DOI: 10.1007/s11099-015-0114-5 PHOTOSYNTHETICA 53 (2): 299-305, 2015

Genetic basis of traits related to stomatal conductance in wheat cultivars in response to drought stress

S.G. WANG[*], S.S. JIA[*], D.Z. SUN[*,+], H.Y. WANG[*], F.F. DONG[*], H.X. MA[*], R.L. JING[**,+], and G. MA[***]

College of Agronomy, Shanxi Agricultural University, Taigu, Shanxi 030801, China[*];
Institute of Crop Science, Chinese Academy of Agricultural Sciences, Beijing 100081, China[**]
Wheat Research Institute, Shanxi Academy of Agricultural Sciences, Linfen, Shanxi 041000, China[***]

Abstract

The genetic basis of stomatal conductance (g_s), net photosynthetic rate (P_N), and transpiration rate (E) was explored by using a wheat doubled haploid population from a cross of Hanxuan10 and Lumai 14. The above three traits were evaluated in wheat flag leaves at 10, 20, 30 days after anthesis under drought stress (DS) and well-watered (WW), and quantitative trait loci (QTL) were analyzed. Expression of the traits during the grain filling stage showed downward trends under both conditions, but expression of three phenotypes were stronger under WW than those under DS. Extremely significant positive correlations were established among the traits at all growth stages under both conditions. A total of 18 additive QTLs for those traits were identified on 10 chromosomes. Among them, two batches of nine additive QTLs were associated with the target traits under DS and WW, respectively. Two additive QTLs for g_s and E, two for g_s and P_N, six for g_s, P_N, and E clustered at the same or near the region (colocation) of chromosomes 4A, 2B, and 7B, respectively. This provided genetic basis for close phenotype correlations among g_s, P_N, and E. Furthermore, QTLs for g_s, P_N, and E near Xgwm577 and Xgwm611 located on 7B chromosome were linked to previously reported QTLs regulating a SPAD value and the chlorophyll *a/b* ratio under dark-induced condition. This finding indicated that these QTLs on 7B chromosome might be involved in the process of wheat leaf senescence.

Additional key words: drought stress; photosynthetic rate; quantitative trait loci; stomatal conductance; transpiration rate; wheat.

Introduction

Stomata are the main channel for the gas flow in and out of plant leaves. Stomata movements were closely related to leaf photosynthesis, respiration, and transpiration, and are affected by environmental conditions (Hetherington *et al.* 2003, Casson *et al.* 2008). Under drought stress, stomatal conductance (g_s), mesophyll CO_2 concentration, net photosynthetic rate (P_N), and transpiration rate (E) decreased, but stomatal resistance increased (Zhang *et al.* 2011). Many studies showed that increased g_s can improve crop photosynthesis and increase crop yield (Gillon *et al.* 2000, Miyashita *et al.* 2005, Franks *et al.* 2009).

It was found that the yield of spring wheat was positively correlated with the g_s and P_N of plants under irrigation, but extreme drought had adverse effects on these traits and wheat yield (Shimshi *et al.* 1975, Fischer *et al.* 1998, Lu *et al.* 2003). Moreover, these studies focused only on some particular growth stages and the changes of g_s, P_N, and E during wheat leaf senescence were neglected. Zheng *et al.* (2011) showed the relationship between traits related to g_s and the wheat yield. Further studies revealed that P_N played a major role for the wheat yield at heading, flowering stage, and 10, 20, 30 d after anthesis. Meanwhile, Yang *et al.* (2001) reported that the changes of g_s were closely related to leaf senescence. However, changes of g_s, P_N, and E have not been studied under different water conditions.

