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Mapping QTLs with additive effects and additive × additive epistatic interactions for harvest index in wheat (*Triticum aestivum* L.)

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Abstract

To map quantitative trait loci (QTL) for harvest index, 148 recombinant inbred lines and their parents, Yecora Rojo and an Iranian landrace line (No. 49), were evaluated under normal and terminal water deficit stress conditions in the research stations of Mahabad University and Miyandoab Agricultural Research Center, Iran, during 2014 and 2015. The experiment was carried out as design alpha lattice design with two replications. A linkage map of 51 retrotransposon and 177 microsatellite markers was used in this investigation. Quantitative trait loci (QTL) for additive effects and additive × additive interactions were determined by QTL Network 2.0 software using CIM and mixed-linear methods. QTL analysis revealed that under normal condition, six QTLs (R^2_A= 0.04 to 12.0%), two QTL × environment (E) interactions (R^2_{AE}= 6.28%), five additive × additive epistatic effects (R^2_{AA}= 0.7 to 8.68%) and 12 additive × additive × E (R^2_{AAE}= 3.76 to 11.4%) were significant. Under water deficit stress conditions, two QTLs (R^2_A= 5.0 to 7.0%), two additive × additive interactions (R^2_{AA}= 3.72 to 5.48%) and seven additive × additive × E interactions (R^2_{AAE}= 8.04 to 9.58) were identified. Among the eight QTLs identified, three QTLs were located on chromosome 2D, suggesting the importance of this chromosome in controlling harvest index, which may be used for marker assisted selection in breeding programs.

Keywords: Epistasis; Harvest index; Microsatellite marker; QTL; Retrotransposon; Wheat.

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Introduction

Bread wheat (*Triticum aestivum* L.) is the most important food crop in the world (Wei *et al.* 2014). Harvest index in wheat reflects the ability of a crop in converting photosynthetic products into the sink (grain yield). In wheat, harvest indexes are generally lower than the theoretical upper limit of 62, as estimated by Austin (1980). Therefore, there is a room for increasing harvest index to reach the theoretical maximum (Calderini *et al.* 1995). Although it has been reported that harvest index is relatively constant among varieties of wheat and barley under normal or mild water deficit stresses conditions (Gallagher and Biscoe 1978), it decreases when the severity of stress increases (Fereres and Soriano 2007).

The improvement of harvest index in wheat has been mostly due to introduction of dwarfing alleles, *Rht-D1b* and *Rht-B1b*, into the background of modern cultivars. These genes reduced plant height and improved availability of assimilates, which increased kernel number and grain yield (Rebetzke *et al.* 2012).

Apart from understanding the physiological basis of the harvest index, knowledge about its QTL/genes is crucial for indirect selection of grain yield in wheat breeding programs. Cuthbert *et al.* (2008) reported five QTL for harvest index on chromosomes 1A, 3A, 3B, 5A and 5B. El-Feki (2010) detected eight harvest index QTLs on different wheat chromosomes. Kumar *et al.* (2007) detected QTLs for harvest index on chromosomes 2DS, 3BL, 4BL and 6AL. McIntyre *et al.* (2010) evaluated 149 recombinant inbred lines (RIL) of wheat in eight environments and detected five QTLs for harvest index on three types of homeologous chromosomes (1B, 1D, 4D, 6A and 7A).

The objective of this study was to mapping QTLs with additive effects and additive × additive interactions for harvest index using a RIL population of wheat.

Materials and Methods

The mapping population consisted of 148 F_8 RIL of wheat produced by crossing Yecora Rojo with a line (called #49). Yecora Rojo is a modern spring cultivar bred in CIMMYT (). The line #49 is a tall late spring landrace collected from Baluchestan province of Iran. This line was produced in University of California, Riverside, USA, and provided through the Center of Excellence in Cereal Molecular Breeding, University of Tabriz, Iran.

The RILs and their parents were evaluated in the research stations of Mahabad University and Miyandoab Agricultural Research Center, Iran, during 2014 and 2015 growing seasons. These locations are from the semi-arid areas of Iran. In both experimental sites, the experiment was conducted as alpha lattice design with two replications. Each plot consisted of two rows with 2.5 m long and the inter-row and inter-plant spacing of 20 cm and 5 cm, respectively.

