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ORIGINAL PAPER

Variation at the vernalisation genes *Vrn-H1* and *Vrn-H2* determines growth and yield stability in barley (*Hordeum vulgare*) grown under dryland conditions in Syria

Jarod A. Rollins · B. Drosse · M. A. Mulki · S. Grando · M. Baum · M. Singh · S. Ceccarelli · M. von Korff

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Abstract
Key message **Spring growth in barley controlled by natural variation at Vrn-H1 and Vrn-H2 improved yield stability in marginal Syrian environments.**
Abstract The objective of the present study was to identify QTL influencing agronomic performance in rain-fed Mediterranean environments in a recombinant inbred line (RIL) population, ARKE derived from the Syrian barley landrace, Arta and the Australian feed cultivar, Keel. The population was field tested for agronomic performance at two locations in Syria for 4 years with two sowing dates, in autumn and winter. Genotypic variability in yield of the RIL population was mainly affected by year-to-year variation presumably caused by inter-annual differences in rainfall distribution. The spring growth habit and early flowering inherited from the Australian cultivar Keel increased plant height and biomass and improved yield stability in Syrian environments. QTL for yield and biomass coincided with the map location of flowering time genes, in particular the vernalisation genes *Vrn-H1* and *Vrn-H2*. In marginal environments with terminal drought, the *Vrn-H1* allele inherited from Keel improved final biomass and yield. Under changing climate conditions, such as shorter winters, reduced rainfall, and early summer drought, spring barley might thus outperform the traditional vernalisation-sensitive Syrian landraces. We present the ARKE population as a valuable genetic resource to further elucidate the genetics of drought adaptation of barley in the field.

J.A. Rollins and B. Drosse contributed equally to the paper.

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J. A. Rollins · B. Drosse · M. A. Mulki · M. von Korff (✉)
Max Planck Institute for Plant Breeding Research,
Carl-von-Linné-Weg 10, 50829 Cologne, Germany
e-mail: korff@mpipz.mpg.de

M. A. Mulki · S. Grando · M. Baum · M. Singh · S. Ceccarelli
The International Center for Agricultural Research in the Dry Areas (ICARDA), P.O. Box 5466, Aleppo, Syria

Present Address:
S. Grando · S. Ceccarelli
ICRISAT, Patancheru 502 324, Andhra Pradesh, India

M. von Korff
Institute of Plant Genetics, Heinrich-Heine-University,
40225 Düsseldorf, Germany

Introduction

Marginal farmlands constitute the majority of the land used for agriculture and therefore offer the greatest opportunity to substantially increase worldwide food production (Tester and Langridge 2010). Marginal environments are characterised by abiotic stress, such as heat and drought, the occurrence of which strongly varies over space and time (Blum 1996, Baum et al. 2007). In contrast to favourable environments with stable conditions, marginal Mediterranean environments are thus characterised by high environmental fluctuations which result in low trait heritability and high genotype-by-environment interactions (Voltas et al. 2002).

Barley is the second most widely cultivated crop in marginal Mediterranean environments and is often the most common crop in the driest rain-fed farming areas as it is well adapted to abiotic stresses (Baum et al. 2007). Selection and breeding have resulted in landraces and modern genotypes adapted to stress-prone environments, and both

germplasm groups are under cultivation in these environments. While landraces are characterised by high yield stability and intermediate yield levels under low input agriculture, modern cultivars are often bred for high yield potential under favourable conditions (Zeven 1998, Pswarayi et al. 2008). There are two schools of breeding philosophy: breeding for adaptation to a specific agroecological environment (specific adaptation) or breeding for wide adaptation across agroecological environments (Ceccarelli 1989). Breeding for specific adaptation has been used in particular for adaptation to marginal environments with high variation in climatic and edaphic conditions (Atlin and Frey 1990; Ceccarelli et al. 1992). In this context, it is essential to identify similar stress-prone agroecological environments which can be geographically distant, for effective breeding and germplasm exchange (Windhausen et al. 2012). An example of the adaptation of breeding material to geographically distant locations is given by the adaptation of the barley germplasm bred by the International Center for Agricultural Research in the Dry Areas (ICARDA), Syria for the drought stress environments of West Asia and Northern Africa (WANA) to the dry Southern Australian environments (Coventry et al. 2004). Barley lines from WANA (ICARDA) tested in Southern Australia displayed favourable levels of abiotic stress resistance, and a significant number of barley genotypes performed at least as well as the best Australian feed varieties (Eglinton et al. 2001). In some instances, Australian breeding lines have also been tested for adaptation to dry locations in Syria and results suggested that these lines and derived crosses performed well in wetter locations in Syria (Shakhatreh et al. 2001). This reciprocal adaptation is a typical case of wide "geographical" adaptation but not necessarily of wide "environmental" adaptation as abiotic stresses are the main yield-limiting factors in both environments. It is, however, interesting because ICARDA and Australian germplasm represent very different genetic backgrounds and breeding histories. While ICARDA lines often represent selections from the landraces commonly grown by subsistence farmers as feed barley, Australian genotypes are bred for high yield potential as malting or feed barley. Despite the high economic value of germplasm exchange (Gepts 2006), the genetic basis of adaptation of genetically diverse germplasm to drought-prone environments in Syrian and Southern Australia, is not yet understood.

Previous QTL studies for agronomic performance in dry Mediterranean environments have found that differences in reproductive development were one of the key factors determining adaptation under water-limiting conditions (Francia et al. 2011; Cuesta-Marcos et al. 2008). Barley is characterised by two major growth types: winter and spring. Winter growth types are defined here as genotypes which show accelerated flowering after vernalisation, the prolonged exposure to cold temperature. In contrast, spring barley does not respond to vernalisation. However, there exists a continuous gradient from typical spring to extreme winter growth (vernalisation requirement). The growth habit is determined by the interaction of *Vrn-H2*, a strong inhibitor of flowering under long-day conditions and *Vrn-H1* which is upregulated during vernalisation and represses *Vrn-H2* (Yan et al. 2003, 2004). A recessive deletion of the *Vrn-H2* locus and dominant alleles at *Vrn-H1*, resulting from deletions in the first intron, are associated with the increased *Vrn-H1* expression in the absence of cold treatment, reducing or eliminating the requirement for vernalisation. Variation in the size of the first intron of *Vrn-H1* thus causes quantitative differences in *Vrn-H1* expression and in vernalisation requirement (Hemming et al. 2009). Vernalisation response is often associated with strong photoperiod sensitivity, dominant alleles of the photoperiod response gene *Ppd-H1* induce early flowering under long-day conditions as an adaptation to short growing seasons in Mediterranean environments. A recessive mutation in the gene prevalent in spring barley causes reduced photoperiod sensitivity and delayed flowering as an adaptation to Northern European environments (Turner et al. 2005). *Ppd-H1*, *Vrn-H1* and *Vrn-H2* converge on the floral inducer *HvFT1* (*Vrn-H3*); *Vrn-H2* represses *HvFT1* to counteract the *Ppd-H1*-dependent long-day induction of *HvFT1* before vernalisation (Hemming et al. 2008; Campoli et al. 2012b). Under long days, high levels of *Vrn-H1* expression positively correlate with *HvFT1* expression and time to flowering. Genetic variation in the first intron of *HvFT1* has been linked to differences in *HvFT1* expression and flowering in response to vernalisation (Yan et al. 2006, Casas et al. 2011). However, a recent study showed that *HvFT1* copy number variation determined the growth type, while differences in the intron sequence did not clearly associate with flowering time, suggesting that other linked, unknown polymorphisms may determine *HvFT1* expression (Nitcher et al. 2013). Most wild ancestors of domesticated barley, *H. vulgare* ssp. *spontaneum,* are classified as having a winter growth habit and early flowering under long day (Takahashi et al. 1963 in Saisho et al. 2011), indicating that the winter growth habit is ancestral in barley. In Mediterranean areas and the Near East, cultivated barley is generally sown in autumn and typically shows an intermediate vernalisation requirement as determined by partial deletions in the *Vrn-H1* intron, or by a spring growth habit due to deletions of *Vrn-H2* and/or in the intron of *Vrn-H1*. The spring growth type is more common in coastal areas and Southern parts of the Fertile Crescent where winter temperatures are mild (Weltzien 1988, 1989), but cultivars with and without vernalisation response occupy similar cultivation areas (Saisho et al. 2011). It is thus interesting to study the effects of spring versus winter growth habit on yield and

yield component traits in marginal Mediterranean environments with cold winters and dry summers.

The objectives of the present study were to: (1) analyse the genetic basis of adaptation to dry environments in a Syrian landrace and an Australian cultivar; (2) test the effects of spring versus winter growth on agronomic performance in marginal environments; (3) characterise the magnitudes of trait variation between locations and between years within locations in dry Mediterranean environments.

A QTL analysis for agronomic performance was conducted in a recombinant inbred line population termed ARKE derived from two genetically diverse parental lines, the Syrian landrace selection and winter barley, Arta and the Australian spring cultivar, Keel. The analysis showed that year-to-year variation had stronger effects on agronomic performance than variation across two contrasting locations in Syria. QTL for yield coincided with QTL for plant height and flowering time suggesting that improved growth and early flowering increased yield in dry environments. Many QTL clusters coincided with known flowering time genes and loci, in particular the vernalisation genes *Vrn-H1* and *Vrn-H2* at which the Keel alleles accelerated heading date, plant growth and improved yield in the majority of tested environments. The spring growth habit inherited from the Australian cultivar Keel thus caused early flowering, and was correlated with increases in plant height and biomass, and improved yield stability. We present the ARKE population as a valuable genetic resource to further elucidate the genetics of drought adaptation in barley.

Materials and methods

Plant material

The Syrian barley, 'Arta' and the Australian feed barley cultivar, 'Keel' were used to develop a population of 499 recombinant inbred lines (RILs) at ICARDA. Arta is a two-row pure line selected from the Syrian white-seeded landrace, Arabi Abiad. Arta is a winter barley and is well adapted to the driest sites in Syria (Baum et al. 2003); it was officially released by the Syrian Ministry of Agriculture and Agrarian Reform in 1994 with the name of "Arabi Abiad Improved". Keel is a two-row spring feed barley variety, which was developed by the South Australian Barley Improvement Program from a cross between Clipper, CPI18197, and WI 2645. Keel is well suited to low rainfall areas where it showed a clear yield advantage over most current Australian feed varieties (South Australian Field Crop Evaluation Program and Field Crop Pathology, SARDI, and the South Australian Barley Improvement Program, University of Adelaide).

Arta was crossed with Keel to generate the uniformly heterozygous F1 generation. By selfing the F1 population, the F2 population was created. The F2 plants were then selfed and 500 heads were collected. The seeds of each head were grown in 1-m-long single rows as F3 generation. From each F3 family, one head was collected at random and grown as F4 generation in a 1-m-long single row. The population, henceforth designated as ARKE, was then advanced to F8. Field data were collected for all 499 ARKE lines, but only 188 randomly selected lines were genotyped.

The RIL population and the parental lines were scored for 11 agronomic traits (Table 1) in the field from 2006 to 2009 at two locations in Syria, Tel Hadya (36.01°N; 36.56°E, elevation 284 m asl) and Breda (35.56°N, 37.10°E, elevation 300 m asl) with a long-term average rainfall of 303 mm (27 seasons) and 275 mm (25 seasons), respectively. The soil of Tel Hadya is classified as very fine clay, thermic, Chromic Calcixerert, while the soil of Breda is a loamy, thermic, Calcixerollic Xerochrept with a lower calcium carbonate (5 %) compared to the Tel Hadya soil (20 %) (Ryan et al. 1997). Both soils have similar pH values (7.9–8.1) and are deficient in phosphorus and nitrogen.

At each location, the RIL population was sown in autumn and in winter of each year between 2005 and 2009 except for the winter of 2006 (Supplementary Table 1 for sowing and emergence dates). Thus, the population was tested in 14 different environments. However, the trial at Breda sown in winter in 2008 was not scored as most lines did not flower due to severe water limitations. Environments are abbreviated as follows: B for Breda, T for Tel Hadya, then two digits for the year (example 07 = 2007), A for autumn sowing and W for winter sowing. The field trials were set up in a row and column unreplicated design with the two parents as systematic checks (50 plots of Keel and 51 of Arta) with a total of 600 plots (4 m^2 each, 8 rows of 2.5 m at 20 cm distance) and with a different randomisation in each combination of location and year (Gleeson 1997; Kempton and Gleeson 1997). The sowing density was 300 seeds/m^2 for all entries and planting was performed with a plot drill. A plot combine was used for harvesting and the seeds were subsequently ventilated before taking the weight. The field management, net plot size, and seed density were according to the local practice. Climate data were recorded on a daily basis as summarised in Table 2.