Received 26 February 2014, *accepted* 2 September 2014.
[+]Corresponding authors; phone: 0086-354-6288706, fax: 0086-354-6388344, e-mail: sdz64@126.com (D.Z. Sun); phone and fax: 0086 10 8210 5829; e-mail: jingrl@caas.net.cn (R.L. Jing)
Abbreviations: C_i – intercellular CO_2 concentration; cM – centimorgan; DHL – doubled haploid line; DS – drought stress; E – transpiration rate; ES – early grain-filling stage; g_s – stomatal conductance; H10 – Hanxuan 10; L14 – Lumai 14; LOD – likelihood of odd; LS – late grain-filling stage; MS – middle grain-filling stage; P_N – net photosynthetic rate; QTL – quantitative trait loci; WW – well watered.
Acknowledgements: This work was supported by National Science and Technology Major Projects for Cultivation of New Transgenic Varieties (2014ZX0800203B-003), the Specialized Research Fund for the Doctoral Program of Higher Education (20121403110005), CGIAR Generation Challenge Programme (GCP, G7010.02.01), and the Natural Science Foundation of Shanxi Province (2014011004-3). The first two authors contributed equally to this work. We also appreciate the editors and the anonymous reviewers for their valuable comments on the manuscript.

The objective of the current study was to gain insights into the changing pattern of g_s, P_N, and E during wheat leaf senescence under DS and WW conditions and to elucidate the molecular basis of g_s, P_N, and E in wheat cultivars in response to drought stress.

Materials and methods

Plant material and field design: Two wheat cultivars with significantly different drought resistance, Hanxuan 10 (H10) and Lumai 14 (L14), were selected for this study. H10 is a drought-tolerant cultivar developed by the Shanxi Academy of Agricultural Sciences in 1966. It is still grown in arid and barren areas. L14 is a high yielding cultivar, adapted to abundant water and fertile conditions, from Yantai Institute of Agricultural Sciences, Shandong, China, which was widely grown during the 1990's in northern China. A double haploid (DH) population derived from a cross of the two cultivars was developed at the Institute of Crop Sciences, CAAS, Beijing（Jing *et al.* 1999). All of the 150 lines and their parents were grown at the experimental farm (37°25′N, 112°35′E, 799.6 m a.s.l.) of Shanxi Agricultural University in 2009. The experimental field was divided into two parts for different water environments. The field design of each part consisted of randomized complete blocks with three replications. Each plot was two rows of 2 m, with 0.25 m between rows, 40 seeds were sown in each row. The DS environment was based on the rainfed water regime with a total of 198.2 mm rainfall during the whole growing season. The WW environment was supplied with 65 mm applied prior overwintering, during seedling establishment, jointing, and at mid-grain filling stages, respectively.

Using the DH population, g_s, P_N, and E of wheat flag leaves were measured at the early grain-filling stage [ES, 10 d after anthesis (DAA)], the middle grain-filling stage (MS, 20 DAA), and the late grain-filling stage (LS, 30 DAA) under two water regimes. QTLs controlling these traits were identified.

g_s, P_N, and E: Ten flowering plants from each line and parents were tagged. Gas-exchange characteristics of wheat flag leaves were measured with portable photosynthetic apparatus of *CI-340* (*CID*, Camas, WA, USA) from 9:00 to 11:30 h in the morning under the sunny condition. A gas buffer system was connected with an apparatus well before measuring to ensure that CO_2 concentration in the leaf chamber was stabilized at about 350 ± 10 μmol mol^{-1}. The relative humidity in the leaf chamber was set to about 40%, and quantum flux density (PAR) was stabilized at about 1,200 ± 20 μmol m^{-2} s^{-1}, temperature was set at 25°C. Measurements were carried out at 10, 20, and 30 DAA. The air temperatures were 23 ± 2, 24 ± 2, and 27 ± 3°C during the measurement, respectively. Due to large sample population, three replicates were performed for each of the three measurements. One replicate included the traits measurement under both DS and WW conditions. Three plants from each lines were measured in each replicate.

Data analysis: A genetic linkage map, consisting of 395 marker loci, including 132 amplified fragment length polymorphisms (AFLP), and 263 simple sequence repeats (SSRs), was constructed from the 150 DHLs using *MAPMAKER/Exp version 3.0* software (Hao *et al.* 2003, Zhou *et al.* 2005). The map covered 3,904 centimorgans (cM) with an average distance of 9.9 cM between adjacent markers.

Analyses of variance (*ANOVA*) and correlation of the data were conducted using software *SPSS 17.0*. QTLs for g_s, P_N, and E under two water regimes were detected using *QTL Mapper version 2.0* (Wang *et al.* 1999) for composite interval mapping (CIM) of a mixed linear model with a threshold of LOD score 2.5. QTLs were named according to the rule of "QTL + trait abbreviation + chromosome".

