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Mapping of quantitative trait loci for agronomic and morpho-physiological traits under drought environments in spring barley (*Hordeum vulgare* L.)

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Abstract

Barley production is severely affected by drought caused by the unpredictable Mediterranean weather patterns, which include uneven rainfall and extreme temperatures. This leads to a decrease in crop yield. However, to tackle this issue, landraces and wild species are crucial sources of variation for stress adaptive traits. By incorporating these traits into improved varieties, we may see an increase in yield and stability under drought conditions. Seventy-six quantitative traits loci (QTLs) identified traits were mapped using recombinant inbred lines (RIL) population Arta × Harmal-2//Esp/1808-4L, evaluated at six dry and semi-dry areas over 3 years. The study investigated traits such as grain yield, biological yield, harvest index, kernel weight, seed per head, days to heading, kernel filling duration, growth vigour, growth habit, lodging and plant height. Numerous QTLs were discovered that are associated with various phenotypic traits related to grain yield, kernel yield, duration of filling period and days to heading. For areas with less than 250 mm/annum of rainfall, QTLs were identified on chromosome 2H for biological yield, days to heading, and kernel weight, on 1H for harvest index, and on 2H, 4H, and 5H for kernel weight. For semi-dry areas with rainfall less than 450 mm, QTLs were found on chromosome 6H for grain yield, 2H and 5H for kernel weight, 1H and 6H for seed per head, and 2H for days to heading. Notably, these QTLs significantly explain more than 10% of phenotypic variation. The 2H chromosome was found to have the most important QTL and pleiotropic effect for yield and its components, such as kernel weight, days to heading, and biological yield. The cross Arta/Harmal was adapted, and mechanisms were developed to cope with drought stress, reflected by the significant and positive correlation of biological yield and harvest index with grain yield. Chromosomes 1H, 2H, 4H and 5H harbour more than 60% of mapped QTLs for dry areas. It is worth noting that the QTLs mentioned earlier, along with the kernel weight QTLs (QKW 1.5, QKW2.7b, QKW4.1, QKW6.7, QKW6.9), have consistently exhibited positive effects on crop yield in semi-dry and dry areas, making them potential candidates for breeding drought-tolerant crops. Genomic co-localisation of the QTL for Arta/Harmal

population suggested that selection for drought through linked markers can be an option for drought tolerance selection for barley in dry areas.

KEYWORDS
adaptation, barley, drought stress, genotype × environment, mapping population, pleiotropy, QTL, yield

1 | INTRODUCTION

Barley is well adapted to drought conditions in the Mediterranean basin, where unpredictable climatic conditions, particularly rainfall, rainfall distribution and high and low temperatures, may lead to dramatic decreases in yield. Barley genotypes, particularly landraces and wild species, represent an important source of variation for adaptive traits that may contribute to increased yield and yield stability under drought conditions and that could be introgressed into improved barley varieties. Drought is one of the most adverse abiotic factors limiting the growth and productivity of crops (Gudys et al., 2018). It varies in occurrence, duration and severity from location to location and in the same location from year to year. The most difficult task for cereal breeders in Mediterranean countries is to develop varieties able to tolerate drought stress fluctuating across years and environments, improving yield stability (Teulat et al., 2002). Over the last two decades numerous QTLs controlling agronomic performance and yield components under drought stress have been identified for barley (Baum et al., 2003; Cuesta-Marcos et al., 2009; Kalladan et al., 2013; Mansour et al., 2014; Talamé et al., 2004; Teulat et al., 2001; Tondelli et al., 2014; von Korff et al., 2008). A large number of morphological and physiological traits are linked to drought tolerance in barley (Chen et al., 2010; Del Pozo et al., 2012), which exhibits strong environmental interactions (Tondelli et al., 2006). Increasing tolerance to drought stress has become a major goal for barley breeding programmes, particularly in light of prolonged drought periods as a result of climate change (Wehner et al., 2015). The risk of drought is greatest at the end of the cropping season, but drought caused by a late start of the rainy season may also occur at the beginning of the cropping season. Eventually, drought spells may occur at any time during the cropping season.

Therefore, cultivars that are successful in one dry year may fail in another, or cultivars resistant to terminal drought may not be resistant to intermittent drought or drought occurring early in the season (Turner, 2002). In addition, drought seldom occurs in isolation and often interacts with other abiotic stresses (particularly temperature extremes) or biotic stresses (e.g. root diseases and nematodes).

To determine the genetic basis of complex traits, important genetic and genomic resources have been developed in a wide range of species (Kota et al., 2003; Mora et al., 2015), including barley (Close et al., 2009; Gudys et al., 2018; Kota et al., 2003; Wójcik-Jagła et al., 2013; Zhang et al., 2017; Zhou et al., 2015). Empirical breeding for such a complex target environment can be equivalent to pyramiding genes in breeding for disease resistance. This is because most traits directly or indirectly affecting drought resistance have a complex genetic basis. The process is time consuming and expensive. Therefore, it will considerably benefit from the possibility of more precisely controlling the accumulation of favourable alleles at the several loci that control relevant characters.

The use of molecular markers could provide a useful tool to complement phenotypic selection by identifying and selecting individual loci controlling quantitative traits loci (QTLs). The efficient use of markers in a plant breeding programme requires the identification of a close association between a marker and a trait that is repeatable across a wide range of crosses. Molecular markers have led to the creation of molecular genetic linkage maps of several species, including barley (Graner et al., 1991; Ramsay et al., 2000), and linked markers have been identified for numerous traits.

Association between markers and traits of interest can be revealed from studies based on measurements of the trait in mapping populations. Such studies have led to the mapping of previously unassigned qualitative loci as well as quantitative traits that are important for practical barley breeding such as barley yellow dwarf virus (Najar et al., 2017; Niks et al., 2004), scald (Sayed et al., 2004; Sayed & Baum, 2018) and many other traits through classical QTL analysis (Backes et al., 1995, 2003; Baum et al., 2003, 2007; Forster et al., 2000; Grando et al., 2005; Hayes et al., 1993; Marquez-Cedillo et al., 2001; Teulat et al., 2002, 2001) or advanced backcross QTL analysis (von Korff et al., 2010, 2004, 2006, 2008; Li et al., 2005; Pillen et al., 2003, 2004), and numerous QTLs controlling agronomic performance and yield components under drought stress for barley have also been developed (Baum et al., 2003; Cuesta-Marcos et al., 2009; Kalladan et al., 2013; von Korff et al., 2006, 2008; Mansour et al., 2014; Talamé et al., 2004; Teulat et al., 2001; Tondelli et al., 2014).

In the present article, we report the use of QTL analysis of agronomic traits, including yield characters, measured in 3 years of field trials in semi-dry and dry areas. The evaluation of relevant genetic material across years and locations is necessary to isolate gene effects dependent on the environment from Genotype × Environment (GE) Interaction effects. The objective of this study was to identify trait-marker linkages in a population of recombinant inbred lines (RILs) of a cross between two barley cultivars using QTL mapping for agronomic traits that are relevant in breeding barley for dry areas.

2 | MATERIALS AND METHODS

2.1 | Plant material and growth conditions

A spring barley population of 94 F7-derived RILs was generated during the 1999–2000 to 2000–2001 cropping seasons from the cross

Arta × Harmal/Esp//1808-4L. Both parents are two-rowed barley cultivars well adapted to low rainfall environments (250–375 mm annual rainfall) and are characterised by good yield stability (Grando et al., 2001). Arta is derived from a selection of the Syrian, white-seeded landrace Arabi Abiad and is well adapted to Syrian dry areas, combining high yield potential through a large number of tillers, and thus kernels per m^2 and high kernel weight. Arta is susceptible to lodging under high-yielding conditions and becomes very short under dry conditions. Harmal/Esp//1808-4L (hereafter abbreviated as Harmal) is an improved ICARDA (International Center for Agricultural Research in the Dry Areas) breeding line resistant to lodging. The main objective of the Arta × Harmal-2/Esp//1808-4L cross was to develop lines combining the grain yield architecture of Arta with the plant height, lodging resistance and adaptation to drought stress conditions of Harmal. The parental lines and 88 RILs out of the 94 RILs were planted at the ICARDA research stations located at Tel Hadya (36_01°N; 37_20°E, elevation 300 m asl) and Breda (35_56°N; 37_10°E, elevation 354 m asl.) in Syria during the 1998–1999 to 2000–2001 cropping seasons and at four additional sites Khanasri (32_24°N; 36_03°E, elevation 700 m asl.), Ramtha 32_46°N; 33_45°E, elevation 520 m asl.), Rabba (31_16°N; 35_45°E, elevation 933 m asl.) and Gweer 31_14°N; 35_45°E, elevation 820 m asl.) in Jordan during the 1999–2000 to 2000–2001 cropping seasons.

The α-lattice design with blocks of 10 plots arranged in an array of rows and columns, allowing a two-dimensional spatial analysis was conducted (Singh et al., 2003). A different randomisation was used for each location and year combination. The plot size was 5 m^2 (eight rows, 25-cm apart and 2.5-m long), sown at a seeding rate of 140 Kg. ha^{-1} of seeds per plot in the locations in Jordan, whereas in Syrian locations, the plot size was 4 m^2 (eight rows, 20-cm apart and 2.5-m long), sown at a seeding rate of 175 Kg.ha^{-1} of seeds per plot. Only the inner six rows were harvested to avoid edge effects.

In all locations, rainfall distribution is typically unimodal: the cropping season is between November and May. Low rainfall sites are characterised by a short rainy season. For example, in Khanasri and Ramtha, the rainy season is between December and March. Temperature data were fully available only for the two locations in Syria. As in the case of rainfall, the temperature has an unimodal pattern with a minimum in winter, often < 0 °C, and maximum temperatures close to 40°C. *Minimum* temperature coincides with the wettest period of the year when plant growth is mostly limited by temperature. Temperatures start increasing at the end of the rainy season, and therefore, the period with optimum temperature and water availability is very short. Annual rainfall data for all sites are reported in Figure 1.

The Syrian environment at Tel Hadya was consistently the highest rainfall, receiving >250 mm annual rainfall (semi-dry areas) in all years, whereas Breda rainfall was intermediate between that of Tel Hadya and the locations in Jordan. Only Rabba and Gweer in Jordan received more than 250-mm rainfall during the 2000–2001 growing season, and generally, the 2000–2001 cropping season had high rainfall in all locations except Khanasri in Jordan, where low rainfall prevented the crop from reaching heading.