Plots were irrigation after 90 mm evaporation from class A pan under both normal and water deficit stress conditions; however, irrigation was stopped at heading stage under water deficit stress conditions. Biomass and grain yield were measured at physiological maturity by harvesting the whole experimental unit. Then, harvest index was determined by dividing the grain yield by biomass for each plot.

For the QTL analysis a linkage map consisting of 51 retrotransposons and 177 microsatellite markers were used. Among the 228 markers studied, 202 markers were associated with 36 linkage groups and 26 markers didn’t belong to any linkage group. Among linkage groups, 34 linkage groups corresponded with 19 wheat chromosomes. The adjacent markers had an average distance of 3.42 cm. The QTL network 2.0 and QTL Cartographer 2.5 software were utilized to do the QTL analysis using mixed-linear and composite interval mapping (CIM) methods.

Results

Phenotypic performance of RIL lines and parents

There was a significant difference between two parents in terms of harvest index at both irrigation conditions (tables not shown). Due to substantial transgressive segregation, some RILs had higher harvest index as compared with the parents under both irrigation conditions (Table 1). In both environmental conditions, the values of skewness and kurtosis were less than 1 for harvest index indicating a normal distribution with polygenic inheritance, suitable for the QTL analysis (Table 1; Figures 1 and 2).

Table 1. Summary of descriptive statistics for harvest index of wheat in relation to Yecora Rojo and No. 49 parents and their recombinant inbred lines (RILs) in two locations and two years under normal and water deficit stress conditions.

Statistics	Normal	Water deficit stress
Yecora Rojo	54.33	52.66
No. 49	52.61	59.45
RILs mean	48.03	42.68
Minimum	34.13	24.83
Maximum	63.56	67.83
Std. Deviation	0.62	0.79
Skewness	0.22	0.25
Kurtosis	-0.024	0.32

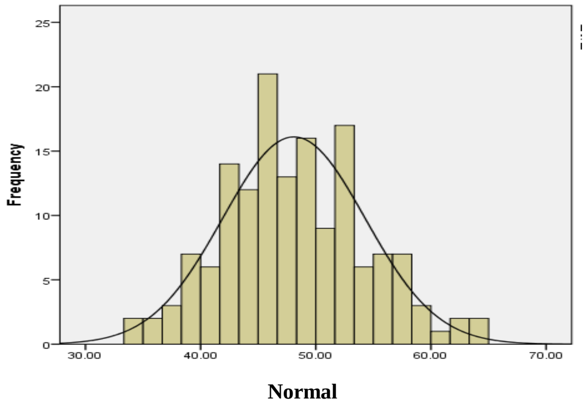

Figure 1. Frequency distribution of harvest index for the studied wheat RILs under normal irrigation conditions, averaged over locations and years.

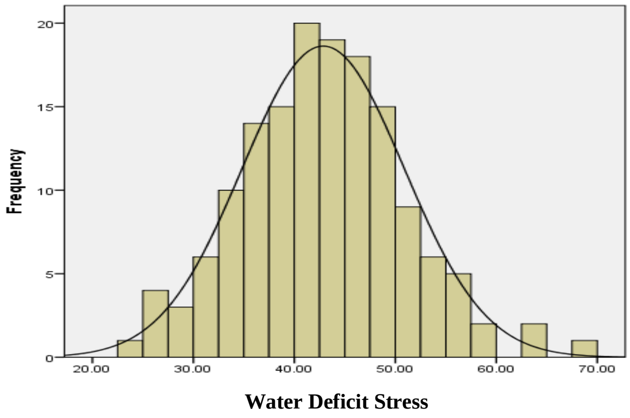

Figure 2. Frequency distribution of harvest index for the studied wheat RILs under water deficit stress conditions, averaged over locations and years.

QTL mapping

Under normal condition, six QTLs (R^2_A= 0.04 to 12.0%), two QTL × environment (E) (R^2_{AE}= 6.28%), five additive × additive (R^2_{AA}= 0.7 to 8.68%) and 12 additive × additive × E (R^2_{AAE}= 3.76 to 11.4%) interactions were significant. Under water deficit stress conditions, two QTLs (R^2_A= 5.0 to 7.0%), two additive × additive (R^2_{AA}= 3.72 to 5.48%) and seven additive × additive × E (R^2_{AAE}= 8.04 to 9.58) interactions were identified (Tables 2 and 3; Figures 3 and 4).