Results

Variations of g_s, P_N, and E: The g_s, P_N, and E of DHLs and their parents showed significant differences under both water conditions (Table 1). In H10, DS decreased g_s, P_N, and E by 3.9–30.4%, 5.9–27.4%, and 7.3–20.5%, respectively, while in L14 the parameters were reduced by 8.0–27.1%, 3.5–31.7%, 7.9–19.8%, respectively. In DHLs, the trait values declined by 26.6–36.4%, 13.9–24.9%, 3.6–14.6%, respectively. In addition, expression of phenotypic values for all target traits from the female parent H10 were much stronger than those from the male parent L14 at various growth stages (Table 1). The averages of DHLs were lower than those of the parents with low mean values. The g_s, P_N, and E of DHLs showed a wide range of distribution and transgressive segregation (Table 1).

Correlation analysis: Significant positive correlations existed between g_s, P_N, and E under both water conditions at various growth stages (Table 2). In addition, all of the correlation coefficients under DS were higher than those under WW (Table 2).

Table 1. Phenotypic variation of traits related to stomatal conductance in DH lines and their parents at various growth stages under two water regimes. g_s – stomatal conductance; P_N – photosynthetic rate; E – transpiration rate; ES – early grain-filling stage; MS – middle grain-filling stage; LS – late grain-filling stage; DS – drought stress; WW – well-watered. CV – coefficient of variation.

Parameter	Treatment	Stage	Parent		DH line		
			Hanxuan10	Lumai14	Mean	Variation	CV [%]
g_s [mmol(H_2O) m^{-2} s^{-1}]	DS	ES	204.50	156.42	136.51	68.35–208.98	30.0
		MS	154.48	121.22	88.13	34.15–156.18	29.0
		LS	102.10	88.98	63.00	26.53–107.84	36.8
	WW	ES	294.20	200.24	186.09	109.79–420.38	29.9
		MS	179.39	166.21	121.57	73.69–250.43	31.7
		LS	106.25	96.72	99.05	53.66–198.45	40.8
P_N [μmol(CO_2) m^{-2} s^{-1}]	DS	ES	21.61	15.26	14.38	6.26–24.37	25.9
		MS	21.65	13.85	10.38	2.57–21.80	29.8
		LS	9.33	8.19	5.45	1.57–9.81	45.7
	WW	ES	27.09	19.16	17.26	6.66–35.98	31.1
		MS	23.01	14.35	12.05	7.23–26.16	32.8
		LS	12.85	11.99	7.26	3.11–18.65	54.4
E [mmol(H_2O) m^{-2} s^{-1}]	DS	ES	3.18	2.64	2.52	1.10–3.89	26.2
		MS	3.31	2.54	2.71	1.21–4.51	26.6
		LS	2.53	2.32	2.14	0.96–3.98	32.4
	WW	ES	4.00	3.29	2.95	1.31–8.13	28.9
		MS	3.60	3.08	2.81	1.13–8.13	31.6
		LS	2.73	2.52	2.41	1.02–4.97	40.5

Table 2. Relationship between stomatal conductance, photosynthetic rate, and transpiration rate. g_s – stomatal conductance; P_N – photosynthetic rate; E – transpiration rate; ES – early grain-filling stage; MS – middle grain-filling stage; LS – late grain-filling stage; DS – drought stress; WW – well-watered.

Parameter	Stage	Treatment	E [mmol(H_2O) m^{-2} s^{-1}]	P_N [μmol(CO_2) m^{-2} s^{-1}]
g_s	ES	WW	0.730**	0.730**
		DS	0.769**	0.852**
	MS	WW	0.682**	0.792**
		DS	0.690**	0.797**
	LS	WW	0.776**	0.872**
		DS	0.840**	0.875**
P_N	ES	WW	0.829**	
		DS	0.811**	
	MS	WW	0.746**	
		DS	0.797**	
	LS	WW	0.746**	
		DS	0.797**	

Additive QTL for g_s, P_N, and E: Under DS, 9 additive QTLs were identified for g_s, P_N, and E at ES, MS, and LS stages with LOD ranging from 2.5 to 2.97 and the phenotypic variations explained by each QTL ranged from 7.2% to 17.2%. Among these QTLs, the QTL linked to g_s and P_N was located between marker Xgwm429 and Xgwm388 on chromosome 2B and favorable alleles were contributed from L14; at the same time, the QTL for g_s and E were identified at the marker region P3446.2–CWM145 on chromosome 4A, and favorable alleles were also donated by L14 (Table 3, Figs. 1, 2).