Statistical analyses

For each trait at each available combination of location, sowing date and year, the best linear unbiased estimates (BLUEs) of the genotype effects were calculated using the most suitable spatial model determined for the

Table 1 List of 11 quantitative traits investigated in a total of thirteen different environments

Abbreviation	Trait	Units	Method of measurement	Environment
BY	Biological yield	kg/ha	Vegetative biomass	B08A B09A B09W T08A T08W T09A T09W
DH	Days to heading	days	Days from emergence to heading	T06A T07A T07W T08A T08W T09A T09W
GH	Growth habit		As a visual score from 1 = erect to 5 = flat at the 5–6 leaf stage	B09A T06A T07A T07W T08A T09A T09W
GV	Growth vigour		As a visual score from 1 = poor vigour to 5 = good vigour at the 5–6 leaf stage	B06A B07A B07W B08A B09A T06A T07A T07W T08A T08W T09A T09W
GY	Grain yield	kg/ha	Measured after threshing the harvested sample	B06A B07A B07W B08A B09A B09W T06A T07A T07W T08A T08W T09A T09W
HI	Harvest index		Ratio of generative to vegetative biomass	B08A B09A B09W T08A T08W T09A T09W
KW	Kernel weight	g	Measured as the average of 3 samples of 100 kernels per plot	B07A B07W B08A B09A B09W T07A T07W T08A T09A T09W
PED	Peduncle length	cm	Measured from the last node to the bottom of the spike	B06A B07A B07W B08A B09A B09W T06A T07A T08A T08W T09A T09W
PEDEX	Peduncle extrusion	cm	Measured from the ligule of flag leaf to the bottom of the spike	B06A B07A B07W B08A B09A B09W T06A T07A T08A T08W T09A T09W
PH	Plant height	cm	Measured from soil surface to the bottom of the spike	B06A B07A B07W B08A B09A B09W T06A T07A T07W T08A T08W T09A T09W
SL	Spike length	cm	Spike length excluding the awns	B06A B07A B07W B08A B09A B09W T06A T07A T07W T08A T08W T09A T09W

Environment designed as a combination of the location (*B* Breda, *T* Tel Hadya), the year (2006 = 06, 2007 = 07, 2008 = 08, 2009 = 09) and the planting date (*A* autumn, *W* winter). In 2007, 2008 and 2009 additional planting in winter was carried out to extend the generative phase of plants into the summer drought

associated individual field layout. The procedure of Singh et al. (2003), which was developed for an incomplete block design, was further modified to suit an unreplicated trial in a rectangular field layout as in the present study, where there were no blocks and the spatial variability was gauged by the best of the nine applicable models. These models comprised factorial combinations of: (1) three ways of accounting for linear trends in column direction, with or without a linear trend and random cubic smoothing spline (CS) in column number; and (2) three structures for plot errors, first-order autoregressive (AR) errors along rows, first-order autoregressive (AR) errors along rows as well as AR along columns, and independent errors. These are listed as:

1. Crd (completely randomised design) is a non-spatial design and serves as a control model to compute the efficiency of other models which have one or more features of spatial variability.
2. CrdAr, using a completely randomised design with first-order auto-correlated (AR) errors along rows.
3. CrdArAr, using a completely randomised design with first-order auto-correlated (AR) errors along rows and along columns.
4. CrdL, using a completely randomised design with linear trends along rows.
5. CrdLAr, using a completely randomised design with linear trends along rows and first-order auto-correlated (AR) errors along rows.
6. CrdLArAr, using a completely randomised design with linear trends along rows, and first-order auto-correlated (AR) errors along rows and along columns.
7. CrdCS, using a completely randomised design with linear trends along rows and random cubic smoothing spline in column numbers.
8. CrdLCSAr, using a completely randomised design with linear trends along rows, random cubic smoothing spline in column numbers and first-order auto-correlated (AR) errors along rows.
9. CrdLCSArAr, using a completely randomised design with linear trends along rows, random cubic smoothing spline in column numbers and first-order auto-correlated (AR) errors along rows and along columns.

Each of the above models was fitted for the data of each trial by expressing the plot position in row and column number. The REML (restricted maximum likelihood) method of the Genstat software (Payne 2011) was used to fit the model by setting the associated directives, VCOMPONENTS to declare the fixed and random components in the model and VSTRUCTURE to declare the error structures (for example, first-order auto-correlated errors along

Table 2 Ecological data and mean grain yield (kg/ha), in four different years and two different locations

Env	Tm	Ts	Tj	Tdd	Ts	Rc	Rn	Hu-an	Ev	PAR	RAD	So	GY RILS A	GY RILs W	GY A/W Arta	GY A/W Keel
B05-06	13	22	7	15	18	237	62	67	5	nd	nd	Loam	2,821	nd	2,970/nd	3,440/nd
B06-07	12	24	6	14	18	224	60	62	4.5	nd	nd	Loam	1,037	108	975/6	1,030/174
B07-08	14	19	3	13	19	174	37	54	5.6	nd	nd	Loam	1,539	0	1,181/0	1,449/0
B08-09	14	21	6	14	19	247	72	56	4.8	nd	nd	Loam	1,226	660	1,486/568	1,219/801
Breda	**13**	**22**	**6**	**14**	**19**	**221**	**58**	**60**	**5**	**nd**	**nd**	**Loam**	**1,656**	**256**	**1,653/191**	**1,785/325**
T05-06	14	23	6	13	17	302	82	63	4.2	27	15	Clay	4,930	nd	4,610/nd	4,962/nd
T06-07	13	24	6	16	16	290	74	61	3.6	27	16	Clay	2,269	701	2,251/241	2,366/941
T07-08	14	21	3	16	15	223	58	58	4.8	28	15	Clay	4,160	888	2,905/143	4,094/1,592
T08-09	14	20	8	14	15	291	89	65	3.2	25	13	Clay	2,490	291	2,830/1,452	2003/1,303
Tel Hadya	**14**	**22**	**6**	**15**	**16**	**277**	**76**	**62**	**4**	**27**	**15**	**Clay**	**3,462**	**627**	**3,144/612**	**3,356/1,279**

All climatic measurements represent annual means from September to October. Temperature °C: *Tm* mean annual temperature, *Ts* mean May temperature, *Tj* mean January temperature, *Tdd*= mean annual day–night temperature difference, *Ts* mean annual soil temperature at 5 cm. Water availability: *Rc* cumulative rainfall in mm, *Rn* number of rainy days, *Hu-an* mean annual humidity, *Ev* mean annual evaporation. Solar radiation: *PAR* photosynthetically active radiation, *Rad* total daily solar radiation, *So* soil type, *GY* yield in kg/h in *A* (autumn-sown) and *W* (winter-sown) experiments, *nd* not determined

rows/columns). To select the best model out of the nine models, we used Akaike information criterion expressed in terms of a quantity called 'deviance' produced by Genstat. The 'deviance' is minus twice the REML log-likelihood ignoring a constant depending on the fixed terms, and thus Akaike information criterion expressed as deviance is AICD = deviance + twice the number of linear and non-linear variance components of the models and was used to compare models with the same fixed effect terms (Singh et al. 2003). The best model out of the nine models was used for estimating the experimental error variance and genetic parameters. Means of the genotypes were estimated as best linear unbiased estimates (BLUEs) by fitting the model with genotype effects assumed as fixed.

We used the BLUEs in the GGE biplot to indicate possible specific adaptations of lines to the environments. The biplot was environment scaled/focused (Yan et al. 2000). The BLUEs were also used for all further analyses including the subsequent QTL detection. We further carried out estimation of variance components associated with genotypes (G) and partitioning of genotype × environment components where the environments was partitioned into location (L), sowing time (S), interaction L × S, years within location (Y(L)), years within sowing time (Y(S)) and the remainder. The main effects of L and S and their interaction were assumed fixed, while the genotype, G, and its interaction with (a) fixed environment effects, G × L, G × S and G × L × S and random environment effects involving years, G × Y(L) and G × Y(S) were assumed random. Assessment of these interactions is relevant in discussing breeding strategies related to wide and specific adaptation. The highest order interaction (G × Y × L × S) was treated as random error. For the traits which were recorded at either only one locations or year, the highest available three-factor interaction was taken as random error. We used REML directive of Genstat (Payne 2011) to estimate the variance components. Statistical significance of various genotypic variance components was carried out by treating the estimate divided by its standard error as an approximation by standard normal variate.

The procedure MEANS (SAS ver. 9.2, SAS Institute 2009) was used to calculate means and standard deviations for each trait in the RIL population, Arta and Keel at each location and sowing date, separately. Significant differences between means were identified with the Duncan test (Duncan 1955). Genetic correlations were determined separately for autumn and winter sowings using means calculated across environments and years for each RIL.

Genotyping and linkage map construction

Arta, Keel, and 188 RILs were genotyped with 103 microsatellites (SSR markers), 623 DArT-markers and

ten gene-specific PCR markers (*Vrn-H1*, *Vrn-H2*, *Vrn-H3*, *HvFT3*, *HvCO1*, *HvCO2*, *HvVrt2*, *HvGI*, *HvPRR1* and *HvA1*; Supplementary Table 2 for primer information). *Vrn-H3*, *HvFT3*, *HvCO1*, *HvCO2*, *HvVrt2*, *HvGI*, *HvPRR1* were sequenced in Arta and Keel and SNPs between both genotypes were targeted for genotyping using high-resolution melting (HRM) in the Roche Lightcycler 480. Amplifications were carried out with 100–150 ng of DNA, 0.4 U of GoTaq Flexi DNA polymerase (Promega), 0.2 mM dNTP, 2.5 mM $MgCl_2$, 0.4 μM of each primer, and 0.75 μL of EvaGreen (Biotium). Reactions were performed with the following amplification conditions: 95 °C for 3 min, 45 cycles of 95 °C for 15 s and 56 °C for 30 s. High-resolution melting included a first-step heating to 95 °C for 5 min and a melting program that went from 65 to 95 °C. Melting curve analysis was performed on the LightCycler 480 with the gene-scanning module (version 1.3).

DArT genotyping was carried out by Triticarte Pty. Ltd. (http://www.tritcarte.com.au). Markers with a segregation distortion higher than 20 % in 188 RILs were excluded from linkage map construction. SSR markers were assigned to barley chromosomes based on a previously published barley consensus map (Alsop et al. 2011). Linkage groups of SSR-, DArT- and PCR-markers were calculated with the mapping software JoinMap3.0 (van Ooijen and Vorrips 2001). Genetic distances between markers were calculated with the Haldane mapping function and a LOD threshold of 3.0.

QTL analysis

The QTL analysis was conducted with the program MultiQTL Version 2.5 (Korol et al. 2005) using the MULTIPLE ENVIRONMENT OPTION which calculates significant effects across all environments, but reports effects for each environment separately After performing simple-interval mapping (SIM) for each trait, significances of detected QTL were estimated by permutation tests ($N = 1{,}000$). For the entire genome analysis, we included all chromosomes with significant ($P < 0.05$) putative QTL detected by SIM into the multiple-interval mapping (MIM) model to reduce "background" variation by taking into account QTL effects from other chromosomes. QTL obtained with MIM were tested for significance ($P < 0.001$) with a global permutation test ($N = 10{,}000$) and QTL effects and percentage of explained variance reported are inferred from the multi-locus model. The most significant marker interval is reported in Table 5. In addition, pairwise interaction effects between flowering time genes were calculated for each environment for all traits within MultiQTL.

