A, and 5B were embedded between Flt and Hd QTLs, indicating a connection with *EPS* (chromosome 2D), *VRN-A1* (chromosome 5A), and *VRN-B1* (chromosome 5B) genes, as stated before (Chen et al., 2010; Lombardo et al., 2019; Milec et al., 2012).

Seed or kernel traits of wheat are quantitative in nature with a strong influence from different environments that exhibit strong genotype–environment interactions (Cao et al., 2020). The 43 Tkw QTLs (seven in US and 18 each in German and Russian environments) on chromosomes 1A, 1B, 2B, 2D, 3A, 4A, 4B, 4D, 5A, and 5B and group 6 and 7 chromosomes indicate the polygenic character of the trait, which makes candidate gene identification difficult. For example, out of 17 QTLs of Tkw detected in (Li et al., 2018), only three candidate genes could be identified for QTLs on chromosomes 3B (*TaGS5*), 5AL (*isoamylase 3* gene), and 6AL (*TaTPP-6AL1*). To add to it, the polyploid nature of the wheat genome forced the use of comparative genomics to clone Tkw genes in wheat on chromosomes 4AL (*TaTGW6*; Hu et al., 2016a), 6A (*TaGW2*; Su et al., 2011), and 7A (*TaTGW-7A*; Hu et al., 2016b). Important QTLs with respect to grain weight were located on chromosomes 1A (two QTLs at 219–220 cM), 2D (two QTLs at 283–426 cM), 6A (two QTLs at 236 cM), and 7B at (two QTLs at 55–64 cM). Here, 23 of the 43 Tkw QTLs were co-located with spike-related traits such as SI, Sps, Swps, Spklt, Dens, and GMSp, whereas some others were co-located with Ht, Pdl, Hd, and other traits.

Four TPP QTLs (on chromosomes 4A, 6D, and 7A) and four HI QTLs (on chromosome 2D) have been reported before (Kumar et al., 2007), whereas those on chromosomes 1B, 2A, 3B, 5A, and 5B were novel. Mostly, the HI and TPP QTLs were independent of other traits. Some of them, however, did co-locate with F_spklt QTLs on chromosomes 2A, 2D, 6D, and 7A, whereas one QTL on 2D of HI co-located with Yd and BY QTLs.

Disease resistance traits (Pm, Lr, Yr, and Fhs). Out of 83 disease resistance QTLs (19 Lr, seven Yr, 52 Pm, and five Fhs), 74 were potentially novel. Among them, the Yr QTL on chromosome 2BS could represent genes *Yr27* or *Yr53* (depending on the centromere location of chromosome 2B) (Wang and Chen, 2017), whereas the cluster on 7DS (*Q. Lr_Mo05-7D*, *Q. Lr_Pu09-7D*, *Q. Yr_SFS99-7D*, and *Q. Pm_GFS98-7D*) could be the same QTL as *Q. Yr.7DS_Opata85* at *Yr18* reported earlier (Singh et al., 2000). However, this site also harbored the *Lr34* (Nelson et al., 1995c) and *Pm15* (Tosa and Sakai, 1990) genes. A QTL cluster at 43–53 cM on 3BS was believed to be *Lr27* reported by Börner et al. (2002). Likewise, the leaf rust resistance QTLs on chromosomes 2A and 3B were reported before (Börner et al., 2002).

Several *Pm* resistance genes have been identified, where we have located novel Pm QTLs. For example, *Pm28* resides on chromosome 1B (Peusha et al., 2000), whereas *Pm24* is located on chromosome 1DS (Huang et al., 2000). Likewise, at least four genes, viz. *Pm6*, *Pm33*, *Pm42*, and *Pm51*, are located on chromosome 2B (Hua et al., 2009; Marone et al., 2013; Zhan et al., 2014; Zhu et al., 2005). *Pm13* was initially located on chromosome 3B (Ceoloni et al., 1992), though it was later discovered to be located on chromosome 5BL (Blanco et al., 2008). In addition, at least seven and six powdery mildew resistance genes are located on chromosomes 7B and 7A, respectively (Shah et al., 2018). However, chromosome 5A was reported to harbor only *Pm23* (Hao et al., 2008) and we have potentially new Pm QTLs on 5A not previously reported in the ITMI/MP. Another six and three Pm QTLs on chromosomes 5B and 5D, respectively, could be paralogs to the ones

discovered on 5A, although *Pm30* (Liu et al., 2002) and *Pm34* and *Pm35* (Miranda et al., 2006, 2007) were reported to be on the short and long arms of 5B and 5D, respectively.