Under WW condition, another 9 additive QTLs were found for the three target traits at various growth stages with LOD ranging from 2.5 to 3.3 and their phenotypic variations ranged from 6.6% to 10.5%. Out of these QTLs, *Qg*$_s$ *-7B-2* detected at LS, *QP*$_N$*-7B-1* at MS, *QE-7B-2* and *QE-7B-3* at LS were located near marker Xgwm577 on chromosome 7B, and favorable alleles of *Qg*$_s$ *-7B-2*, *QE-7B-2,* and *QE-7B-3* were from H10, but *QP*$_N$*-7B-1* was from L14. In addition, *QP*$_N$*-7B-2* and *QE-7B-1* were detected at another marker region P1123.2–Xgwm611 on chromosome 7B at MS, and favorable alleles also came from L14 (Table 3, Figs. 1, 2).

Discussion

Under both water conditions, g_s, P_N, and E of DHLs and their parents showed downward trends, and the phenotypic values under DS were lesser than those under WW at various growth stages. This indicated that the changes in g_s, P_N, and E of wheat flag leaves were not only influenced by stomatal traits, but also determined by the physiological function of the flag leaves. This might explain why wheat plants adapted to the DS exhibited lower g_s and its related traits. On the other hand, under both water conditions, the coefficients of variation of the three traits were larger, and became higher and higher along with the developmental stage in DHLs. A possible reason is due to enlarged differences in leaf senescence among DH lines at the later growth stage.

A total of 18 additive QTLs were detected for g_s, P_N, and E under both water conditions. Only two of these QTLs explained more than 10% of the phenotypic variation, suggesting that all target traits were quantitative and controlled by multiple genes. Some studies showed that QTLs for closely correlated traits may be located at, or near, the same chromosomal position (Veldboom *et al.* 1994, Yu *et al.* 1997). Several tightly linked genes, or the gene, which affects multiple traits located at the same marker region, were called "gene linkage" or "pleiotropism". In the present study, four regions of pleiotropism or gene linkage were found at three developmental stages under two water conditions. These included the marker interval Xgwm429–Xgwm388 on chromosome 2B, where *Qg*$_s$ *-2B* and *QP*$_N$*-2B* were located, P3446.2–CWM145 on chromosome 4A, where *Qg*$_s$ *-4A* and *QE-4A* were detected, P1123.2–Xgwm611 on chromosome 7B, where *QP*$_N$*-7B-2* and *QE-7B-1* were mapped, and the marker region WMC276–Xgwm577–CWM96.1 on chromosome 7B, where *Qg*$_s$ *-7B-2*, *QP*$_N$*-7B-1*, *QE-7B-2*, and *QE-7B-3* were detected. Moreover, it was also found that QTLs affecting P_N, g_s, E, and intercellular CO_2 concentration (C_i) in rice were clustered in the same genomic region on choromosome 11 (Zhao *et al.* 2008). Similarly, QTLs for P_N and E in sunflower were at the same marker region on group XIV (Hervé *et al.* 2001). The colocation of QTLs for the target traits might be a genetic basis for the significantly phenotypic correlation between g_s, P_N, and E reported in rice and sunflower studies and also present in our study (Hervé *et al.* 2001, Zhao *et al.* 2008). Authors also suggested that the close genetic relationship existed between the target traits. Although it is not clear if these genes (QTLs) are pleiotropism or linkage, these regions are potential "hot spots" regions with a high possibility for the g_s, P_N, and E.

Table 3. Additive effect QTLs for stomatal conductance, photosynthetic rate, and transpiration rate. g_s – stomatal conductance; P_N – photosynthetic rate; E – transpiration rate; ES – early grain-filling stage; MS – middle grain-filling stage; LS – late grain-filling stage; DS – drought stress; WW – well-watered. ** and * represent the significance level in $P<0.001$ and $P<0.005$, respectively; Site (cM) means genetic distance of the putative QTL from the left flanking marker; A – additive effect, a positive value indicates the allele is from H10, while a negative value means the allele is from L14; H^2 indicates the phenotypic variance explained by the additive QTL.