Results

Phenotypic variation is high across years and locations

The largest climatic differences between locations were recorded for cumulative rainfall, number of rainy days and soil temperature (Table 2). Between years, the largest climatic variation was observed for cumulative rainfall and number of rainy days. Cumulative rainfall showed the highest correlation with yield in autumn-sown (0.71) and winter-sown experiments (0.79). Yield in autumn-sown field trials was lower in Breda with an average yield of 1,656 kg/ha as compared with Tel Hadya with an average yield of 3,462 kg/ha. Yield was strongly reduced in winter-sown field trials in both locations; average yield levels were 256 kg/ha in Breda and 627 kg/ha in Tel Hadya. The lowest average rainfall of 174 mm in Breda and 223 mm in Tel Hadya was recorded in 2007–2008, when we recorded only 37 rainy days at Breda and 58 rainy days at Tel Hadya. The GGE biplot for yield performance separated the autumn and winter-sown trials, while the autumn-sown experiments in 2008 clustered between the autumn and winter-sown trials (Fig. 2). The parental line Keel yielded higher than Arta in all environments except those in 2009 autumn sowing (Table 2). In particular, Keel showed higher yields in the environments with low rainfall in 2008 and the winter-sown experiments, while Arta yielded higher in the 2009 autumn-sown experiments which were characterised by more favourable climatic conditions. Keel thus demonstrated a higher yield stability as compared to Arta.

In all environments, the RIL population showed significant transgressive segregation for yield and biomass (Fig. 1a, b; Table 3).

The correlation analysis revealed significant and positive correlations of GY with BY, and HI with correlation coefficients of 0.54 and 0.45 in the autumn-sown and 0.60 and 0.79 in the winter-sown trials, respectively (Table 4). GY also showed positive correlations with KW (0.42), PED (0.44), PH (0.33), and SL (0.48) in the winter-sown trials, but not in the autumn-sown trials. Additionally, DH showed high negative correlations with yield component traits such as GY in autumn-sown trials (−0.26) and winter-sown trials (−0.66), KW in autumn-sown (−0.28) and winter-sown trials (−0.57), and SL (−0.71) only in the winter-sown trials. In addition, DH was negatively correlated with BY (−0.33) and PH (−0.30) in autumn-sown trials and with BY (−0.24) and PH (−0.39) in winter-sown trials. The analysis revealed more significant and higher correlations coefficients in the winter-sown than in the autumn-sown trials. Partitioning of phenotypic variation revealed a high variation

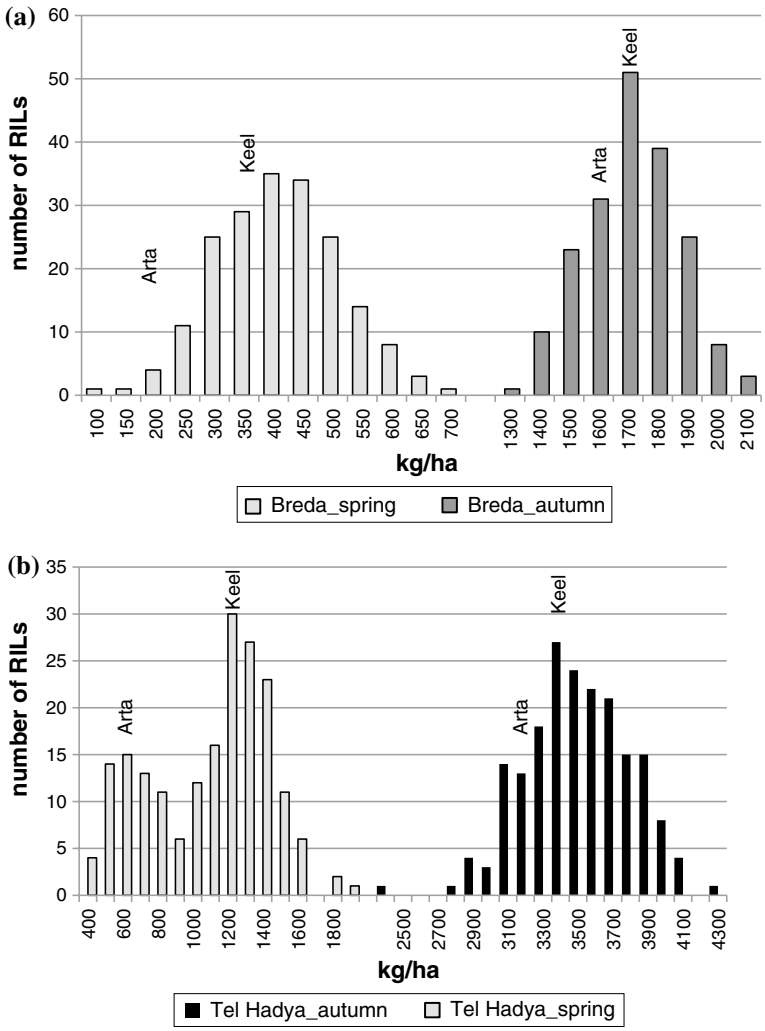

Fig. 1 Frequency distribution of grain yield at different sowing times (autumn, winter) across 4 years in different locations: **a** Breda and **b** Tel Hadya. The mean performance of the parental lines Arta and Keel is indicated above the bars

and significant effects of the genotype (DH, GH, GV, GY, HI, KW, PED, PEDEX and PH), its interaction with sowing date (DH, GH, GV, KW, SL), its interaction with year within locations (BY, GV, HI, PED, PEDEX, PH) and with year within sowing date (BY, GV, KW, PED, PEDEX, PH, SL). There was no significant variation due to genotype and location interaction, while the interactions between genotypes and years within locations were significant. Where estimable, the genotype and year interactions within location or sowing date were either stronger in significance or higher in magnitude compared to the genotype (BY, GV, GY, PED, PEDEX, PH, SL except KW) (Supplementary Table 3).

Taken together, the year-to-year variation in total rainfall and rainfall distribution had the strongest effects on traits expression. Early flowering was correlated with increased biomass, plant height and yield in autumn and winter-sown trials. The early flowering spring barley Keel showed improved yield in the majority of environments and in particular in environments with low rainfall (Table 2).

Genetic marker map and QTL analysis

A recombination map was constructed for the ARKE RIL population with 554 DArT markers, 101 SSR markers, and 10 STS markers derived from 9 genes involved in the control of reproductive development and the stress response gene *HvA1* (Cseri et al. 2011). Sequencing of candidate genes revealed that both parents carried the dominant allele of *Ppd-H1* (Turner et al. 2005). The parental lines showed functional polymorphism in *Vrn-H1* (Hemming et al. 2009) and *Vrn-H2* (Karsai et al. 2005), and were differentiated by an insertion/deletion polymorphism of 4 bp in the promoter of *Vrn-H3* (*HvFT1*) and silent SNPs in the remaining genes (Supplementary Table 2). A total of 665 markers clustered into 11 linkage groups with a total map size of 1,129 cM and an average marker distance of 1.7 cM (Supplementary Table 4). Two linkage groups were found for chromosome 1H and 2H and three linkage groups for chromosome 7H, thus separate linkage groups were designated as 1Ha/1Hb, 2Ha/2Hb and 7Ha/7Hb/7Hc, respectively. Most markers

Table 3 Recorded traits, abbreviations and number of environments, in which the 11 traits were measured

Abbreviations	Trait	#env[a]	Means B-A			Means B-W			Means T-A			Means T-W		
			RILs[b, c]	Arta	Keel	RILs[b, c]	Arta	Keel	RILs[b, c]	Arta	Keel	RILs[b, c]	Arta	Keel
BY	Biological yield (kg/ha)	7	3,042 ± 703a	2726aef	2811ae	1,848 ± 364c	2172cef	1697c	6,552 ± 1496b	5876d	6090d	3,695 ± 1740a	2398ae	3885a
DH	Days to heading (days)	7	nd	nd	nd	nd	nd	nd	98 ± 9a	100a	98a	53 ± 8b	60c	50b
GH	Growth habit	7	2.3 ± 0.2a	2.4a	2.5a	nd	nd	nd	2.5 ± 0.4a	2.3a	2.5a	2.4 ± 0.8a	3.4b	2.0a
GV	Early growth vigour	12	2.4 ± 0.7ab	2.0a	2.8a	2.4 ± 0.8a	3.5b	2.1a	2.3 ± 0.7a	2.4a	2.6a	2.5 ± 0.9a	3.2ab	2.3a
GY	Grain yield (kg/ha)	12	1,681 ± 755a	1652a	1784a	256 ± 308c	191c	325c	3,455 ± 1272b	3149b	3356b	1,091 ± 565d	611c	1279d
HI	Harvest index	7	0.45c	0.45c	0.46c	0.20a	0.18a	0.21a	0.52bc	0.57bc	0.48bc	0.39c	0.28a	0.46c
KW	Kernel weight (g)	10	36 ± 4a	35a	36a	31 ± 5c	29c	31c	41 ± 8bd	39d	41bd	40 ± 9bd	36a	39d
PED	Peduncle length (cm)	12	12 ± 5dg	11gh	11gh	7 ± 3b	5f	8bc	16 ± 7a	15a	15a	10 ± 3c	8bc	11gh
PEDEX	Peduncle extrusion (cm)	12	−7 ± 5ae	−5b	−9cf	−9 ± 2cf	−7ae	−10f	−4 ± 7b	−2d	−5b	−8 ± 3ce	−8ae	−9cf
PH	Plant height (cm)	12	35 ± 12a	31a	36ac	21 ± 6ef	16f	23eh	53 ± 22b	51b	52b	33 ± 7ac	29ch	34ac
SL	Spike length (cm)	12	6.8 ± 1.0a	6.8a	6.8a	5.0 ± 1.8b	3.2f	5.5b	7.3 ± 1.0de	7.5e	7.1ad	6.1 ± 0.9c	6.1c	6.1c

Means and standard deviations are calculated for the RIL population, and means for Arta and Keel, for the two locations and for sowing in autumn and winter, separately

[a] Number of environments in which the trait was measured (see "Materials and methods"; Table 1)

[b] Means of the RIL population, Arta and Keel are calculated for the four combinations of locations and sowing dates separately. Significant differences between means of RILs and parents and between the different locations are indicated with different letters according to the Tukey–Kramer test for multiple comparisons ($P < 0.05$)

[c] Standard deviation for RILs (means)

adjacent to gaps within chromosomes also showed segregation distortion (Supplementary Table 4). Linkage groups within chromosomes were ordered according to information of the consensus map of Alsop et al. (2011).

Single-trait analysis with single-QTL-per-chromosome model and MIM-single-trait analysis was employed to detect QTL. A total of 86 QTL were detected for 11 traits (Fig. 3). Significant QTL, additive effects, and phenotypic variance explained are listed for each environment separately in Table 5. Multi-environment QTL analysis demonstrated that QTL effects were relatively stable for the traits DH and PH; the Arta allele at the majority of significant markers caused either an increase or a reduction of trait values across all tested environments. In contrast, QTL effects for the traits GY and KW showed cross-over effects, the Arta allele at the majority of significant loci had opposing effects on the trait in different environments. Strong variation in QTL effects across environments corresponded to strong interaction effects between the genotype and year and sowing date for yield related traits (Supplementary Table 3).

