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QTLs for agronomic traits from a Mediterranean barley progeny grown in several environments

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Abstract In order to identify quantitative trait loci (QTLs) controlling agronomic trait variation and their consistency under Mediterranean conditions in barley, a progeny of 167 recombinant inbred lines (RILs) and the parents Tadmor and Er/Apm, originating from the Mediterranean basin, were grown under Mediterranean conditions in 1995, 1996, 1997 and 1999. For the 2 first years (M95 and G96), one replicate was grown, but for the latter (M97 and M99) two rainfed (rain) and two irrigated (ir) replicates were produced. M95, G96, M97rain, M97ir, M99rain and M99ir were considered as six different environments and were compared in terms of their meteorological conditions and water supply. Grain yield and yield components were assessed, as well as heading date and plant height. Highly significant differences were noted between environments. QTLs were obtained from each environment separately and from a multiple environment analysis (simple interval mapping and simplified composite interval mapping). Despite heterogeneity between environments, numerous QTLs were common to several environments. This was particularly true for traits like plant height and thousand-grain weight. The most reliable QTLs which explained the largest part of the phenotypic variation were obtained for plant height on chromosomes 3 (3H) and 6 (6H). The multiple-environment analysis provided an opportunity to identify consistent QTLs for agronomic traits over six Mediterranean environments. A total of 24 consistent QTLs were detected. Out of these, 11 presented main effects, seven presented QTL×E interaction, and six presented both effects. In addition, 18 of the consistent QTLs were common to other published work and six seemed specific to this study. These latter QTLs could be involved in Mediterranean adaptive specificities or could be specific to the studied genetic background. Finally, when the rainfed and the irrigated environments of M97 were considered separately, a total of 16 QTLs presenting main effects over the two water conditions were identified, whereas five QTLs seemed dependent on the water conditions.

Keywords Mediterranean climate · Barley · Drought tolerance · Yield · QTL · QTL×E interaction

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Introduction

One of the major goals for plant breeders is to develop genotypes with a high yield potential and the ability to maintain yield across environments. This is particularly true in the Mediterranean basin where harsh and fluctuating climatic conditions lead to high Genotype×Environment (G×E) interactions (Acevedo et al. 1991). With the development of molecular markers, breeders have a complementary tool to traditional selection, and markers linked to the variation in a trait of interest could be used to assist breeding programs. However, the identification of relevant markers linked to the variation of yield components and stability is difficult and time-consuming. Nevertheless, numerous studies reported quantitative trait loci (QTLs) for such traits in barley (Hayes et al. 1993; Thomas et al. 1995; Kjaer and Jensen 1996; Bezant et al. 1997; Mather et al. 1997; Yin et al. 1999; Zhu et al. 1999) and QTLs consistent over 30 environments were described by Tinker et al. (1996). These studies were mostly performed in Northern European and American conditions. A few compared QTLs detected under water-stressed and irrigated conditions in cereals (Ribaut et al. 1996 in corn and Lafitte and Courtois 1999 in rice, as examples) and, except the study by Baum et al. (1996), no work was really concerned with QTLs for barley agronomic performance in the Mediterranean basin. As the Mediterranean area is often drought-prone (low rainfall, high temperature and light intensity leading to high evaporative demands), the identification of QTLs for agronomic traits in barley in some

Mediterranean environments will be of interest for yield improvement in this area.

Several authors have focussed their efforts on the dissection of drought tolerance in traits that have a positive impact on yield stability (Acevedo 1987; Monneveux 1991). Osmotic adjustment and carbon isotope discrimination (Δ) are such traits (Morgan 1983; Farquhar and Richard 1984; Blum 1988; Craufurd et al. 1991; Acevedo 1993; Merah et al. 2001). In Teulat et al. (1998, 2001) traits related to plant water status and OA were measured in controlled conditions and QTLs identified at two soil-moisture contents. Experiments performed under controlled conditions present advantages because the traits are evaluated theoretically with limited environmental fluctuations (Price and Courtois 1999). They are particularly adapted for traits such as OA where measurements are difficult and time-consuming in field conditions (numerous measurements simultaneously, importance of the management, and timing of the water stress). On the other hand, field experiments represent realistic conditions (Price and Courtois 1999). In such a context, the co-location of QTLs for drought tolerance-related traits such as OA or relative water content, measured in controlled conditions, and of QTLs for agronomic traits, measured in several Mediterranean field conditions, would reinforce the value of such criteria. Indeed, once genetic markers associated with field performance are identified, it will become possible to study which adaptive traits co-segregate with yield or yield components. The comparison between loci involved in these complex traits, as well as the study of their relationships and their genetic basis could help in the identification of the relevant drought tolerance criteria and of the key chromosomal regions involved. Favourable alleles at the nearest markers could then be selected to improve the yield performance of barley in the Mediterranean area.

In this context, the objectives of the present paper were to identify QTLs affecting agronomic trait variation and their stability across several Mediterranean environments in a recombinant inbred line (RIL) progeny from a Mediterranean two-row barley cross. The ultimate objective will be a comparison of the locations of these QTLs to the ones involved in the variation of adaptive traits with an impact on yield stability in the Mediterranean area. The comparison of those QTLs with QTLs previously reported for the same traits in other barley genetic backgrounds and in other conditions, as well as the differences between QTLs identified for traits measured under rainfed conditions and those obtained under irrigated conditions, may provide new information on yield stability in the Mediterranean area.

Materials and methods

A progeny of 167 two-row barley RILs and the two parents, Tadmor (selected by ICARDA from Arabi Aswad, a Syrian landrace) and Er/Apm (a selected line, released in Tunisia) were grown in field conditions under two water treatments in 1997 and 1999

Table 1 Means of temperature and cumulated rainfall (R), Penman evapotranspiration (ET) and R/ET during the months of the growth cycle of the six environments: M95: Montpellier 1995, South of France; G96: Granada 1996, South of Spain; M97rain and M97ir: Mauguio 1997, South of France; M99rain and M99ir, Montpellier 1999; rain: rainfed conditions; ir: irrigated conditions