Trait	Treatment	Stage	QTL	Flanking marker	Site [cM]	LOD	A	H^2 [%]
g_s	DS	ES	*Qg*$_s$ *-6D*	Xgwm325–WMC113	5.5	2.5	11.21*	7.18
		MS	*Qg*$_s$ *-2D*	WMC453.1–WMC18	15	2.66	7.81**	9.36
		LS	*Qg*$_s$ *-2B*	Xgwm429–Xgwm388	0.2	2.62	–6.49**	7.79
			Qg$_s$ *-4A*	P3446.2–CWM145	11.3	2.78	–7.29**	9.90
	WW	LS	*Qg*$_s$ *-7B-1*	WMC526–WMC273	11	2.53	11.94*	8.74
			Qg$_s$ *-7B-2*	Xgwm577–CWM96.1	7.2	2.6	10.87**	7.27
P_N	DS	LS	*QP*$_N$*-2B*	Xgwm429–Xgwm388	0.2	2.52	–0.68**	7.51
			QP$_N$*-3B*	Xgwm299–M539.1	4.59	2.79	0.75**	8.20
	WW	ES	*QP*$_N$*-3A*	P8422–CWM539.2	11.1	2.58	1.38*	6.59
		MS	*QP*$_N$*-7B-1*	Xgwm577–CWM96.1	0.2	3.04	–1.18**	8.96
			QP$_N$*-7B-2*	P1123.2–Xgwm611	5.2	3.29	–1.29**	10.52
E	DS	ES	*QE-1D*	P8443.1–P3616.2	0	2.55	0.18*	7.53
		MS	*QE-6A*	CWM487–P3465.4	0	6.16	–0.30**	17.22
		LS	*QE-4A*	P3446.2–CWM145	8.8	2.54	–0.20*	8.49
	WW	ES	*QE-5B*	Xgwm408–Xgwm604	11.2	2.56	–0.22*	6.82
		MS	*QE-7B-1*	P1123.2–Xgwm611	8.2	2.61	–0.26*	8.62
		LS	*QE-7B-2*	WMC276–Xgwm577	0.2	2.6	0.26**	7.22
			QE-7B-3	Xgwm577–CWM96.1	7.2	2.6	0.27**	7.87