With regards to Fhs, Yi et al. (2018) have located stable QTLs at 44.4–50.9 cM, whereas our QTL on chromosome 2D was located at 70 cM and the similarity to (Yi et al., 2018) can only be speculated. Many meta-QTLs for Fhs have been reported on chromosomes 7A and 7D (Venske et al., 2019), and our QTLs of Fhs might coincide. In cultivar 'Catbird', Cativelli et al. (2013) have located a QTL for Fhs at approximately 8–40 cM (Cativelli et al., 2013), and our QTL on chromosome 7D was located at 41.5–56.5 cM, which is comparable. The Fhs QTL on chromosome 6BS was detected at approximately 54–55 cM (Börner et al., 2002), and we mapped its position to 204 cM. Its similarity to the *Fhb2* gene, which was mapped at approximately 13 cM (Cuthbert et al., 2007), is worth noting.

Significance of new map

Since the map has been generated from only 92 individuals, which is considered to be a low number, especially in a RIL population genetic distances increase about twofold compared to an F_2 or fourfold compared to a DH population, we have compared and validated the marker order from the generated map with available mapping data from the ITMI-DH population (Sorrells et al., 2011) and the published Wheat Genome sequence (IWGSC et al., 2018). The results of this comparison (as far as the respective coordinates were available in the ITMI-DH population or could be determined and assigned unambiguously in the genome sequence based on the marker sequence context) indicate that the marker order of the two maps and the genome sequence agree quite well (except for some chromosome orientations) (Table S9). Based on these data, the QTL mapping results generated from the wealth of information described in this paper can now be compared easily to any marker data with available marker sequences generated from both the ITMI/MP and DH populations as well as any other population based on the sequence coordinates.

The genetic map with 7584 SNP markers and an average marker density of 1.02 markers per cM makes it unlikely that major QTLs for the analyzed traits are missed so that the set of identified QTLs should be rather comprehensive. Large physical gaps between markers are essentially limited to one region on each chromosome (Figure 2; Figure S2b), which correspond to the respective centromeric region, which display very low levels of recombination.

EXPERIMENTAL PROCEDURES

The population was created by crossing the spring wheat variety 'Opata85' with the synthetic hexaploid wheat 'W7984', which was generated via an interspecific cross of the *Triticum tauschii* accession 'CIGM86.940' (DD) with the tetraploid wheat 'Altar 84' (AABB) at the International Maize and Wheat Improvement Center (CIMMYT) in Mexico (Börner et al., 2002; Lohwasser et al., 2005). Two new populations were created using the same parents that complement the original ITMI/MP for mapping traits (Sorrells et al., 2011). A total of 150 RILs were originally developed by single-seed descent to the F_8 or F_9 at Cornell University, Ithaca, USA (Börner et al., 2002). Here, we have used (i) one new dataset generated in the US experiments between 2015 and 2017 and (ii–iv) three already existing phenotypic datasets, which were (ii) generated in Germany between 1997 and 1999 and reported in Börner et al. (2002), (iii) generated in Russia between 2005 and 2009 and reported in Chesnokov et al. (2013), and (iv) generated in India between 2001 and 2002 and reported in Kumar et al. (2007). The details of each dataset are provided below.

US experiments

The US dataset consisted of 16 traits measured in a total of three experiments carried out at the University of California Intermountain Research and Extension Center, Tulelake, California in 2015 (Tlk15), 2016 (Tlk16), and 2017 (Tlk17).

Experimental design. The population along with parents and standard check varieties was sown from mid-April to early May, depending on the rainy season, and harvested in early September in two replicates per year in a randomized complete block design using a mechanical plot planter, where the seeding rate was about 300 seeds/m^2. Final plot size was 3 m $\times$ 1.5 m with seven rows per RIL per replicate, which were 15 cm apart. Fertilizers were applied according to standard practices of the area. The experiments were subjected to sprinkler irrigation (i) at pre-emergence, (ii) before heading, and (iii) after heading. Harvest was carried out on a per plot basis in early September using a Wintersteiger harvester.