2.2 | Agronomic traits

The traits recorded were measured as described by Zadoks et al. (1974) Ceccarelli et al. (1991) and Baum et al. (2003) with minor modifications. Eleven agronomic and morpho-physiological quantitative traits were studied in up to 14 sites in semi-dry areas (rainfall > 250–400 mm/annum) and in dry areas (rainfall < 250 mm/annum) in Syria and Jordan (Table 1).

2.3 | Statistical analysis

The data were analysed with the spatial analysis described by Singh et al. (2003) using Genstat (2014). Means and ranges from a normal distribution for the 14 agronomic and morpho-physiological traits were calculated (Table 2). The genotypic standardised BLUPs (Best Linear Unbiased Prediction) were used to analyse genotype × environment interactions (GEI) using the site regression (SREG) model; the response variable is modelled as a function of both fixed effects and random effects. The fixed effects represent the overall relationship between the response variable and the predictor variables, whereas the random effects capture the site-specific variations or deviations from the fixed effects. The basic structure of the SREG model can be represented as follows (Crossa & Cornelius, 1997) in the GGEbiplot software (Yan et al., 2000):

$$Y\_ij = \beta\_0 + \beta\_1X\_1 + \beta\_2X\_2 + \ldots + \beta\_p{}^*X\_p + B\_i + \varepsilon\_ij$$

where

Y_ij is the response variable for the *i*-th site and *j*-th observation.

X_1, *X_2*, ..., *X_p* are the predictor variables.

β_0, β_1, β_2, ..., β_*p* are the fixed effect coefficients representing the overall relationship between the response and predictor variables.

B_i is the random effect representing the site-specific deviation from the fixed effects.

ε_*ij* is the residual or error term.

Components of variance (%) using multiple regression analysis for the six locations and years were calculated. Genotypes were considered fixed effects, whereas environment and year were assumed to be random effects (Salarpour et al., 2020; Thomason & Phillips, 2006). Simple correlation coefficients were also calculated based on the BLUPs. These are estimates of genetic correlation coefficients because the use of different randomisations made the estimates of environmental correlation equal to zero.

The genetic correlation coefficients were calculated between locations for any pair of characteristics in the same or different years, as indicated by Falconer (1989):

$$r = \frac{cov_{XY}}{\sqrt{var_X\, cov_Y}}$$

where cov_{xy} is the 'cross-covariance', and var_x and var_y refer to the components of variance and covariance of each character

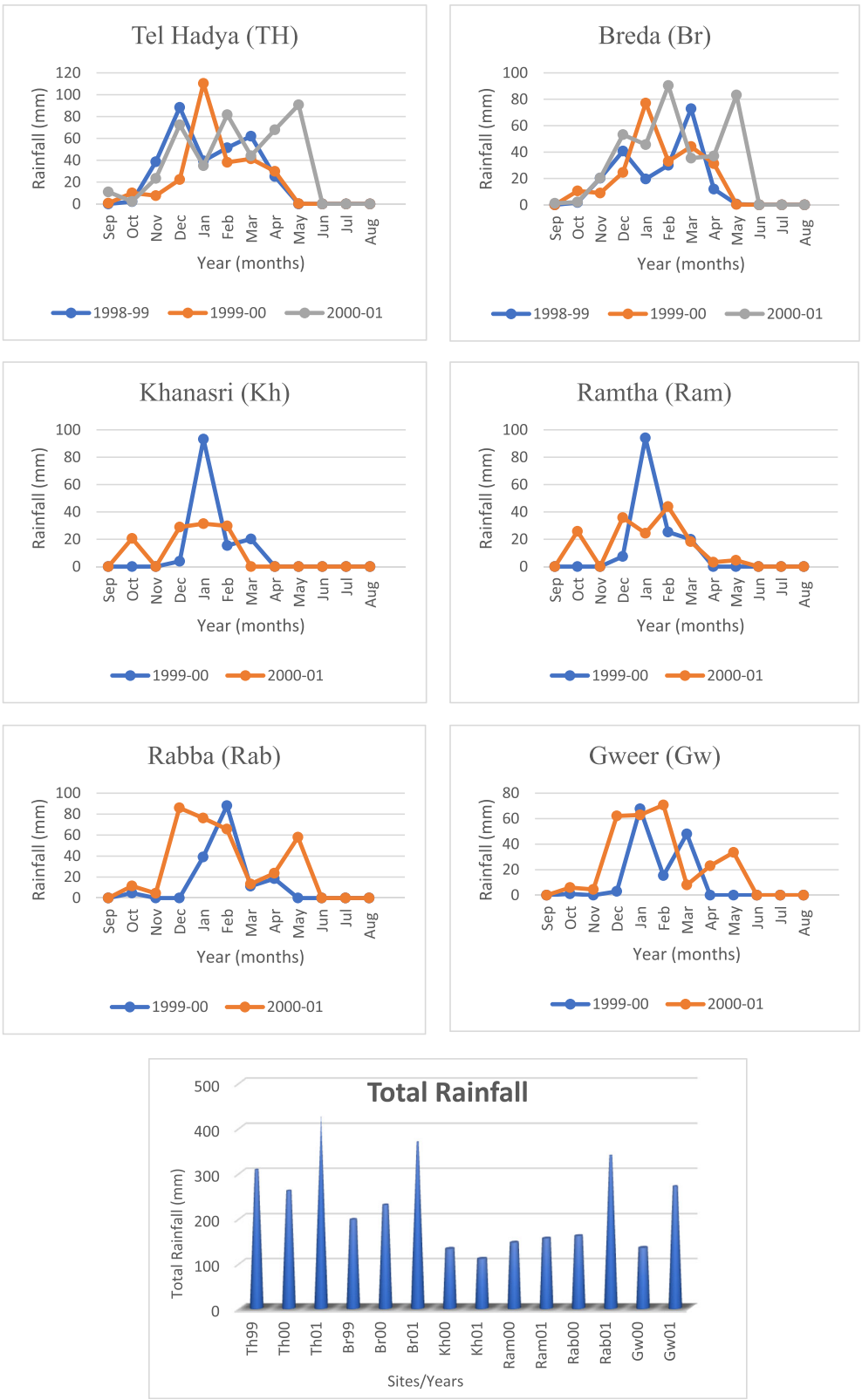


FIGURE 1 Rainfall (mm) in the growing seasons 1998–1999, 1999–2000 and 2000–2001 in Tel Hadya, Breda, Khanasri, Ramtha, Rabba and Gweer research stations in Syria and Jordan. Total rainfall in three growing seasons (1998–1999, 1999–2000 and 2000–2001) and six locations (Tel Hadya, Breda, Khanasri, Ramtha, Rabba and Gweer) in Syria and Jordan. Th99 (Tel Hadya 1998–1999), Th00 (Tel Hadya 1999–2000), Th01 (Tel Hadya 2000–2001), Br99 (Breda 1998–1999), Br00 (Br 1999–2000), Br01 (Br 2000–2001), Kh00 (Khanasri 1999–2000), Kh01 (Khanasri 2000–2001), Ram00 (1999–2000), Ram01 (2000–2001), Rab00 (Rabba 1999–2000), Rab01 (Rab 2000–2001), Gw00 (Gweer 1999–2000), Gw01(2000–2001).

separately. The genetic correlation coefficient, denoted by 'r' ranges between −1 and +1, similar to simple correlation coefficients. However, in the context of genetic correlations, the coefficient represents the genetic relationship between traits rather than a direct linear association.

Genotype-by-Environment Interaction Model (G × E) model was used to take into account the interactions between genetic factors and different environments. It partitions the environmental variance (*Ve*) into genetic variance specific to each environment (*Vg* × *E*) and residual variance (*Vr*).

TABLE 1 Eleven agronomic and morpho-physiological quantitative traits were investigated in up to 14 sites in Syria and Jordan.

Trait	Abbr.	Method of measurement	Units/scale	Environment tested
Grain yield	GY	Measured after threshing the harvested sample.	kg.ha^{-1}	Br00, Br01, Br99, Gw00, Gw01, Kh00, Rab00, Rab01, Ram00, Ram01, Th00, Th01, Th99
Biological yield	BY	Measured by hand harvesting the six central rows of each plot for the entire plot length.	kg.ha^{-1}	Br00, Gw00, Gw01, Kh00, Kh01, Rab00, Rab01, Ram00, Ram01, Th00
Harvest index	HI	Measured as ratio GY/BY.	-	Br00, Gw00, Gw01, Kh00, Rab00, Rab01, Ram00, Ram01, Th00
Kernel weight	KW	Measured as the average of three samples of 100 kernels.	g	Br00, Br01, Br99, Gw00, Gw01, Kh00, Rab00, Rab01, Ram00, Ram01, Th00, Th01, Th99
Number of kernels per spike	SEED	Measured by the average number of kernels from three spikes.	g	Gw01, Rab01
Days to heading	HD	Number of days from emergence to awn appearance in 50% of the plants in a plot.	Number days	Gw00, Gw01, Kh00, Rab00, Rab01, Ram00, Th01, Th99
Kernel filling period	FP	Measured as the difference between DM and HD.	Number days	Gw01, Rab01
Early growth vigour	GV	Measured as a visual score at the 5–6 leaf stage, using a scale from 1 = good vigour to 5 = poor vigour.	Scale 1–5	Br00, Gw00, Kh00, Kh01, Rab00, Ram00, Th00, Th01, Th99
Growth habit	GH	Measured as a visual score at the 5–6 leaf stage, using a scale from 1 = erect to 5 = prostrate.	Scale 1–5	Gw00, Kh00, Kh01, Rab00, Ram00, Th00, Th01, Th99
Lodging	LDG	Measured using a visual score from 0 = not lodged to 9 = completely lodged.	Scale 1–9	Th01, Th99
Plant height	PH	Measured in cm from ground level to the spike base at physiological maturity.	cm	Br00, Br01, Br99, Gw00, Gw01, Kh00, Rab00, Rab01, Ram00, Th00, Th01, Th99

Grain yield (GY in Kg.ha^{-1}), biological yield (BY in Kg.ha^{-1}), harvest index (HI), kernel weight (KW), number of kernels per head (SEED), heading date (HD), duration of filling period in days (FP), early growth vigour (GV), growth habit (GH), lodging (LDG) and plant height (PH) in centimeter in three growing seasons (1998–1999, 1999–2000 and 2000–2001) and six locations (Tel Hadya, Breda, Khanasri, Ramtha, Rabba and Gweer) in Syria and Jordan. Th99 (Tel Hadya 1998–1999), Th00 (Tel Hadya 1999–2000), Th01(Tel Hadya 2000–2001), Br99 (Breda 1998–1999), Br00 (Br 1999–2000), Br01 (Br 2000–2001), Kh00 (Khanasri 1999–2000), Kh01 (Khanasri 2000–2001), Ram00 (1999–2000), Ram01 (2000–2001), Rab00 (Rabba 1999–2000), Rab01 (Rab 2000–2001), Gw00 (Gweer 1999–2000) and Gw01(2000–2001).

$$Ve = Vg \times E + Vr$$

These models allow for the estimation of various genetic parameters, such as heritability (H^2), which quantifies the proportion of total phenotypic variance attributable to genetic factors. It is estimated as

$$H^2 = Vg/Vp$$

where *Vg* is the genetic variance and *Vp* is the phenotypic variance.