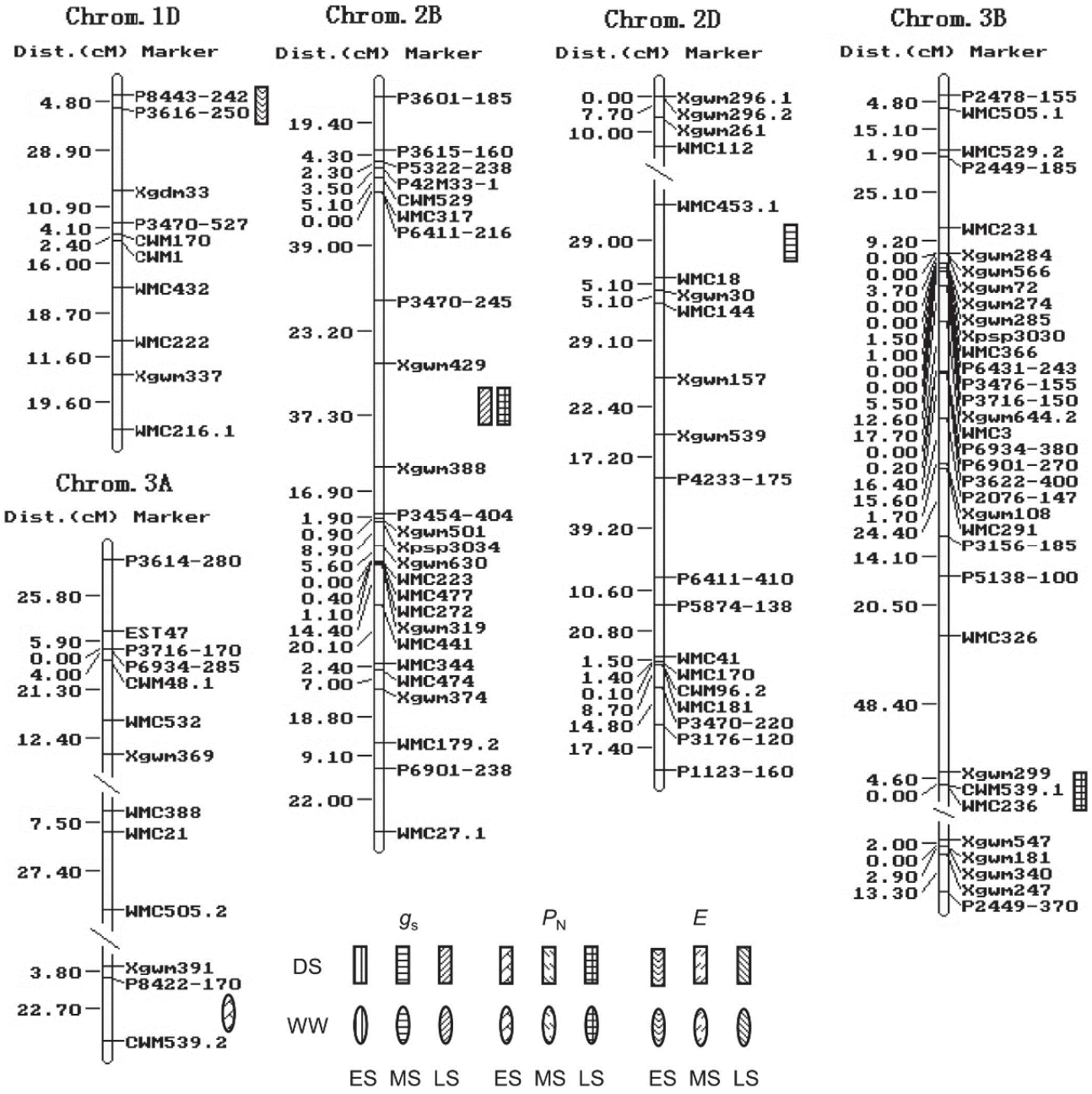

Fig. 1. QTL position for stomatal conductance (g_s), net photosynthetic rate (P_N), and transpiration rate (E) on the genetic linkage groups (chromosome 1D, 2B, 2D, 3A, 3B) constructed on the DH population derived from a cross of (Hanxuan 10 × Lumai 14). ES – early grain-filling stage; MS – middle grain-filling stage; LS – late grain-filling stage; DS – drought stress; WW – well-watered.