The QTL analysis revealed nine QTL for GY. At six QTL the Keel allele improved GY in the majority of environments and at three loci Arta improved GY in the majority of environments. QTL for GY located close to QTL for PH, PED and PEDEX on chromosomes 2Ha and 3H, where increased PH, PED and PEDEX contributed by Keel at the QTL on 2Ha and by Arta on 3H, improved GY (Fig. 3). QTL for GY on chromosomes 2Hb, 4H, 5H, 7Hb and 7Hc coincided with QTL for DH, KW, PH, PED, PEDEX and SL, where reduced DH correlated with increased GY, KW, PH, PED, PEDEX, and SL. Co-segregation of QTL for traits which also showed high correlation coefficients suggested causal relationships between different traits. With the exception of the QTL on 7Hc, the Keel allele accelerated DH, increased PH, BY and GY at these QTL clusters in the majority of the autumn and winter-sown trials. The strongest effects on GY and all other traits were recorded at the marker intervals spanning the position of the vernalisation genes *Vrn-H1* and *Vrn-H2*. Genotyping revealed that Arta carries the *Vrn-H2* locus and the vernalisation-responsive *Vrn-H1-6* allele (Casao et al. 2011a, b; Hemming et al. 2009; Cockram et al. 2007). In contrast to Arta, Keel carries a deletion of the *Vrn-H2* locus and is characterised by the *Vrn-H1-4* allele, which shows a reduced vernalisation requirement as compared to *Vrn-H1-6* (Hemming et al. 2009). Significant, but relatively small, delays in flowering were already correlated with significant yield reductions, particularly in low rainfall environments. For example, the Arta allele at *Vrn-H1* delayed flowering by one day and reduced yield by 271 kg/ha in Tel Hadya 2008, autumn-sown. Calculation of pairwise marker interactions between

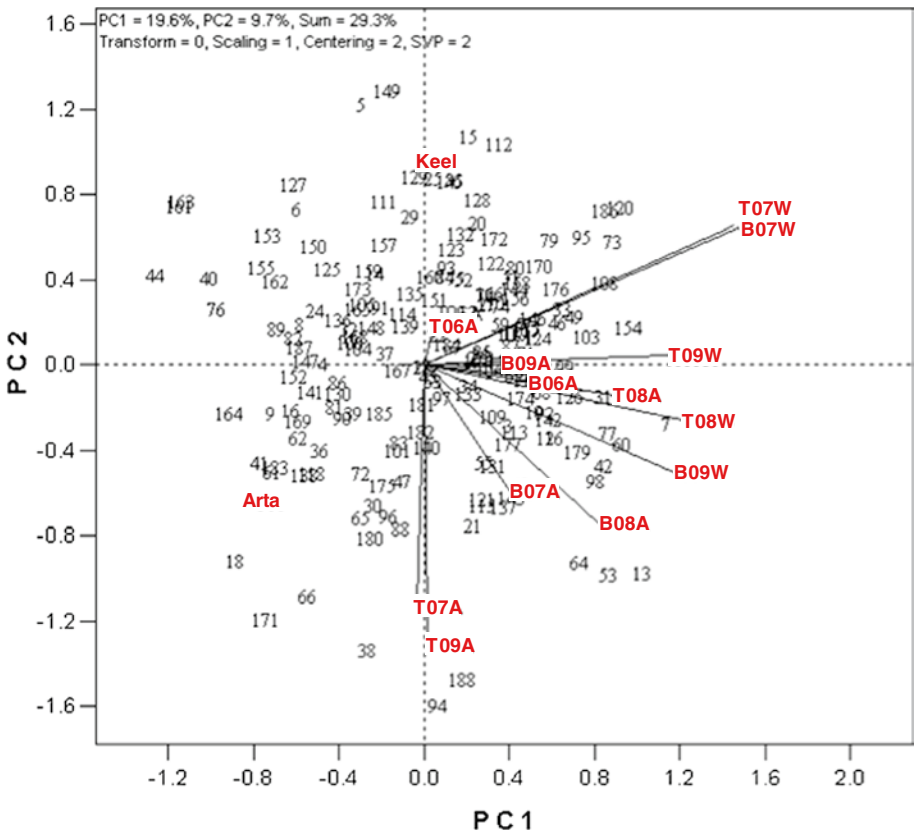

Fig. 2 GGE biplot based on best linear unbiased estimates for yield. *T* Tel Hadya, *B* Breda, 06 = 2005–2006, 07 = 2006–2007, 08 = 2007–2008, 09 = 2008–2009, *A* autumn sowing, *W* winter sowing

Table 4 Correlation coefficients (*r*) according to Pearson between 11 agronomic traits

	BY	DH	GH	GV	GY	HI	KW	PED	PEDEX	PH	SL
BY		−0.33***	−0.09	−0.29***	0.54***	0.09	−0.07	0.09	0.01	0.14*	0.00
DH	−0.24***		0.35***	0.52***	−0.26***	−0.15	-0.28***	−0.22***	0.03	−0.30***	0.12
GH	−0.40***	0.79***		0.48***	−0.16*	−0.01	−0.16*	−0.10	0.06	−0.22***	0.01
GV	−0.43***	0.76***	0.84***		−0.27***	−0.06	−0.23***	−0.02	0.09	−0.19*	0.05
GY	0.60***	−0.66***	−0.63***	−0.66***		0.45***	−0.03	0.09	0.01	0.10	−0.01
HI	0.28***	−0.47***	−0.45***	−0.45***	0.79***		−0.07	0.11	0.16*	−0.06	−0.08
KW	0.16*	−0.57***	−0.53***	−0.51***	0.42***	0.24***		0.18*	−0.03	0.33***	0.30***
PED	0.20***	−0.46***	−0.39***	−0.40***	0.44***	0.34***	0.37***		0.52***	0.66***	0.23***
PEDEX	0.08	−0.03	−0.07	−0.12	0.07	0.08	0.00	0.45***		0.19*	−0.03
PH	0.28***	−0.39***	−0.48***	−0.47***	0.33***	0.14	0.43***	0.62***	0.16*		0.36***
SL	0.13	−0.71***	−0.57***	−0.53***	0.48***	0.34***	0.49***	0.42***	−0.10	0.45***	

For calculating correlations the means of the trait performance of each RIL averaged for each location and sowing time were used. In the upper triangular area correlations based on means averaged across autumn sowing (moderate stress), and in the lower triangular area means averaged across environments with winter sowing (more severe stress) are depicted. Significant correlations are indicated * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

QTL for DH revealed significant interactions between *Vrn-H2* and *Vrn-H1*, but not between other loci (Table 6). Variation at *Vrn-H1* and *Vrn-H2* caused significant differences in time to flowering in the autumn and winter-sown trials 2008 and 2009 and in the winter-sown experiment 2007 in Tel Hadya. A significant delay in DH was recorded for genotypes with the Arta allele at *Vrn-H1* and *Vrn-H2*, while genotypes with other combinations of Arta and Keel alleles at both loci flowered earlier, but not significantly different from each other. Only in T08A, the genotypes with Keel alleles at both loci flowered even significantly earlier than genotypes with a combination of Arta and Keel alleles at both genes. Significant interactions between *Vrn-H1* and *Vrn-H2* were also observed for BY, GV, GY, PED, PEDEX and SL. Genotypes with the Keel alleles at *Vrn-H1* and *Vrn-H2* showed the highest yield in all environments, with the exception of B08A and T09A, where genotypes with the Arta allele at *Vrn-H2* and the Keel allele at *Vrn-H1* were yielding highest. Faster development as inherited by the Keel allele at *Vrn-H1* and *Vrn-H2* also increased BY, SL and PED, in particular in the winter-sown experiments. Interactions between *Vrn-H1* and *Vrn-H2* had thus strong effects not only on time to flowering, but also on growth rate, spike length and yield. In short-season environments due to low rainfall (2008) or late sowing in winter, faster development was beneficial for yield. In more favourable environments as represented by T09A, an intermediate phenotype as determined by the Arta allele at *Vrn-H2* and the Keel allele at *Vrn-H1* was beneficial. However, the Keel allele at *Vrn-H1* caused a yield increase in 11 out of 13 tested environments and was thus overall beneficial under winter and standard autumn-sown conditions.

Taken together, the QTL analysis showed that genetic variation in biomass accumulation/plant height and in reproductive development primarily determined yield in the ARKE RIL population grown in Syrian environments. Fast reproductive development primarily inherited by Keel accelerated plant growth and thus increased final PH and BY in environments with short seasons due to terminal stress. Interaction effects at the vernalisation genes *Vrn-H1* and *Vrn-H2* had the strongest effects on DH and correlated traits BY, GY, PED, PEDEX and SL. The Keel allele at *Vrn-H1* and *Vrn-H2* caused earlier DH and increased BY and GY in the winter-sown and most autumn-sown experiments.

Discussion

High environmental fluctuations in dry Mediterranean environments

Previous studies have identified high environmental variation between barley trials in different Mediterranean

Table 5 QTLs for agronomic traits detected across all environments

Chr	Marker/interval	Pos	LOD	B06A	B07A	B07W	B08A	B09A	B09W	T06A	T07A	T07W	T08A	T08W	T09A	T09W
BY																
2Hb	bPb09199-bPb02244	92.3–92.5	10				−249	108	**14**				−535	**−329**	−43	**−184**
							4.5 %	0.8 %	**0.0 %**				11.2 %	**2.8 %**	0.1 %	**1.6 %**
3H	Scssr25691-bPb01681	89.3–102.9	6				295	−156	**131**				403	**239**	94	**−82**
							6.3 %	1.7 %	**2.8 %**				6.4 %	**1.5 %**	0.3 %	**0.32 %**
4H	*Vrn-H2*-HvM67	160.7–164.0	10				−195	−62	**−195**				−297	**−654**	−211	**−199**
							2.8 %	0.3 %	**6.3 %**				3.5 %	**11.2 %**	1.3 %	**1.9 %**
5H	bPb04988-*Vrn-H1*	140.0–140.9	12				−26	−211	**15**				−56	**−907**	58	**68**
							0.0 %	3 %	**0.0 %**				0.1 %	**21.5 %**	0.1 %	**0.2 %**
DH																
1Ha	bPb03451-bPb07112	0–0.2	6							−0.1	0.5	**2.4**	0.3	**0.1**	0.3	**0.6**
										0.01 %	0.05 %	**0.04 %**	0.04 %	**0.02 %**	0.04 %	**0.04 %**
2Hb	bPb03575-bPb03950	81.6–82.0	16							0.2	0.8	**2.8**	0.8	**0.8**	0.7	**1.3**
										0.45 %	7.6 %	**3.7 %**	7.2 %	**4.2 %**	7.7 %	**12.9 %**
3H	bPb04156-bPb03109	157.0–157.6	16							0.5	0.7	**3.9**	0.8	**1.1**	0.5	**1.1**
										3.1 %	6.5 %	**7.5 %**	7.1 %	**7.1 %**	3.3 %	**9.2 %**
4H	Bmag419A-*Vrn-H2*	149.9–153.5	44							0.1	0.4	**8.2**	0.9	**1.2**	0.4	**1.6**
										0.3 %	1.6 %	**35 %**	8.7 %	**7.5 %**	2.9 %	**20 %**
5H	*Vrn-H1*-bPb03910	140.9–142.3	53							0.3	0.9	**6.5**	1.0	**1.1**	0.7	**1.6**
										1.2 %	10 %	**22 %**	10.1 %	**6.2 %**	7.1 %	**21 %**
6H	bPb01982-bPb02054	133.0–138.3	11							0.4	0.8	**0.7**	0.6	**−0.7**	0.5	**0.5**
										1.9 %	7.4 %	**0.2 %**	4.1 %	**2.4 %**	3.4 %	**1.9 %**
7Hb	Vrn-H3-bPb09907	7.2–8.0	9							0.3	0.1	**2.6**	−0.4	**0.6**	0.2	**0.6**
										1.2 %	0.1 %	**3.7 %**	1.4 %	**2.1 %**	0.6 %	**3 %**
7Hc	Bmag0011-BMS64	13.9–18.9	11							−0.2	−0.1	**−4.0**	−0.3	**−0.3**	−0.3	**−1.0**
										0.6 %	0.1 %	**7.7 %**	0.9 %	**0.7 %**	1.3 %	**7.3 %**
GH																
1Ha	GBM5162-HvFT3	102.3–108.6	14					−0.09		−0.03	−0.16	**−0.25**	−0.22		−0.02	**−0.16**
								3.3 %		0.1 %	6.1 %	**2 %**	8.1 %		0.4 %	**2.4 %**
2Ha	-bPb03608	0.0–1.7	9					−0.07		−0.06	−0.16	**−0.05**	−0.20		−0.02	**−0.10**
								2.2 %		0.5 %	6.3 %	**0.1 %**	6.8 %		0.4 %	**0.9 %**
2Hb	GBM1047-bPb05942	88.2–89.4	13					0.05		0.06	0.16	**0.44**	0.20		0.01	**0.37**
								0.9 %		0.4 %	5.9 %	**5.8 %**	6.3 %		0.0 %	**11.3 %**
3H	Ebmac705-HVLTPPB	23.0–24.8	13					0.08		0.12	0.19	**0.24**	0.24		0.05	**0.12**
								2.6 %		1.8 %	8.3 %	**1.9 %**	10 %		2.2 %	**1.2 %**