The expected mean squares approach is used to estimate these genetic components by comparing the mean squares of different sources of variation, such as genetic effects, environmental effects and interactions. By comparing these mean squares and their expected values under the assumption of a specific genetic model, one can estimate the contribution of each component and calculate the corresponding genetic parameters.

The genetic variance (Vg) is the portion of the phenotypic variance attributable to genetic factors, whereas the phenotypic variance (Vp) represents the total variance observed in the phenotype.

Combining analysis of variance (ANOVA), the method was used to examine the effects of multiple categorical independent variables (factors) on a continuous dependent variable. Mean squares (MS) were calculated by dividing the sum of squares (SS) for each factor and interaction by their respective degrees of freedom (DF).

QTL × Environment (E) interaction analysis is calculated to investigate how genetic loci affect traits under different environmental conditions. This analysis is performed using a mixed linear model, which estimates both fixed and random effects, as well as the QTL × E interaction effect. The equation for this model is calculated using GENSTAT software (2014).

$$Yijkl = \mu + Qi + Ej + (QxE)ij + (QxG)ik + (E \times G)jk + \varepsilon ijkl$$

where *Yijkl* is the observed trait value for the *i* genotype, *j* environment, *k* replicate and *l* individual.

μ is the overall mean of the trait.

Qi is the effect of the *i* QTL.

Ej is the effect of the *j* environment.

$(Q \times E)ij$ is the interaction effect between the *i* QTL and the *j* environment.

$(Q \times G)ik$ is the interaction effect between the *i* QTL and the *k* genotype.

TABLE 2 Means and ranges for grain yield (GY in Kg.ha^{-1}), biological yield (BY in Kg.ha^{-1}), harvest index (HI), kernel weight (KW), number of kernels per head (SEED), heading date (HD), duration of filling period in days (FP), early growth vigour (GV), growth habit (GH), lodging (LDG), plant height (PH) in centimeter, in three growing seasons (1998–1999, 1999–2000 and 2000–2001) and six locations (Th = Tel Hadya, Br = Breda, Kh = Khanasri, Ram = Ramtha, Rab = Rabba and Gw = Gweer) in Syria and Jordan.

Trait	Unit	Th99 *Mean (range)*	Th00 *Mean (range)*	Th01 *Mean (range)*	Br99 *Mean (range)*	Br00 *Mean (range)*	Br01 *Mean (range)*	Kh00 *Mean (range)*	Kh01 *Mean (range)*	Ram00 *Mean (range)*	Ram01 *Mean (range)*	Rab00 *Mean (range)*	Rab01 *Mean (range)*	Gw00 *Mean (range)*	Gw01 *Mean (range)*
GY	Kg.ha^{-1}	4800 (3500–5600)	2900 (2400–3600)	3600 (3100–4200)	1400 (1200–1700)	1300 (0900–1600)	2000 (1300–2600)	400 (100–700)	-	900 (500–1500)	50 (10–100)	800 (400–1400)	1000 (700–1200)	600 (400–800)	700 (500–1100)
BY	Kg.ha^{-1}	-	7400 (6700–8100)	-	-	3400 (3200–3700)	-	1300 (1000–1800)	100 (0–100)	4100 (3500–4900)	1000 (700–1300)	-	7600 (7100–8700)	2000 (1600–2500)	4100 (3700–4500)
HI	-	-	0.41 (0.35–0.47)	-	-	0.36 (0.27–0.43)	-	0.30 (0.12–0.39)	-	0.23 (0.13–0.32)	0.02 (0.01–0.06)	-	0.13 (0.11–0.15)	0.30 (0.23–0.38)	0.19 (0.13–0.31)
KW	g	41.5 (32.6–5.0)	48.1 (40.6–54.2)	44.5 (38.7–51.6)	32.9 (28.4–41.2)	36.9 (31.1–46.1)	41.3 (33.0–49.4)	26.1 (17.1–30.2)	-	26.6 (22.9–30.4)	27.5 (24.6–31.6)	27.5 (22.1–32.0)	31.7 (28.6–35.1)	26.5 (21.8–31.5)	-
SEED	g	-	-	-	-	-	-	-	-	-	-	-	22.4 (18.6–42.4)	-	17.8 (11.8–27.4)
HD	Days	95 (91–101)	92 (89–98)	83 (78–89)	-	-	-	90 (84–93)	-	83 (78–89)	-	74 (70–78)	90 (85–94)	86 (82–92)	93 (88–98)
FP	Days	-	-	-	-	-	-	-	-	-	-		22 (19–26)	-	25 (20–29)
GV	1–5	2.4 (1.8–3.0)	2.0 (1.4–2.8)	2.6 (1.7–4.0)	-	2.6 (1.7–3.7)	-	2.8 (2.4–3.3)	2.8 (2.3–3.3)	2.8 (1.7–3.6)	-	3.2 (2.4–3.3)	-	3.3 (2.2–4.1)	-
GH	1–5	2.7 (1.7–3.9)	1.9 (1.3–2.5)	3.0 (2.6–3.5)	-	-	-	3.3 (2.5–3.8)	2.8 (1.5–3.6)	2.6 (1.7–3.8)	-	3.1 (2.3–4.1)	-	3.6 (2.4–4.0)	-
LDG	1–9	1.1 (0.0–8.0)	-	2.7 (0.4–4.6)	-	-	-	-	-	-	-	-	-	-	-
PH	cm	63.3 (73.4–85.6)	59.6 (48.6–66.9)	72.0 (64.2–83.6)	40.8 (32.7–49.7)	28.5 (23.5–35.7)	53.7 (66.3–46.8)	27.9 (23.6–34.9)	-	43.6 (36.9–50.9)	-	41.1 (35.5–48.3)	59.1 (50.6–70.2)	36.0 (29.2–44.3)	32.9 (29.3–37.3)

$(E \times G)jk$ is the interaction effect between the j environment and the k genotype.

$\varepsilon ijkl$ represents the residual error or random variation.

Likelihood ratio tests are used to determine the significance of $QTL \times E$ interactions.

2.4 | DNA extraction

Genomic DNA was extracted from 0.3–0.4 g of lyophilised tissue from 3- to 4-week-old seedlings according to the cetyltrimethylammonium bromide (CTAB) protocol (Saghai-Maroof et al., 1984) with minor modifications.

2.5 | Map construction

Genetic mapping was performed using amplified fragment length polymorphic (AFLP) and simple sequence repeat (SSR) markers. Two sources of SSRs were used in this study: database-derived repeats (described by Becker & Heun 1995; Liu et al., 1996) and repeats derived from an enriched genome library. Isolation of microsatellite-containing clones, sequencing and primer design was as described by Powell et al. (1996). SSR assays were performed according to standard protocols (Sayed et al., 2002). The reaction mixture consisted of 5 µM of each dNTP, 10 pM of each primer, 25 ng template DNA, 0.2 units *Taq* DNA polymerase, 10 mM Tris–HCl, 50 mM KCl and 2 mM $MgCl_2$. Polymerase chain reaction (PCR) products were separated using a 6% polyacrylamide sequencing gel system (GIBCO/BRL, Life Technologies) and visualised by silver staining (Bassam et al., 1991). All the SSR markers used in mapping are described in Table S1.

AFLP was performed following the methodology of Zabeau and Vos (1993) with minor modifications. Restriction enzymes used were *Pst*I and *Mse*I, and pre-amplification was performed with 1-bp or 2-bp extension primers. Selective amplification of restriction fragments was performed using primers with two, three, or four selective nucleotides. PCR amplifications were separated on 6% denaturing polyacrylamide gels and stained with silver nitrate. AFLP adapters, the preamplification primer and primers for main amplification are described in Tables S2 and S3.

2.6 | Linkage mapping

Segregation analysis was performed using the JoinMap v.2.0 (Stam & Van Ooijen, 1995) software package. Recombination fractions were converted to centiMorgans (cM) according to the Kosambi mapping function (Kosambi, 1944). To identify linkage groups, pairwise comparisons and grouping markers were performed at logarithm of odds (LOD) threshold 6.0 and at a maximum distance of 25 cM. The marker order was confirmed by ripple command. Then, the linkage groups were assigned to seven chromosomes (Table S4).

2.7 | QTL analysis

Using a reduced map method, QTL analysis was performed with PLABQTL v1.1 (Utz & Melchinger, 1996) for 11 agronomic and morpho-physiological traits. The 189 mapped markers were reduced according to 5-cM walk speed to 84 markers. QTLs were first mapped using simple interval mapping (SIM), followed by simplified composite interval mapping (sCIM) procedures for PLABQTL. This programme uses an interval mapping approach by multiple regressions with flanking markers using the marker closest to the peak at each putative QTL as a cofactor. SIM uses multiple regression of phenotypic data on marker genotypic data with 1000 permutations to identify the minimum significant LOD score (logarithm of the odds) to be considered per trait. Then sCIM was used to consider more than one QTL per linkage group and unbalanced QTL genotype frequencies. The cofactors (representing potential QTL) are automatically selected by forward stepwise regression. Markers to be included as cofactors in the regression to increase the detection's power and reduce the bias in the estimated QTL positions and effects (Utz & Melchinger, 1994) were selected through stepwise regression. In this study, the LOD thresholds for the respective traits are empirical thresholds obtained by 1000 permutations. A permutation test can be used to determine the critical LOD threshold from 2.5 to 3.5 (depending on the trait) to establish the presence of significant QTLs ($P < .05$). Confidence intervals for the QTLs were estimated based on a two-LOD support interval by taking two positions around the peak of the LOD profile, which had LOD values of 2.0 less than the maximum.