Item	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Total
M95										
Rainfall (mm)	108	51	27	8	12	50	29	2	–	287
Temperature (°C)	14.3	9.6	8	11.2	10.5	14.4	16.9	21.5	–	13.3
ET (mm)	16	8.0	18	29	66	85	114	152	–	488
R/ET	6.75	6.38	1.5	0.28	0.18	0.59	0.25	0.01	–	0.59
G96										
Rainfall (mm)	–	148	173	57.2	47.6	36	109	11	8.2	590 (442[a])
Temperature (°C)	–	9.12	9.53	7.1	10.28	14.42	16.48	22.15	22.65	13.97
ET (mm)	–	na[b]	25.5	39.8	55.1	83.03	110.36	181.77	239.30	734.86[a]
R/ET	–	na[b]	6.78	1.44	0.86	0.43	0.99	0.06	0.03	0.60[a]
M97rain										
Rainfall (mm)	–	166	133	2.6	0.2	12	26.8	128.8	–	469.4
Temperature (°C)	–	8.61	7.61	10.09	13.48	14.04	17.75	19.94	–	13.07
ET (mm)	–	29.1	32.8	57.9	116.3	141.2	136.1	128.1	–	641.5
R/ET	–	5.70	4.05	0.04	0.002	0.08	0.20	1.01	–	0.73
M97ir										
Rainfall and irrigation (mm)	–	166	133	18.6	45.2	57	46.8	128.8	–	637.0
R/ET	–	5.70	4.05	0.32	0.39	0.40	0.34	1.01	–	0.99
M99rain										
Rainfall (mm)	13.5	55.5	50.5	0	46.0	51.0	140.5	22.5	–	379.5
Temperature (°C)	9.2	8.0	9.1	8.3	12.09	14.4	18.7	21.4	–	12.61
ET (mm)	18.6	10.0	13.1	31.3	49.4	73	86.9	125.6	–	401.9
R/ET	0.73	5.50	3.85	0	0.93	0.71	1.62	0.18	–	0.93
M99ir										
Rainfal and irrigation (mm)	13.5	55.5	50.5	37.5	46.0	111	140.5	22.5	–	477.0
R/ET	0.73	5.50	3.85	1.20	0.93	1.54	1.62	0.18	–	1.17

[a] Without december; [b] na: non-available

(M97rain and M99rain; rainfed conditions and M97ir and M99ir; with an irrigation supply) with two blocks per treatment. The plants were sown on November 3rd in Mauguio at the INRA field station (South of France) in 1997 and on November 20th in the experimental field of the ENSAM campus (Montpellier, South of France) in 1999 in a random complete block design. In each block, two rows per line were grown. For each year, 101 kg/ha of PK was supplied before sowing and then 124 kg/ha of Nitrogen (Ammonitrate) was added twice.

Two other trials conducted in 1995 and 1996, with only one replicate of RILs per trial, were also considered for a contribution to the detection of consistent QTLs across environments. In 1995 (M95), the trial was carried out in Montpellier on the ENSAM campus under rainfed conditions. For each RIL, 40 seeds were sown in two rows, 3-m long, spaced 25 cm apart on November 22th 1994. Eighty kg/ha of P_2O_5 and K_2O were added to the plot before sowing and 110 kg/ha of Nitrogen (Ammonitrate) was supplied three times. In 1996 (G96), parcels of $3m^2$ with a seeding rate of 220 seeds/m^2 were sown on December 5th (1995) at CIDA (Centro de Investigación y Desarrollo Agrario), Granada (South of Spain). Fertiliser was added once (147 kg/ha of Nitrogen Urea 46.5%). The trial was conducted under rainfed conditions.

M95, G96, M97rain, M97ir, M99rain and M99ir were considered as six different environments. Table 1 describes the monthly temperature, rainfall (R) and Penman evapotranspiration (ET) means during each trial period. The environments differed in total cumulative rainfall (and water supply for M97ir and M99ir) as well as rainfall distribution (Table 1). In M95, the total rainfall during the experiment was 287 mm which was quite low for the region. Sixty five percent of these seasonal precipitations were received during the beginning of the growth cycle (November to January). A drought period occurred from February until the end of the cropping cycle with a decrease of water availability as the growth cycle progressed. In G96, the total rainfall was high (590 mm) and more than 86% fell during the 3 first months with a mean R/ET ratio for January and February of 3.53. The last 4 months were characterised by a terminal water stress (mean R/ET ratio of 0.27). This stress was more marked in June and in the beginning of July (i.e. during grain filling) when the R/ET ratio decreased to 0.05 so that in this environment, 35.9% of the rainfall (211.8 mm) was used for plant development (tillering to maturity stages). In M97rain, plants received 469 mm, with about 64% falling during the 2 first months of the cycle. A long period of drought was noticed between February and May with a mean R/ET ratio of 0.09. In M99rain, plants have received 379 mm. Contrary to the other environments, only a third of the cumulative recorded rainfall fell during the 3 first months. Three drought periods were observed during this plant cycle. The early one occurred in November after the sowing. The second one took place in February which was the driest month (0 mm rainfall). May was a rainy month followed by the last drought period in June with a R/ET ratio of 0.18. Plants of irrigated blocks received 126 and 98 mm of additional water 6-times in M97ir and M99ir respectively so that, in both M97 and M99, the irrigated E differed from the rainfed ones in water availability.

Measurements

In M95, plant height (PH), dry aerian biomass production *per* plant (DAB), the number of grains *per* ear (NGE), and the number of fertile tillers *per* plant (NFT) were measured at maturity on ten plants *per* RIL. Grain yield *per* plant (GY) was assessed on the entire two rows. Harvest index was calculated as HI=GY/DAB. Then, 1000-grain weight (TGW) was evaluated from a sample of grains harvested for each RIL. In G96, heading date (HD), PH, NGE (ten plants *per* RIL) and TGW were recorded, but GY was not available in this environment. In M97rain, M97ir, M99rain and M99ir, a global note of HD was recorded for the two rows *per* RIL in each block. At maturity, five plants *per* RIL and *per* block were harvested. Plant height, DAB, GY, HI and TGW were measured on these plants. In M97rain and M97ir, NGE and NFT were additionally recorded. For all environments, HD was evaluated by the number of days from sowing until the emergence of 50% of the heads on main tillers, and PH was measured from the soil surface to the top of the ear including awns.

Statistical analysis of field data

Analyses of variance were performed using the GLM procedure of the SAS program (SAS Institute 1987, Cary N.C., USA). Because of heterogeneity in trait measurements in each environment (PH was evaluated directly in the field by a mean in G96, and on several plants per RIL in M95 for example) and lack of replicates for M95 and G96, the G×E interactions were evaluated only with M97rain, M97ir, M99rain and M99ir. As for these four environments a high significant block effect was noticed for most traits, and the adjusted means generated by fixing the block effect were used in all analyses. The G×E interactions were also approached by the study of the phenotypic correlations of a given trait across environments and of the stability of QTLs across the six environments.