Traits measured. The following traits were measured on each plot before harvest. Heading date (Hd) was measured as the number of days from emergence to 50% flowering, DMT was measured as the number of days from emergence to senescence, and GFD was recorded as the difference between Hd and DMT. Lodging (Ld) was measured as the visual percentage of plot lodged about 10 days before harvest and height (Ht) was recorded in cm from soil level to mid-spike of each RIL.

Post-harvest, grains were weighed as a harvest-run sample from each plot. Separate weights were taken for unthreshed spikelets. Percent hulls was determined on a sample of about 10 RILs that were not completely free-threshing and the mean was used to compute the weight of grain in unthreshed spikelets. This amount was added to the threshed grain sample for the computation of grain yield per plot. Harvest area in ft^2 was computed for each plot as well as grain yield (Yd) in lb/acre. Test weight (Tw) was determined by the standard USDA volumetric method to determine grams/quart and converted to lb/bushel. The non-threshability index (NT_Ind) was calculated as % weight of unthreshed spikelets.

Spike-related traits were based on the spike-based scoring of two spikes per RIL per replicate. Spike length (Sl) was recorded in mm from collar to tip of the apical spikelet. Fertile spikelets per spike (F_spklt) were noted as the number of spikelets with seed. Basal node sterility (S_spklt) was recorded as the number of spike nodes with aborted or absent spikelet structures. Seeds per spike (Sps) was taken as the number of seeds counted after threshing. Seed weight per spike (Swps) was expressed in grams as weight of all seeds from each measured spike. Individual seed weight

was expressed in milligrams and calculated as Swps/Sps × 1000. The number of seeds per spikelet (Seed_spklt) was computed as Sps/F_spklt and the spike density (Dens) was recorded as Sl/(F_spklt + S_spklt). All traits were recorded in all three environments except GMT and GFD, which were missing in Tlk15 for a total of 46 traits (Table S10).

German dataset

Fifteen traits from Börner et al. (2002), including awn color (Awnc), glume color (Gc), waxiness (Wax), height (Ht), peduncle length (Pdl), leaf erectness (Ler), heading (Hd), flowering time (Flt), lodging (Ld), spike length (Sl), seed weight per spike (Swps), thousand kernel weight (Tkw), powdery mildew (Pm), yellow rust (Yr), leaf rust (Lr), and fusarium (Fhs), recorded during eight experiments in Germany between 1997 and 1999, were used. The eight experiments included one growth chamber experiment at Gatersleben in 1997 (GC97), one glass house experiment at Gatersleben in 1997 (GGH97), and field experiments in 1998 and 1999 at Gatersleben (GFS98 and GFS99), Hohenthurm (HFS98 and HFS99), and Silstedt (SFS98 and SFS99). Not all traits were scored at all locations. The traits recorded in the eight experiments ranged between five (GGH97) and 11 (GFS98) for a total of 69 traits (Table S11). Details of trait measurements are provided in Börner et al. (2002).

Russian dataset

The Russian dataset included data for 25 traits, that is, awn length (Awn), flag leaf length (Fll), flag leaf position (Flp), flag leaf width (Flw), heading (Hd), flowering time (Flt), height (Ht), peduncle length (Pdl), glume color (Gc), grain mass per spike (GMsp), kernel color (KC), stem waxiness (Wax), leaf waxiness (Lwax), spike waxiness (Swax), seeds per spike (Sps), seed number per spikelet (Sespklt), fertile spikelets per spike (F_spklt), spike length (Sl), thousand grain weight (Tkw), seed weight per spike (Swps), non-threshability index (NT_Ind), leaf rust (Lr), yellow rust (Yr), and powdery mildew (Pm), which were recorded at three locations in various years. These locations included Mikhnevo (Moscow District) in 2005, 2006, 2007, 2008, and 2009 (Mo05, Mo06, Mo07, Mo08, and Mo09, respectively), Pushkin (suburb of St. Petersburg) in 2005, 2006, 2007, and 2009 (Pu05, Pu06, Pu07, and Pu09, respectively), and Bezenchuk (Samara District) in 2009 (Sa09). Again, not all traits were recorded at all sites. The traits recorded across 10 experiments ranged between six (Pu06) and 22 (Pu07 and Pu09), whereas the total number of traits recorded was 149 (Table S12). Further details are available in Chesnokov et al. (2013).