At the normal condition, six QTLs were mapped on 2D1, 6A, 2D2, 4B, 7B and 1A chromosomes for harvest index. Amount of additive value of these QTLs (QHI2D1-N, QHI6A-N, QHI2D2-N, QHI4B-N, QHI7B-N, QHI1A-N) were -0.019, -0.016, 0.016, 0.022, -0.017 and -0.017, respectively, which accounted for 37.04% of total phenotypic variation. Positive values show that the alleles from Yecora Rojo increase the harvest index and negative values indicate that the alleles from No. 49 increase the harvest index value. Thus, four QTLs of QHI2D1-N, QHI6A-N, QHI7B-N and QHI1A-N were contributed by the No. 49 parent and two QTLs of QHI2D1-N and QHI4B-N were contributed by the Yecora Rojo parent. Also, two significant interactions between QHI2D1-N and environments of Mahabad and Miandoab (R^2_{AE} of 6.28%) were found. Therefore, under normal conditions, alleles of the No. 49 parent in Miandoab decreased the amount of harvest index by 0.022, and alleles of Yecora Rojo parent in Mahabad increased harvest index by 0.019 units (Table 2). Furthermore, five additive × additive epistatic interactions between QTLs on chromosome combinations of 5A × 6A, 3A × 6A, 3A × 6A, 2B × 7A and 1B × 1B were significant for harvest index under normal condition (Table 3). Amount of additive × additive value for these effects were -0.031, 0.009, 0.009, -0.014 and 0.043, respectively; and these effects controlled 18.76% of the total phenotypic variation. A positive value (i.e., 3A × 6A, 3A × 6A and 1B × 1B interactions) shows that the parents' effect is larger than the recombinant effect, and a negative value (i.e., 5A × 6A and 2B × 7A interactions) indicates that the recombinant effect is larger than that of parents (Li *et al.* 2014). In addition, under this condition 12 additive × additive × environment interactions were detected, which contributed to 31.98% of the total phenotypic variation (Table 3). In the normal condition, the contribution of additive QTL to total phenotypic variation was larger than additive × environment effects, which indicated that additive QTLs were less influenced by the environmental conditions. In additions, the phenotypic variation explained by additive × additive effects, was smaller than additive QTL effects. Thus, additive QTLs were more important than epistatic QTLs in controlling harvest index, Furthermore, under normal condition, additive × additive effects were influenced by the environment because R^2_{AA} value was smaller than R^2_{AAE}.

In water deficit stress condition, two QTLs on chromosomes 6A and 2D were detected for harvest index (Table 1). The additive value of these QTLs were -0.02 and 0.02, which explained 12.0% of the total phenotypic variation. Both parents carried QTL alleles that increased phenotypic values.

Table 2. Detected QTL for harvest index in a RIL population of wheat derived from the Yecora Rojo × No. 49 cross in two locations under normal and water deficit stress conditions, averaged over two years.

Chr.	QTL	Marker interval	Position (cM)	A	R^2_A (%)	AE	R^2_{AE} (%)
			Normal				
2D1	QHI2D1-N	Wms515 - Gwm349	21.5	-0.019	0.04	AE_2= -0.022 AE_4 = 0.019	6.28
6A	QHI6A-N	Barc113 - Gwm570	22.4	-0.016	6	-	-
2D2	QHI2D2-N	Wmc18 -Wms515	1	0.016	6	-	-
4B	QHI4B-N	Gwm6 - Sukkula/ISSR7.390	51.5	0.022	12	-	-
7B	QHI7B-N	Sukkula/Nikita.520 - Wms297	21.4	-0.017	7	-	-
1A	QHI1A-N	Gwm135 - Wmc333	7	-0.017	6	-	-
Total					37.04		6.28
			Water deficit stress				
6A	QHI6A-WD	Nikita/ISSR9.650 - Cfa2114	37.3	-0.02	7	-	-
2D	QHI2D-WD	Wmc18 - Wms515	0.0	0.02	5	-	-
Total					12	-	-

A: additive effect; R^2: coefficient of determination; AE= additive × environment interaction; AAE2= additive × additive × environment (Miandoab, water deficit stress condition); AE4= additive × additive × environment (Mahabad, water deficit stress condition); Chr.: chromosome.

