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Meta Analysis of Quantitative Trait Loci (QTL) for Growth and Yield Related Traits under Drought Stress in Wheat (*Triticum aestivum* L.)

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ABSTRACT

Wheat is a critical crop in temperate climate zones, with demand rising in both urbanized and industrialized countries. However, drought stress significantly impacts global wheat yield, highlighting the need for breeding programs focused on drought tolerant wheat. This study conducted a QTL meta analysis to identify growth characteristics and yield related traits associated with drought tolerance in wheat. Stable QTLs were targeted across different varieties and experimental environments to ensure the success of these breeding programs. The study compiled drought tolerant QTLs from 27 previous studies, identifying a total of 951 QTLs, which were used to create a consensus map. Of these, 538 QTLs were related to yield characteristics, while 413 were linked to growth characteristics associated with drought tolerance. BioMercator V4.2.3 software was employed to generate consensus maps and perform the meta analysis. The consensus map, derived from the combined data, consisted of 457 QTLs spanning a total genetic map length of 727,819 cM. The meta analysis identified 140 MQTLs, with MQTL 5B:7 and 3B:4 emerging as the most significant, harboring 24 and 20 QTLs, respectively. These chromosomes contain major QTLs associated with drought tolerance. The findings provide valuable insights that can be utilized in breeding programs to enhance drought tolerance, yield, and growth in wheat.

Keywords:
Meta analysis; drought; yield, growth; wheat

1. Introduction

Wheat (*Triticum* spp.), a staple crop of global significance, has its origins traced back between 11,000 and 9,500 years ago in the fertile regions of Southeast Turkey and Northern Syria, often referred to as the "cradle of agriculture" [1]. Over millennia, wheat has undergone significant evolutionary changes, evolving from its wild ancestors, such as the diploid wild wheat (*Triticum urartu*) and goat grass (*Aegilops speltoides*), into the complex polyploid species we cultivate today [2].

Modern wheat cultivation is dominated by two species: hexaploid bread wheat (*Triticum aestivum*) and tetraploid durum wheat (*Triticum turgidum* ssp. durum). Bread wheat, accounting

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for approximately 95% of global wheat production, is especially valued for its adaptability and its large, complex genome (16,979 Mbp), making it the most significant grain crop globally [3]. Despite its global importance, wheat is not cultivated in Malaysia due to unfavorable climatic conditions. Instead, Malaysia relies heavily on wheat imports to meet domestic demands, primarily from the United States and Australia [4]. The growing demand for high quality wheat products, driven by economic growth and changing consumer preferences, underscores the need for a stable and sustainable wheat supply.

One of the most pressing challenges in wheat production is the threat of abiotic stress, particularly drought, which is exacerbated by climate change. Drought not only reduces crop yield but also impacts the nutritional quality of the grain, posing a significant threat to food security [5]. The development of drought tolerant wheat varieties through genetic and molecular approaches is crucial for mitigating these impacts and ensuring the sustainability of wheat production in the face of global climate challenges [6,7]. Molecular breeding techniques, including the identification and mapping of quantitative trait loci (QTLs) associated with drought tolerance, have become essential tools in developing resilient wheat cultivars [8]. These approaches enable the selection of traits that enhance water use efficiency, root architecture, and other physiological adaptations critical for survival under drought conditions [9].

Wheat is a staple food globally, but Malaysia's tropical climate, marked by high humidity, temperatures, and rainfall, poses significant challenges for its cultivation. These conditions are unfavorable for wheat, which typically thrives in temperate climates with cooler temperatures and less moisture [10]. In Malaysia, rice remains the primary staple food, with per capita consumption significantly higher than that of wheat. According to the Food and Agriculture Organization (FAO), the average Malaysian consumes about 80–90 kilograms of rice annually. In contrast, wheat consumption is considerably lower, with the average per capita consumption ranging between 30–40 kilograms per year. While rice is deeply rooted in the Malaysian diet and culture, wheat-based products like bread, noodles, and pastries have grown in popularity, particularly in urban areas. The rising demand for wheat products is partly due to the influence of Western diets and the convenience of wheat-based foods [11].

As a result, Malaysia is heavily reliant on wheat imports to meet domestic demand. The country imports around 1.6 million metric tons of wheat annually, mainly from Australia and the United States . This dependence on imports exposes Malaysia to global market fluctuations and supply chain disruptions, such as those caused by climate change and geopolitical events like the Russia-Ukraine conflict, which have impacted wheat production and export globally. Droughts in key wheat-producing regions, including the U.S., Canada, and France, have led to reduced yields, exacerbating supply challenges and driving up global wheat prices [12]. This situation highlights the vulnerability of Malaysia's wheat supply chain and underscores the need for exploring potential domestic wheat cultivation, even on a small scale, to enhance food security [12].

In this context, understanding the genetic and physiological mechanisms underlying wheat's response to drought stress is imperative. The integration of genetic mapping with advanced genomic techniques offers new opportunities for developing drought tolerant wheat varieties, thereby contributing to global food security in an increasingly unpredictable climate [8,13]. This study aims to provide insights into the molecular mechanisms of drought tolerance in wheat, focusing on the identification and characterization of key QTLs that can be leveraged in breeding programs to enhance the resilience of wheat crops under adverse environmental conditions. In addition, the genes that are identified within the identified key QTLs can be a source of genes used for genetic modification of crops especial cereal crop like rice.

2. Methodology

2.1 QTL Data Collection and Synthesis

QTL data related to drought tolerance in wheat were gathered through a review of previous wheat QTL mapping studies. Credible sources such as Google Scholar, PubMed, and Scopus were used to identify relevant articles. Twenty seven resources were selected to ensure comprehensive and reliable data. Keywords like "drought tolerance," "drought stress," and "water deficit" were employed to locate pertinent studies. While the publication date was flexible, recent articles were prioritized to ensure up to date information. The collected data were compiled into input files, including key details such as the genus and species, donor and recipient varieties, breeding type, population size, molecular markers, and their positions (in cM). For any incomplete genetic map data, the Gramene database (Gramene) was referenced for molecular marker positions. QTL data were similarly compiled, including QTL names, traits, locations, LOD scores, phenotypic variance (R^2), and positions. Major QTLs were defined by an average LOD score > 3.0 and an average phenotypic variance > 10%, with stable QTLs consistently appearing across at least four different environments [14] (please refer to supplementary data and Table 1 for this information).

2.2 QTL Mapping

The collected genetic map and QTL (Table 1 and supplementary file) data were organized into input files in both Microsoft Excel and Text (Tab Delimited) formats. BioMercator V4.2.3 bioinformatic software was used for QTL mapping, where the positions of QTLs and molecular markers were displayed. Special care was taken to ensure the accuracy of input file formats to avoid mapping errors.

2.3 Consensus Mapping and QTL Projection

Using BioMercator, a consensus map was generated by integrating the data from previous studies onto a reference map by Qu *et al.*, [15]. This process included various types of molecular markers, with a focus on Short Simple Sequences (SSR), among others. Inconsistent marker sequences were filtered out to ensure accuracy. QTL projection was then performed by aligning the QTLs from the original maps onto the reference map. This projection was based on LOD scores, variance values, and QTL locations. The 95% confidence interval (CI) of QTLs on the original maps was estimated using the method by Darvasi and Soller [16]: $CI = 503/NR^2$, where N is the population size and R^2 is the variance.