QTL detection

For all the data sets, phenotypes of the 167 RILs were analysed using 123 molecular markers arranged on a map including mostly RFLP, AFLP and SSR markers. PCR amplification products using specific primer pairs WG940, TB4TB5 and ABC454, kindly made available by T.K. Blake (Montana State University, Bozeman, USA), were also used as markers indicated by s. For SSR, primer sequences were kindly made available by M. Macaulay and R. Waugh (Scottish Crop Research Institute, UK). MAPMAKER (Lander et al. 1987) was used to estimate the marker order and centiMorgan (cM) distances (Kosambi 1944). The base map consisted of 1300 cM, and gaps were present on chromosomes 7H, 2H, 3H, 1H and 5H. The organization of the chromosomes is presented in Fig. 1.

To examine the influence of environment on trait expression and on QTLs in the Mediterranean progeny, QTLs from each environment were first assessed with the trait means generated from each of the six E separately. These analyses were performed with MAPMAKER/QTL version 1 (Lander and Botstein 1989). The putative QTLs were declared significant when the LOD score was ≥2.0. In a second step, simple interval mapping (SIM) and simplified composite interval mapping (sCIM) analyses were performed using the software package MQTL, adapted for the evaluation of progeny in multiple environments to identify QTLs that exhibit, or do not exhibit, QTL×E interaction (Tinker and Mather 1995a, b). The software allows one to identify QTLs based on approximately the same approach as that of Zeng (1994) (see details in Tinker and Mather 1995a, b). For sCIM, 33 background markers, well scattered along the chromosomes and at QTLs previously detected by MAPMAKER/QTL for the traits studied, were used as cofactors to control the effect of the genetic background. They are indicated in Fig. 1. The sCIM analysis makes it possible to improve the precision and accuracy of the QTL location and effect (Tinker and Mather 1995b). A test statistic (TS) value (Haley and Knott 1992) was produced for both QTL main effect and QTL×E interaction at each marker locus, and for each trait for both SIM and sCIM. To estimate significant thresholds, the TS values generated were divided by the one obtained by 1000 random permutations of the data performed for each trait during SIM analysis. Corrected TS values (cTS) were obtained. When cTS was higher than 1, the QTL was accepted (type-I error rate below 5). As in Tinker et al. (1996), when evidence for a QTL main effect and a QTL×E interaction were found near the same position, a single QTL was inferred based on the effect that seemed the strongest. Primary QTLs were those obtained when cTS are significant with SIM and when sCIM cTS are also strong. Secondary QTLs were those obtained when only SIM or sCIM gave evidence of a QTL. For primary QTLs, the positions indicated correspond to the maximum cTS obtained by sCIM analysis. For secondary QTLs, the positions are those corresponding to the maximum cTS with SIM or sCIM.

Table 2 Trait means, standard deviation, minimum and maximum values obtained from each environment. M95: Montpellier 1995; G96: Granada 1996; M97rain and M97ir: Mauguio 1997 rainfed and irrigated; M99rain and M99ir: Montpellier 1999, rainfed and irrigated. The environment and genotype effects are indicated. Means not sharing a common letter are significantly different according to Duncan's test (P=0.05). LSD: least significant difference

Trait	Environment	Mean	SD	Min	Max	Environment effect	Genotype effect
Plant height (cm) LSD: 1.70	M95	86.6C	8.7	66.0	109.6	0.0001***	0.0001***
	G96	104.5A	11.0	74.0	137.0		
	M97rain	61.6E	6.3	47.4	81.4		
	M97ir	85.5C	6.8	60.4	101.4		
	M99rain	83.6D	6.4	68.0	104.0		
	M99ir	95.5B	5.7	81.5	112.0		
Number of grains per ear LSD: 0.47	M95	25.9B	2.0	20.6	31.6	0.0001***	0.0001***
	G96	28.3A	2.8	20.6	37.0		
	M97rain	21.0D	1.9	16.6	25.9		
	M97ir	21.9C	2.1	15.8	27.2		
Number of fertile tillers LSD: 0.92	M95	25.0A	5.2	15.8	52.4	0.0001***	0.0513ns
	M97rain	10.4C	3.7	4.6	21.8		
	M97ir	20.5B	3.9	13.0	34.2		
Thousand-grain weight (g) LSD: 0.90	M95	40.2B	5.2	20.8	68.7	0.0001***	0.0001***
	G96	36.4D	4.7	21.4	49.0		
	M97rain	44.0A	4.0	33.7	55.7		
	M97ir	44.2A	3.7	32.6	53.9		
	M99rain	40.5B	3.5	33.1	50.8		
	M99ir	37.6C	3.8	25.2	46.8		
Dry aerian biomass per plant (g) LSD: 1.38	M95	35.2B	8.0	18.9	64.3	0.0001***	0.0053**
	M97rain	16.3E	5.0	7.5	33.1		
	M97ir	37.7A	6.7	23.8	59.9		
	M99rain	27.5D	6.4	14.0	57.8		
	M99ir	30.4C	6.0	16.1	46.3		
Grain yield per plant (g) LSD: 0.55	M95	12.5B	3.4	3.4	22.2	0.0001***	0.0003***
	M97rain	6.6D	1.9	3.2	13.6		
	M97ir	13.5A	2.7	7.1	21.9		
	M99rain	9.7C	2.3	4.9	17.7		
	M99ir	9.2C	2.4	3.4	14.5		
Harvest index LSD: 0.12	M95	0.35B	0.09	0.10	0.74	0.0055*	0.0001***
	M97rain	0.41A	0.04	0.22	0.60		
	M97ir	0.36B	0.05	0.20	0.46		
	M99rain	0.36B	0.04	0.21	0.52		
	M99ir	0.30C	0.05	0.17	0.45		
Heading date (days after sowing) LSD: 0.50	G96	117.2D	1.4	114.0	122.0	0.0001***	0.0001***
	M97rain	146.7C	2.2	142.0	151.0		
	M97ir	146.9C	1.8	143.5	153.5		
	M99rain	149.4B	3.3	140.0	154.7		
	M99ir	151.0A	2.4	142.0	156.0		

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability level

Results

Trait variation within and across environments and G×E interactions analysis

Table 2 describes the trait values for each environment. Considering all environments, a significant RIL effect was obtained for plant height (PH), the number of grains *per ear* (NGE), thousand-grain weight (TGW), grain yield (GY), heading date (HD), harvest index (HI) and for dry aerian biomass (DAB), and a non-significant RIL effect for the number of fertile tillers (NFT). The progeny showed a large variation for all traits within each environment and the trait distributions were approximately normal. As an example, GY values ranged from 3.4 g *per* plant to 22.2 g in M95, and from 7.1 g to 21.9 g in M97ir. There were also significant differences between environments for all traits, and trait means presented large differences among the six environments (Table 2).