Indian dataset

The Indian dataset included seven traits related to or contributing to yield, viz. tillers per plant (TPP), biological yield (BY), grain yield (GY), harvest index (HI), spike length (Sl), fertile spikelets per spike (F_spklt), and seeds per spike (Sps), recorded across four locations, viz. Meerut in 2000–2001 (M01), Meerut in 2001–2002 (M02), Pantnagar in 2001–2002 (P02), and Ludhiana in 2001–2002 (L02). The total number of traits was 28 (Table S13). Relevant experimental data and procedures are available elsewhere (Kumar et al., 2007).

Data analysis, genotyping, and genetic mapping

Basic phenotypic data analysis, ANOVA, and correlation analysis including visualization were carried out in RStudio version 1.0.153.

For genotyping, DNA from fresh leaves was extracted and used for genotyping using the Illumina (San Diego, CA, USA) Infinium technology. An optimized array (wheat 20K Infinium SNP array) was used. This array is an optimized and reduced 15K version (Soleimani et al., 2020) of the 90K iSELECT SNP-chip described previously (Wang et al., 2014) to which 5385 markers from the 35K Wheat Breeders Array (Allen et al., 2017) have been added. All sequences of markers on this array can be found in Table S14. A genetic map was constructed using Joinmap software (Ooijen and Voorrips, 2002). A list of 92 ITMI/MP RILs out of the original population of 114 RILs is provided in Table S15.

Mean values of all traits measured in all environments were used for QTL analysis, inclusive composite interval mapping (ICIM), performed with IciMapping 4.1 (http://www.isbreeding.net/), in order to detect putative additive QTLs, where the step size chosen for all QTLs was 1.0 cM. An LOD score of $2 < \text{LOD} \leq 3$ was applied to detect QTLs as significant and $\text{LOD} > 3.0$ was applied to detect highly significant QTLs. We chose ICIM because it has advantages over composite interval mapping (CIM) implemented in other QTL mapping software programs like QTLCartographer as it avoids the possible increase of sampling variance and the complicated background marker selection process implemented in CIM (Meng et al., 2015). In addition, simulated investigations using different genomes and various genetic models indicate that ICIM has higher detection power, a reduced false detection rate, and less biased estimates of QTL effects compared to CIM in additive mapping. QTLs were designated following the rules set out in the Catalog of Gene Symbols (McIntosh et al., 2008) and according to a previous report (Arif and Börner, 2019).

CONCLUSIONS

To conclude, we accomplished the genetic dissection of the performance of the wheat ITMI/MP population for a total of 292 traits measured across four countries and three continents over a period of 20 years (1997–2017) using 7584 high-quality SNPs. We detected a total of 874 significant QTLs (including 432 being highly significant). Our study corroborated previous findings and detected new QTLs that were undiscovered. This investigation showed that dense genetic maps and phenotyping in different ecological zones supported by modern QTL detection software may provide new insights into the trait architecture in a given genetic population like ITMI/MP. Moreover, this study will serve as a foundation for similar studies because much more phenotypic data have already been generated from the same population for a plethora of traits. Additionally, comparison of the mapping data from the ITMI-RIL population with the ITMI-DH population and the wheat genome sequence (Table S8), each QTL can be compared to all other published data from any map for which sequence information is available for the markers. To add to it, since this population and the new reconstructed populations are available to researchers and scientists across the world, breeders can use the QTL information to make crosses with desired RILs to improve their traits of interest.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All relevant data can be found within the manuscript and its supporting materials.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Figure S1. Correlation heatmap of heading time (Hd), days to maturity (DMT), grain filling duration (GFD), height (Ht), lodging (Ld), test weight (Tw), yield (Yd), non-threshability index (NT_Ind), spike length (Sl), fertile spikelets per spike (F_spklt), sterile spikelets (S_spklt), seeds per spike (Sps), seed weight per spike (Swps), individual seed weight (SeedWt), seeds per spikelet (Sespklt), and spike density (Dens) (mean values of traits from each experiment were used) in US experiments. Red to blue indicate positive to negative correlations and the color intensity indicates the magnitude of correlation; white color indicates an absence of any correlation.