2.4 Meta QTL Analysis for Drought Tolerance

Following the consensus mapping and QTL projection via the bioinformatic platform, a meta-QTL analysis was conducted using BioMercator V4.2.3. This analysis integrated QTLs related to growth and yield traits across different populations, locations, or environmental conditions. The number of meta-QTLs per chromosome was determined using five Model Selection Criteria: AIC (Akaike Information Content), AICc (AIC Correction), AIC3 (AIC 3 Candidate Models), BIC (Bayesian Information Criterion), and AWE (Average Weight of Evidence). The optimal meta QTL was identified based on the highest number of QTLs across these models, calculated with a 95% confidence interval.

3. Results and Discussion

3.1 QTL Data Collection from Previous Studies

A total of 27 [17-43] research articles related to drought tolerance in wheat were collected for further analysis. These studies provided detailed information on wheat varieties, population sizes, breeding types, and environmental conditions. From these 27 articles, 37 genetic maps related to drought tolerance in wheat were extracted and integrated into a comprehensive genetic map (Table 1). Additionally, 951 QTLs associated with drought tolerance were identified and recorded, covering 15 growth traits and 16 yield related traits (Table 2 and supplementary file). The collection also included 6,907 molecular markers such as Short Simple Sequences (SSR), Restriction Fragment Length Polymorphisms (RFLP), Random Amplified Polymorphic DNA (RAPD), Sequence Tagged Sites (STS), Amplified Fragment Length Polymorphisms (AFLP), Microsatellites (STMS), Microsatellite Primed Polymerase Chain Reaction (MPPCR), Expressed Sequence Tags (EST), and Single Nucleotide Polymorphisms (SNP).

Hotspot regions for QTLs related to drought tolerance were identified, along with stable QTLs across various wheat varieties, breeding methods, and environments. These stable hotspots can be further utilized in breeding programs. Among the 951 QTLs, 538 were associated with yield traits, and 413 were related to growth traits, with yield traits being more frequently studied. The data collected emphasized that traits such as root system characteristics and senescence are crucial for growth under drought conditions, as roots play a significant role in accessing water from deeper soil layers during water scarcity.

Agronomic traits like plant height, harvest index, total biomass, number of productive tillers, grain weight per spike, and physiological traits such as canopy temperature, chlorophyll content, photosynthetic rate, and water soluble carbohydrates were found to significantly contribute to grain yield in wheat. Enhanced biomass production, driven by higher photosynthesis rates, stomatal conductance, leaf chlorophyll content, and radiation use efficiency, was also linked to increased yield. Both growth and yield traits are interdependent and vital for producing healthy and high quality wheat (Table 2).

3.1 Consensus Map Results

For this study, the bioinformatics software BioMercator V4.2.3 was used for QTL mapping and identifying molecular markers flanking QTL regions associated with drought tolerance in wheat. The consensus map was generated from 37 genetic maps obtained from previous studies. QTL regions related to drought tolerance were identified on each chromosome. A total of 457 QTLs were identified on the consensus map, with an overall map length of 727,819 cM. The reduction in QTLs from 951 to 457 occurred as BioMercator V4.2.3 automatically removed inverted co-located loci.

Of the 457 QTLs collected through the consensus map, chromosome 3B recorded the highest number with 68 QTLs, followed by chromosome 5A with 54 QTLs. The chromosome with the fewest QTLs was chromosome 4D, with no QTLs detected. Chromosome 3B influences grain weight stability in crops exposed to brief heat shocks during early grain filling [43]. Additionally, the region on chromosome 3B is associated with QTLs for the number of tillers that can survive under drought and heat stress, grain number, biomass, and harvest index in well-watered conditions, all traits needed to produce good yield [28,44]. Wheat chromosome 5A is known to carry several genes affecting adaptation and productivity [45]. Most beneficial QTLs were located on chromosomes 3B, 5B, 7A, and 7D, with no beneficial QTLs detected on chromosomes 1A, 4D, 5A, and 6B [46]. This indicates that the observation of the highest number of QTLs on chromosome 3B and the lowest on

4D from the consensus map aligns with previous studies. Table 3 shows the number of QTLs for each chromosome on the generated consensus map. Although consensus maps were generated for all the chromosomes in wheat, Figure 1(a) only displays the two chromosomes of significance in this study.

Table 1
The list of 27 publications used in this study

Title of Journal	Population Size	Donor variety	Recipient Variety	Type of Breeding	Type of drought treatment and duration	Reference
Mapping QTL for chlorophyll fluorescence kinetics parameters at seedling stage as indicators of heat tolerance in wheat	150	Hanxuan 10	Lumai 14	DHL	While this study primarily focuses on heat stress, drought stress may also be applied by withholding water to induce soil moisture deficit during seedling stages to assess combined heat and drought tolerance. However, the main focus is on high temperature stress.	Azam *et al.*, [17]
Mapping of QTLs associated with abscisic acid and water stress in wheat	150	Pavon76	Yecora Rojo	RIL	Drought stress was imposed by withholding water at critical growth stages, often reducing soil moisture to simulate drought conditions. The level of water reduction is closely monitored, and abscisic acid levels were measured as a physiological response to the water-deficit conditions.	Barakat *et al.*, [18]
Mapping QTLs for grain yield components in wheat under heat stress	397	HD2808	HUW510	F6	This study mainly addresses heat stress, but drought is often applied as a combined treatment by limiting water supply during reproductive stages to induce water stress, alongside heat treatments.	Bhusal *et al.*, [19]
QTL for root angle and number in a population developed from bread wheats (*Triticum aestivum*) with contrasting adaptation to water-limited environments	184	SeriM82	Hartog	DHL	The study involves controlled drought stress by reducing irrigation to simulate water-limited environments. Soil moisture content is typically monitored and maintained at lower levels to observe root growth traits under drought conditions.	Christopher *et al.*, [20]
QTL associated with heat susceptibility index in wheat (*Triticum aestivum L.*) under short-term reproductive stage heat stress	64	Halberd	Cutter	F5	Though the primary stress in this study is heat during the reproductive stage, short-term drought stress may also be applied by restricting irrigation to simulate conditions often seen in water-scarce environments during the reproductive phase of wheat growth.	Mason *et al.*, [21]
Detection of consensus genomic regions associated with root architecture of bread wheat on groups 2 and 3 chromosomes using QTL meta–analysis	206	WL711	C306	RIL	Drought stress was applied through controlled water-limiting conditions where irrigation is withheld or reduced to observe root architecture traits, such as root angle and root length, under water-deficit environments.	Darzi-Ramandi *et al.*, [22]