When the rainfed and irrigated plants grown at the same site in 1997 and 1999 were considered and compared, differences were also noted. The rainfed and irrigated environments of each year mostly differed in water availability (Table 1). Significantly lower PH and DAB values were obtained under the two rainfed, compared to the two irrigated, conditions (P<0.0001***). As an example in M97, a RIL mean of 61.6 cm was obtained for PH under rainfed conditions and a mean of 85.52 cm un-

Table 3 Phenotypic correlation coefficients between thousand-grain weight in the six environments: M95, G96, M97rain, M97ir, M99rain and M99ir; ir: irrigated trial; rain: rainfed trial

Environment	M95	G96	M97rain	M97ir	M99rain	M99ir
M95	–					
G96	0.141*	–				
M97rain	0.275**	0.327***	–			
M97ir	0.312***	0.300***	0.505***	–		
M99rain	0.338***	0.281**	0.547***	0.552***	–	
M99ir	0.300***	0.195*	0.332***	0.350***	0.543***	–

*, **, *** Correlation significant at the 0.05, 0.01, 0.001 probability level

der irrigated conditions (Table 2). For NGE and NFT measured only in M97rain and M97ir, values were also significantly higher under irrigated, compared to rainfed, conditions (P<0.0001***). By contrast, a higher HI was obtained under rainfed conditions (P<0.0001***). TGW was significantly higher in M99rain compared to M99ir (P<0.0001***) whereas no differences were obtained between M97rain and M97ir. An environmental effect was also obtained for GY and HD (P<0.0001***) but no significant differences were noticed between M99rain and M99ir for GY, and between M97rain and M97ir for HD. Finally, for all the traits common to M97 and M99, the RIL effect was significant (P<0.017* for DAB, P<0.009** for GY, and P<0.0001*** for PH, TGW and HD) whereas G×E interactions were not significant for any trait.

Considering all environments, the G×E interactions were evaluated by a correlative approach: indeed, if all RIL means were significantly correlated across environments for one given trait, this meant that the RIL ranking remained mostly consistent across environments. Table 3 shows, as an example, that correlations between means for TGW across the six environments are significant. With the same procedure, the RIL ranking for PH, NGE and HD was also shown to be consistent across the environments considered, suggesting low G×E interactions acting on these traits.

QTL analysis

QTL identified from the six environments separately

QTLs obtained within each environment are presented in Table 4 and Fig. 1. A total of ten QTLs was identified for M95: for PH on chromosomes 7H, 3H and 6H, for NGE on 4H, for NFT on 3H, for TGW on chromosomes 3H and 6H, for DAB on 4H, and for GY on chromosomes 7H and 4H. In G96, nine QTLs were identified: three for PH on chromosomes 2H, 3H and 6H, one for NGE on 3H, two for TGW on 6H and 5H, and three HD on chromosomes 3H, 1H and 5H. The rainfed environment M97rain and the irrigated environment M97ir differed in water availability. When considering each of these environments separately, some QTLs were common to both water conditions (Table 4). For example, common QTLs were mapped on chromosomes 3H and 6H for PH and 6H for TWG. The significance of these QTLs was higher for the irrigated environment M97ir. As an example, the highest LOD peak of the study was obtained for PH on chromosome 6H (6.97) for M97ir, whereas a LOD peak of 2.20 was found for the same trait for M97rain (Table 4). The other QTLs were found to be specific to one environment, with one water treatment: on chromosomes 4H (M97rain) and 5H (M97ir) for TGW and on chromosomes 2H, 4H and 5H (M97ir) for PH. For GY, no QTL was found either in M97rain or in M97ir with MAPMAKER/QTL but a QTL was detected for M97rain by ANOVA. This QTL was closest to WG286 on chromosome 6H (P<0.0037). As the marker flanks a gap of 31 cM between WG286 and *dhn4*, the existence of a QTL for GY on this portion of chromosome was only putative. At the WG286 locus, Tadmor alleles conferred a higher GY. In addition, ten QTLs were obtained for M97ir compared to eight QTLs for M97rain. However, the differences between the two water conditions in terms of the number and location of QTLs depended on the trait considered. For example, for TGW two QTLs were identified in both treatments but one was mapped on chromosome 4H for the rainfed conditions and one was mapped on chromosome 5H for the irrigated conditions. The other QTLs detected in M97 were mapped on chromosomes 4H for NFT, 3H and 5H for HI, and 2H for HD for the rainfed conditions. Concerning the irrigated conditions, one QTL was additionally significant for NFT on 6H and two for NGE on 3H and 4H. In M99, numerous QTL locations differed between the two water conditions. For this site, nine QTLs were obtained for M99ir compared to ten QTLs for M99rain. The QTLs identified only under rainfed conditions were located on chromosomes 3H and 6H (nearby pAF93) for PH, on 2H, 4H, 1H and 6H (nearby BCD348B) for TGW, on 7H for HI. The QTLs identified only under irrigated conditions were mapped on chromosomes 5H for TGW, on 6H for DAB, on 5H for GY, on 4H for HI, and on 7H and 6H for HD. However, only a few QTLs seemed common to the two water treatments: on 6H nearby BCD348B for PH and nearby BCD1 for TGW, and on 3H for HD.