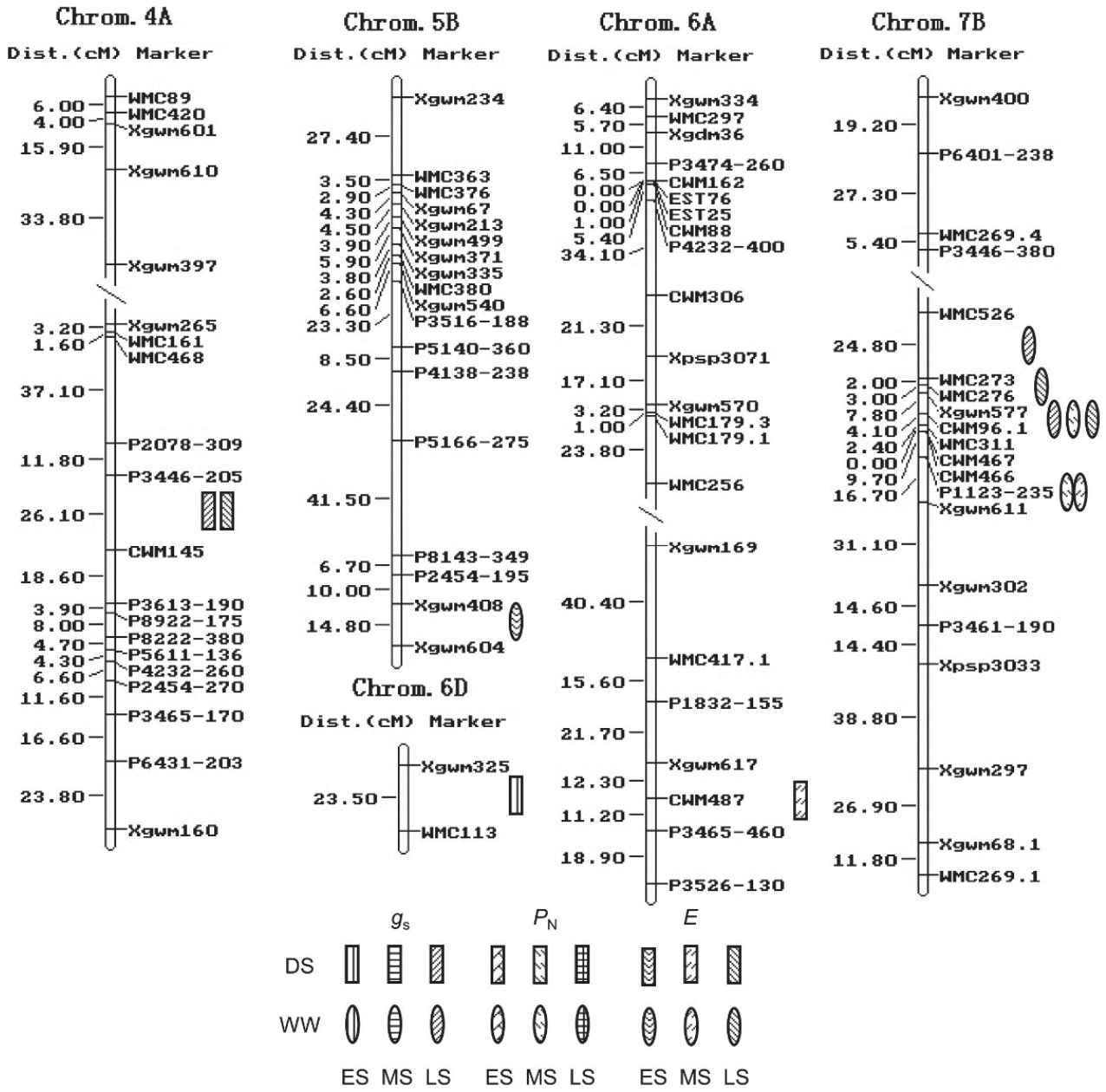

Fig. 2. QTL position for stomatal conductance (g_s), net photosynthetic rate (P_N), and transpiration rate (E) on the genetic linkage groups (chromosome 4A, 5B, 2D, 6A, 6D, 7B) constructed the DH population derived from a cross of (Hanxuan 10 × Lumai 14). ES – early grain-filling stage; MS – middle grain-filling stage; LS – late grain-filling stage; DS – drought stress; WW – well-watered.

Vijayalakshmi *et al.* (2010) detected some QTLs for traits related to leaf senescence under normal temperature and heat stress using Ventnor/Karl 92 RIL population, in which *QSpad^o.ksu-7B* on chromosome 7B and *QChl a/b.igdb-7B*, detected under dark-induced condition (Li *et al.* 2012), were all located at the vicinity of Xgwm577 and Xgwm611. In this study, *Qg$_s$ -7B-2*, *QP$_N$-7B-1*, *QE-7B-2*, and *QE-7B-3* detected under WW linked with Xgwm577, while *QP$_N$-7B-2* and *QE-7B-1* linked with Xgwm611, indicating there are some genes related to leaf senescence traits near the two makers on chromosome 7B. It is necessary to construct near-isogenic lines of these regions for fine mapping in order to make clear that the QTLs are "pleiotropism" or "gene linkage".

Among 18 additive QTLs for g_s, P_N, and E detected in this study under two water conditions, none was simultaneously detected under DS and WW. This finding indicated that g_s, P_N, and E are governed by a set of additive and epistatic QTLs under DS and WW, respectively; DS can induce the expression of genes that are silent under WW condition.

References

Casson S., Gray J.E.: Influence of environmental factors on stomatal development. – New Phytol. **178**: 9-23, 2008.

Fischer R.A., Rees D., Sayre K.D. *et al.*: Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. – Crop Sci. **38**: 1467-1475, 1998.