Conditional and unconditional QTL mapping of drought-tolerance-related traits of wheat seedling using two related RIL populations	302	Weimai 8	Yannong 19	RIL	Applied through soil moisture reduction and maintained at controlled levels during seedling stages.	Zhang *et al.,* [23]
QTL analysis of drought tolerance for seedling root morphological traits in an advanced backcross population of spring wheat	177	Devon	Syn084	F3	Reduced irrigation to control water availability and impose water-deficit conditions.	Ibrahim *et al*., [24]
QTL Mapping of Wheat Double Haploids for Chlorophyll Content and Chlorophyll Fluorescence Kinetics Under Drought Stress Imposed at Anthesis Stage	140	Opata	SH223	DH	Imposed through a water-withholding treatment at anthesis to simulate terminal drought conditions.	Ilyas *et al*., [25]
QTLs for cell membrane stability and flag leaf area under drought stress in a wheat RIL population	206	WL711	C306	F3	Drought was simulated by withholding irrigation at the critical flag leaf stage.	Khanna-Chopra *et al*., [26]
Quantitative Trait Loci for Grain Yield and Adaptation of Durum Wheat (*Triticum durum Desf.*) Across a Wide Range of Water Availability	249	Kofa3	Svevo	F7	Controlled water regimes ranging from irrigated to rain-fed environments were used to apply varying levels of drought.	Maccaferri *et al*., [27]
Mapping of QTLs Associated with Yield and Yield Related Traits in Durum Wheat (*Triticum durum Desf.*) Under Irrigated and Drought Conditions	109	Omrabi 5	Belikh 2	Biparental	The stress was induced by managing different irrigation levels to simulate drought and fully irrigated conditions.	Arif *et al*., [28]
QTL mapping for physiological maturity in synthetic hexaploid wheat (*Triticum aestivum L.*) under drought stress	84	Opata	SH349	DHL	Drought was imposed by limiting water supply during critical growth stages, particularly during grain-filling.	Fatima [29]
Genetic basis of traits related to stomatal conductance in wheat cultivars in response to drought stress	150	Hanxuan 10	Lumai 14	RIL	Water-deficit was imposed by withholding irrigation to reduce soil water content during key growth stages.	Wang *et al*., [30]
Genomic regions associated with grain yield under drought stress in wheat (*Triticum aestivum L.*)	206	WL711	C306	RIL	Stress was applied by subjecting the plants to low water conditions and rain-fed environments.	Shukla *et al*., [31]
Mapping QTLs associated with agronomic and physiological traits under terminal drought and heat stress conditions in wheat (*Triticum aestivum L.*)	167	SeriM82	Babax	F7	Water-withholding treatments were applied at late developmental stages to simulate terminal drought stress.	Tahmasebi *et al*., [32]

Genetic Mapping of Potential QTLS Associated with Drought Tolerance in Wheat	180	6544-6	Chakwal-86	F2	Simulated by reducing water supply during key growth phases, especially post-anthesis.	Malik *et al*., [33]
QTL on wheat (*Triticum aestivum L.*) chromosomes 1B, 3D and 5A are associated with constitutive production of leaf cuticular wax and may contribute to lower leaf temperatures under heat stress (2008)	121	Halberd	Karl92	F7	Imposed through controlled water-deficit treatments.	Mondal *et al*., [34]
Mapping QTL for the traits associated with heat tolerance in wheat (*Triticum aestivum L.*)	96	Ventnor	Karl92	RIL	Water withholding was applied during specific growth stages in combination with high-temperature treatments.	Talukder *et al*., [35]
QTL mapping for nine drought-responsive agronomic traits in bread wheat under irrigated and rain-fed environments	192	Excalibur	Kukri	DH	Applied using rain-fed conditions as the primary method of simulating drought.	Gahlaut *et al*., [36]
Modeling and mapping QTL for senescence-related traits in winter wheat under high temperature	101	Ventnor	Karl 92	RIL	Reduced irrigation along with high-temperature conditions were used to simulate stress.	Vijayalakshmi *et al.*, [37]
Mapping QTLs for Heat Tolerance in Wheat	144	Kauz	MTRWA116	F9	Water-deficit imposed in combination with high temperatures.	Mohammadi *et al.*, [38]
Mapping QTLs for stomatal density and size under drought stress in wheat (*Triticum aestivum L.*)	150	H10	L14	DH	Imposed by withholding water at key stages to induce drought.	Wang *et al*., [39]
Mapping QTLs for seedling root traits in a doubled haploid wheat population under different water regimes	150	Hanxuan 10	Lumai 14	DHL	Different water regimes, including drought through reduced irrigation.	Liu *et al*., [40]
QTL mapping for yield and photosynthetic related traits under different water regimes in wheat	131	Chuan 35050	Shannong 483	RIL	Applied through controlled irrigation levels to simulate drought.	Feng *et al*., [41]
Quantitative Trait Loci Mapping for Chlorophyll Fluorescence and Associated Traits in Wheat (*Triticum aestivum*)	150	Hanxuan 10	Lumai 14	RIL	Imposed by reducing water availability during the grain-filling period.	Yang *et al*., [42]
Genomic dissection of drought resistance in durum wheat ¥ wild emmer wheat recombinant inbreed line population	152	Langdon	G1816	RIL	Controlled water-deficit conditions applied through soil moisture reduction to specific levels.	Peleg *et al*., [43]

RIL (*Recombinant Inbred Lines*), DHL (*Doubled Haploid Lines*), DH (*Doubled Haploid*), F2 (*second filial*), F3 (*third filial*), F5 (*fifth filial*), F6 (*sixth filial*), F7 (*seventh filial*), F9 (*ninth filial*), Biparental.

Table 2
Shows the list of growth traits and yield traits involved in drought tolerance in wheat

List of Growth Traits	**List of Yield Traits**
Plant height	Grain yield
Days to anthesis	Total grains per spikelet
Abscisic acid	Total grain weight per spikelet
Days to maturity	Leaf length/width
Senescence	Days to flowering
Total root length	Grains per grain
Root surface area	Total chlorophyll
Average root diameter	Membrane stability
Estimated days to anthesis	Photosynthetic rate
Maximum root length/length of root spikes	Productive tillers
Maximum number of root spikes	Harvest index
Grain filling rate	1000 grain weight
Days to flowering	Grain filling duration/rate
Total root length	Leaf blade length/width
Harvest index	Coleoptile length
Chlorophyll fluorescence	

Table 3
Shows the number of QTLs for each chromosome on the consensus wheat map generated

Chromosome	Number of QTLs
1A	13
1B	17
1D	16
2A	35
2B	47
2D	14
3A	14
3B	68
3D	5
4A	25
4B	9
5A	54
5B	36
6A	12
6B	6
6D	3
7A	37
7B	33
7D	23
Total	457

3.2 Meta-QTL Analysis

Meta-QTL analysis, derived from previous studies, enables the integration of QTL information. The software BioMercator V4.2.3 was used to analyze the number of meta-QTLs (MQTLs) on each chromosome based on model selection criteria, including AIC, AICc,AIC3, BIC, and AWE. The selected values were based on the criteria where at least three out of the five generated models were consistent. Additionally, molecular markers flanking the mQTLs were identified. Table 4 below summarizes all the mQTLs obtained using BioMercator V4.2.3, including the number of chromosomes involved for each model and the traits associated with drought tolerance in wheat.