Table 5 continued

Chr	Marker/interval	Pos	LOD	B06A	B07A	B07W	B08A	B09A	B09W	T06A	T07A	T07W	T08A	T08W	T09A	T09W
4H	*Vrn-H2*-HvM67	160.7–164.0	26					0.07		0.15	−0.02	**0.78**	0.06		0.03	**0.35**
								2.1 %		3.1 %	0.1 %	**19.2 %**	0.6 %		0.6 %	**10.7 %**
5H	bPb03246-bPb06676	114.9–115.0	52					0.02		0.03	0.14	**1.16**	0.22		−0.01	**0.43**
								0.1 %		0.1 %	4.9 %	**43 %**	8.2 %		0.0 %	**17 %**
6H	HvCO2-GBM1400	95.2–99.0	14					0.09		0.09	0.16	**0.45**	0.24		0.04	**0.32**
								3.5 %		1.2 %	5.8 %	**6 %**	9.6 %		1 %	**8.5 %**
7Hb	Vrn-H3-bPb-9907	7.2–7.9	9					0.00		−0.05	−0.03	**0.39**	−0.10		0.01	**0.17**
								0.0 %		0.4 %	0.3 %	**4.8 %**	1.8 %		0.1 %	**2.7 %**
GV																
1Ha	GBM5162-HvFT3	102.3−108.6	15	0.07	−0.38	**−0.39**	0.01	−0.32		−0.09	−0.37	**−0.40**	−0.06	**−0.12**	−0.29	**−0.15**
				0.5 %	5 %	**6 %**	0.0 %	7.3 %		1.2 %	6.7 %	**6.4 %**	0.2 %	**0.5 %**	4.2 %	**1.3 %**
2Ha	bPb07831-bPb02827	2.9−3.7	8	0.03	0.15	**−0.01**	−0.02	−0.23		−0.03	−0.15	**−0.23**	−0.16	**−0.10**	−0.12	**−0.26**
				0.1 %	0.8 %	**0.0 %**	0.0 %	3.7 %		0.2 %	1.1 %	**2.1 %**	1.3 %	**0.3 %**	0.8 %	**4.2 %**
2Hb	bPb00886-GBM1047	87.7−88.2	24	0.02	0.36	**0.43**	0.15	0.27		0.03	0.29	**0.45**	0.47	**0.51**	0.37	**0.36**
				0.0 %	4.5 %	**7.3 %**	1.7 %	5.3 %		0.1 %	4 %	**8.3 %**	12 %	**8.3 %**	6.8 %	**7.9 %**
3H	bPb04004-bPb08441	0−9.2	14	−0.09	0.15	**0.19**	0.14	0.24		0.03	0.29	**0.17**	0.49	**0.03**	0.25	**0.08**
				0.9 %	0.8 %	**1.4 %**	1.4 %	4.2 %		0.1 %	4.1 %	**1.2 %**	12.7 %	**0.0 %**	3 %	**0.4 %**
3H	bPb00104-bPb08504	151.6−155.4	13	−0.06	0.21	**0.13**	0.28	0.21		0.12	0.34	**0.06**	0.38	**0.32**	0.23	**0.13**
				0.4 %	1.5 %	**0.7 %**	5.5 %	3.3 %		2.1 %	5.4 %	**0.1 %**	7.8 %	**3.2 %**	2.5 %	**1 %**
4H	Bmag419A-*Vrn-H2*	153.5−160.7	29	0.04	−0.22	**0.55**	0.02	0.02		0.02	−0.19	**0.60**	−0.01	**0.71**	0.14	**0.22**
				0.2 %	1.7 %	**12.2 %**	0.0 %	0.0 %		0.0 %	1.7 %	**15 %**	0.0 %	**16.3 %**	0.89 %	**2.9 %**
5H	*Vrn-H1*-bPb03910	140.9−142.3	71	0.00	0.48	**0.78**	0.15	0.22		0.08	0.16	**0.96**	0.25	**1.03**	−0.01	**0.25**
				0.0 %	8 %	**22 %**	1.5 %	3.3 %		1 %	1.2 %	**38 %**	3.3 %	**34 %**	0.0 %	**4 %**
6H	bPb07068-bPb00386	8.7−9.0	24	0.05	−0.24	**−0.44**	−0.10	−0.36		0.02	−0.02	**−0.57**	−0.22	**−0.56**	−0.09	**−0.36**
				0.39 %	2.1 %	**7.4 %**	0.7 %	9.2 %		0.1 %	0.0 %	**13.2 %**	2.8 %	**10 %**	0.4 %	**8 %**
6H	bPb01982-bPb02054	132.9−138.3	18	−0.02	0.46	**0.23**	0.10	0.20		0.05	0.45	**0.30**	0.19	**0.14**	0.24	**0.14**
				0.1 %	7.4 %	**2.1 %**	0.7 %	3 %		0.4 %	10 %	**3.6 %**	1.9 %	**0.6 %**	2.8 %	**1.2 %**
7Hc	bPb00259-Bmag135	80.7−82.2	10	−0.07	0.30	**0.17**	0.15	−0.02		−0.07	0.13	**0.07**	0.38	**0.13**	0.26	**0.03**
				0.6 %	3.2 %	**1.1 %**	1.7 %	0.0 %		0.7 %	0.8 %	**0.2 %**	7.7 %	**0.6 %**	3.3 %	**0.0 %**
GY																
2Ha	bPb04447-GBM1052	28.9−29.7	11	76	−58	**−27**	−226	−68	**−72**	205	94	**−7**	4	**−182**	−104	**−156**
				1.1 %	3.1 %	**2.3 %**	6.8 %	1.3 %	**3.5 %**	1.5 %	2.6 %	**0.0 %**	0.0 %	**2.3 %**	1.3 %	**6.4 %**
2Hb	bPb08302-bPb03925	81.6−82.0	10	−70	−3	**−31**	−26	−35	**−48**	4	12	**−57**	−428	**−275**	121	**−45**
				1 %	0 %	**3.2 %**	0.1 %	0.4 %	**1.5 %**	0 %	0 %	**0.8 %**	9.8 %	**6.5 %**	1.9 %	**1 %**
3H	bPb00285-HvGI	54.2−57.7	12	86	−22	**32**	254	−9	**64**	−154	60	**94**	172	**182**	151	**41**

Table 5 continued

Chr	Marker/interval	Pos	LOD	B06A	B07A	B07W	B08A	B09A	B09W	T06A	T07A	T07W	T08A	T08W	T09A	T09W
				1.4 %	0.4 %	**3.2 %**	8.6 %	0.0 %	**2.7 %**	1.0 %	1 %	**2.3 %**	1.6 %	**2.4 %**	2.8 %	**0.4 %**
3H	bPb01609-bPb012026	151.6–155.4	13	7	47	**−36**	19	−108	**−44**	−25	−27	**−181**	−288	**−278**	−15	**−15**
				0 %	2.1 %	**4.4 %**	0 %	3.2 %	**1.3 %**	0 %	0.2 %	**8.4 %**	4.4 %	**6.6 %**	0 %	**0.1 %**
4H	Bmag419A-*Vrn-H2*	153.5–160.7	37	−51	−15	**−83**	41	41	**−91**	−191	−42	**−280**	−14	**−507**	97	**−131**
				0.5 %	0.2 %	**22 %**	0.2 %	0.48 %	**5.6 %**	1.3 %	0.5 %	**21 %**	0.0 %	**19 %**	1.2 %	**4.5 %**
5H	bPb04988-*Vrn-H1*	140.0–140.9	47	−67	−33	**−73**	−57	−142	**−86**	−103	19	**−310**	−271	**−537**	67	**−81**
				0.9 %	1 %	**17 %**	0.4 %	5.6 %	**5 %**	0.4 %	0.1 %	**25 %**	3.9 %	**21 %**	0.6 %	**1.7 %**
6H	bPb07143-Scssr09398	0.0–4.5	8	−46	−34	**11**	122	107	**73**	−219	14	**133**	87	**167**	78	**74**
				0.4 %	1 %	**0.4 %**	2 %	3.2 %	**3.6 %**	1.7 %	0.1 %	**4.5 %**	0.41 %	**2.4 %**	0.8 %	**1.4 %**
7Hb	bPb09269-bPb08049	14.5–14.6	8	−172	−47	**−1**	151	−7	**−33**	52	145	**22**	77	**34**	−64	**12**
				5.7 %	2.1 %	**0.0 %**	3 %	0.0 %	**0.7 %**	0.1 %	6.1 %	**0.1 %**	0.3 %	**0.1 %**	0.5 %	**0.036 %**
7Hc	Bmag0011-BMS64	13.9–18.9	9	0	−65	**−8**	5	14	**15**	−183	−141	**19**	−259	**−170**	−56	**64**
				0 %	4 %	**0.2 %**	0.0 %	0.1 %	**0.2 %**	1.2 %	5.8 %	**0.1 %**	3.6 %	**2.1 %**	0.4 %	**1.1 %**
HI																
2Hb	bPb04837-Bmag829	11.4–13.2	7				−0.004	0.013	**0.010**				0.007	**0.035**	0.023	**0.021**
							0.1 %	2.3 %	**0.5 %**				0.4 %	**2.1 %**	5.8 %	**3.4 %**
3H	bPb04371-bPb06785	35.1–35.4	8				0.034	0.004	**0.032**				0.009	**0.025**	0.007	**0.021**
							3.9 %	0.16 %	**4.7 %**				0.6 %	**1.1 %**	0.6 %	**3.3 %**
4H	Bmag419A-*Vrn-H2*	153.5–160.7	9				−0.006	0.007	**−0.017**				0.004	**−0.097**	0.012	**−0.020**
							0.1 %	0.7 %	**1.3 %**				0.2 %	**16.3 %**	1.6 %	**3.1 %**
5H	bPb04012-bPb05951	139.5–140.0	16				−0.011	−0.017	**−0.031**				−0.019	**−0.088**	0.000	**−0.027**
							0.4 %	3.8 %	**4.6 %**				3.1 %	**13.7 %**	0.0 %	**5.8 %**
6H	bPb00432-Scssr103	121.8–128.5	7				−0.014	0.010	**0.027**				0.003	**0.018**	0.021	**0.019**
							0.65 %	1.3 %	**3.4 %**				0.1 %	**0.6 %**	4.8 %	**2.8 %**
7Hc	Bmag0011-BMS64	13.9–18.9	13				0.030	0.019	**0.061**				−0.010	**0.036**	0.022	**0.025**
							3.2 %	4.8 %	**17.7 %**				0.89 %	**2.2 %**	5.5 %	**4.7 %**
KW																
2Ha	bPb09404-bPb06755	36.52–38.2	8		−1.1	**0.0**	−1.1	−0.8	**−0.4**		−0.2	**−0.7**	−0.3		−1.0	**−0.8**
					4.3 %	**0.0 %**	3.7 %	1.8 %	**0.5 %**		0.2 %	**1 %**	0.5 %		2.2 %	**0.9 %**
2Hb	Ebmac415-bPb02329	82.6–82.8	37		−0.9	**−1.6**	−0.8	−0.5	**−2.0**		−0.8	**−0.9**	−1.9		0.5	**−2.9**
					2.5 %	**8.1 %**	1.7 %	0.77 %	**11.8 %**		3 %	**1.7 %**	16.8 %		0.62 %	**12.7 %**
3H	Bmag0606-bPb04209	136.4–137.9	24		0.2	**1.1**	1.2	0.9	**1.1**		1.3	**1.2**	1.9		0.6	**1.2**
					0.2 %	**3.4 %**	4.3 %	2.6 %	**6.1 %**		3.3 %	**6.7 %**	8.3 %		0.6 %	**4.5 %**
4H	VRNH2-HVM67	160.7–164.0	18		0.1	**−0.6**	0.2	0.6	**−1.1**		1.0	**0.8**	−0.4		1.2	**−2.0**