The percentage of phenotypic variation (R^2) explained by each QTL was calculated, and a QTL was considered major when it explained >10% of the phenotypic variation (Gudys et al., 2018; Kumar et al., 2017). The additive genetic effects were also calculated for the QTLs, and the source of the increased trait value caused by the parents Arta or Harmal allele was indicated.

3 | RESULTS

3.1 | Variation in meteorology data

The meteorological data representing total rainfall in the six trial sites during the three years of the experiments are summarised in Figure 1. Most of the precipitation occurred from early September and stopped in April or May except Th, Br, Rab and Gw during the season 2000-2001. The year 2000 was much drier in all the sites than in 2001 and 1999. Meteorological data showed that the RIL Arta/Harmal population experienced drought stress with low rainfall during the grain set period except in the case of TH and Br sites, relatively (Figure 1).

3.2 | Effect of drought, its components and phenotyping

The RIL population showed a large variation for all the traits evaluated (Table 2). Grain yield varied from 4800 Kg.ha^{-1} in Th99 to only 100 Kg.ha^{-1} in Ram01, with an average of 3500–5600 Kg.ha^{-1} in Th00 and 1.0–100 Kg.ha^{-1} in Ram01. Tel Hadya was consistently the highest-yielding location, whereas the locations in Jordan were consistently the lowest yielding, with average yields always below 1000 Kg.ha^{-1}, and Breda was intermediate. This yield trend across locations followed that of the average rainfall. There was also a large variation within the RILs. For example, in Th99 and Th01, the two highest-yielding locations, the range for grain yield was about 2000 Kg.ha^{-1}, and in three of the four lowest-yielding locations (Seed00, Gw00 and Gw01), the range was about 500 Kg.ha^{-1}. There was also a large phenotypic variation between the RILs for all the other traits. A reduction in yield components such as harvest index, kernel weight and number of seeds per head accompanied the reduction in grain yield across environments.

3.3 | Heritability (h^2)

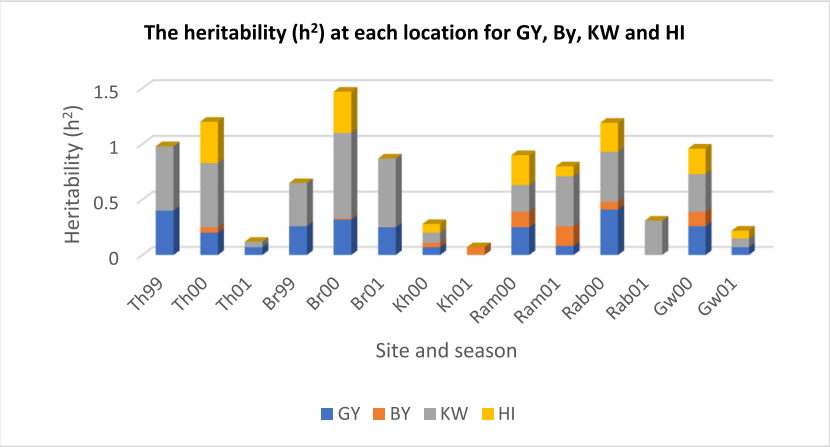
The heritability (h^2) estimates of traits at each site in each year are illustrated in Figure 2. The results showed the presence of genotypes by environmental interactions, and the environments were defined as high or low heritability based on their values. Th99 and Br00 were the environments with the greatest heritability for grain yield, kernel weight, growth vigour and plant height. Rab00 was an exception for grain yield with high heritability even though it is classified as a dry area (Table S5 and Figure 2).

3.4 | Linkage map

Two hundred and fifty-four molecular markers (80 SSR, 174 AFLP) were mapped in the RIL population, and 16 markers were excluded after testing for segregation distortion (chi-square test at $P = .05$ and $P = .01$). Linkage groups were created using a LOD threshold 6, with 189 markers assigned to the seven chromosomes (28 on 1H, 42 on 2H, 16 on 3H, 15 on 4H, 16 on 5H, 35 on 6H and 37 on 7H). For QTL analysis, a reduced map containing 84 marker loci (38 SSRs and 46 AFLPs) was constructed. The map spans over 691 cM and has an average interval length of 8.8 cM (Figure 3).

3.5 | GE interaction

The analysis of the genotype × environment interactions (GEI) of the traits evaluated in the six locations (Table 3) showed that, as expected,



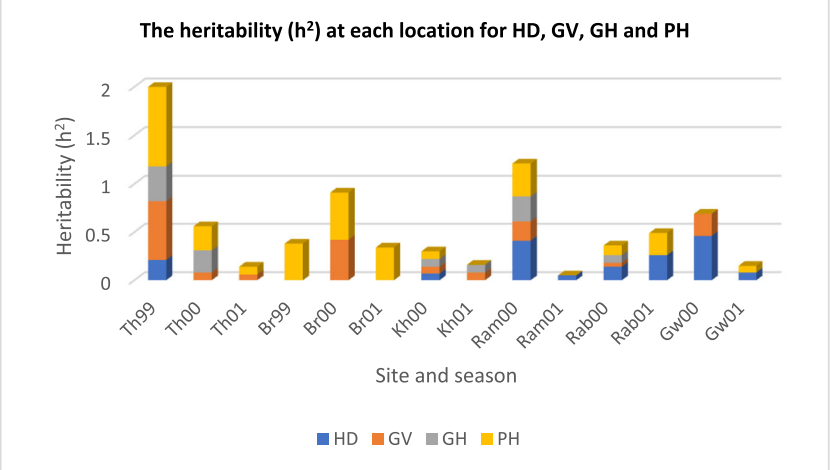


FIGURE 2 The heritability (h^2) estimates of traits at each site in each year for grain yield (GY), biological yield (BY), harvest index (HI), kernel weight (KW), heading date (HD), early growth vigour (GV), growth habit (GH), plant height (PH) in three growing seasons (1999, 2000 and 200) at six locations (Th = Tel Hadya, Br = Breda, Kh = Khanasri, ram = Ramtha, Rab = Rabba and Gw = Gweer) in Syria and Jordan. (refer to Table S5).

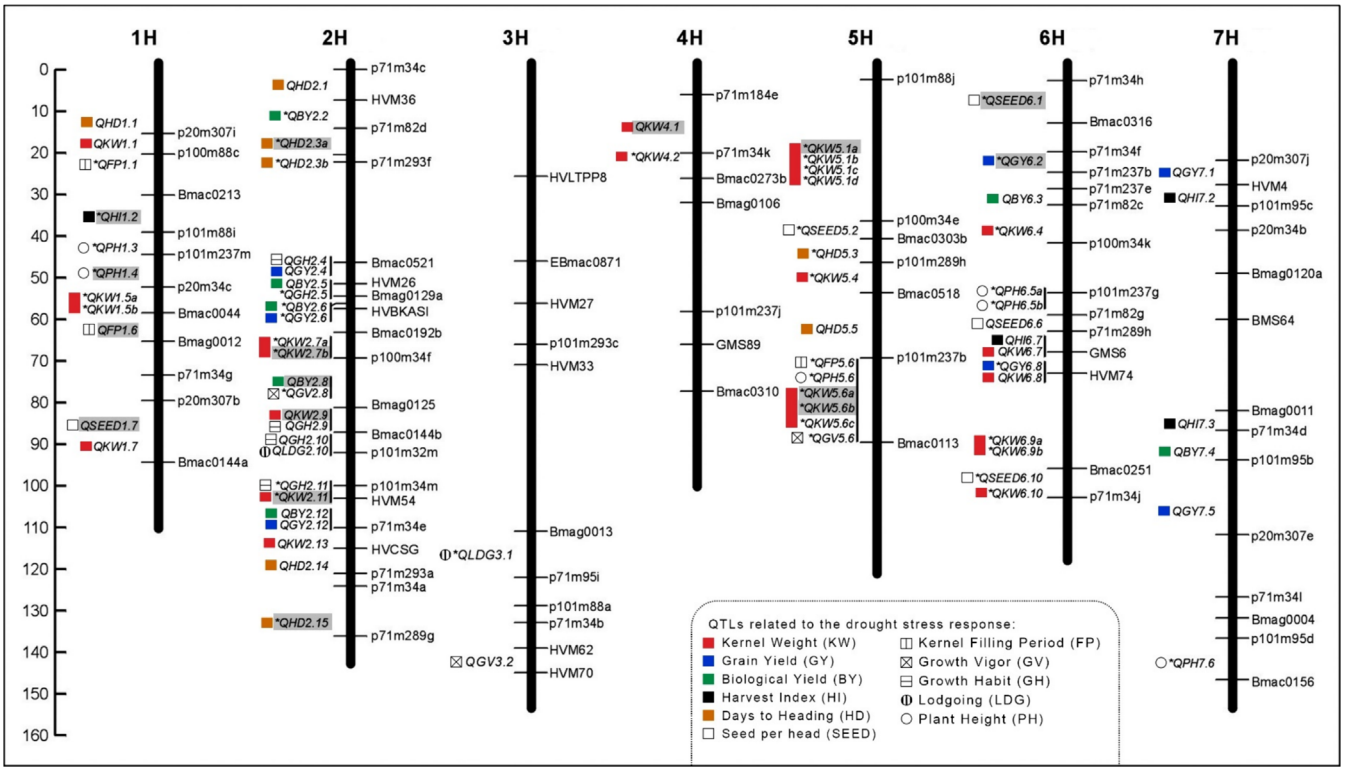


FIGURE 3 The QTL map of Arta × Harmal-2/Esp//1808-4L population shows 76 putative QTLs detected for 11 agronomic traits in dry and semi-dry areas based on SSR and AFLP markers. Linkage groups are orientated with short arms at the top. The order of SSR markers and distances in centiMorgans (cM), according to Kosambi mapping units, is based on the barley molecular consensus map (Liu et al., 1996; Ramsay et al., 2000). The centiMorgan scale is given on the left. SSR markers are indicated by a name or prefix. AFLP markers are designated by the code for the PstI+2, 3, 4 and MseI+2, 3, 4 selective primers followed by a letter. Locus names are indicated on the right side of the chromosomes. QTL are indicated to the left of the chromosomes by a 'Q' prefix followed by a trait code, chromosome and running number (e.g. *QGY2.4* corresponds to the *GY* on chromosome 2H with the running number on 2H). (*) indicates a higher trait value source of allelic QTL effect from Harmal parent. The abbreviations of the QTL follow Tables S6 and 6.