A total of 140 MQTLs were identified, encompassing 456 QTLs overall. This represents a slight reduction from the 457 QTLs initially mapped, as one QTL from the consensus map was not included in the mQTL region due to its membership probability being less than 50%. In the mQTL analysis, 19 chromosomes were involved, while two chromosomes, 4D and 5D, did not produce MQTLs. Chromosomes 4D and 5D were less frequently reported in previous studies, which led to BioMercator being unable to generate a mQTL map for these chromosomes. Chromosomes 4D and 5D analyses were found on 20 different chromosom, excludinal locations excluding both these chromosome [36]. Chromosomes 2A, 3A, 4A, and 5D each contributed less than 3.3% of genetic variance [27]. Furthermore, according to Xin *et al.,* [48], QTLs were identified for all 21 chromosomes except for 1A, 1B, 4B, 4D, and 5D, with individual QTLs contributing only 10% of phenotypic variation. As a result, 19 out of 21 chromosomes were successfully included in the mQTL analysis. Figure 1(b) shows the selected MQTL maps of two selected chromosome of significance in this study.

Table 4
Provides details on mQTLs and the traits associated obtained with BioMercator V4.2.3. Only chromosomes with QTLs and traits related to yield and growth under drought stress are listed below

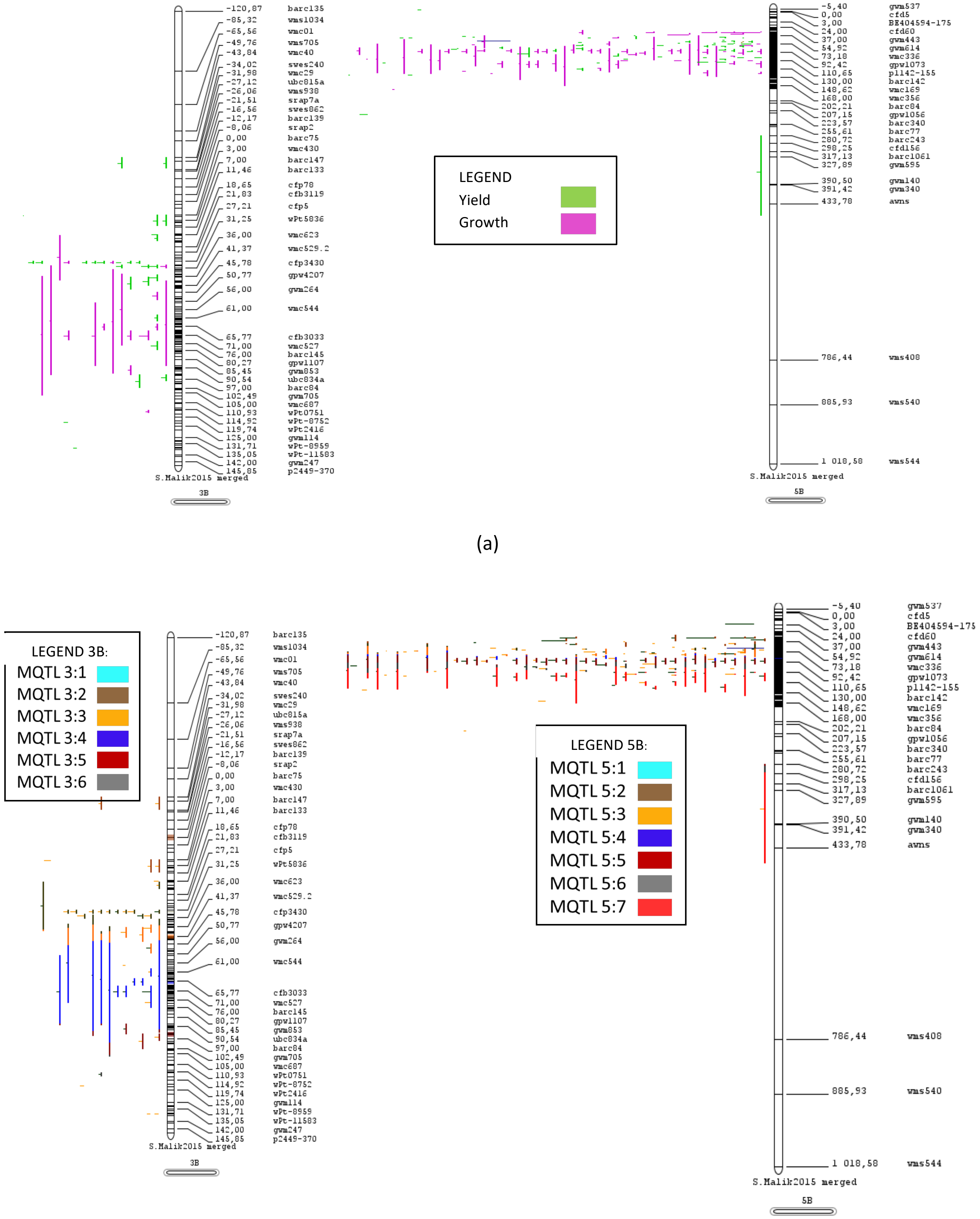
Chromosome	MQTL	Position (cM)	Number QTL	No Traits	Traits Involved
1A	MQTL 1:1	67.52	8	8	Fv, Fm, CL, TRL, Fv/Fm, SH, CTWD, KN
	MQTL 1:2	73.87	1	1	RL
	MQTL 1:7	87.43	3	3	GY, SK, sd
1B	MQTL 1:1	25.05	1	1	Htscc
	MQTL 1:7	29.36	3	3	PH, HI, Yd
	MQTL 1:8	32.19	3	3	GFD, Sps, sl
	MQTL 1:9	37.69	8	6	FO, Fo, Fo, FLCW, TC, GY, Sps, Phr
1D	MQTL 1:1	4.1	2	2	RDW, E
	MQTL 1:3	49.78	3	3	TGWWD, PHE, GFD
	MQTL 1:7	72.71	7	7	Da, Tip, Crs, Frk, Sra, Trl, SPLS
	MQTL 1:8	93.95	1	1	FLW
	MQTL 1:9	135.65	3	3	YLD, DHE, DMA
2A	MQTL 2:1	6.62	2	2	GFD, KN
	MQTL 2:2	26.65	3	3	Fv/Fm, SSS, SCN
	MQTL 2:3	45.86	16	5	RL, RN, HI, RA, RV, RA, RA, RV, RA, RL, RN, RN, RA, RV, RL, RV
	MQTL 2:5	53.44	9	8	RL, Rv, Trl, Frk, Sra, HI, RV, KNS, FSS
	MQTL 2:6	60.47	3	3	FLRI, TSS, SDM
	MQTL 2:7	89.04	2	2	RWC, SK
2B	MQTL 2:1	7.3	7	1	RL, RL, RL, RL,RL, RL, RL
	MQTL 2:2	31.85	4	3	RDW, RDW, FLW, SK
	MQTL 2:4	44.62	9	8	KN, KW, RN, HI, CL, GS, SRN, PN, RN
	MQTL 2:5	67.91	11	8	RA, SRA, GY, GFD, SRA, HD, TC, FLRI, RA, Fo, SRA
	MQTL 2:6	77.44	5	5	CL, HIWD, RSA, PRA, CHLC
	MQTL 2:7	88.01	1	1	SRA
	MQTL 2:8	91.62	4	4	HI, sd, HD, Crs
	MQTL 2:9	100	5	4	DPH, GY, GY, PH,, Htpmd
	MQTL 2:10	347.02	1	1	RN
2D	MQTL 2:1	4.2	1	1	GNWD
	MQTL 2:2	30.67	6	5	FLLWD, FLAWD, FLWWD, FLAWD, CMSWD, DTFWD
	MQTL 2:3	51.17	7	7	Sra, Trl, Frk, MRL, sw, Crs, GS,
3A	MQTL 3:1	3.91	2	2	Sw, MRL
	MQTL 3:2	27.68	1	1	sd