Table 3. Additive × additive epistatic QTL and additive × additive × environment interaction for harvest index in two locations under normal and water deficit stress conditions, averaged over two years.

Env.	Chr. i	Marker interval	Pos.	Chr. j	Marker interval	Pos.	AA	R^2_{AA}	AAE	R^2_{AAE}
Normal	5A	Barc330 - Gwm617	4.0	6A	Wms334 - Gwm459	375.7	-0.031	5.82	$AAE_2 = -0.03$ $AAE_3 = 0.02$ $AAE_4 = 0.03$	6.46
	3A	Wmc505 - Wms566	65.3	6A	Barc113 - Gwm570	35.6	0.009	1.88	-	3.76
	3A	Wmc505 - Wms566	25.8	6A	Wmc256 - Barc113	48.6	0.009	0.7	$AAE_1 = 0.02$ $AAE_2 = 0.009$ $AAE_3 = -0.02$ $AAE_4 = -0.02$	6.10
	2B	Gwm501 - 3.LTR.105	76.8	7A	Gwm282 - Gwm63	80.2	-0.014	1.68	$AAE_2 = -0.04$ $AAE_3 = 0.03$ $AAE_4 = -0.03$	11.44
	1B	Gwm18 - Gwm413	141.6	1B	Wmc216.2 -Wms131	95.7	0.043	8.68	$AAE_2 = 0.03$ $AAE_3 = -0.02$	4.22
	Total							18.76		31.98
Water deficit stress	5A	Wms154 - Gwm304	41.0	3A	Gwm666 - Wms155	19.3	0.025	3.72	$AAE_1 = 0.03$ $AAE_2 = 0.03$ $AAE_4 = -0.05$	9.58
	7B	Wmc3 - Barc164	80.2	2B	Gwm501 -3.LTR.105	135.2	-0.02	5.48	$AAE_1 = -0.02$ $AAE_2 = -0.02$ $AAE_3 = 0.05$ $AAE_4 = 0.02$	8.04
	Total							9.2		17.62

AA: additive× additive effect; R^2: coefficient of determination; AAE1= additive × additive × environment (Miandoab, normal condition); AAE2= additive × additive × environment (Miandoab, water deficit stress condition); AE3= additive × additive × environment (Mahabad, normal condition); AE4= additive × additive × environment (Mahabad, water deficit stress condition); Env.: environment; Chr.: chromosome; Pos.: position.

It should be noted that the QTL on chromosomes 2D flanked by Wms18-Wmc515 markers were located at the same marker interval, but at different locations. Also, two pairs of additive × additive effects were identified. These epistatic effects were located between QTLs on chromosome combinations 5A × 3A and 7B × 2B with additive × additive values of 0.025 and -0.024, respectively, and explained 9.2% of the total phenotypic variation (Table 3). The epistatic effect of QHI5A-WD × QHI3A-WD increased the values of the parental types and the QHI7B-WD × QHI2B-WD