Considering all six environments, some QTLs for NGE, PH and TGW were common to several or all environments. For these QTLs, no change was observed in the direction of the allele effect across environments. These common QTLs were found for traits presenting a consistent RIL ranking across environments from the correlative approach. For PH, a QTL was found at the same location for all environments on chromosome 6H,

Table 4 QTLs detected by Interval Mapping with MAPMAKER/QTL for some agronomic traits measured in one, three, five or all six environments independently: the name of the trait is followed by numbers corresponding to the environments where they were measured. %Var: individual variance explained by the QTL. [1]M95, [2]G96, [3]M97rain, [4]M97ir, [5]M99rain, [6]M99ir. PH: plant height, NGE: number of grains *per* ear, NFT: number of fertile tillers, TGW: thousand-grain weight, DAB: dry aerian biomass (*per* plant), GY: grain yield (*per* plant), HI: harvest index, HD: heading date

Trait		Marker (distance to peak LOD value in cM)	Chromosome	Magnitude of peak LOD	Var (%)	Estimated genetic additive effect[a]
PH[all]	M95	BCD1066+1	7H	2.03	5.9	5.152
		Bmag0136+0	3H	5.22	13.8	7.857
		CDO497+0	6H	2.30	6.2	5.276
	G96	HVM54+5	2H	2.30	8.0	–6.325
		BCD263+0	3H	2.56	7.6	6.092
		BCD348B+2	6H	3.91	12.8	7.877
	M97rain	MWG582B+3	3H	2.54	7.7	3.459
		Bmag0009+2	6H	2.20	7.1	3.329
	M97ir	HVM54+4	2H	2.05	6.7	–3.558
		Bmag0136+0	3H	5.58	14.4	5.151
		MctgEaccC+4	4H	3.05	9.5	–4.199
		CDO497+0	6H	6.97	17.5	5.691
		BCD298+17	5H	2.07	6.1	3.356
	M99rain	MWG582B+4	3H	2.67	7.4	3.463
		BCD348B+3	6H	3.64	10.9	4.228
		pAF93+9	6H	3.66	13.6	4.719
	M99ir	BCD348B+1	6H	4.72	14.5	4.312
NGE[1234]	M95	MctgEaccC+1	4H	4.18	12.8	–1.435
	G96	MWG582B+1	3H	4.38	14.0	2.081
	M97ir	BCD1127+2	3H	3.52	11.4	1.409
		MctgEaccC+3	4H	3.63	11.7	–1.429
NFT[124]	M95	BCD263+0	3H	2.60	7.7	–2.864
	M97rain	HVM67+2	4H	2.78	8.8	–1.113
	M97ir	BCD348B+0	6H	3.57	9.4	–2.413
TGW[all]	M95	MWG595+1	3H	2.23	6.7	–2.683
		BCD1+6	6H	2.79	10.8	–3.421
	G96	BCD348B+0	6H	2.96	8.6	2.737
		CDO385+3	5H	2.26	7.9	–2.638
	M97rain	HVM67+4	4H	2.43	8.0	2.235
		BCD348B+2	6H	2.58	8.3	2.274
	M97ir	CDO497+0	6H	4.02	10.6	2.401
		CDO400+2	5H	3.08	9.1	2.225
	M99rain	CDO1417+11	2H	2.45	9.2	2.111
		HVRCABG+8	4H	2.03	7.1	1.855
		WG983+1	1H	3.19	9.3	–2.113
		BCD348B+2	6H	2.10	7.3	1.881
		BCD1+4	6H	3.72	14.1	–2.621
	M99ir	BCD1+3	6H	2.91	10.2	–2.403
		WG564+5	5H	2.03	7.7	–2.104
DAB[13456]	M95	WG114+4	4H	3.17	10.0	–5.035
	M99ir	BCD348B+1	6H	3.04	9.4	1.841
GY[13456]	M95	WG380+0	7H	2.14	5.9	–1.623
		WG114+6	4H	2.18	7.3	–1.806
	M99ir	CDO344+0	5H	2.12	5.7	–5.738
HI[13456]	M97rain	Bmag0209+0	3H	4.56	12.0	–0.0309
		WG908+13	5H	2.26	6.8	–0.0232
	M99rain	BCD1066+0	7H	2.39	6.4	0.0218
	M99ir	MctgEaccC+1	4H	2.75	10.0	–0.0296
HD[23456]	G96	Bmac0209+0	3H	2.54	7.2	0.771
		WG983+0	1H	2.65	8.3	–0.824
		Bmag0223+23	5H	3.71	23.6	1.391
	M97rain	CDO1417+5	2H	2.57	10.2	–1.423
	M99rain	HVM62+2	3H	3.35	11.2	–2.230
	M99ir	WG380+0	7H	2.11	5.7	1.129
		Bmag0013+12	3H	2.32	7.8	–1.323
		BCD1+13	6H	2.10	6.2	1.182

[a] Genetic effect expressed as the change in the value of each trait due to the contribution of an allele from Tadmor compared to Er/Apm