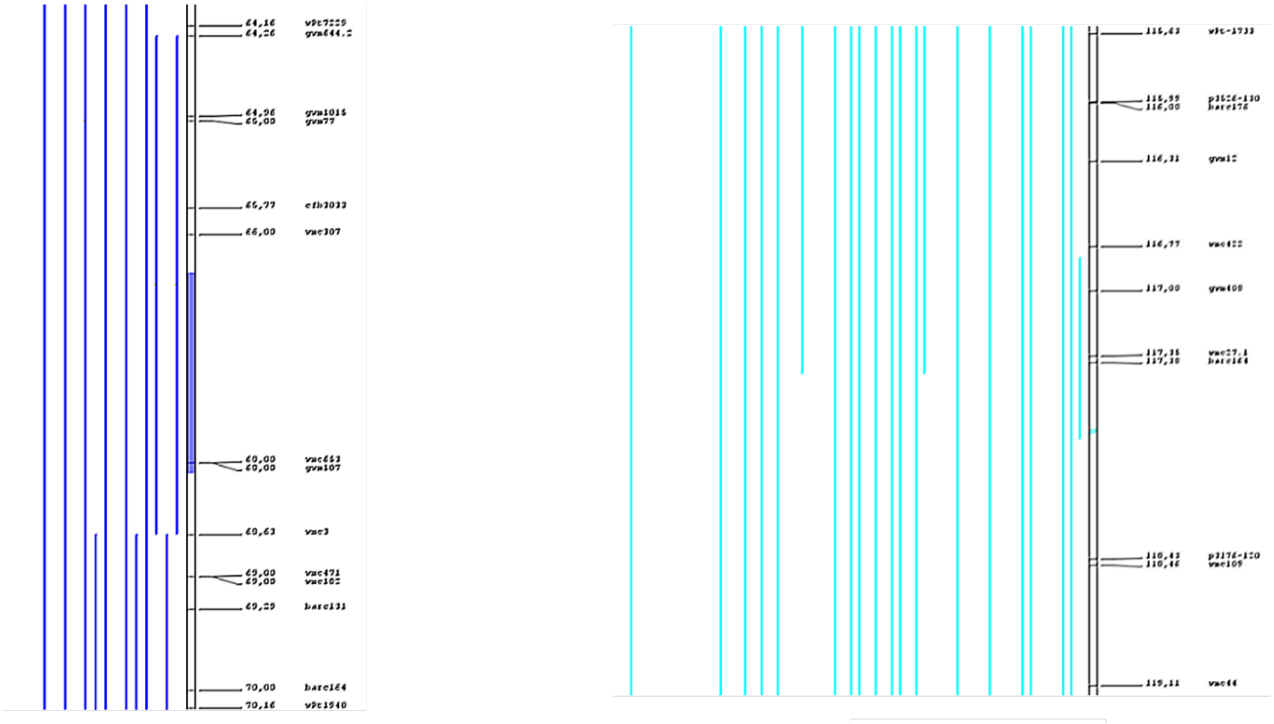
	MQTL 3:3	51.28	3	3	RN, RN, PH
	MQTL 3:4	71.79	6	3	RV, RV, RL, RL, RA, RA
	MQTL 3:5	86.34	2	2	Rv, RL
3B	MQTL 3:1	11.81	6	6	FLL, KN, PN, KNS, BMWD, TGWWD
	MQTL 3:2	28.4	17	12	CTWD, SPNWD, TNWD, GNWD, HIWD, BMWD, TNWD, CMSWD, GYWD, CMSWD, SPNWD, TKW, TGWWD, GYWD, DTFWD, GNWD, RDi
	MQTL 3:3	41.79	7	7	FLAWD, PHTWD, DSIGY, HIWD, TDS, HI, GYWD
	MQTL 3:4	67.22	20	16	RL, RA, RA, RL, RA, SRA, FVFM, TRL, FVFM, TDFL, CL, SpsD, GrD, SwD, RSA, PRA, ScD, SRN, SCN, RDW
	MQTL 3:5	95.13	6	6	RN, HI, DSIGY, TGWWD, Bm, KW
	MQTL 3:6	119.55	11	8	HI, ST, MP, Sps, MP, PH, Yd, HI, Sw, PhrD, PhrD
	MQTL 3:7	39.26	5	4	GYWD, HIWD, PHTWD, BMWD, PHTWD
4A	MQTL 4:1	219.4	1	1	TC
	MQTL 4:2	6.92	10	10	RL, Fm, sd, KN, Rv, Fv, Tip, Fv/Fm, SCN, CL
	MQTL 4:3	39.92	4	4	SK, HI, SDM, CHLC
	MQTL 4:4	50.82	2	2	E, GS
	MQTL 4:5	51.85	3	3	DHM, GY, SDM
	MQTL 4:6	56.49	1	1	RDW
	MQTL 4:10	89.92	4	4	HI, Mrso, DSIGY, GYWD
4B	MQTL 4:1	33.62	2	2	DHM, DPH
	MQTL 4:6	34.69	2	2	FLRI, PHTWD
	MQTL 4:8	35.87	3	3	GNWD, GY, TDM
5A	MQTL 5:1	20.1	5	4	RSFWR, Ptm, RFW, Da, Dm
	MQTL 5:2	53.08	7	7	CHL, FLCW, SpsD, TDM, HI, TDS, DPH
	MQTL 5:3	58.68	10	10	Ph, Bm, CHLC, Tkw, TDFL, Hd, MP, 75Gh, Mrso, KN
	MQTL 5:4	81.06	17	14	FLRI, DHM, E, FLWWD, DRI, HdD, Gr, Da, Da, Yd, Gp, Dm, Dm, Da, SK, Gfd, ST
	MQTL 5:5	131.35	10	10	Wue, SwD, GS, sd, Sc, PhD, Tr, DPH, TkwD, SL
	MQTL 5:6	166.09	5	5	GY, sl, sd, KW, SCN
5B	MQTL 5:1	56.92	7	7	Trl, Sra, GM2, ROL, Dm, TrD, Sps
	MQTL 5:2	67.58	2	2	PHE, KN
	MQTL 5:3	75.64	3	3	FLRI, SCOM, MRL
	MQTL 5:7	117.75	24	20	Sps, YDd, HID, TC, GrD, GrD, Tip, Sps, Tr, DRI, RSA, Gr, Gr, Sw, Sw,FLL, CHLC, Sc, Bm, TRL, Gfd, FLW, Wue, PRA
6A	MQTL 6:1	4.08	4	4	SCOM, RN, GY, RA
	MQTL 6:6	39.85	2	2	BMWD, TGW
	MQTL 6:7	46.56	1	1	FVFM
	MQTL 6:8	98.03	5	5	FV/FM, sd, sl, sd, E
6B	MQTL 6:1	35.75	3	3	SSS, PN, HI
	MQTL 6:3	51.85	1	1	FLRI
	MQTL 6:6	30.58	3	3	Tip, KW, GFD
7A	MQTL 7:1	27.04	2	2	Ht, FLW
	MQTL 7:2	47.76	14	8	Da, Da, Tgw, Dm, Da, Gfd, Dm, Da, Dm, Dm, SDM, STI, ScD, PH
	MQTL 7:3	59.66	4	4	BmD, SwD, Fm, TDM
	MQTL 7:4	69.6	3	3	FM, FV, SRN
	MQTL 7:5	76.39	7	6	CHLC, CL, Tmrso, Htpmd, Htpmd, Fv/Fm, Htscc
	MQTL 7:6	105.2	4	4	SK, Tkw, SID, CMSWD