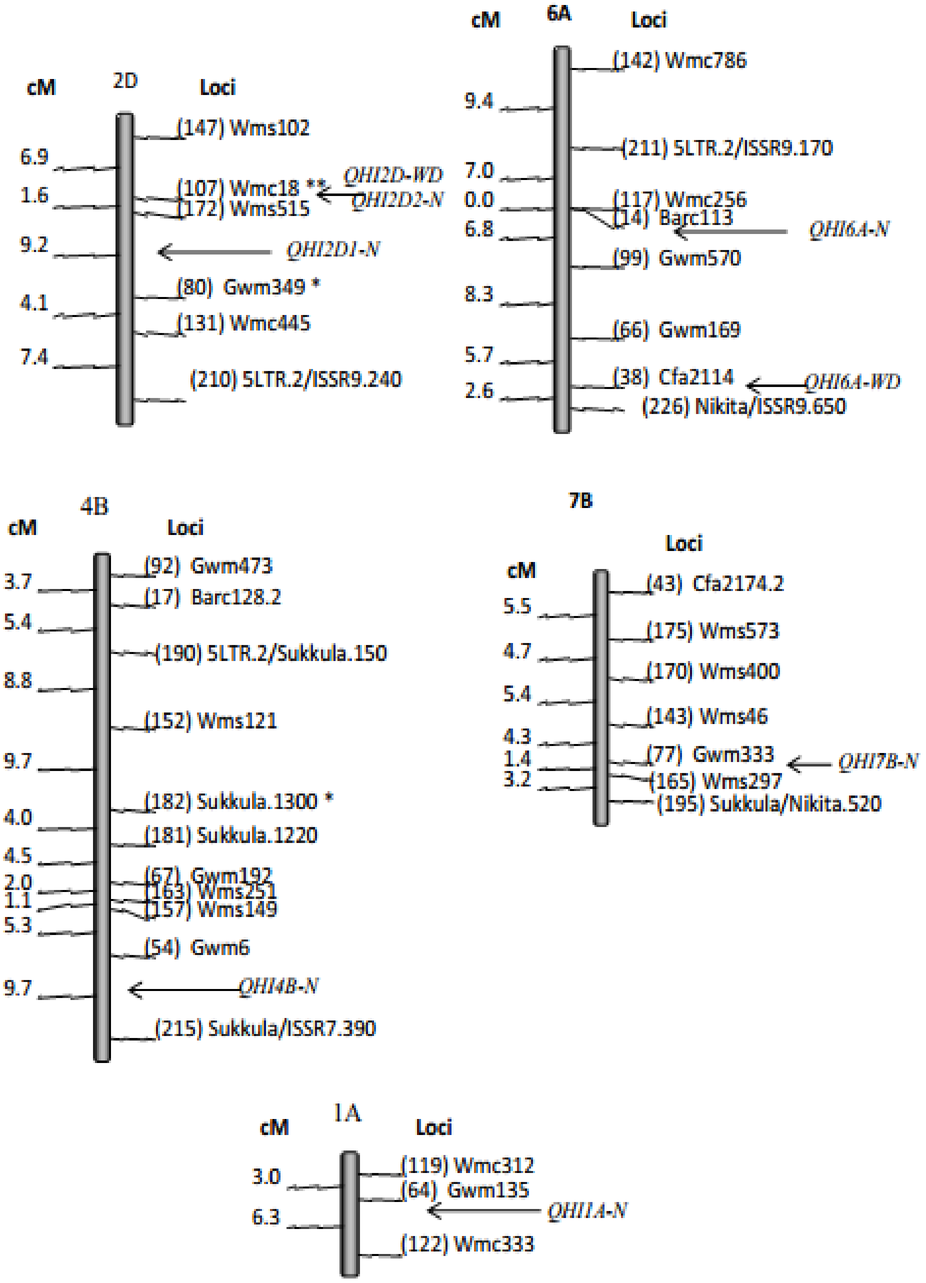

Figure 3. Map location of QTLs identified for harvest index using a RIL population derived from Yecora Rojo × No. 49 cross on the average of two locations, two years and two irrigation conditions.