TABLE 3 Components of variance (%) using multiple regression analysis across the six locations and years for grain yield (GY), biological yield (BY), harvest index (HI), kernel weight (KW), days to heading (HD), early growth vigour (GV), growth habit (GH), and plant height (PH) in three seasons (1999, 2000 and 2001) and six locations (Th = Tel Hadya, Br = Breda, Kh = Khanasri, ram = Ramtha, Rab = Rabba and Gw = Gweer) in Syria and Jordan.

Source of variation	*GY*	*BY*	*HI*	*KW*	*HD*	*GV*	*GH*	*PH*
Genotype (G)	0.52[b]	0.15[c]	0.41[c]	3.89[a]	4.30[a]	11.79[b]	19.72[a]	1.36[b]
Environment (location × year)	98.05	99.16	96.44	91.82	91.44	55.29	58.90	96.09
(G × E) Interaction	1.43[b]	0.60[c]	3.15[c]	4.29[a]	4.26[a]	32.92[b]	21.38[a]	2.55[b]

Note: All values were significantly different from zero and ranged from 0 to 100.
[a]Less affected by G × E interaction (G = GEI).
[b]More affected by G × E interaction (between 1/2 and 1/3 of GEI).
[c]Strongly affected by G × E interaction (G = 1/4 and 1/10 of GEI).

the environments (location × year) were always the largest source of variation. The importance of the variation between genotypes (G) in relation to GE interactions varied with the trait. The traits less affected by GE interactions were KW, HD and GH, for which G and GE were nearly equivalent, whereas in the case of GY, GV and PH, G was between one half to one third of GE. The traits most strongly affected by GE were BY and HI, for which G was one quarter and one tenth of GE, respectively (Table 3).

3.6 | Correlation among traits

The estimates of genetic correlation coefficients were calculated between the measured traits in all environments, therefore between 76 pairs of the traits in the 14 environments. Eleven traits were highly significant; $P < .01$, values ranged from 0.29 to 0.77, which indicates the resemblance between relatives in a manner analogous to the estimation of heritability values shown in Table S5 and Figure 2.

Table 4 displays the study's results on 12 traits with their genetic correlation coefficient. Grain yield (GY) showed a positive correlation with KW, BY, HI and FP, along with PH ($P < .01$). However, biological yield (BY) had a negative correlation with GV ($P < .01$) and GH ($P < .05$). Growth habit (GH) showed a positive correlation with GV and HD but had a negative correlation ($P < .01$) with FP, PH, and SEED. On the other hand, growth vigour (GV) had a negative correlation with FP, PH and BY. Plant height (PH) was positively associated with FP but negatively correlated with GH, GV and HD. Moreover, HI was positively correlated with FP and KY ($P < .01$) but negatively correlated with HD.

3.7 | QTL detection

Seventy-six QTLs were identified for 11 agronomic traits in six environments (Tables 5 and 6 and Figure 3).

3.8 | Grain yield (GY)

In five different environments (Rab01, Rab00, Th99, Br99 and Gw00), several QTLs were detected that affected grain yield on chromosomes 2H, 6H and 7H. We found QGY QTLs on chromosome 2H in two clusters: one at 45–60 cM (QGY2.4 and QGY2.6 in Rab01 and Th00, respectively) and the other at 100–110 cM (QGY2.12 in Rab00). QGY2.4 and QGY2.12 had a higher trait value sourced from Arta alleles, which conferred additive effects of 66 and 153 Kg.ha^{-1}, respectively. QGY2.6, on the other hand, had a higher trait value sourced from Harmal alleles, conferring an additive effect of 164 Kg.ha^{-1}. Two QTLs on 6H (*QGY6.2* and *QGY6.8*) were identified in Th99 and Br99 with a higher trait value sourced from Harmal alleles conferring additive effects of 230 and 81 Kg.ha^{-1}, respectively. Two QTLs on chromosome 7H (*QGY7.1* and *QGY7.5*) were identified in Rab00 and Gw00, respectively, with Arta alleles conferring higher trait values.

3.9 | Biological yield (BY)

QTLs for biological yield (*QBY*) were detected in four environments (Th00, Kh01, Ram00 and Rab00) on chromosomes 2H, 6H and 7H. The chromosome 2H QTL *QBY2.2* with a higher trait value sourced from Harmal alleles conferring greater BY was located between the heading date QTL *QHD2.1* with a higher trait value from Harmal alleles and *QHD2.3a*, *b* with a higher trait value from Arta alleles. *QBY2.5* and *QBY2.6* were located proximal to GH *and GY*, respectively. *QBY2.8* was located proximal to the growth vigour QTL *QGV2.8*. Other QTLs for biological yield (*QBY6.3* and *QBY7.4*) were detected in Ram00 and Seed01, respectively, with a higher trait value from Arta alleles conferring larger trait values. Arta contributed the larger value allele for biological yield in drought environments. The additive effect of the QTL ranged from 3.0 to 337 Kg.ha^{-1}. The phenotypic variation explained by *QBY* was between 0.2% and 10.6%, and the phenotypic variation for all QTL added up to 27.9%.

3.10 | Harvest index (HI)

In three different environments (Th00, Br00 and Gw00), QTLs for harvest index (*QHI*) have been detected on chromosomes 1H, 6H and 7H. The QTL *QHI1.2*, with an additive effect of 0.02 from Arta alleles, explained 11.5% of the variation. At QTL *QHI6.7*, the Arta allele had an additive effect of 0.02, explaining 4.8% of the variation. Moreover, Arta alleles at *QHI7.2* and *QHI7.3* on chromosome 7H have been found to confer higher trait values detected in Gw00 and Th00, respectively.

3.11 | Kernel weight (KW)

Several kernel weight (QKW) QTLs were identified on chromosomes 1H, 2H, 4H, 5H and 6H. Four QTLs (QKW1.1, QKW1.5a,

TABLE 4 Genetic correlation coefficients[a] (*r*) among grain yield (GY), biological yield (BY), harvest index (HI), kernel weight (KW), number of kernels per head (SEED), heading date (HD), duration of filling period in days (FP), early growth vigour (GV), growth habit (GH), lodging (LDG) and plant height (PH).

Trait	GH	GV	HD	FP	LDG	PH	SEED	BY	GY	HI
GV	**.58****									
HD	**.43****	**.43****								
FP	*−.32***	*−.34***	*−.78***							
LDG	−.02	−.18	−.20	.27*						
PH	*−.39***	−.51**	*−.35***	**.29****	.25*					
SEED	*−.32***	−.14	−.19	0.13	−.04	.15				
BY	−.22*	*−.39***	−.14	.03	−.08	**.41****	.23*			
GY	−0.10	−.20	*−.32***	.13	−.04	0.10	0.24*	**.57****		
HI	−0.21*	−.20	*−.53***	**.36****	.20	.20	.15	.28*	**.77****	
KW	−0.13	−.09	−.20	.12	−.08	**.47****	.15	**.34****	.27*	**.37****

Note: Bold genetic values indicate a positive correlation between the traits concerned. Italic genetic values indicate a negative correlation between the traits concerned.

[a]Values are significantly different from zero at (* = $P < .05$, ** = $P < .01$).

TABLE 5 QTLs detected in each environment.

Trait	Th99	Th00	Th01	Br99	Br00	Br01	Kh00	Kh01	Ram00	Ram01	Rab00	Rab01	Gw00	Gw01	TOTAL
GY	6H	2H	-	6H	-	-	-	-	-	-	2H*,7H*	2H*	7H*	-	**7**
BY	-	2H	-	-	-	-	-	2H,2H*, 7H*	2H*,2H*	-	2H	-	-	-	**7**
HI	-	7H*	-	-	6H	-	-	-	-	-	-	-	1H,7H*	-	**4**
KW	6H*, 6H	2H	1H,1H*, 6H	-	1H*,4H*,4H,5H, 5H,5H	1H,5H	-	-	2H*,6H*	6H	5H	2H,2H*, 5H,5H	2H,6H	5H	**25**
SEED	-	-	-	-	-	-	-	-	-	-	-	1H*,5H, 6H,6H*, 6H	-	-	**5**
HD	-	-	2H*,2H,2H*,2H	-	-	-	-	-	-	-	2H	5H,5H*	-	1H*	**8**
FP	-	-	-	-	-	-	-	-	-	-	-	5H	-	1H,1H*	**3**
GV	-	-	5H	-	-	-	3H*	2H	-	-	-	-	-	-	**3**
GH	2H*	-	2H,2H*	-	-	-	-	-	-	-	2H*,2H	-	-	-	**5**
LDG	2H*	-	3H	-	-	-	-	-	-	-	-	-	-	-	**2**
PH	-	1H,6H	-	-	6H	-	-	-	1H,5H, 7H	-	5H	-	-	-	**7**
TOTAL	**5**	**6**	**11**	**1**	**8**	**2**	**1**	**4**	**7**	**1**	**8**	**13**	**5**	**4**	**76**

Note: The 76 QTLs identified for 11 traits detected at two locations in Syria (Th = Tel Hadya, Br = Breda) during 1999–2001 and four locations in Jordan (Kh = Khanasri, ram = Ramtha, Rab = Rabba and Gw = Gweer) during 2000–2001. The location codes are combined with the growing season in which the trial was grown to give the environment in which a QTL was detected. (* indicates a higher trait value source of allelic QTL effect from Arta parent).

TABLE 6 Summary of the major QTLs detected for eight agronomic and morpho-physiological traits at two locations in Syria (Th = Tel Hadya, Br = Breda) during 1999–2001 and four locations in Jordan (Kh = Khanasri, Ram = Ramtha, Rab = Rabba and Gw = Gweer) during 2000–2001.