	MQTL 7:7	159.39	3	3	Crs, gwe, Trl
	MQTL 7:2	15.54	4	4	GY, SDM, CL, HI
	MQTL 7:5	53.4	7	7	SI, Sw, FLRI, Phr, WueD, SpsD,Bm
	MQTL 7:7	70.82	9	7	HI, Bm, TrD, Yd, YdD, BmD, SSS, Ph, Tr
	MQTL 7:8	90.84	2	2	TKW, CHL
	MQTL 7:9	109.36	8	8	TGWWD, 25Go,GYWD, KW, SI, PH, Fo, Spado
7D	MQTL 7:1	26.52	4	4	Tip, Trl, Sra, Frk
	MQTL 7:2	42.77	1	1	FVFM
	MQTL 7:3	55.02	1	1	FVFO
	MQTL 7:4	64.84	6	6	FVFO, YLD, GM2, SPLS, DMA, SPAD
	MQTL 7:5	72.43	5	5	DHE, ROL, TGW, PHE, FV
	MQTL 7:6	87.36	3	3	Fo, 25Go, Tmrso
	MQTL 7:7	107.51	3	3	FVFM, FV, FO

Legend:

Yield (YLD) and growth (GW) are critical traits, with measurements like initial fluorescence (FO), maximum fluorescence (FM), and variable fluorescence (FV) used to assess photosynthetic efficiency. The maximum quantum efficiency of photosystem II (FV/FM) and maximum fluorescence yield (FVFO) are essential indicators, alongside abscisic acid (ABA) levels that influence stress responses. Grain characteristics, including grain weight per spike (GWS/GSP), grain filling duration (GFD), grain number per spike (GNS), and thousand grain weight (TGW), are crucial for yield determination. The grain filling rate (GFR) and grain yield (GY/YLD) are also important. Root traits such as seminal root angle (RA/SRA), seminal root number (RN/SRN), and root length (RL) contribute to drought tolerance and nutrient uptake. Flag leaf traits like length (FLL), width (FLW), and area (FLA) are significant for photosynthesis. Days to flowering (DTF), coleoptile length (CL), seedling height (SH), and seedling fresh (SFW) and dry weight (SDW) are vital growth parameters. The root-to-shoot fresh weight ratio (RSFWR), root diameter (RD), root volume (RV), and average root diameter (ArD) are indicators of root system architecture. Root crossings (CRS), forks (FRK), tips (Tip), surface root area (SRA), and total root length (TRL) are also essential. Total chlorophyll content (TC), cell membrane stability (CMS), heading rate (HD), and plant height (PH/RPH/PHT/PHE/HT) are critical for stress tolerance. Germination (Gr) and heading time (Hd) are key developmental traits. Transpiration rate (TRD), stomatal conductance (Sc/GS), and photosynthetic rate (PHR) influence water use efficiency (WUE), while spike length (Sl), spike weight (SW), seeds per spike (SPS), and thousand kernel weight (TKW) impact yield..Biomass yield (Bm), harvest index (HI), stress tolerance index (STI), mean productivity (MP), and stress tolerance (ST) are critical for drought resistance. Days to physiological maturity (DPMS) and control (DPMC) define maturity stages. Grain number (GN), tiller number (TN), and spike number (SPN) are yield components, while drought stress index (DSI), canopy temperature (CT), leaf rolling (ROL), and spikelet per spike (SPLS) indicate stress adaptation. Spikelet compactness (SCOM/SCN), grain per square meter (GM2), days to maturity (DMA/DM), and chlorophyll content (SPAD/CHLC) are additional important traits. Relative water content (RWC), flag leaf cultivar waxes (FLCW), temperature depression of flag leaf (TDFL) and main spike (TDS), thylakoid membrane damage (TMD), SPAD chlorophyll content (SCC), and plasma membrane damage (PMD) are crucial for assessing plant health. Germination percentage (GP), days to anthesis (DA), productive tillers per square meter (PTM), and grain weight per ear (GWE) are vital for crop yield. The grain yield per plot (GYPP), green heat (75GH, 25GO, 50GO), maximum rate of senescence (MRS), time to maximum rate at senescence (TMRS), stomatal density (SD), stomatal length (SL), and stomatal width (SW) influence photosynthetic efficiency. Maximum root length (MRL), total root length (TRL), projected root length (PRA), and root surface area (RSA) are critical for root system function. Kernel number per spike (KNS), kernel weight per spike (KWS), total spikelet number per spike (TSS), sterile spikelet number per spike (SSS), and fertile spikelet number per spike (FSS) are key for grain yield. Above-ground dry matter (DM), net photosynthetic rate (PN), intracellular CO2 concentration (CI), transpiration rate (E), leaf water use efficiency (LWUE), and spike dry matter (SDM) are essential physiological traits for crop performance. TDM(total dry matter), FLRI(flag leaf rolling index), CL(culm length), DPH(days from plant)