Franks P.J., Drake P.L., Beerling D.J.: Plasticity in maximum stomatal conductance constrained by negative correlation between stomatal size and density: an analysis using *Eucalyptus globulus*. – Plant Cell Environ. **32**: 1737-1748, 2009.

Gillon J.S., Yakir D.: Internal Conductance to CO_2 diffusion and $C^{18}OO$ discrimination in C_3 leaves. – Plant Physiol. **123**: 201-214, 2000.

Hao Z.F., Chang X.P., Guo X.J. *et al.*: QTL mapping for drought tolerance at stages of germination and seedling in wheat (*Triticum aestivum L.*) using a DH population. – Agric. Sci. China **2**: 943-949, 2003.

Hervé D., Fabre F., Berrios E.F. *et al.*: QTL analysis of photosynthesis and water status traits in sunflower (*Helianthus anuus* L.) under greenhouse conditions. – J. Exp. Bot. **362**: 1857-1864, 2001.

Hetherington A.M., Woodward F.I.: The role of stomata in sensing and driving environmental change. – Nature **424**: 901-908, 2003.

Jing R., Chang X., Jia J. *et al.*: Establishing wheat doubled haploid population for genetic mapping by anther culture. – Biotechnology **9**: 4-8, 1999.

Li H., Lin F., Wang G. *et al.*: Quantitative trait loci mapping of dark-induced senescence in winter wheat (*Triticum aestivum*). – J. Integr. Plant Biol. **54**: 33-44, 2012.

Lu J.Y., Shan L., Gao J.F. *et al.*: Effect of drought stress on photosynthesis and some other physiological characteristics in flag leaf during grain filling of wheat. – Agr. Res. Arid Areas **21**: 77-81, 2003.

Miyashita K., Tanakamaru S., Maitani T. *et al.*: Recovery responses of photosynthesis, transpiration, and stomatal conductance in kidney bean following drought stress. – Environ. Exp. Bot. **53**: 205-214, 2005.

Shimshi D., Ephrat J.: Stomatal behavior of wheat cultivars in relation to their transpiration, photosynthesis, and yield. – Agron. J. **67**: 326-331, 1975.

Veldboom L.R., Lee M., Woodman W.L.: Molecular marker-facilitated studies in an elite maize population: I. Linkage analysis and determination of QTL for morphological traits. – Theor. Appl. Genet. **88**: 7-16, 1994.

Vijayalakshmi K., Fritz A.K., Paulsen G.M. *et al.*: Modeling and mapping QTL for senescence-related traits in winter wheat under high temperature. – Mol. Breeding **26**: 163-175, 2010.

Wang D.L., Zhu J., Li Z.K. *et al.*: Mapping QTLs with epistatic effects and QTL×environment interactions by mixed linear model approaches. – Theor. Appl. Genet. **99**: 1255-1264, 1999.

Yang H.M., Wang G.X.: Leaf stomatal densities and distribution in *Triticum Aestivum* under drought and CO_2 enrichment. – Acta Phytoecol. Sin. **25**: 312-316, 2001.

Yu S.B., Li J.X., Xu C.G. *et al.*: Importance of epistasis as the genetic basis of heterosis in an elite rice hybrid. – P. Natl. Acad. Sci. USA **94**: 9226-9231, 1997.

Zhang Y.Q., Lin Q., Liu J.B. *et al.*: Effects of drought stress on photosynthetic characteristics and yield of different fertilizer and water types of wheat. – J. Triticeae Crops **31**: 724-730, 2011.

Zhao X.Q., Xu J.L., Zhao M. *et al.*: QTLs affecting morph-physiological traits related to drought tolerance detected in overlapping introgression lines of rice (*Oryza sativa* L.). – Plant Sci. **174**: 618-625, 2008.

Zheng T.C., Zhang X.K., Yin G.H. *et al.*: Genetic gains in grain yield, net photosynthesis and stomatal conductance achieved in Henan Province of China between 1981 and 2008. – Field Crop. Res. **122**: 225-233, 2011.

Zhou X.G., Jing R.L., Hao Z.F. *et al.*: Mapping QTL for seedling root traits in common wheat. – Sci. Agric. Sin. **38**: 1951-1957, 2005.