Table 5 continued

Chr	Marker/interval	Pos	LOD	B06A	B07A	B07W	B08A	B09A	B09W	T06A	T07A	T07W	T08A	T08W	T09A	T09W
					0.0 %	**1 %**	0.1 %	1 %	**3.5 %**		4.9 %	**1.2 %**	0.8 %		3.3 %	**6 %**
5H	GBM1399-Bmag812	90.8–108.0	18		−1.2	**−1.7**	−1.5	−2.0	**−1.7**		−1.5	**−2.5**	−1.2		−1.7	**−1.6**
					5.1 %	**8.6 %**	6.4 %	12.5 %	**8.2 %**		10.8 %	**13 %**	7 %		6.8 %	**3.9 %**
6H	bPb06034-GMS6	70.1–71.8	23		1.0	**−1.4**	0.2	1.1	**0.8**		1.8	**−0.5**	1.0		1.1	**0.5**
					3.4 %	**6 %**	0.12 %	3.5 %	**2 %**		14.8 %	**0.6 %**	4.7 %		2.6 %	**0.5 %**
7Hb	bPb028890-Vrn-H3	6.6–7.2	18		−0.8	**−0.2**	−0.9	−0.7	**−1.5**		−0.6	**0.3**	−0.3		−1.1	**−1.6**
					2 %	**0.2 %**	2.2 %	1.6 %	**6.3 %**		1.5 %	**0.1 %**	0.4 %		2.9 %	**3.9 %**
7Hc	bPb09912-bPb01596	24.8–24.9	20		1.4	**1.4**	1.0	1.2	**1.3**		0.5	**0.3**	0.4		1.3	**1.8**
					6.9 %	**6.1 %**	2.8 %	4.5 %	**5.3 %**		1.3 %	**0.2 %**	0.9 %		4 %	**5.1 %**
PH																
1Ha	bPb09360-Bmag718	48.6–49.2	23	−0.2	1.2	**1.5**	1.6	0.5	**1.4**	−1.1	3.8	**1.8**	1.6	**0.9**	2.5	**1.2**
				0.0 %	2.5 %	**5.4 %**	3 %	0.4 %	**3.2 %**	0.5 %	11.4 %	**4.2 %**	4.1 %	**1.4 %**	4.5 %	**1.8 %**
2Ha	bPb06755-bPb05326	38.2–39.9	19	−1.7	−1.6	**−1.1**	−1.9	0.1	**−1.6**	−0.2	−0.7	**−1.2**	−1.2	**−1.1**	−2.3	**−1.8**
				3.2 %	4.3 %	**3.1 %**	4.2 %	0.02 %	**3.7 %**	0.024 %	0.44 %	**1.9 %**	2.5 %	**2.4 %**	3.8 %	**3.9 %**
2Hb	bPb02329-bPb02948	82.8	62	0.6	−3.4	**−1.5**	−2.5	−2.3	**−2.9**	1.1	−3.0	**−2.6**	−2.8	**−2.8**	−2.5	**−3.2**
				0.3 %	19.8 %	**5.7 %**	7.1 %	7.2 %	**13 %**	0.6 %	7.3 %	**9.2 %**	13.8 %	**14.7 %**	4.8 %	**12.6 %**
3H	Bmag209-bPb06554	75.1–77.4	12	0.6	1.2	**−0.3**	1.2	0.2	**1.1**	1.7	3.1	**1.1**	0.1	**−0.3**	2.2	**1.5**
				0.4 %	2.3 %	**0.3 %**	1.6 %	0.1 %	**1.9 %**	1.4 %	7.7 %	**1.7 %**	0.0 %	**0.2 %**	3.6 %	**2.7 %**
3H	bPb01390-bPb07684	187.4–187.8	19	−1.1	−1.3	**−1.2**	−1.3	−2.5	**−1.0**	−0.2	−2.7	**−2.1**	−1.5	**−2.1**	−1.4	**−1.6**
				1.4 %	2.8 %	**3.1 %**	2.1 %	8.9 %	**1.5 %**	0.0 %	5.6 %	**6.5 %**	3.8 %	**8.8 %**	1.6 %	**3 %**
4H	bPb04699-GBM1143	2.9–6.5	29	0.7	1.9	**1.3**	2.0	1.7	**2.0**	3.2	2.9	**1.9**	3.0	**2.1**	2.5	**2.6**
				0.6 %	5.8 %	**3.8 %**	4.8 %	4.1 %	**6.1 %**	5.1 %	6.4 %	**5.4 %**	15 %	**8.5 %**	4.7 %	**7.9 %**
4H	*Vrn-H2*-HvM67	160.7–164.0	24	−0.7	−0.7	**−0.4**	−2.0	−2.3	**−2.8**	0.4	−1.6	**−2.4**	−1.6	**−1.4**	−1.6	**−1.9**
				0.6 %	0.9 %	**0.3 %**	4.4 %	7.4 %	**11.6 %**	0.1 %	2.1 %	**7.8 %**	4.3 %	**3.5 %**	1.9 %	**4.4 %**
5H	bPb06579-bPb05271	132.7–133.6	15	0.1	−1.9	**−0.1**	−1.5	−1.8	**−1.4**	−0.1	−1.0	**−2.3**	−1.0	**−1.8**	−0.7	**−1.9**
				0.0 %	6.1 %	**0.1 %**	2.7 %	4.7 %	**2.8 %**	0.0 %	0.9 %	**6.9 %**	1.6 %	**5.9 %**	0.4 %	**4.5 %**
6H	bPb04190-bPb05515	139.1–140.8	26	−0.2	−2.6	**−1.0**	−2.4	−2.5	**−2.1**	−0.1	−2.3	**−1.3**	−2.1	**−1.7**	−2.7	**−1.8**
				0.0 %	11 %	**2.5 %**	7 %	8.9 %	**6.8 %**	0.0 %	4.1 %	**2.3 %**	7.1 %	**5.8 %**	5.6 %	**3.9 %**
7Hb	Vrn-H3-bPb09907	7.2–8.0	29	−1.8	−1.7	**−0.9**	−1.6	−1.3	**−1.8**	−3.1	−3.1	**−2.6**	−3.0	**−1.6**	−2.4	**−2.4**
				3.8 %	4.6 %	**1.7 %**	3.2 %	2.3 %	**5.2 %**	4.6 %	7.7 %	**9.6 %**	14.4 %	**4.9 %**	4.3 %	**7.1 %**
7Hc	bPb00235-Bmac0755	55.4–59.2	25	0.1	−1.6	**−1.2**	−2.1	−2.1	**−1.6**	−0.5	−3.5	**−2.2**	−2.5	**−1.9**	−2.1	**−2.1**
				0.0 %	4.4 %	**3.3 %**	5.2 %	6.7 %	**3.8 %**	0.1 %	9.8 %	**7.3 %**	10.4 %	**7.2 %**	3.3 %	**5.3 %**
PED																
1Ha	bPb09360-Bmag718	48.6–49.2	17	0.21	1.11	**0.28**	0.99	0.30	**0.29**	−0.75	2.08		0.40	**1.18**	1.38	**0.73**
				0.1 %	5.9 %	**0.7 %**	2.5 %	0.4 %	**0.3 %**	0.7 %	11.4 %		1.0 %	**7.8 %**	4.6 %	**1.7 %**

Table 5 continued

Chr	Marker/interval	Pos	LOD	B06A	B07A	B07W	B08A	B09A	B09W	T06A	T07A	T07W	T08A	T08W	T09A	T09W
2Ha	bPb09404-bPb06755	36.6−38.2	11	−1.22	−1.08	**−0.32**	−1.23	0.23	**−0.69**	−0.22	−0.18		−0.36	**−0.58**	−0.87	**−1.10**
				3.5 %	5.5 %	**0.9 %**	4 %	0.2 %	**1.9 %**	0.1 %	0.1 %		0.8 %	**1.9 %**	1.8 %	**3.8 %**
2Hb	bPb03925-Ebmac415	82.1−82.6	16	−0.65	−1.38	**−0.33**	−0.41	−0.29	**−1.19**	−0.46	−0.68		−0.91	**−0.79**	−0.92	**−1.35**
				1.0 %	9.1 %	**1 %**	0.4 %	0.4 %	**5.6 %**	0.3 %	1.2 %		4.9 %	**3.4 %**	2 %	**5.7 %**
3H	Bmac0209-bPb06554	75.1−77.4	11	0.29	1.12	**0.38**	0.94	0.56	**0.81**	0.76	1.67		0.35	**0.16**	0.39	**1.00**
				0.19 %	6 %	**1.3 %**	2.3 %	1.4 %	**2.6 %**	0.77 %	7.4 %		0.71 %	**0.14 %**	0.37 %	**3.2 %**
4H	Bmag419A-*Vrn-H2*	153.5−160.7	18	−0.12	−0.53	**0.26**	−1.00	−1.09	**−2.05**	−1.13	−1.24		−0.82	**0.26**	0.41	**−1.82**
				0.03 %	1.3 %	**0.6 %**	2.6 %	5.2 %	**16.6 %**	1.7 %	4.1 %		4 %	**0.4 %**	0.4 %	**10.5 %**
5H	Bmag5-Bmag105b	55.8−56.3	9	−0.16	−0.39	**−0.18**	−0.31	−0.71	**−0.13**	0.35	−1.77		0.05	**−0.42**	−0.67	**−0.78**
				0.1 %	0.7 %	**0.3 %**	0.2 %	2.2 %	**0.1 %**	0.2 %	8.2 %		0.0 %	**1.0 %**	1.1 %	**1.9 %**
5H	*Vrn-H1*-bPb03910	140.9−142.3	8	−0.11	−0.72	**−0.08**	−0.31	−0.36	**−0.54**	−1.08	0.18		−0.64	**−0.48**	−0.59	**−1.82**
				0.0 %	2.5 %	**0.1 %**	0.3 %	0.6 %	**1.2 %**	1.6 %	0.1 %		2.4 %	**1.3 %**	0.9 %	**11 %**
7Hc	bPb02620-bPb09865	79.0−79.3	7	0.28	−0.42	**0.78**	−0.27	−0.55	**−0.81**	0.79	−0.57		0.14	**0.42**	0.65	**−0.16**
				0.2 %	0.9 %	**5.4 %**	0.2 %	1.3 %	**2.6 %**	0.8 %	0.8 %		0.1 %	**1.0 %**	1 %	**0.1 %**
PEDEX																
1Ha	bPb09256-bPb01604	40.2	21	−0.09	0.87	**0.11**	1.13	0.21	**1.09**	−1.35	1.31		0.79	**0.56**	1.14	**1.06**
				0.0 %	5.9 %	**0.1 %**	6.5 %	0.24 %	**7.3 %**	2.7 %	8.9 %		5.2 %	**1.5 %**	2 %	**5.1 %**
1Ha	Bmag105a-bPb04041	61.0−64.6	14	0.88	1.15	**1.02**	1.53	0.36	**0.43**	−0.65	0.83		0.73	**0.82**	1.40	**0.29**
				1.9 %	10.3 %	**6.4 %**	11.8 %	0.7 %	**1.2 %**	0.6 %	3.7 %		4.5 %	**3.1 %**	3.1 %	**0.4 %**
2Ha	bPb09404-bPb06755	36.6−38.2	10	−1.16	−0.41	**−0.28**	−0.79	−0.16	**−0.78**	−0.12	−0.25		−0.39	**0.07**	−1.80	**−0.35**
				3.3 %	1.3 %	**0.5 %**	3.2 %	0.14 %	**3.8 %**	0.0 %	0.31 %		1.3 %	**0.0 %**	5.1 %	**0.54 %**
2Hb	bPb08033-bPb023426	79.9−80.1	7	0.59	0.33	**0.83**	0.72	0.51	**−0.10**	1.41	0.16		0.75	**0.07**	−0.16	**−0.21**
				0.9 %	0.8 %	**4.3 %**	2.6 %	1.5 %	**0.1 %**	2.9 %	0.1 %		4.7 %	**0.0 %**	0.0 %	**0.2 %**
3H	bPb02119-bPb05145	64.7−69.6	17	−0.26	0.72	**−0.21**	0.69	0.54	**0.37**	1.46	1.11		0.90	**0.19**	1.08	**1.31**
				0.2 %	4 %	**0.3 %**	2.5 %	1.6 %	**0.9 %**	3.1 %	6.4 %		6.8 %	**0.2 %**	1.8 %	**7.9 %**
4H	bPb03847-Bmag419B	143.4−149.9	9	0.32	0.46	**1.29**	0.59	0.75	**−0.30**	−0.58	−0.12		0.37	**1.16**	0.17	**−0.75**
				0.3 %	1.7 %	**10.2 %**	1.7 %	3.1 %	**0.6 %**	0.5 %	0.1 %		1.2 %	**6.2 %**	0.1 %	**2.8 %**
5H	*VrnH1*bPb03910	140.9−142.3	13	−0.16	0.11	**1.19**	−0.14	−0.25	**−0.39**	−0.24	0.30		−0.01	**0.17**	0.45	**−1.77**
				0.1 %	0.1 %	**8.5 %**	0.1 %	0.3 %	**1.0 %**	0.1 %	0.5 %		0.0 %	**0.1 %**	0.3 %	**14.2 %**
7Hb	Vrn-H3-bPb09907	7.2−8.0	14	0.56	1.09	**0.99**	1.27	0.92	**−0.19**	−0.43	0.27		0.85	**0.37**	0.29	**−0.11**
				0.8 %	9.2 %	**6.1 %**	8.2 %	4.7 %	**0.2 %**	0.3 %	0.4 %		5.9 %	**0.6 %**	0.1 %	**0.1 %**
7Hc	BMS64-bPb01847	18.9−24.7	10	−0.08	0.68	**−0.46**	0.23	0.35	**0.88**	0.49	0.76		−0.06	**−0.18**	1.25	**1.02**
				0.0 %	3.6 %	**1.2 %**	0.3 %	0.7 %	**4.7 %**	0.4 %	3 %		0.0 %	**0.1 %**	2.5 %	**4.7 %**