Trait/QTL (QTL code)	Chromosome	QTL interval (cM)	Environment	Drought[a]	LOD	Additive effect (higher allelic source)	QTL x E effect[b]	R^2 [%][c]
Grain yield (GY)								
QGY6.2	6H	19–24	Th99	SD	2.7	230 (Harmal)	NS	15.5**
Biological yield (BY)								
QBY2.8	2H	77–83	Ram00	D	2.6	153 (Arta)	NS	10.6**
Harvest index (HI)								
QHI1.2	1H	30–39	Gw00	D	2.6	0.02 (Harmal)	NS	11.5**
Kernel weight (KW)								
QKW2.7b	2H	67–70	Rab01	SD	3.3	0.60 (Harmal)	NS	10.2**
QKW2.9	2H	80–85	Rab01	SD	4.7	0.80 (Arta)	NS	15.1**
QKW2.11	2H	100–104	Th00	D	3.3	1.80 (Harmal)	NS	10.8**
QKW4.1	4H	5–15	Br00	D	4.5	1.04 (Arta)	4.46	13.1**
QKW5.1a	5H	0–14	Rab01	SD	6.1	0.65 (Harmal)	NS	14.2**
QKW5.6a	5H	76–92	Gw01	D	3.1	0.53 (Harmal)	NS	12.9**
QKW5.6b	5H	82–92	Br00	D	4.1	0.90 (Harmal)	NS	16.1**
SEED per head (SEED)								
QSEED1.7	1H	80–92	Rab01	SD	3.3	1.30 (Arta)	NS	10.4**
QSEED6.1	6H	0–10	Rab01	SD	3.4	1.86 (Harmal)	NS	11.5**
Days to heading (HD)								
QHD2.3a	2H	14–22	Rab00	D	2.6	0.84 (Harmal)	NS	11.9**
QHD2.15	2H	127–133	Th01	SD	2.9	0.68 (Harmal)	NS	10.1**
Kernel filling period (FP)								
QFP1.6	1H	57–65	Gw01	D	3.5	0.97 (Arta)	NS	11.9**
Plant height (PH)								
QPH1.4	1H	42–52	Th00	D	4.1	2.40 (Harmal)	NS	10.9**

Note: The location codes are combined with the growing season in which the trial was grown to give the environment in which a QTL was detected. The 'Q' prefix indicates the QTL detected, followed by the trait code, chromosome and a sequential number. The QT interval related to marker positions in grey is highlighted in Figure 3.

[a](D) = dry season (rainfall <250 mm/annum), (SD) = semi-dry season (rainfall >250 mm < 400 mm/annum).

[b](NS) not significant.

[c](R^2) percentage of phenotypic variation explained by individual QTL.

**Major QTL significantly explained more than 10% of the phenotypic variation in dry areas.

QKW1.5b and QKW1.7) were detected in Br00, Br01 and Th01. Other QTLs (QKW2.7a,b, QKW2.9, QKW2.11 and QKW2.13) were identified in single environments. The major QTL *QKW2.9* was on chromosome 2H (0.8 g additive effect, LOD 4.7) and explained %15.1 of phenotypic variation, *QKW4.1* on chromosome 4H (1.04 g additive effect, LOD 4.5) explained %13.1 of phenotypic variation. Many QTLs for kernel weight were found on chromosome 5H (QKW5.1a,b,c,d, QKW5.4, QKW5.6a,b,c) with an additive effect of 0.48 to 1.82 g with a higher trait value from Harmal alleles. *QKW5.1a* (0.65 g additive effect, LOD 6.1) that explained %14.2 of phenotypic variation and *QKW5.6b* (0.90 g additive effect, LOD 4.1) that explained 16.1% of phenotypic variation were the strongest. Additional QTLs for kernel weight were detected on chromosome 6H (QKW6.4, QKW6.7, QKW6.8, QKW6.9a,b, QKW6.10) with additive effects of 1.18 g to 2.24 g and LOD 2.8–3.7 from Harmal and Arta alleles.

3.12 | Kernel number per spike (SEED)

QTLs for SEED per spike *(QSEED)* were detected on chromosomes 1H, 5H and 6H in one environment (Rab01). One QTL *QSEED1.7* was detected on chromosome 1H, had an additive effect of 1.3 with a higher trait value from Arta alleles and explained 1.4% of the phenotypic variation. *QSEED5.2* had an additive effect of 1.26 from Harmal alleles and explained 2.9% of the phenotypic variation. *QSEED6.1*, *QSEED6.6* and *QSEED6.10* had additive effects of 1.86, 1.15, and 0.98, respectively.

3.13 | Heading date (HD)

Multiple QTLs responsible for the heading date (QHD) were detected on chromosomes 1H, 2H and 5H. Among them, QHD1.1 was identified in Gw01 and explained 8.5% of the phenotypic variation. The Arta allele showed a higher trait value, resulting in an average 1-day delay in flowering. On chromosome 2HS, three QTLs (QHD2.1, QHD2.3a and QHD2.3b) were detected, located around the approximate position of ppd-H1. Additionally, on 2HL, two QTLs (QHD2.14 and QHD2.15) were identified. On the other hand, QHD5.3 and QHD5.5 were detected in Rab01, and the Harmal and Arta alleles showed positive effects, explaining 3.4% and 6% of the phenotypic variation, respectively.

3.14 | Duration of filling period (FP)

In the GW01 and Rab01 environments, only three QTLs (QFP1.1, QFP1.6 and QFP5.6) were identified for the kernel filling duration. QFP1.1 and QFP1.6, located on chromosome 1H, had an additive effect of 0.8 day and 1 day, respectively, explaining 8% and 11.9% of the variation. Harmal and Arta alleles were the sources of higher trait values. For the QTL (QFP5.6) detected in Rab01, Harmal allele had an additive effect of 0.78 days on the kernel filling duration.

3.15 | Growth habit (GH)

Five QTLs for growth habit (*QGH2.4*, *QGH2.5*, *QGH2.9*, *QGH2.10* and *QGH2.11*) were detected in three environments (Th00, Th01 and Rab00) and located on chromosome 2H. At *QGH2.10* and *QGH2.9*, the Arta allele exhibited a significant effect at QGH2.10 and QGH2.9, explaining 5.7% and 5.5% of the phenotypic variance, respectively.

3.16 | Early growth vigour (GV)

QTLs for early vigour (QGV) have been identified on chromosomes 2H, 3H and 5H in three environments Th01, Kh00 and Kh01. These QTLs explained 3.4%, 1.4% and 6.3% of the total phenotypic variation in early vigour. Among these QTLs, *QGV2.8* showed an additive effect of 0.13 because of the contribution of the Harmal alleles. For the remaining QTLs, *QGV3.2* and *QGV5.6* found in Kh00 and Th01, respectively, the Arta alleles had additive effects of 0.09 and 0.19. The QTLs accounted for 11.1% of the additive phenotypic variation in early vigour.

3.17 | Lodging (LDG)

The lodging trait of QLDG was assessed in two different years, Th99 and Th01. During Th99, a QTL *QLDG2.10* was detected, which had an additive effect of 0.4 from Arta alleles and explained 5.5% of the phenotypic variation. In Th01, a second QTL *QLDG3.1* was identified, which had an additive effect of 0.44 and explained 2.1% of the phenotypic variation with Harmal alleles.

3.18 | Plant height (PH)

A study found that four QTLs on chromosomes 1H, 5H, 6H and 7H are responsible for determining the height of plants in very dry environments. The QTL on chromosome 1H was found to explain the most variance in plant height (10.9%) and had an additive effect of 2.4 cm. This QTL was only detected in the growing season of 1999–2000 at two locations, Ram00 and Th00 (*QPH1.3* and *QPH1.4*). Additionally, QTL for plant height was detected on chromosome 5H in Ram00 and Th00 (*QPH5.6a*, *b*) and on chromosome 6H in Br00 and Th00 (*QPH6.5a*, *b*). Meanwhile, the QTL *QPH7.6* was only detected in Ram00. The Harmal alleles had a larger effect on plant height.

As a result of this study, the QTLs identified showed LOD scores ranging from 2.6 to 6.1 and explained 0.4% to 16.1% of the observed variation (R2). Using the criterion (LOD > 2.5), we identified 76 significant QTLs for 11 traits out of a total of 15 agronomic and morpho-physiological traits related to drought tolerance in barley (Tables S6 and 6). The QTL QBY2.12 for biological yield was found to be located within a 10-cM interval that also contained the QTL QKW2.11 for kernel weight and QGY2.12 for grain yield. All three QTLs were contributed with a high allelic value by Arta alleles. Additionally, three QTLs for kernel filling duration were found to be collocated with the QTL for kernel weight. Among the QTLs for kernel filling duration, QFP1.1 was identified in the same environment (Gw01) as the QTL for days to heading (QHD1.1) and a kernel weight QTL from a different environment (Br00). Another QTL, QFP1.6, was also identified in Gw01 and was collocated with kernel-weight QTLs detected in Br01 and Th01.

3.19 | Co-location of QTL

The biological yield QTL *QBY2.12* was collocated within a 10-cM interval containing the kernel weight QTL *QKW2.11* and grain yield QTL *QGY2.12*. Both QTL for biological and grain yield were contributed from Arta alleles. The three QTLs for the kernel filling duration were collocated with kernel weight QTL. *QFP1.1* collocated with a QTL for days to heading (*QHD1.1*) in the same environment (Gw01) and with a kernel weight QTL from a different environment (Br00). The QTL *QFP1.6* was also identified in Gw01 collocated with kernel weight QTL detected in Br01 and Th01.

4 | DISCUSSION

The meteorological data for the six sites showed low precipitation during the reproductive stage of barley growth, demonstrating that

barley encounters low rainfall from June in semi-dry areas like TH and Br sites and from May in dry areas like Kh, Ram, Rab and Gw sites. This implies the need for an efficient selection method to improve drought tolerance for barley and wheat (Salarpour et al., 2020).

Multi-environmental field conditions are commonly used to evaluate the genotype performance (Mathews et al., 2008; von Korff et al., 2008) using a different type of biparental population, for example, RIL population (Mathews et al., 2008; McIntyre et al., 2010), double haploid (DH) population (Obsa et al., 2016; Quarrie et al., 1994) or advanced backcross (Kalladan et al., 2013).

The aim of this study is to identify genes associated with QTL confidence intervals. The environments were a highly significant source of variation for all the traits in all the marker intervals. Overall, there was a small amount of QTL by environment interaction, and this was mostly explained by differences in the magnitude of effect of QTL across environments (Figure 3).