LEGEND
Yield 🟩
Growth 🟪
-120,87 barc135
-85,32 wms1034
-65,56 wmc01
-49,76 wms705
-43,84 wmc40
-34,02 swes240
-31,98 wmc29
-27,12 ubc815a
-26,06 wms938
-21,51 srap7a
-16,56 swes862
-12,17 barc139
-8,06 srap2
0,00 barc75
3,00 wmc430
7,00 barc147
11,46 barc133
18,65 cfp78
21,83 cfb3119
27,21 cfp5
31,25 wPt5836
36,00 wmc623
41,37 wmc529.2
45,78 cfp3430
50,77 gpw4207
56,00 gwm264
61,00 wmc544
65,77 cfb3033
71,00 wmc527
76,00 barc145
80,27 gpw1107
85,45 gwm853
90,54 ubc834a
97,00 barc84
102,49 gwm705
105,00 wmc687
110,93 wPt0751
114,92 wPt-8752
119,74 wPt2416
125,00 gwm114
131,71 wPt-8959
135,05 wPt-11583
142,00 gwm247
145,85 p2449-370
S.Malik2015 merged
3B
-5,40 gwm537
0,00 cfd5
3,00 BE404594-175
24,00 cfd60
37,00 gwm443
54,92 gwm614
73,18 wmc336
92,42 gpw1073
110,65 pl142-155
130,00 barc142
148,62 wmc169
168,00 wmc356
202,21 barc84
207,15 gpw1056
223,57 barc340
255,61 barc77
280,72 barc243
298,25 cfd156
317,13 barc1061
327,89 gwm595
390,50 gwm140
391,42 gwm340
433,78 awns
786,44 wms408
885,93 wms540
1 018,58 wms544
S.Malik2015 merged
5B
(a)
LEGEND 3B:
MQTL 3:1
MQTL 3:2
MQTL 3:3
MQTL 3:4
MQTL 3:5
MQTL 3:6
S.Malik2015 merged
3B
LEGEND 5B:
MQTL 5:1
MQTL 5:2
MQTL 5:3
MQTL 5:4
MQTL 5:5
MQTL 5:6
MQTL 5:7
S.Malik2015 merged
5B
(b)



MQTL3B:4

MQTL5B:7

(c)

Fig. 1. Figure (a) Provides the consensus map for chromosome 3B and 5B of wheat (b) Provides the meta QTL maps for chromosome 3B and 5B, and finally (c) Is the close-up of the two main MQTLs with the highest number of growth and yield trait

For chromosome 1A, the optimal number of MQTL regions identified using the selection criteria model was seven. The selection of the seven regions was based on the fact that the majority of models showed seven as the best value using BioMercator V4.2.3 software. For chromosome 1A, a total of 12 QTLs were identified, involving 12 traits related to drought tolerance in yield and growth characteristics. These traits include Fv, Fm, CL, TRL, Fv/Fm, SH, CTWD, KN, GY, SK, sd, and RL. The highest number of QTLs were found in MQTL 1A:1 and MQTL 1A:7, with QTL membership probabilities ranging from 57% to 100%. For chromosome 1B, nine MQTL regions were identified based on the model selection criteria. A total of 15 QTLs were involved, covering 13 drought-tolerant traits related to yield and growth characteristics such as Htscc, PH, HI, Yd, GFD, Sps, sl, FO, FLCW, TC, GY, Sps, and Phr. The QTL membership probabilities ranged from 87% to 100%, with the highest concentration in MQTL 1B:9, which contained eight QTLs. Chromosome 1D showed the best model with nine MQTL regions. Sixteen QTLs were identified, associated with 16 drought-tolerant traits related to wheat yield and growth, such as RDW, E, TGWWD, PHE, GFD, Da, Tip, Crs, Frk, Sra, Trl, SPLS, FLW, YLD, DHE, and DMA. The QTL membership probabilities ranged from 82% to 100%, with MQTL 1D:7 containing the highest number of QTLs, totaling seven.

For chromosome 2A, the best selection model was identified as model 7, with a total of 35 QTLs involving 23 drought-tolerant traits. The highest MQTL was MQTL 2A:3, with 16 QTLs and five traits, with membership probabilities ranging from 61% to 83%. Chromosome 2B showed an optimal value of 10, selected by the majority of models, with MQTL 2B:5 containing 11 QTLs and eight traits. The membership probabilities for these QTLs ranged from 29% to 100%. For chromosome 2D, all five models selected six MQTL regions. A total of 14 QTLs involving 13 drought-tolerant traits were identified, with MQTL 2D:3 containing seven QTLs. The membership probabilities ranged from 95%

to 100%. Chromosome 3A contained 18 QTLs, with membership probabilities ranging from 98% to 100%. The highest MQTL was MQTL 3A:4, containing six QTLs. Model 5 was selected as the best for chromosome 3A based on majority values. Chromosome 3B, based on the criteria model, generated six MQTL regions with 67 QTLs related to drought tolerance in yield and growth, involving 55 traits. The membership probabilities ranged from 73% to 100%, except for QTL QKW-3B, which had a membership probability of 54%. The second highest MQTL was MQTL 3B:4, containing 20 QTLs and 16 traits. For chromosome 3D, the best model selected nine MQTL regions, with five QTLs and four traits identified. The membership probabilities for these QTLs were 100%.

For chromosome 4A, the best selection model identified was model 10, with a total of 25 QTLs. The highest MQTL was MQTL 4A:2, with 10 QTLs and 10 traits, and membership probabilities ranging from 49% to 100%. For chromosome 4B, eight MQTL regions were selected, with seven QTLs divided into three MQTL regions. The membership probabilities ranged from 49% to 76%, except for three QTLs with lower probabilities. For chromosome 5A, model 6 was identified as the best, with 54 QTLs divided into six regions. The highest MQTL was MQTL 5A:4, with 17 QTLs involving 14 traits, with high membership probabilities, mostly at 100%. For chromosome 5B, the model selection criteria showed a high value of 153 for four models, but only model 7 was usable due to software limitations. The highest MQTL was MQTL 5B:7, containing 24 QTLs and 20 traits, with membership probabilities mostly at 100%. For chromosome 6A, model 8 was identified as the best, with 12 QTLs involving 12 traits. The highest MQTL was MQTL 6A:8, with five QTLs, all with 100% membership probabilities. For chromosome 6B, the selection model showed two MQTL regions, with four QTLs divided between them. The membership probabilities for all QTLs were 100%. For chromosome 6D, model 7 was chosen, with three QTLs and three traits, with membership probabilities at 92%.

For chromosome 7, model 7 was chosen for generating mQTL, with 37 QTLs involving 26 traits divided into seven regions. The highest MQTL was MQTL 7A:2, with 14 QTLs and eight traits, with membership probabilities ranging from 67% to 91%. For chromosome 7B, nine MQTL regions were identified, with 30 QTLs involving 28 traits. The highest MQTL was MQTL 7B:7, with nine QTLs and seven traits, with membership probabilities ranging from 50% to 100%. Finally, for chromosome 7D, model 7 was chosen, with 23 QTLs involving 23 traits, divided into seven regions. The highest MQTL was MQTL 7D:4, with six QTLs and membership probabilities ranging from 40% to 100%.

3.3 Making Sense of Traits and Meta QTL

Two mQTLs were selected from the generated mQTLs based on the maximum number of QTLs and their association with drought tolerance in wheat.