Table 5 continued

Chr	Marker/interval	Pos	LOD	B06A	B07A	B07W	B08A	B09A	B09W	T06A	T07A	T07W	T08A	T08W	T09A	T09W
SL																
2Hb	Bmag749-bPb05642	107.7–109.5	10	0.06	0.15	**0.09**	−0.47	−0.10	**−0.30**	0.01	−0.35	**−0.36**	−0.22	**−0.56**	−0.30	**−0.05**
				0.1 %	0.7 %	**0.1 %**	3.8 %	0.5 %	**3.2 %**	0.0 %	3 %	**2.6 %**	1.5 %	**6.6 %**	2.9 %	**0.1 %**
4H	Bmag419A-*Vrn-H2*	153.5–160.7	23	0.14	0.03	**−1.64**	−0.30	0.27	**−0.29**	0.00	0.29	**−0.56**	−0.06	**−0.78**	0.40	**−0.06**
				0.8 %	0.0 %	**23 %**	1.6 %	3.4 %	**3.1 %**	0.0 %	2 %	**6.4 %**	0.1 %	**13 %**	5 %	**0.2 %**
5H	bPb04012-*Vrn-H1*	140.0–140.9	15	0.18	−0.01	**−1.30**	0.08	0.15	**−0.23**	0.03	0.18	**−0.51**	0.12	**−0.33**	0.26	**0.07**
				1.3 %	0.003 %	**14.3 %**	0.11 %	1 %	**1.9 %**	0.02 %	0.76 %	**5.4 %**	0.43 %	**2.4 %**	2.1 %	**0.24 %**
7Ha	bPb00186-bPb09079	6.4–6.9	12	−0.06	0.39	**−0.03**	0.44	0.28	**0.34**	0.22	0.53	**0.27**	0.18	**0.28**	0.23	**0.21**
				0.2 %	4.7 %	**0.0 %**	3.3 %	3.5 %	**4.1 %**	1 %	6.9 %	**1.4 %**	1 %	**1.7 %**	1.7 %	**2.3 %**
7Hb	bPb028890-Vrn-H3	6.6–7.2	9	−0.05	−0.47	**−0.36**	−0.11	−0.32	**−0.13**	−0.02	−0.21	**−0.02**	−0.34	**−0.26**	0.01	**−0.07**
				0.1 %	7.2 %	**1.1 %**	0.2 %	4.5 %	**0.6 %**	0.0 %	1.1 %	**0.0 %**	3.7 %	**1.5 %**	0.0 %	**0.3 %**

Chromosome, significant marker interval, chromosomal positions and LOD values are given. Additive effects (Arta–Keel) and percentage of explained phenotypic variance (PEV) are listed for each environment separately. Environments in which the seeds were sown in winter are given in bold

environments, but these have not identified the specific contributions of the year and location to the overall environmental variance (Comadran et al. 2011; Francia et al. 2011). In the present study, we dissected the specific contributions of variation between locations, years and sowing dates which allowed a more precise definition of genotype by environment interactions. We selected two geographically close locations which are characterised by different environmental conditions, Tel Hadya represents a favourable Mediterranean environment with deep, clay-rich soils and intermediate rainfall, while Breda is characterised by shallow soils and low rainfall (Ryan et al. 1997). Partitioning of phenotypic variation (Supplementary Table 3) and the GGE biplot (Fig. 2) revealed strong interaction effects between genotype and year within location or within sowing date. A strong gene by year interaction was also observed for QTL effects. In particular, QTL effects for yield and yield component traits exhibited quantitative and qualitative differences between years and sowing dates, while QTL effects for developmental and plant architecture traits were more stable across environments (Table 5). Our results thus indicated that interactions between genotypes/genes and unpredictable (temporal) factors had significantly stronger effects on yield expression than gene interactions with predictable spatial variation. These genotype by year interactions were likely due to pronounced differences in average rainfall between years within locations. Indeed, the highest correlations of yield with ecological factors were observed for the cumulative rainfall supporting results by Francia et al. (2011) who found strong positive correlation between water input and grain yield. The occurrence, severity, timing, and duration of drought thus varied strongly from year to year even at the same location and this year-to-year variation had the strongest effects on yield.

Spring growth improves yield stability

Under variable climatic conditions as encountered in Syrian environments, yield stability is an important breeding goal for subsistence farming. The Australian cultivar Keel showed an overall better agronomic performance and higher yield stability in the Syrian environments compared to the locally adapted landrace Arta. Keel bred for Australian dry environments was thus well adapted to Syrian environments and even outperformed the local landrace Arta in the driest year of 2008 and in the winter-sown experiments. These results thus complement previous observation that germplasm from the Middle East performed well in Australian environments (Eglinton et al. 2001) suggesting that Australian and Mediterranean germplasm are adapted to similar environmental conditions. Yield was correlated

Table 6 Interaction effects of allelic variation at the vernalisation genes *Vrn-H2* and *Vrn-H1* for days to heading and yield component traits in the different environments

Trait	*Vrn-H2*	*Vrn-H1*	LOD	B06A	B07A	B07W	B08A	B09A	B09W	T06A	T07A	T07W	T08A	T08W	T09A	T09W
BY	Arta	Arta	40				3352a	2518a	1848a				7727a	1775a	5201a	4095a
	Arta	Keel					3489a	2721b	1758a				7847a	3446b	5631b	3975a
	Keel	Arta					3390a	2618ab	1853a				7706a	2923bc	5421b	4142a
	Keel	Keel					3440a	2831b	1925a				7841a	3586d	5083a	4226a
DH	Arta	Arta	116							84a	101a	63a	108a	46a	103a	61a
	Arta	Keel								84a	100a	51b	107bc	43b	102b	58b
	Keel	Arta								84a	100a	50b	107b	43b	102b	58b
	Keel	Keel								84a	100a	49b	106c	43b	102b	58b
GV	Arta	Arta	110	2.5a	2.5ab	3.1a	2.1a	2.4a		2.2a	2.0a	3.2a	2.2ab	2.8a	2.6a	3.5a
	Arta	Keel		2.4a	2.6ab	2.0b	2.2a	2.1ab		2.2a	2.0a	2.1b	2.3ab	1.5b	2.4a	3.0b
	Keel	Arta		2.5a	3.1a	2.3b	2.3a	2.3ab		2.3a	2.1a	2.5c	2.4a	2.0bc	2.3a	3.0b
	Keel	Keel		2.5a	1.4b	2.0b	2.1a	2.1b		2.2a	2.0a	1.7d	2.1b	1.3d	2.5a	3.0b
GY	Arta	Arta	89	2776a	1015a	19a	1530a	1276a	543a	4846a	2266a	321a	4070ab	410a	2468a	1372a
	Arta	Keel		2803a	1050a	132b	1643a	1401b	675b	4886a	2247a	859b	4275ab	1176b	2552ab	1533b
	Keel	Arta		2805a	1014a	131bc	1500a	1240a	669b	4907a	2292a	805b	4014a	976c	2498ab	1553b
	Keel	Keel		2903a	1057a	156c	1549a	1415b	716b	5026a	2231a	863b	4323b	1334bc	2353b	1574b
PED	Arta	Arta	45	19a	9a	6a	8a	10a	8a	26a	11a		8a	7a	15a	11a
	Arta	Keel		19a	10b	6a	9b	10a	8a	26a	11a		9b	8b	16a	13b
	Keel	Arta		19a	10b	6a	9b	11a	9b	26a	12a		9b	8b	15a	13b
	Keel	Keel		19a	10b	6a	9b	11a	9b	27b	12a		9b	8b	16a	13b
PEDEX	Arta	Arta	52	−1.4	−8.4a	−6.6a	−9.5a	−7.9a	−9.8a	6.4a	−6.0a		−9a	−9a	−5a	−8a
	Arta	Keel		−0.8	−8.5a	−8.6b	−9.6a	−8.0a	−9.1a	6.4a	−6.5a		−9a	−9a	−5a	−6b
	Keel	Keel		−1.6	−8.7a	−8.4b	−9.6a	−8.2a	−9.3a	7.1a	−6.5a		−9a	−10a	−6a	−6b
	Keel	Arta		−2.1	−8.3a	−8.4b	−9.7a	−8.4a	−9.2a	6.5a	−6.0a		−9a	−9a	−6a	−7b
SL	Arta	Arta	68	6.7a	6.7a	1.9a	6.3a	7.6a	6.3a	7.2a	7.4a	5.4a	7.1a	5.8a	7.9a	6.3a
	Arta	Keel		6.7a	6.7a	4.5b	6.3a	7.6a	6.3a	7.0a	7.4a	6.0b	7.2a	6.0ab	7.8a	6.2a
	Keel	Arta		6.7a	6.7a	4.7b	6.7a	7.5a	6.7a	7.1a	7.3a	6.0b	7.3a	6.3bc	7.8a	6.4a
	Keel	Keel		6.5a	6.9a	4.4b	6.4a	7.4a	6.4a	7.1a	7.0a	6.3b	7.1a	6.5c	7.4b	6.3a

Arta allele from Arta, *Keel* allele from Keel, *T* Tel Hadya, *B* Breda, *A* autumn sowing, *W* winter sowing

Effects with different letter codes (a, b, and c) are significantly different ($P < 0.5$)