Assuming that the proportion of phenotype variation explained by a major QTL should be >10% (Gudys et al., 2018; Kumar et al., 2017), as much as 21% of the QTLs identified in our study can be considered major QTLs, including all 16 QTLs detected under drought stress (Table S6 and Table 6). Similarly, the 11 significant QTLs detected by Liu et al. (2017) can be classified as major QTLs, as each explained at least 11.2% of the variation. Grain yield (GY) and HI, the significant and positive correlation of biological yield and harvest index with grain yield, show that the cross Arta/Harmal was adapted, and mechanisms were developed to cope with drought stress. In areas with less than 260 mm of rainfall, six QTLs related to grain yield (GY) were detected across five environments (Rab01, Rab00, Th99, Br99 and Gw00). Out of the seven QTLs identified, QGY2.4, QGY2.12, QGY6.2, QGY6.8, QGY7.1 and QGY7.5 were found to be associated with grain yield.

Hayes et al. (1993) and Romagosa et al. (1996, 1999) found a total of 14 QTLs for grain yield in better agronomic environments, five of these on chromosomes 2H, 3H, 5H and 6H were reconfirmed as discussed by Li et al. (2005). Li et al. (2005) identified three and six QTLs for grain yield in two advanced backcross populations, but only one QTL at the photoperiod gene *Ppd-H1* locus on 2H was reconfirmed in both populations (Laurie et al., 1994). This *Ppd-H1* on 2H locus showed pleiotropic effects of the photoperiod gene on many agronomic traits, especially earliness. Yield QTL at the *Ppd*-H1 locus was also identified by Pillen et al. (2004) and Marquez-Cedillo et al. (2001). Pillen et al. (2003) found QTL for kernel weight associated with the HvBKASI locus. In that region, we found QTL for kernel weight QKW2.7a, b (68 cM) and biological yield QBY2.8 (80 cM). The third location on 2H that harbours grain yield QTL is QGY2.12 around the HVCSG locus (105 cM). Pillen et al. (2003) also identified yield QTL at this location. The yield QTL on 6H *QGY6.1* (23 cM) and *QGY6.7* (69 cM) and 7H location *QGY7.1* (22 cM) and QGY7.5 (105 cM) might correspond to the yield QTL that was identified in other studies (Marquez-Cedillo et al., 2001; Pillen et al., 2003). Interesting to note is that the grain yield QTL on 6H *QGY6.1* (23 cM) co-located with a QTL for the number of kernels per spike (*QSEED6.1*), which might be the reason for the increased grain yield at this location. The grain yield QTL *QGY6.8* (69 cM) co-locates with a QTL for kernel weight (*QKW6.7*), indicating that increased kernel weight is associated with increased grain yield alleles.

The location of QBY2.6 (55 cM) for biological yield on chromosome 2H coincides with QGY2.6, a QTL for grain yield. Similarly, QBY2.12 (105 cM) for biological yield is co-located with QGY2.12 for grain yield. The QTL location on chromosome 2H for biological yield is consistent with the findings of other studies on QTL locations for kernel weight and yield (Pillen et al., 2003).

A number of kernel weight (KW) QTLs were consistent with other studies (Backes et al., 1995; Baum et al., 2003; Bezant et al., 1997; Hayes et al., 1993; Marquez-Cedillo et al., 2001; Pillen et al., 2003 and 2004; Teulat et al., 2001 and 2002). Teulat et al. (2001) identified a chromosome 6H kernel weight QTL important in Mediterranean environments that collocated to the regions found in this study (*QKW6.4*, *QKW6.7*, *QKW6.8*, *QKW6.9a*, *b and QKW6.10*). Additive effects ranged between 0.6 g for *QKW2.7b* and 1.2 g for *QKW2.7a* from Harmal alleles, indicating a QTL × E effect since these QTLs are controlled by the same locus.

Pillen et al. (2003, 2004) identified QTL for seeds per spike (*SEED*) on chromosomes 1H and 5H, whereas Li et al. (2005) detected QTLs on all chromosomes except 6H. In this study, *QSEED* was collocated with kernel weight (KW) on 1H and twice on 6H, which could be expected because the traits are correlated.

Heading date (HD) is influenced by various environmental cues. Temperature and photoperiod are the two most important in temperate cereals (McMaster & Moragues, 2019). Heading date (HD), one of the most important traits for adaptation to drought conditions, was negatively correlated with PH and FP (early genotypes are taller and have a longer filling period). This study detected several QTLs for heading date in four environments on chromosomes 1H, 2H and 5H. Backes et al. (1995) reported QTL for heading date on chromosomes 2H and 7H. Marquez-Cedillo et al. (2001) reported QTL for HD on all the chromosomes except 6H. Baum et al. (2003) reported QTL for heading on 2H, 3H, 4H, 5H and 7H; the alleles from parent Arta always contributed with the same sign, whereas in this study, the QTLs for heading were affected by alleles from both parents Arta and Harmal. Pillen et al. (2003 and 2004) reported QTL for HD on all seven chromosomes but not in dry areas. Key pathways involved have been reviewed for cereals by Comadran et al. (2012) and Monteagudo et al. (2019). Two major genes involved in photoperiod response have been identified and characterised: Photoperiod-H1, Ppd-H1 on chromosome 2H (Turner et al., 2005) and Photoperiod-H2, Ppd-H2 on chromosome 1H (Kikuchi et al., 2012). We have identified several QTLs for heading dates under drought environment on 2H. QTL QHD2.3a and QTL2.3b might be located close to the potential Ppd-H1 locus (Laurie et al., 1994; Turner et al., 2005) on chromosome 2H. In this study, the QTL QHD2.3a and QHD2.3b explained 11.9% and 4.7% of the total phenotypic variation of flowering date, which seems related to the locus Ppd-H1. Also, in this study, the QTL on 1H (QHD1.1 18 cM) clustered with the QTL for kernel filling duration (QFP1.1). Interestingly, a QTL for heading date on 1H (Marquez-Cedillo et al., 2001) co-located with a QTL for kernel plumpness and

one for plant height. Most other studies using Australian mapping populations have found that the Ppd-H1 has the largest effect on phenology and agronomic performance in barley (Boyd et al., 2003; Coventry et al., 2003). Conversely, Obsa et al. (2016) failed to find any significant QTL associated with Ppd-H1 on chromosome 2H. One other QTL (QHD5.3) for heading date (HD) was found on chromosome 5H close to the position of a heading data QTL identified by Pillen et al. (2003).

Marquez-Cedillo et al. (2001) identified QTLs for kernel plumpness on chromosomes 1H, 2H, 4H, 5H and 7H. Hayes et al. (1993) reported QTLs on chromosome 1H. In this study, QTLs for three traits, duration of filling period QFP1.1 (18 cM), days to heading QHD1.1, and kernel weight, were mapped to the same location on chromosome 1H. Furthermore, QTL for the filling period (QFP1.6, 60 cM) is also present on chromosome 1H. Lastly, the third QTL for the QFP5.6, 80 cM was mapped on chromosome 5H. This QTL was found in an interval where QTLs for early vigour, kernel weight, and plant height were found in the drier environments, including Rab01, Br00, Gw01, Ram00 and Rab00.

A QTL for growth habit (GH) was identified on 2H (*QGH2.9*), which was closely located to a QTL for kernel weight (*QKW2.9*) and lodging (*QLDG 2.10*). Baum et al. (2003) reported QTL for growth habit on chromosomes 1H and 6H in the Arta × *Hordeum spontaneum 41-1* cross. Meanwhile, Thabet et al. (2018) reported only one QTL on chromosome 1H for growth habit.

Baum et al. (2003) identified a QTL for early growth vigour on chromosome 6H. Similarly, Borràs-Gelonch et al. (2010) and Obsa et al. (2016) reported a QTL on chromosome 2H that accounted for 8.5% and 7.8% of the phenotypic variation, respectively. In this study, it was observed that genotypes with good early growth in winter (GH and GV) had negative correlations with FP (filling period) and positive correlations with LDG (lodging). This means that erect genotypes with good early growth in winter have a longer filling period, making them more susceptible to lodging.

In drought-prone environments, early vigour enables early resource acquisition (Maydup et al., 2012; Tiyagi et al., 2011) and reduces evapotranspiration of water for the soil surface (Kosová et al., 2014), leaving more water available for the crop. Obsa et al. (2016) mentioned that the identification of QTL for this trait in Australian elite barley germplasm is an important step towards improving the trait through molecular breeding for drought. However, several authors comment that yield may be enhanced by improved early vigour and rapid development of maximum leaf area (El Hafid et al., 1998; Lu & Neumann, 1998). López-Castañeda and Richards (1994) reported that, on average, barley has a greater yield in water-limited environments compared to wheat, triticale and oats. As part of a possible explanation, they pinpointed the faster and more vigorous growth of barley during vegetative development. Variation in this trait is, therefore, likely to be in direct relation to drought stress tolerance and yield (Honsdorf et al., 2014, 2017).

Hayes et al. (1993) detected QTLs for lodging (LDG) on all chromosomes except 1H, Backes et al. (1995) detected QTL on 2H, 3H, 4H and 5H, and Pillen et al. (2003, 2004) detected them on 1H, 2H and 5H. In this study, the second QTL *QLDG3.1* on chromosome 3H was identified in Th01 with Harmal alleles conferring an additive effect of 0.44 and in the region of the *sdw1* semi-dwarfing gene.