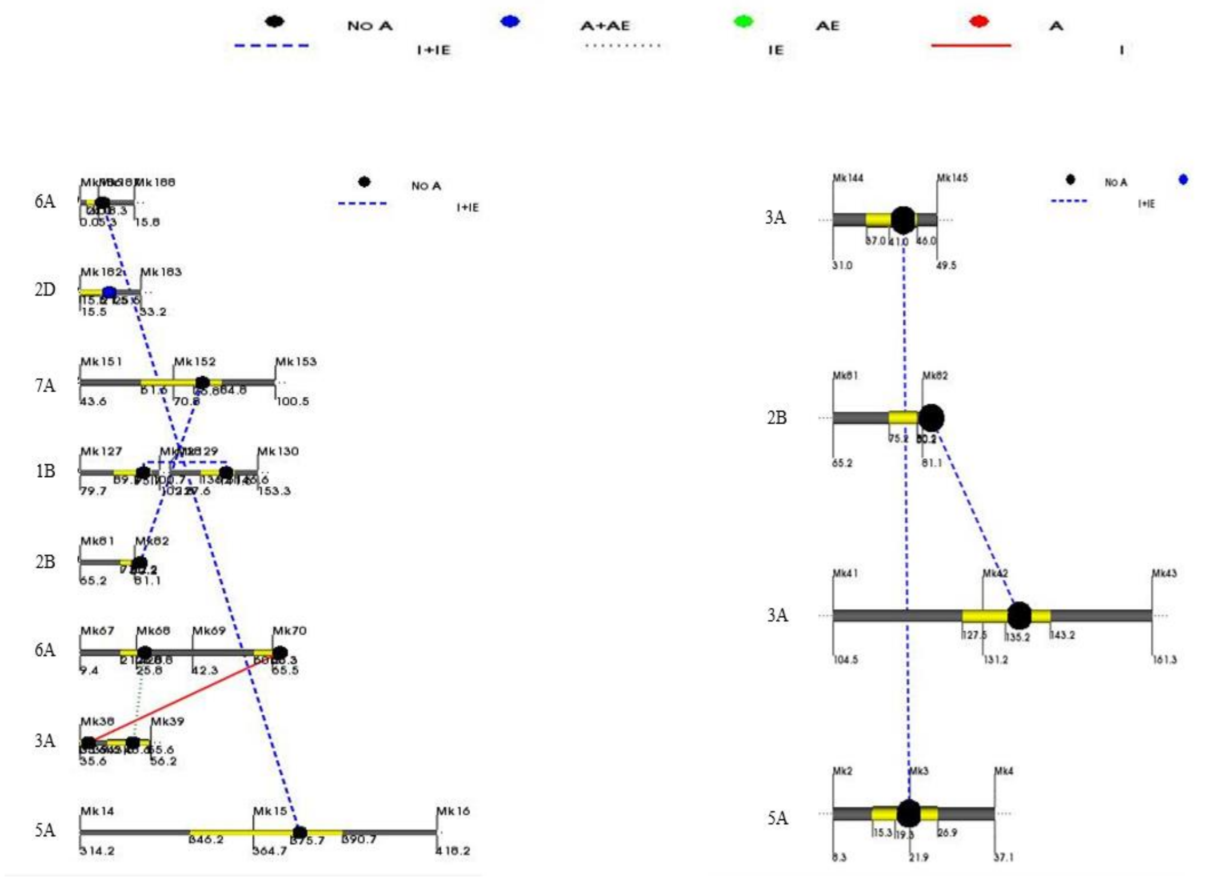

Figure 4. Location of QTLs for harvest index and epistasis among them under normal (left) and water deficit stress (right) conditions.

interaction increased the values of recombinant types. Also, two additive × additive × environment interactions with total R^2_{AAE} of 17.62% were detected (Table 3). Furthermore, under this condition additive × additive epistatic effects were influenced by environment because of R^2_{AA} was smaller than R^2_{AAE}.

Discussion

Under normal condition, six QTLs on 2D1, 6A, 2D2, 4B, 7B and 1A chromosomes and under water deficit two QTLs on chromosomes 6A and 2D significantly contributed to harvest index. In the present study, three QTLs on chromosome 2D, two QTLs on chromosome 6A and only one QTL on chromosomes 4B, 7B, 1A and 7A were found for harvest index. It can be expressed that chromosome 2D played more important role in controlling of harvest index. Furthermore, two QTLs were found on chromosome 2D, flanked by *Wms18- Wmc515* markers under both conditions, but at different locations on this chromosome. These QTLs may be used for marker assisted selection of harvest index in breeding programs. Kumar *et al.* (2007) found four QTLs for harvest index on different chromosomes in wheat. El-Feki (2010) mapped a total of eight harvest index QTLs on chromosomes 1A, 1B, 2B (2), 2D (2), 3A and 6B. McIntyre *et al.* (2010) detected five QTLs, which significantly controlled phenotypic variation of harvest index in wheat. Dodig *et al.* (2012) reported repeatable marker-trait associations on chromosomes 1DL and 2DS for harvest index. McIntyre *et al.* (2010) detected five QTLs for harvest index on chromosomes 1B, 1D, 4D, 6A and 7A. According to Cuthbert *et al.* (2008) five QTLs explained 4.2-11.9% of the phenotypic variation. Markers Xwmc28-5B, Xgwm148-2B and Xcfa2114-6A were identified for harvest index under different environmental conditions in a study by Golabadi *et al.* (2011).