Figure S2. (a) The number of SNPs mapped to each chromosome against respective chromosome length in 92 RILs of ITMI/MP. (b) Physical distance of the SNP markers based on the wheat genome sequence for the three genomes. The largest physical distances between markers are always in the regions of the centromeres.

Figure S3. A SNP-based genetic map of ITMI of homoeologous group 1 (i), 2 (ii), 3 (iii), 4 (iv), 5 (v), 6 (vi), and 7 (vii) chromosomes where SNPs are given on the right side and the position in cM is given on the left side of the chromosomal bars.

Figure S4. Distribution of 183 QTL clusters in the wheat genome. Green lines in the outer track indicate the SNP positions on each chromosome; red bars in the inner track indicate QTL clusters whose lengths correspond to the number of QTLs that each cluster carries; the blue lines under the track circle indicate the span of QTL clusters on respective linkage groups with small vertical lines indicating the central point of each cluster.

Figure S5. Chromosomal distribution of quantitative trait locus (QTLs) (blue in US, black in German, green in Russian and red in Indian environments) where each chromosome is drawn according to its own scale depending on number of markers and QTLs residing on it. QTLs with a limit of detection score of >3.0 are underlined. Certain chromosomes are shown in two (chromosomes 2A, 2B, 3A, 3B, 4A, 5A, 5B, and 7A) or three (chromosome 2D) parts to accommodate the entire length and all the QTLs. Only QTL peak positions (thick horizontal line) and single nucleotide polymorphisms (SNPs) linked to any QTL are shown on the right side and the distance (in cM) is shown on the left side.

Table S1. Correlations among various traits (mean values) measured in US environments. *$P < 0.05$, **$P < 0.01$, - = no correlation.

Table S2. Range and mean ± standard error of various traits evaluated in German environments.

Table S3. Range and mean ± standard error of various traits evaluated in Russian environments.

Table S4. Range and mean ± standard error of various traits evaluated in Indian environments.

Table S5. Number of SNPs, distance, and density per chromosome, per group, and per genome in the ITMI population.

Table S6. Complete list of QTLs identified throught composite interval mapping. Left and right flanking markers linked to QTL are also provided along with LOD, PVE, and additive effect (+ = provided by Opata and − = provided by W7984 parent). Blue indicates QTLs in US environments, gray indicates QTLs in German environments, pink indicates QTLs in Russian environments, and orange indicates QTLs in Indian environments. Asterisks (*) indicate novel QTLs.

Table S7. A summary of the number of significant or highly significant (bold and underlined) QTLs observed on each chromosome.

Table S8. List of QTL clusters alongside intervals, with the number of QTLs linked to traits in those clusters.

Table S9. Comparison of the genetic maps from ITMI RIL and ITMI-DH and the wheat genome sequence. Column A: marker name; column B: chromosome assignment in the ITMI_RIL map; column C: genetic position in the respective chromosome of the ITMI_RIL map; column D: chromosome assignment in the ITMI_DH map; column E: genetic position in the respective chromosome of the ITMI_DH map; column F: chromosome assignment in the wheat genome sequence; column G: physical position in the respective chromosome in the wheat genome sequence.

Table S10. List of 16 traits recorded in Tulelake in the USA across three environments (Tlk-15 = Tulelake in 2015, Tlk-16 = Tulelake in 2016 and Tlk-17 = Tulelake in 2017).

Table S11. List of various traits recorded in German environments from Börner et al. (2002).

Table S12. List of various traits recorded in Russian environments from Chesnokov et al. (2013).

Table S13. List of various traits recorded in Indian environments from Kumar et al. (2007).

Table S14. Complete sequence of SNPs for the 20K array used in the genotyping of ITMI RILs.

Table S15. List of ITMI RILs used in genotyping.

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