Decreasing barley plant height (PH) was the main strategy for improving grain yield and harvest index through reduced lodging (Bezant et al., 1997). The relationship between plant height and heading date was mentioned by Lin et al. (1995), and some other alleles are day-length sensitive (Wang et al., 2010). Plant height (PH) is a quantitative trait controlled by many genes, including dwarfing, semi-dwarfing and many additional loci (Yu et al., 2010). QTL for plant height was identified in this study on chromosomes 1H, 5H, 6H and 7H in only four environments in the year 2000, with the height alleles coming from the Harmal parent. The year 2000 was much drier than 2001 and 1999, reducing plant height overall in most locations. PH genes have been mapped to the short arm of chromosome 2H (Wang et al., 2010) and the long arm of chromosome 4H (Hackett et al., 1992). Baum et al. (2003) reported QTLs on chromosomes 3H and 4H in an Arta × *H. spontaneum 41-1* population but with increased plant height originating from *H. spontaneum 41-1*. Hayes et al. (1993) reported QTL for plant height on chromosomes 2H, 3H, 4H, 5H and 7H, with Steptoe contributing the larger value alleles for the QTL on chromosomes 4H and 7H. Marquez-Cedillo et al. (2001) and Pillen et al. (2003, 2004) reported QTL for plant height on almost all chromosomes. The location on 1H identified by Pillen et al. (2003) seems identical to the QTL position identified in this study (*QPH1.3* and *QPH1.4)*. Also, the location for plant height QTL on 7H (*QPH7.6* 140 cM) corresponds to the height QTL identified by Pillen et al., 2004 and Li et al., 2005. However, Arifuzzaman et al. (2014) found two QTLs on 2H, 3H and 4H. The exotic allele at QTL *QPH1.4* on chromosome 1 showed a great increase in PH by explaining about 11% of the genetic variance in the dry environment. PH is not a desirable breeding trait but an important adaptive trait for drought escape (Arifuzzaman et al., 2014). The PH QTLs in this study, identified on chromosomes 1H, 5H, 6H and 7H, support the cumulative response of PH genes from the Syrian landrace Harmal. Wang et al. (2014) found plant height QTL that positively affects barley agronomic traits and grain yield. In this study, PH, a crucial trait for farmers in environments with low rainfall, was positively associated with KW, BY and FP and negatively correlated with GH and GV (genotypes with erect habit and good early vigour tend to be taller). Through Genome-Wide Association Studies (GWAS), Pasam et al. (2012) and Pauli et al. (2014) detected many QTL for barley plant height overlapping with previously mapped QTL and known genes. However, natural variation in plant height is still insufficient to understand the importance of this trait with respect to other agronomical traits. Thus, tools like GWAS analyses using high-density genetic maps based on different population structures are crucial to increasing our knowledge concerning genetic factors controlling plant height (Alqudah et al., 2016).

The process of mapping QTL helps identify genomic regions linked to drought tolerance by using a DNA marker for Marker-Assisted Selection (MAS) programmes. This approach has been studied and reported by Zhou et al. in 2015. In the current study, markers

closely linked to the QTL of Arta/Harmal cross will be utilised for MAS to enhance drought tolerance.

4.1 | Pleiotropic effects observed in marker interval

A number of QTLs were found for all agronomically important characters in this cross. Some had genetic correlations and mapped to similar positions. Several marker intervals harboured more than one QTL or had pleiotropic effects on several traits. The interval p20m307i – p100m88c (15–20 cM) on chromosome 1H had QTL/pleiotropic effects on days to heading, kernel filling duration and kernel weight; the intervals Bmac0129a – HVBKASI (54-57 cM) and HVM54 – P71m34e on chromosome 2H on biological yield and grain yield; the interval P10034f – Bmag0125 on chromosome 2H on biological yield and growth vigour; the interval Bmac0521 – HVM26 on chromosome 2H on grain yield and growth habit; the interval Bmac0144b – p101m32m on chromosome 2H on growth habit and lodging; the interval p101m237b – Bmag0113 on chromosome 5H on kernel filling duration, growth vigour, kernel weight and plant height; and the interval p71m289h – GMS6 – HVM74 on chromosome 6H on grain yield and kernel weight. Similarly, Hayes et al. (1993) reported that grain yield QTL coincided with height and lodging QTL. Baum et al. (2003) found pleiotropic effects for the region around the *denso* locus on chromosome 3H for plant height, heading date, grain yield and biological yield. Li et al. (2005) found that the chromosome 2H region around the *Ppd*-H1 locus had pleiotropic effects on grain yield, heading date and plant height. Marquez-Cedillo et al. (2001) found the region around the *vrs1* locus having pleiotropic effects on kernel plumpness and test weight.

Over the last two decades, QTLs for a wide range of traits related to drought tolerance, including physiological/agronomic and biochemical characteristics, have been mapped to all seven barley chromosomes (Mir et al., 2012). A precise comparison among these results is not possible owing to the differences in used plant materials and maps, various traits analysed and the diverse methodology applied; however, some interesting observations can be made in regard to the results of the present study.

In our study we identified QTLs that were mapped to all barley chromosomes, with the highest number of QTLs located on chromosomes 1H, 2H, 5H and 6H. We found nine hotspots based on the overlapping confidence intervals, which contained over 50% of mapped QTLs for all the traits, with most on 2H (5), 5H (2) and 6H (2). Previous studies aimed at detecting QTLs underlying yield-related agronomic traits under drought and control conditions (Mikołajczak et al., 2017, 2016; Ogrodowicz et al., 2017) have also reported the important role of the regions on chromosomes 2H. Our results align with a significant QTL hotspot found on 2H, clustering QTLs for the plant height and yield traits (Mikołajczak et al., 2017), as well as heading date (Ogrodowicz et al., 2017). Another region of overlapping QTL hotspots between these studies was found on chromosome 5H, which coincided with our study. Similarly, Mora et al. (2016) revealed the highest number of QTLs for drought-related morphological and physiological traits on chromosomes 2H and 3H, using a distinct barley gene pool and environmental conditions. Recently, a meta-QTL analysis approach has been developed, which is aimed at the integration of data from multiple QTL studies and has a greater statistical power for the detection of so-called meta-QTLs (MQTL) and more precise estimation of their genetic effects (Wu & Hu, 2012). Zhang et al. (2017) performed a meta-QTL analysis of drought tolerance in barley using 72 major QTLs described in several studies, and most of the QTLs were located on chromosomes 2H, 3H, 5H and 7H. As a result, MQTLs, integrating QTLs for barley drought tolerance, have been positioned on chromosomes, with some particularly important regions common to drought and salinity tolerance on 2H (2), 3H (1) and 5H (1).

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4.2 | QTLs detected across environments

Besides identifying numerous QTLs in single environments, QTLs consistent in at least two or more environments were also identified. This suggests that these QTLs are not significantly influenced by specific environmental factors.

The heading date QTL *QHD2.3a, b* identified in Rab00 and Th01 might reflect the influence of the *Ppd*-H1 locus on chromosome 2H in the adapted germplasm. The kernel weight QTLs *QKW 1.5*, *QKW2.7*, *QKW5.1*, *QKW6.7* and *QKW6.9* were identified with consistent expression across a range of environments in semi-dry and dry areas. The QTL *QKW1.5a,b* on chromosome 1H seems to be a new location harbouring kernel weight QTL in semi-dry areas. Chromosome 6H has also been reported as harbouring kernel weight QTL (Baum et al., 2003; Li et al., 2005; Teulat et al., 2001).

Variation in response to drought is mainly because of combined genetic and environmental effects (Sobhaninan et al., 2019). Grain yield and related traits differ in their responses to environmental conditions (Lopes et al., 2012). In the present study, there was an inverse

relationship between days to heading, grain yield and its components (Table 4). This negative correlation was confirmed in other studies on wheat (Olivares-Villegas et al., 2007; Rattey et al., 2009; Sobhaninan et al., 2019; Tahmasebi et al., 2014). This negative correlation may be an escape mechanism from drought. Heading time proved to be a valuable indicator of the drought tolerance genotypes under drought stress conditions (Reynolds et al., 2012). Therefore, identifying genotypes that maintain normal metabolism, growth rate and grain yield under water deficit might help characterise inherent genetic differences in drought tolerance (Sobhaninan et al., 2019).

The significant and positive correlation of biological yield and harvest index with grain yield identified in the present study shows that the cross Arta/Harmal was adapted, and mechanisms were developed to cope with drought stress. These genotypes are often characterised by their ability to use limited water resources efficiently, maintain physiological functions under drought stress and allocate resources effectively towards grain development.

Certain hotspots in QTL analysis have identified shared genetic markers for various barley traits, which can be utilised in marker-assisted breeding programmes to enhance genetic gain. Although there is a great deal of interest in identifying genes that contribute to grain yield and drought tolerance in barley, the complex interactions between these genes have made it difficult to pinpoint the exact responsible genes.

5 | CONCLUSIONS

The present study found that the 2H chromosome harbours the most important QTL and pleiotropic effect for yield and related traits such as kernel weight, days to heading and biological yield. The QTLs, which significantly explained more than 10% of the phenotypic variation in dry areas (rainfall <250 mm/annum), were identified for biological yield, days to heading and kernel weight on chromosome 2H, for harvest index on 1H, for kernel weight on 2H, 4H and 5H, for duration of filling period and plant height on 1H. The QTLs, which significantly explained more than 10% of the phenotypic variation in semi-dry areas (rainfall <450 mm), were obtained for grain yield on chromosome 6H, for kernel weight on 2H and 5H, for seed per head on 1H and 6H, and for days to heading on 2H (Table 6). Importantly, the kernel weight QTLs (*QKW 1.5*, *QKW2.7b*, *QKW5.1*, *QKW6.7*, *QKW6.9*), which were identified with consistent expression across a range of environments in semi-dry and dry areas, can be potentially used for drought tolerance breeding. The crossbreeding of Arta/Harmal has resulted in the development of mechanisms that help the plant cope with drought stress. This has led to a positive correlation among biological yield, harvest index and grain yield. During the Arta/Harmal cross-development, a strategy was proposed to use QTLs to achieve specific objectives. The evaluation revealed that co-localised QTLs for grain yield, plant height and adaptation to drought in the Arta/Harmal cross could be simultaneously improved through MAS. This would allow specific regions to be transferred to elite barley genotypes to simultaneously increase the content of various traits, thereby accelerating progress in barley variety development. To achieve this, an attempt can be made to pyramid QTLs responsible for grain yield, biological yield, harvest index, kernel weight, seed size, heading date, flowering period, grain volume, grain hardness, lodging and plant height. However, it is important to clearly understand the co-localisation of QTLs and their effect on target traits, such as grain yield under drought stress, to use the major effect of QTLs in marker-assisted breeding effectively. The genomic co-localisation of the QTL for the Arta/Harmal population suggests that selection for drought through linked markers can be an option for drought tolerance selection for barley in dry areas. Moreover, we are the first to report the two QTLs for growth vigour on 3H and growth habit on 2H in dry areas.

AUTHOR CONTRIBUTIONS

Haitham Sayed, Salvatore Ceccarelli, Stefania Grando and **Michael Baum** planned the experiments. **Haitham Sayed** conducted the molecular experiments, statistical data analysis and QTL analysis and drafted the manuscript. **Salvatore Ceccarelli** and **Stefania Grando** conducted field experiments at Tel Hadya, Breda and Khanasri sites in Syria. **Adnan Al-Yassin** performed experiments at the Jordan Ramtha, Rabba and Gweer sites. **Haitham Sayed** and **Michael Baum** wrote the manuscript. **Henrik U Stotz** and **Bruce DL Fitt** edited the last version. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

All electronic supplementary material (S1–S6) is available to authorised users.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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