Under normal condition five additive × additive epistatic interactions between QTLs and under water deficit stress condition two additive × additive interactions were recognized. Result showed phenotypic variation explained by the additive × additive effects (R^2_{AA}) was less than the additive QTL effects (R^2_A). Thus, additive QTLs were more important than epistatic QTLs in controlling harvest index in both conditions.

Conclusions

In the represent study, five QTLs in chromosome 2D, two QTLs in chromosome 6A and only one QTL in chromosomes 4B, 7B, 1A, 5B, 7A and 2A were found for harvest index. It can be concluded that chromosome 2D played more important role in controlling of harvest index. Furthermore, one stable QTL was found on chromosome 2D, flanked by Wms18-Wmc515 markers at both irrigation conditions, which may be useful for marker assisted selection of harvest index in breeding programs.

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مکان‌یابی QTLهای با اثرهای افزایشی و اثرهای متقابل اپیستازی افزایشی × افزایشی برای شاخص برداشت در گندم (*Triticum aestivum* L.)

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چکیده

به منظور مکان‌یابی ژن‌های کنترل کننده صفات کمی (QTL) برای شاخص برداشت، ۱۴۸ لاین اینبرد نوترکیب گندم همراه با والدین (YecoraRojo و یک لاین محلی ایرانی با نام No. 49) در شرایط نرمال و تنش کم‌آبی انتهای فصل مورد ارزیابی قرار گرفتند. طرح آزمایشی به صورت آلفا لاتیس با دو تکرار بود که در ایستگاه‌های تحقیقاتی دانشگاه مهاباد و مرکز تحقیقات کشاورزی میاندوآب در طی دو سال زراعی ۱۳۹۳ و ۱۳۹۴ پیاده شد. نقشه پیوستگی مورد استفاده شامل ۱۷۷ نشانگر ریز ماهواره و ۵۱ نشانگر رتروترانسپوزون بود. مکان‌یابی ژن‌های کنترل کننده صفات کمی برای اثرهای افزایشی و اثرهای متقابل اپیستازی افزایشی × افزایشی با استفاده از نرم افزار QTL Network 2.0 و بر اساس روش مکان‌یابی فاصله‌ای مرکب و مدل‌های خطی مخلوط صورت گرفت. نتایج تجزیه QTL نشان داد که در شرایط نرمال شش QTL (R^2_A = ۰/۰۴٪ تا ۱۲٪)، دو اثر متقابل QTL × محیط (R^2_{AE} = ۶/۲۸٪)، پنج اثر متقابل اپیستازی افزایشی × افزایشی (R^2_{AA} = ۰/۰۷٪ تا ۸/۶۸٪) و ۱۲ اثر متقابل افزایشی × افزایشی × محیط (R^2_{AAE} = ۳/۷۶٪ تا ۱۱/۴٪) معنی‌دار بودند. تحت شرایط تنش کم آبی دو QTL (R^2_A = ۵٪ تا ۷٪)، دو اثر متقابل اپیستازی افزایشی × افزایشی (R^2_{AA} = ۳/۷۲٪ تا ۵/۴۸٪) و هفت اثر متقابل افزایشی × افزایشی × محیط (R^2_{AAE} = ۸/۰۴٪ تا ۹/۵۸٪) شناسایی شدند. در مطالعه حاضر سه QTL از هشت QTL شناسایی شده روی کروموزوم شماره 2D مکان‌یابی شد که بیانگر اهمیت این کروموزوم در کنترل شاخص برداشت و امکان استفاده احتمالی از آن در گزینش به کمک نشاگر بود.

واژه‌های کلیدی: اپیستازی؛ رتروترانسپوزون؛ شاخص برداشت؛ گندم؛ نشانگر ریزماهواره؛ QTL.