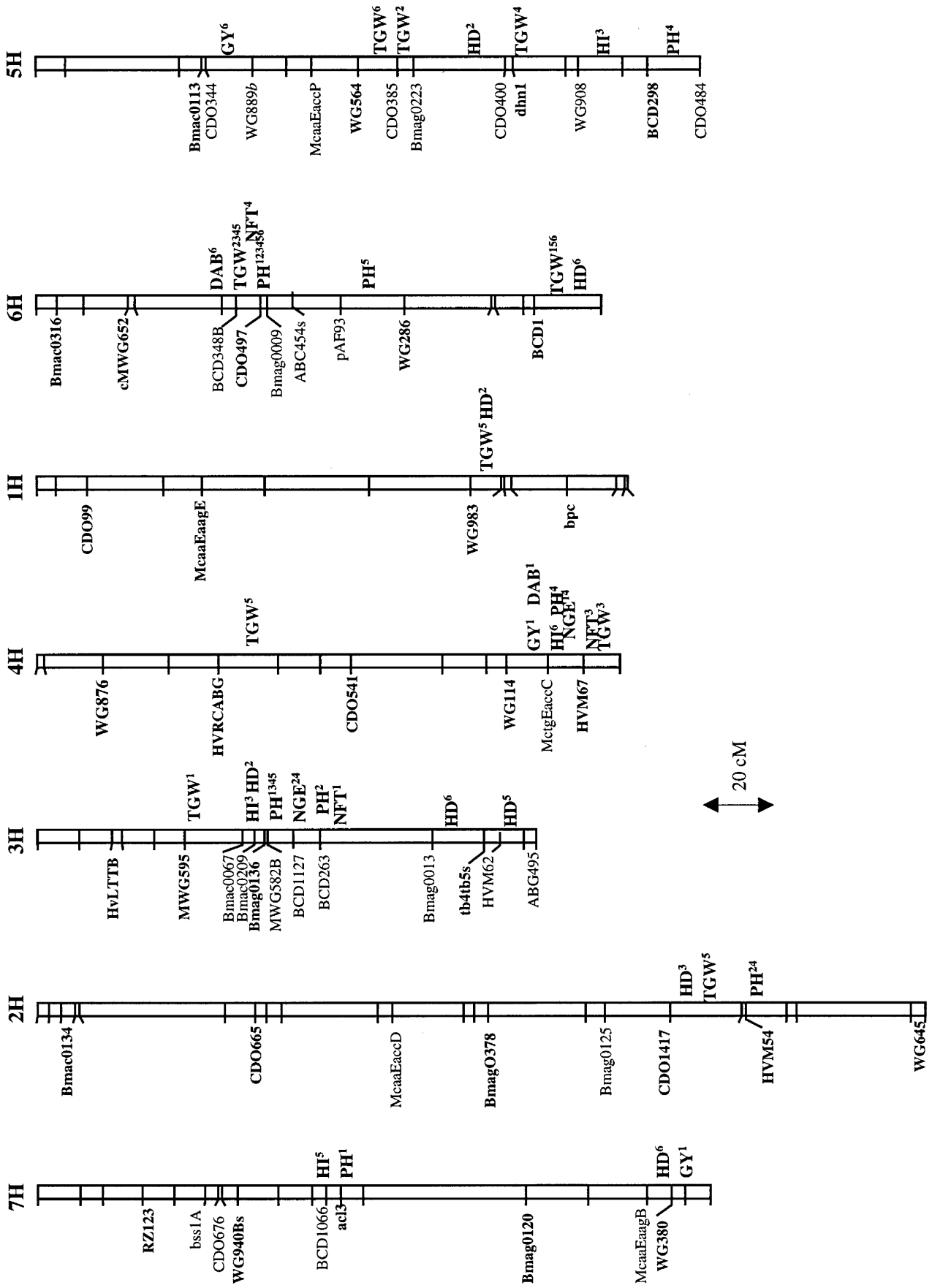
7H
RZ123
bss1A
CDO676
WG940Bs
BCD1066
acl3
HI5
PH1
Bmag0120
MccaEaagB
WG380
HD6
GY1
2H
Bmac0134
CDO665
MccaEaccD
BmagO378
Bmag0125
CDO1417
HD3
TGW5
PH24
HVM54
WG645
3H
HvLTTB
MWG595
TGW1
Bmac0067
Bmac0209
Bmag0136
HI3 HD2
MWG582B
PH1345
BCD1127
NGE24
BCD263
PH2
NFT1
Bmag0013
HD6
tb4tb5s
HVM62
HD5
ABG495
20 cM
4H
WG876
HVRCABG
TGW5
CDO541
WG114
GY1 DAB1
HI6 PH4
NGE4
NFT3
TGW3
MctgEaccC
HVM67
1H
CDO99
MccaEaagE
WG983
TGW5 HD2
bpc
6H
Bmac0316
cMWG652
BCD348B
DAB6
CDO497
TGW2345
PH123458
NFT4
Bmag0009
ABC454s
pAF93
PH5
WG286
BCD1
TGW156
HD6
5H
Bmac0113
CDO344
GY6
WG889b
MccaEaccP
WG564
CDO385
TGW6
Bmag0223
TGW2
HD2
CDO400
dhn1
TGW4
WG908
HI3
BCD298
PH4
CDO484

Table 5 QTLs obtained for all environments where the traits were measured from simple interval mapping (SIM) and/or simplified composite interval mapping (sCIM) analyses performed with the software package MQTL (Tinker and Mather 1995b). The indicated corrected test statistic value (cTS) was produced by dividing the TS obtained at each locus and for each trait for both simple main effect and QTL×E effect, by the significant TS produced for each trait for both effects by analysing 1000 random permutations of the data (for experimentwise P=0.05) during SIM. Primary QTLs (P) are those obtained when peaks are significant with SIM and when sCIM peaks are also strong. All secondary QTLs (S) are QTLs only obtained with sCIM. For primary QTLs, the positions indicated corresponds to the maximum cTS obtained by sCIM analysis. The allele effects are also given (T: Tadmor; E: Er/Apm). PH: plant height, TGW: thousand-grain weight, GY: grain yield *per* plant, HI: harvest index, NFT: number of fertile tillers *per* plant, NGE: number of grains *per* ear, DAB: dry aerian biomass *per* plant, HD: heading date. [1]M95, [2]G96, [3]M97rain, [4]M97ir, [5]M99rain, [6]M99ir

Trait	Location	Chromosome	cTS (simple main effect)	cTS (QTL×E main effect)	Allele effect
PH^{all}	acl3+0	7H	1.32 (S)	1.40 (S)	1.36 (T)
	HVM54+7	2H	1.90 (P)	ns	1.81 (E)
	Bmag0136+0	3H	1.53 (P)	ns	1.46 (T)
	CDO497+0	6H	3.00 (P)	ns	2.06 (T)
NGE^{1234}	MWG595+12	3H	1.20 (P)	1.09 (S)	0.45 (T)
	MctgEaccC+4	4H	2.31 (P)	ns	0.58 (E)
NFT^{134}	Bmac0316+0	6H	ns	1.36 (S)	0.46 (E)
	BCD348B+2	6H	1.70 (P)	ns	0.90 (E)
TGW^{all}	Bmag0378+1	2H	ns	1.34 (S)	0.08 (T)
	MWG595+6	3H	ns	1.06 (S)	0.38 (E)
	HVM67+2	4H	ns	1.40 (S)	0.37 (T)
	WG983+1	1H	1.08 (P)	ns	0.66 (E)
	BCD348B+4	6H	4.22 (P)	1.01 (S)	1.37 (T)
	BCD1+10	6H	1.24 (P)	1.36 (S	0.80 (E)
	dhn1+0	5H	ns	1.09 (S)	0.52 (T)
	BCD298+0	5H	1.38 (S)	1.40 (S)	0.40 (E)
GY^{13456}	HVRCABG+10	4H	ns	1.11 (S)	0.14 (T)
	WG114+12	4H	1.50 (P)	ns	0.42 (E)
	WG889+8	5H	1.27 (S)	ns	0.40 (E)
HI^{13456}	Bmag0136+0	3H	ns	1.11 (S)	0.0022 (E)
HD^{23456}	McaaEaagB+7	7H	1.52 (S)	ns	0.49 (T)
	CDO1417+8	2H	1.09 (S)	ns	0.47 (E)
	Bmag0013+5	3H	2.14 (P)	1.69 (P)	0.65 (E)
	Bmag0223+13	5H	1.15 (S)	ns	0.52 (T)

one QTL was common to five environments on chromosome 3H, and one QTL was common to two environments on 2H. Apart from the latter QTL, Tadmor contributed a higher PH at all consistent loci. For the QTL on chromosome 2H, Er/Apm contributed a higher PH. The significance and magnitude of QTL effects also varied with environments. For example, the consistent QTL for PH on chromosome 6H was detected at a higher LOD score in M96, M97ir and M99ir than in the other environments. For NGE, the QTL accounting for the largest part of the phenotypic variation (14%) was detected in G96 on chromosome 3H. In this segment, Tadmor contributed favourable alleles for the trait. Concerning GY, QTLs were only identified in M95 and M99ir, and did not explain much of the phenotypic variation. For this trait, only Er/Apm contributed to the favourable alleles at the QTLs.