3.3.1 MQTL 5B:7

Figure 1(c) shows the green area representing MQTL 5B.7, which encompasses 24 QTLs related to drought tolerance in wheat. The genetic distance of this MQTL is 117.75 cM, flanked by the molecular markers cfp1676 and cfb3033. The membership probability for MQTL 5B:7 ranges from 76% to 100%. Specifically, three QTLs (QSps-5B.2, QYdD-5B, QHID-5B) have a 76% membership probability, and one QTL (QTC-5B) has a 92% membership probability. Meanwhile, 20 QTLs exhibit a 100% membership probability, including QGrD-5B.3, QGrD-5B.1, QTip-5B, QTr-5B, QDRI-5B, QRSA-5B, QGr-5B.2, QGr-5B, QSw-5B.2, QSw-5B.1, QFLL-5B, QCHLC-5B-1, QSc-5B, QBm-5B, QTRL-5B, QGfd-5B, QFLW-5B, QWue-5B, QPRA-5B, and QSps-5B. Twenty traits associated with yield and growth characteristics related to drought tolerance in wheat were identified for MQTL 5B:7. These traits include Sps (seeds per spike), YDd (yield), HID (harvest index), TC (total chlorophyll), GrD (germination), Tip (root tip number), Tr (total root length), DRI (drought resistance index), RSA (root surface area), Sw (spike weight), FLL (flag leaf length), CHLC (chlorophyll content), Sc (stomatal conductance), Bm (biomass yield), TRL (total root length), Gfd (grain filling duration), FLW (flag leaf width), Wue (water use efficiency), and PRA (projected root length).

Furthermore, four QTLs were associated with germination traits (Gr) in wheat. Seed germination can serve as an early indicator of seed viability [49] and is a crucial parameter for assessing seed functionality in determining germination potential [49]. In addition to gene editing, there is evidence that wheat genetic improvement can also be achieved through genetic techniques. For instance, the introduction of the *AlSAP* gene, which encodes a stress-related protein from the Mediterranean halophytic/salt-tolerant grass *Aeluropus littoralis,* into wheat has been shown to enhance germination rates, biomass, and yield under osmotic and saline stress [50].

Additionally, four QTLs were linked to spike traits (Sps/Sw) in wheat. Spike length is a major factor influencing canopy distribution and light and CO_2 use efficiency, and the average days to maturity (HD) can play a significant role in adaptation to various climates and planting methods [51]. Theoretically, cultivating wheat varieties with longer spike lengths (SL) but denser spike density (SD) is an effective approach to achieving more kernels per spike, which can subsequently increase yield (GY) [52,53], as well as spike fertility [54]. Therefore, spike traits play a critical role in yield and growth characteristics for drought tolerance in wheat.

3.3.2 MQTL 3B:4

The second-highest value MQTL is MQTL 3B:4. Figure 1(c) shows the blue area representing MQTL 3B.4, which comprises 20 QTLs for yield and growth characteristics related to drought tolerance in wheat. The genetic distance of this MQTL is 67.22 cM, flanked by the molecular markers wmc3037 and gwm107. The membership probability for MQTL 3B:4 ranges from 73% to 100%. Fourteen QTLs exhibit a 100% membership probability, including QSRA-3B, QFVFM-3B-1, QTRL-3B, QFVFM-3B-2, QTDFL-3B-1, QCL-3B-1, QSpsD-3B, QGrD-3B, QSwD-3B, QRSA-3B, QPRA-3B, QScD-3B, QSRN-3B, QSCN-3B, and QRDW_3B-1. The remaining QTLs show slightly lower membership probabilities: QRL-3B-1 (73%), QRA_3B-1 (75%), QRA_3B-2 (78%), QRL-3B-2 (89%), QRA_3B-3 (76%), and QRDW_3B-1 (98%). Despite not achieving 100% membership, the percentages obtained are considered high and sufficient for inclusion.

Sixteen traits in wheat were identified that display yield and growth characteristics related to drought tolerance. These traits include RL (root length), RA (root angle), SRA (seminal root angle), FVFM (chlorophyll fluorescence), TRL (total root length), TDFL (flag leaf temperature), CL (culm length), SpsD (seeds per spike), GrD (germination), SwD (spike weight), RSA (root surface area), PRA (projected root length), ScD (stomatal conductance), SRN (seminal root number), SCN (spikelet density), and RDW (root dry weight).

Furthermore, 11 QTLs associated with root traits were predominantly found in MQTL 3B:4. Roots are vital organs as they have the ability to move in search of water and are the first to experience drought stress [55]. Under drought stress, roots continue to grow to seek water and meet cellular water requirements. Increased abscisic acid (ABA) levels have been shown to support root growth while simultaneously suppressing shoot growth [56]. Zinc Finger Proteins (ZFP) with the conserved QALGGH domain are known to be involved in modulating gene expression under drought stress [57]. The role of ZFPs in drought tolerance is well established in wheat, rice, and *Arabidopsis* [58]. Several ZFPs, such as ZFP182 and ZFP252 (rice), ZZ1 (soybean), ZFP1 (*Glycine soja*), and AZF1, AZF2, ZAT10, and ZAT11 (*Arabidopsis*), have been shown to play positive roles in drought stress tolerance [58].

4. Conclusion

Both objectives of this study were achieved, resulting in the identification of 951 QTLs associated with drought tolerance in wheat. A total of 37 genetic maps were recorded and analyzed, focusing on traits related to growth and yield in wheat. The BioMercator V4.2.3 software was utilized to extract data from 27 previous studies. Of the 951 QTLs obtained, 538 were associated with yield traits, while 413 were related to growth traits, all linked to drought tolerance. The number of QTLs was reduced from the original 951 to 457 when BioMercator V4.2.3 automatically removed duplicate and inverted loci. Consequently, 457 QTLs were mapped on a consensus map with a total genetic length of 727819 cM.

Further, a mQTL analysis was performed using BioMercator V4.2.3, resulting in the identification of 140 MQTLs. Two mQTLs from chromosomes 5B and 3B, specifically 5B:7 and 3B:4, were identified as the most suitable for use in breeding for yield and growth under drought conditions. These were selected based on their high QTL counts, with 24 QTLs for chromosome 5B:7 and 20 QTLs for chromosome 3B:4. The membership probability for MQTL 5B:7 was 100% for 20 QTLs, 92% for 1 QTL, and 76% for 3 QTLs, all related to drought tolerance in yield and growth. Similarly, MQTL 3B:4 had a 100% membership probability for 14 QTLs, with the remaining 6 QTLs having probabilities ranging from 73% to 98%. The high membership probabilities for both MQTLs indicate the reliability of these findings. This study, therefore, provides valuable mQTL and molecular marker information that can be utilized to enhance yield and growth in wheat under drought conditions.

The MQTL regions identified in this study can serve as reference points for marker-assisted selection (MAS) in breeding programs aimed at improving drought tolerance in wheat. Additionally, the MQTL information obtained can be useful in synteny studies to determine whether there are similarities in drought resistance mechanisms among different cereal varieties. The polymorphic molecular markers flanking the MQTL regions can be used to screen plants that carry these MQTL regions for breeding programs. Although we do not grow wheat in Malaysia, but the information derived may be used in other cereal crop breeding and also in the improvement of wheat. Finally, future research could focus on gene annotation within the selected regions to identify gene compositions at these loci. This information can help to better understand drought resistance mechanisms and the contribution of these regions to yield and growth improvement. Major genes identified from these regions could also be used in transgenic studies within and across cereal species to enhance drought tolerance, yield, and growth in cereals.

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