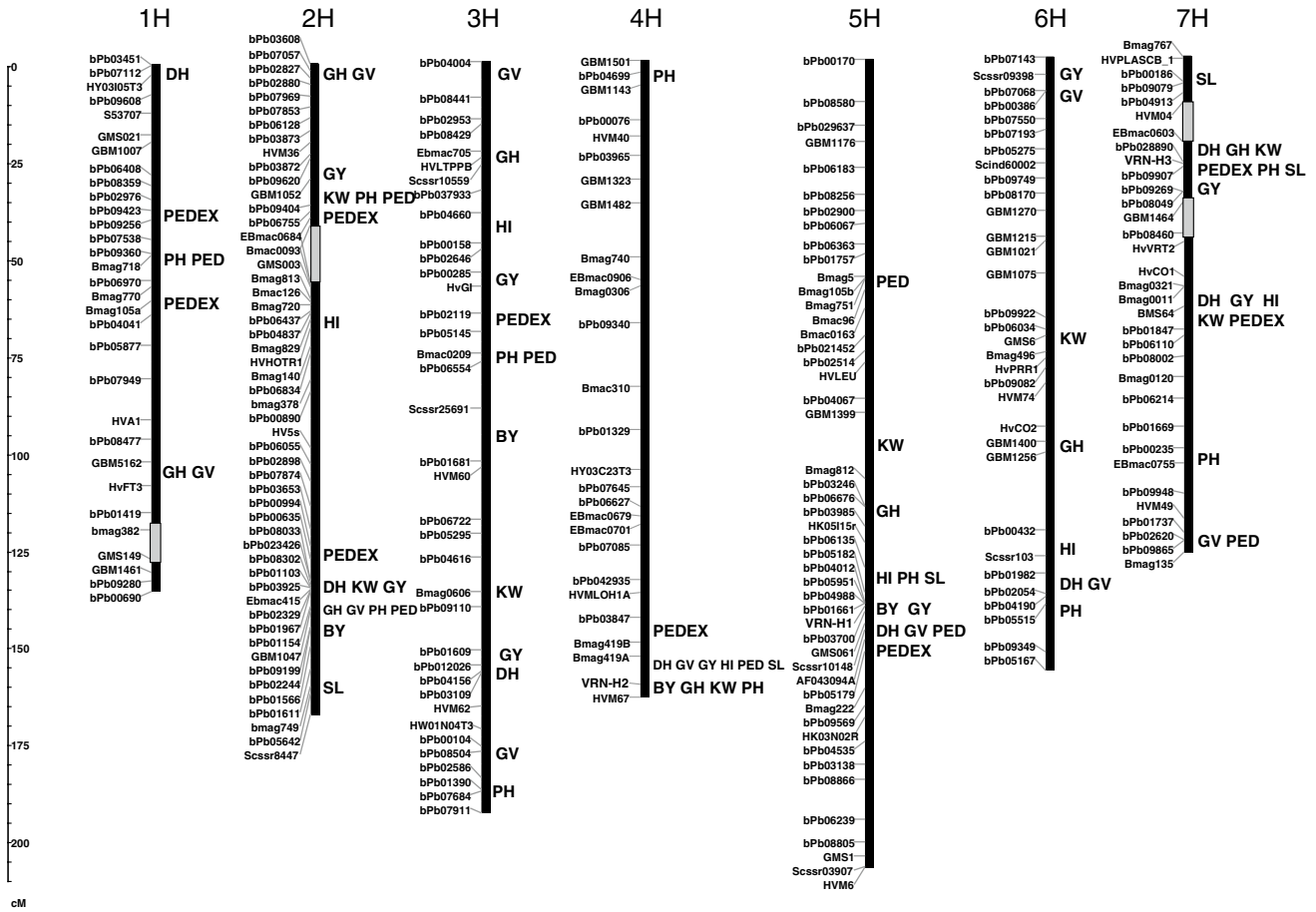

Fig. 3 Seven barley chromosomes with markers indicated to the left and significant QTLs indicated to the right of the chromosomes. *Grey boxes* indicate different linkage groups for chromosomes 1H, 2H and 7H. See Table 1 for trait abbreviations

with biomass, growth vigour and heading in the autumn and winter-sown experiments suggesting that early flowering improved biomass and final yield. Arta and Keel represent two different growth types. Arta has an intermediate vernalisation requirement characteristic of landraces from Syria (Mediterranean environments with cold winters), while Keel shows a spring growth habit with no vernalisation response and a concomitant susceptibility to cold. Late sowing in winter was used to test the performance of the parents and RIL population under more severe conditions of drought and heat, which increased towards the end of the growing season. The bimodal distribution of yield from winter-sown experiments at Tel Hadya (Fig. 1) suggested that the segregation of vernalisation response had a major effect on yield distribution. In the winter-sown trials, Keel and RILs with the erect growth type and faster reproductive development showed a performance superior to Arta and RILs with prostrate growth and vernalisation response. However, also in the autumn-sown experiments 2006–2008 Keel and genotypes with a spring growth habit had higher or the same yield compared to Arta and genotypes with vernalisation response. Francia et al. (2011) have argued that an intermediate vernalisation requirement was beneficial in dry Mediterranean environments as trade-off between cold tolerance during winter and drought escape in summer. In contrast, our results suggested that the spring growth type was beneficial particularly in the low rainfall environments and was not associated with a strong yield penalty due to higher susceptibility to cold as seen in the reduced growth vigour after winter. The spring growth type thus provided a better yield stability in Syrian environments.

Plant growth under drought is positively correlated with yield

A higher yield stability in Keel may have also been achieved by the capacity to maintain growth under stress. Plant growth, peduncle length and peduncle extrusion were strongly affected by drought as seen in the significant differences of these traits between Breda and Tel Hadya and between autumn and winter-sown experiments (Table 3).

Arta showed significantly higher reductions in biomass and plant height in the drier environments than Keel and this was correlated with a yield decrease (Tables 3, 4). Our data suggested that in the field, limiting growth reduction might provide a strategy to increase productivity under stress. These results confirm recent studies in Arabidopsis which demonstrated that mild drought primarily affected plant growth, consistent with the hypothesis that plants reduce their growth as a primary adaptation response to stress rather than as a secondary consequence of resource limitations (Muller et al. 2011; Skirycz et al. 2011). Tisné et al. (2010) showed that high biomass under drought was correlated with a lengthening of the vegetative phase and a reduction of the leaf emergence rate in Arabidopsis grown under controlled conditions. These results suggested a trade-off between water saving strategies such as early flowering and a reduction of leaf area, as compared to maintained growth and photosynthetic activity over a plant cycle. However, our results suggested that in the field with progressively increasing drought, fast development did not only allow plants to set seeds before the drought season, but also to accumulate vegetative biomass faster which in turn supported yield.

Flowering time genes and QTL have pleiotropic effects on yield component traits

Many of the QTL for flowering time, biomass, plant height, peduncle length and yield coincided with the map location of known flowering time genes or loci. Previous studies have identified strong effects of flowering time genes on agronomic performance in Mediterranean environments (Francia et al. 2011; Comadran et al. 2008; 2011; Cuesta-Marcos 2009). *Eam6* at the centromeric region of 2H was commonly identified as a major locus controlling reproductive development in spring by winter barley crosses tested in Mediterranean environments (Cuesta-Marcos et al. 2008; 2009; Francia et al. 2011; Comadran et al. 2011; 2012). In the present study, this locus coincided with a QTL cluster for yield component traits, such as kernel weight, plant height and peduncle length; however, no effects for flowering time were detected at this locus (Fig. 3).

Variation at the interacting vernalisation genes *Vrn-H1* and *Vrn-H2* had the strongest effects on reproductive development, plant growth and yield, where a reduced vernalisation requirement as determined by a deletion of *Vrn-H2* and the Keel allele at *Vrn-H1* improved yield performance. This is in contrast to previous studies which have not identified *Vrn-H1* and *Vrn-H2* as major determinants of performance in Mediterranean environments, neither in standard autumn nor in winter-sown experiments, presumably because vernalisation was always fully satisfied (Francia et al. 2011; Comadran et al. 2011; Ponce-Molina et al. 2012). The strong effects of *Vrn-H1* and *Vrn-H2* on yield may be explained by insufficient vernalisation in the winter-sown experiments and very low rainfall in 2006–2008, when small, delays in flowering were already correlated with significant yield reductions. In addition, variation at *Vrn-H1* and *Vrn-H2* had significant effects on growth vigour, where the Arta allele at both loci increased expression of both traits. Allelic variation at both genes controls expression levels of *Vrn-H1* which negatively affect cold tolerance and thus growth vigour after winter (Dhillon et al. 2010; Stockinger et al. 2007). Growth habit and growth vigour, but not flowering time, were also controlled by a QTL on the long arm of chromosome 1H, close to *HvFT3*, which is the candidate for the photoperiod response locus *Ppd-H2* (Faure et al. 2007; Kikuchi et al. 2009). The functional allele of *HvFT3* causes faster flowering under long or short-day conditions when vernalisation is not fully satisfied (Casao et al. 2011b), while a truncation of the gene primarily observed in winter barley causes a delay of flowering under short days (Kikuchi et al. 2009). Arta and Keel carry the functional form of the *HvFT3* allele, but may show *cis*-regulatory variation, or variation at flowering time regulators in the vicinity of *HvFT3*.

QTL clusters for developmental, plant architecture, and yield component traits were additionally detected on 2Hb, 3H and 7Hb where the Keel allele caused early flowering and an increase in yield and plant height. The QTL on 2H coincides with the location of *HvAP2,* which encodes an AP2 protein with similarity to the wheat domestication gene *Q* (Chen et al. 2009). Gene *Q* from wheat represents a major domestication locus and confers a compact spike, reduced plant height, free threshing grains, a fragile rachis (Simons et al. 2006) and is associated with delayed ear emergence (Kato et al. 1999). Previous QTL studies have detected effects on flowering time and yield in the same region on 2H in Arta × *H. spontaneum* 41-1 (Baum et al. 2003), Tadmor × Er/Apm (Teulat et al. 2001; von Korff et al. 2008), Barke × HOR11508 (Talamé et al. 2004), and Beatrix × SBCC145 (Ponce-Molina et al. 2012) suggesting that this locus shows genetic variation within Mediterranean barley germplasm and influences agronomic performance under dry conditions. The QTL cluster on 3H mapped close to the *sdw1* locus and coincided with QTL for heading date and grain yield identified in crosses involving wild and cultivated or spring and winter barley: Arta × *H. spontaneum* 41-1 (Baum et al. 2003), Tadmor × Er/Apm (von Korff et al. 2008), Barke × HOR11508 (Talamé et al. 2004), and Beatrix × SBCC145 (Ponce-Molina et al. 2012). *Ga20-oxidase*, a gene involved in the synthesis of gibberellin has been recently proposed as a potential candidate for this locus (Jia et al. 2009). The QTL interval on 7Hb that controlled flowering time, plant height, yield, and spike length coincided with QTL for heading

date detected in Arta × *H. spontaneum* 41-1 (Baum et al. 2003), Barke × HOR11508 (Talamé et al. 2004), and Beatrix × SBCC145 (Ponce-Molina et al. 2012). This locus harbours the *Vrn-H3*/*HvFT1* gene (Yan et al. 2006) with homology to the Arabidopsis gene *Flowering Locus T* (*FT*) and to *Hd3a* in rice (Corbesier et al. 2007; Tamaki et al. 2007). Arta and Keel are distinguished by a 4-bp deletion in the promoter region of *HvFT1*, where Arta carried the allele of Calicuchima-sib and Keel the Morex allele (indel 2 in Casas et al. 2011). Casas et al. (2011) have shown that natural variation in the promoter and intron of *HvFT1* causes variation in flowering time and may be important in driving agroecological adaptation of barley.

The QTL cluster on 7Hc, where the Arta allele accelerated time to flowering and increased yield, mapped close to QTL for heading date, plant height, and yield traits detected in crosses between cultivated spring and wild (winter) barley (Pillen et al. 2003; 2004; von Korff et al. 2006; 2010; Talamé et al. 2004; Baum et al. 2003; Lakew et al. 2012). Our study thus revealed a number of flowering time loci segregating in addition to the vernalisation genes between the spring barley Keel and the winter barley Arta. Many of these have previously been shown to differ between spring and winter (wild) barley, suggesting that the evolution of spring and winter growth habit involved allelic changes at a number of flowering time loci. Furthermore, the QTL study suggested that variation at loci controlling reproductive development and plant growth was important for yield stability in the cross Arta × Keel. QTL for biomass, plant height, peduncle extrusion and spike length collocated with known flowering time genes and loci, suggesting that flowering time genes also controlled growth rate and spike development. Earlier studies have identified a strong effect of flowering time genes on yield in dry environments, e.g. early flowering represents a drought escape mechanism through which the plant can reproduce outside the dry season (Acevedo et al. 1991; Francia et al. 2011; Comadran et al. 2011). Our QTL results suggested that flowering time genes had pleiotropic effects on growth, spike architecture and yield. Especially the Arta alleles at *Vrn-H2* reduced biomass and plant height in all tested environments and peduncle extrusion and spike length in the majority of environments (Table 5). The effects of *Vrn-H1* and *Vrn-H2* on growth are likely correlated with their control on the onset and duration of stem elongation (Borràs-Gelonch et al. 2011a, b; Campoli et al. 2012a). Under control condition, the duration of the late reproductive phase of stem elongation in wheat was positively correlated with spike weight and the number of fertile florets at anthesis (González et al. 2002, 2011). In contrast, under terminal drought in the field fast reproductive development increased spike length and kernel weight in the present study. Our results suggested that under changing climate conditions, such as shorter winters, reduced rainfall, and early summer drought, early heading Australian barley genotypes might thus outperform vernalisation-sensitive Syrian landraces.

Finally, the ARKE population and parental lines Arta and Keel represent a valuable resource to study the genetic basis of physiological responses to drought and heat (Rollins et al. 2013).

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Ethical standards All experiments described in this manuscript comply with the current laws of the country in which they were performed.

Conflict of interest The authors declare that they have no conflicts of interests.

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