◀ **Fig. 1** Summary of QTLs obtained for agronomic traits from the study of a 167 recombinant inbred lines of the Mediterranean progeny grown in six environments: Montpellier 1995 (*1*), Granada 1996 (*2*), Mauguio 1997 under rainfed (*3*) and irrigated (*4*) conditions and Montpellier 1999 under rainfed (*5*) and irrigated (*6*) conditions. Background markers are indicated in *bold letters* on the left of chromosomes and additional markers indicated in Tables 4, 5 and 6 in *normal letters*. QTLs identified by interval mapping with MAPMAKER/QTL for each environment separately are indicated on the right of chromosomes (name of trait followed by the number corresponding to the environment where QTLs are significant). Details concerning QTLs are described in Table 4. *PH* plant height, *NGE* number of grains per ear, *NFT* number of fertile tillers, *TGW* thousand-grain weight, *DAB* dry aerian biomass, *GY* grain yield, *HI* harvest index, *HD* heading date

Consistent QTLs over environments and QTLs interacting with the environment

The software package MQTL was used to detect consistent QTLs that exhibit, or did not exhibit, QTL×E interactions in progeny that are replicated across multiple environments (Tinker and Mather 1995a, b). The analysis was first performed considering all the environments where traits were measured, and secondly with only the rainfed and irrigated environments of M97 that have presented the most significant differences between the two water conditions (Table 2). The results are presented in Tables 5 and 6 and Fig. 2.

Table 6 Primary and secondary QTLs obtained from simple interval mapping (SIM) and simplified composite interval mapping (sCIM) analyses with the software package MQTL (Tinker and Mather 1995b) considering the rainfed environment M97rain and the irrigated environment M97ir. The indicated corrected test statistic value (cTS) was produced by dividing the TS obtained at each locus and for each trait for both simple main effect and QTL×E effect, and by the significant TS produced for each trait for both effects by analysing 1000 random permutations of the data (for experimentwise P=0.05) during SIM. The primary QTLs (P) were obtained when peaks were significant with SIM and when sCIM peaks were also strong and the positions correspond to the maximum cTS obtained by sCIM analysis. The secondary QTLs (S) are QTLs only obtained with SIM or sCIM. The allele effects are also given (T: Tadmor; E: Er/Apm). PH: plant height, TGW: thousand-grain weight, GY: grain yield *per* plant, HI: harvest index, NFT: number of fertile tillers *per* plant, NGE: number of grains *per* ear, DAB: dry aerian biomass *per* plant, HD: heading date

Trait	Location	Chromosome	cTS (simple main effect)	cTS (QTL×E main effect)	Allele effect
PH	HVM54+8	2H	1.27 (P)	ns	1.54 (E)
	Bmac0067+2	3H	1.59 (P)	ns	1.61 (T)
	WG876+8	4H	ns	1.46 (S, sCIM)	0.15 (T)
	MctgEaccC+4	4H	1.09 (S, SIM)	ns	1.73 (E)
	Bmag0009+4	6H	2.21 (P)	ns	1.97 (T)
TGW	CDO1417+24	2H	ns	1.13 (S, sCIM)	0.18 (T)
	HVM67+6	4H	1.58 (S, sCIM)	ns	1.00 (T)
	Bmac0032+20	1H	1.06 (S, sCIM)	ns	0.97 (E)
	BCD348B+6	6H	3.49 (P)	ns	1.43 (T)
	CDO400+2	5H	1.83 (S, sCIM)	ns	1.01 (T)
GY	HVRCABG+10	4H	ns	1.09 (S, sCIM)	0.14 (T)
	WG114+12	4H	1.48 (P)	ns	0.42 (E)
	CDO344+6	5H	1.14 (S, sCIM)	ns	0.40 (E)
HI	Bmag0136+0	3H	1.72	ns	1.17 (E)
NFT	WG983+4	1H	ns	1.01 (S, sCIM)	0.08 (T)
	BCD348B+2	6H	1.54 (P)	ns	0.93 (E)
NGE	HVM54+2	2H	ns	1.49 (S, sCIM)	0.06 (T)
	MctgEaccC+6	4H	2.02 (P)	ns	0.60 (E)
DAB	dhn1+2	5H	1.15 (S, sCIM)	ns	1.18 (T)
HD	CDO1417+8	2H	1.34 (S, sCIM)	ns	0.58 (E)
	Bmag0013+4	3H	1.08 (S, sCIM)	ns	1.01 (T)

All environments

A total of 24 putative QTLs were identified (Table 5 and Fig. 2). Out of these, 11 were QTLs presenting only main effects: seven primary QTLs and four secondary QTLs. The primary QTLs were mapped on chromosomes 2H, 3H and 6H for PH, 4H for NGE, 6H for NFT, 1H for TGW, and 4H for GY. One secondary QTL was mapped on chromosome 5H for GY and three on chromosomes 7H, 2H and 5H for HD. For HD, one primary QTL presented both a main effect and an interaction with environment on chromosome 3H. Three primary QTLs for main effect presented secondary QTL×E interaction: on chromosome 3H for NGE and on two regions of chromosome 6H for TGW. Secondary QTLs presenting both a main effect and QTL x E interaction were identified on chromosomes 7H for PH and 5H for TGW. Finally, seven QTLs presenting only QTL×E interaction were additionally found by sCIM: on chromosome 6H for NFT, on chromosome 4H for GY, on chromosome 3H for HI and on chromosomes 2H, 3H, 4H and 5H for TGW. For the latter trait, QTLs interacting with the environment were mostly identified. Finally, regions of chromosomes 3H, 4HL and 6H presented clustered QTLs. For example, on chromosome 3H nearby Bmac0209, QTLs were identified for NGE, TGW, HI and PH (Fig. 2). Except for NFT where positive effects were provided by Er/Apm alleles for the two detected QTLs, both parental genotypes contributed positive allele effects at the loci identified.

Rainfed and irrigated environments for M97

The QTL analysis was completed using the software package MQTL to extract the consistent QTLs across the rainfed environment M97rain and the irrigated environment M97ir, and those presenting QTL x E interaction that could be due to the difference in water availability between the two environments considered (Table 6 and Fig. 2). This analysis was only done for M97 where the differences between the two water conditions were more pronounced (Tables 1 and 2). The eight primary QTLs identified presented a simple main effect. These primary QTLs were three for PH on chromosomes 2H, 3H and 6H, one for TGW on chromosome 6H, one for GY on chromosome 4H, one for HI on chromosome 3H, one for NFT on chromosome 6H and one for NGE on chromosome 4H. Numerous secondary QTLs were also obtained mostly by sCIM analysis. Eight presented main effects:

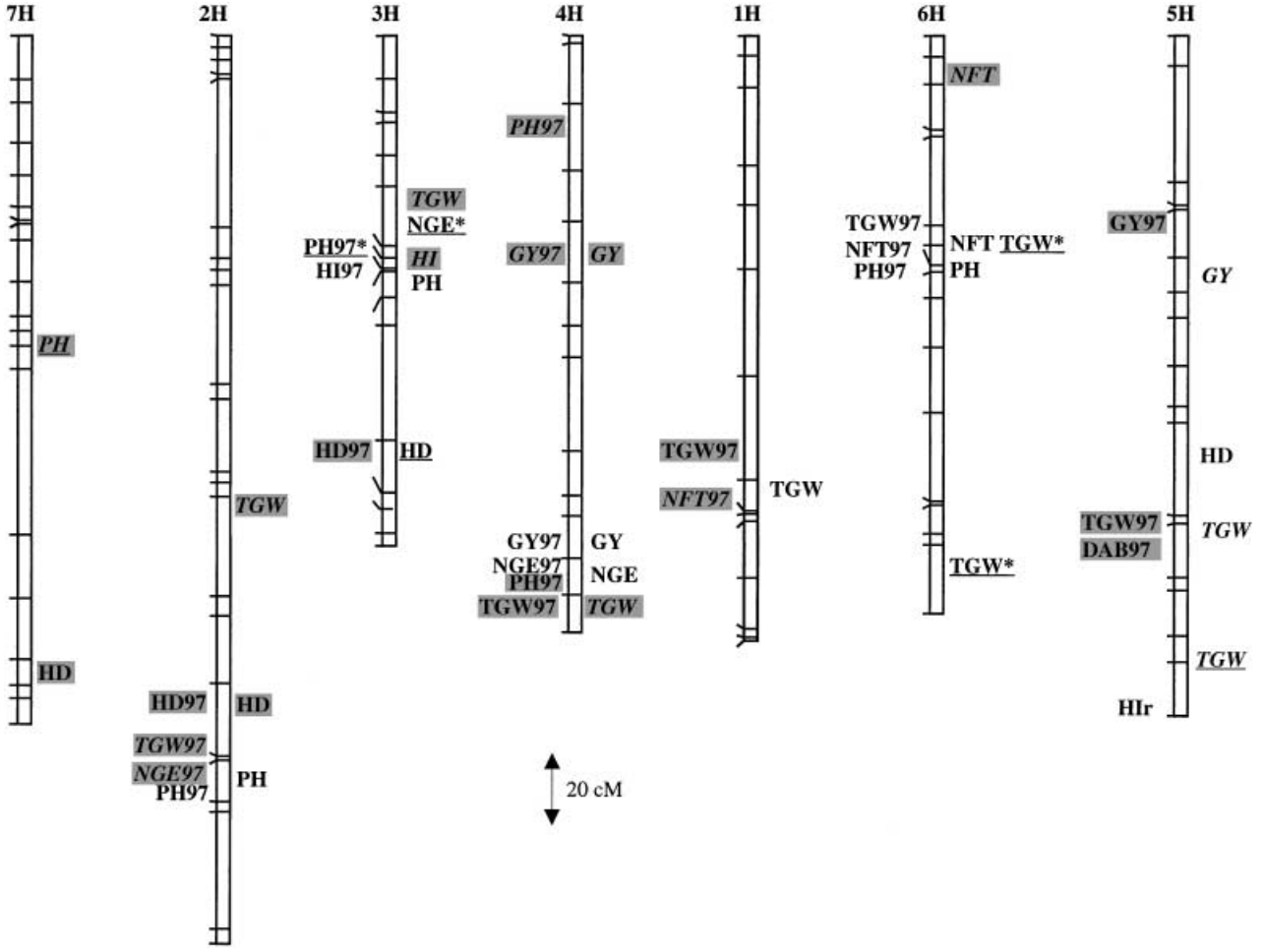

Fig. 2 Summary of QTLs identified with simple interval mapping (SIM) and/or simplified composite interval mapping (sCIM) using MQTL for agronomic traits measured in several Mediterranean environments. The QTLs identified are on the right of the chromosomes. Primary QTLs detected both by SIM and sCIM are in *black* and secondary QTLs detected by one method are in *gray*. QTLs presenting QTL×E interaction are in *italics*. QTLs presenting both effects are *underlined and additionally followed by an asterisk* when the main effect corresponds to a primary QTL and the interaction with E is detected as secondary QTL. QTLs obtained for traits measured in 1997 (M97rain and M97ir) are indicated on the left of chromosomes. Details concerning QTLs are described in Tables 5 and 6. *PH* plant height, *TGW* thousand-grain weight, *DAB* dry aerian biomass, *GY* grain yield, *HI* harvest index, *NGE* number of grains *per* ear, *NFT* number of fertile tillers, *HD* heading date

one for PH on chromosome 4H, three for TGW on chromosomes 4H, 1H and 5H, one for GY on chromosome 5H, one for DAB on chromosome 5H, and two for HD on chromosomes 2H and 3H. The five secondary QTLs presenting interaction with the environment, and thus water availability, were one for PH on chromosome 4H, one for TGW on chromosome 2H, one for GY on chromosome 4H, one for NFT on chromosome 1H and one for NGE on chromosome 2H. These secondary QTLs interacted only with the environment. It could be noted that only the Tadmor alleles conferred a positive effect when the QTLs interacted with the environment. However, these QTLs differed by their cTS: low for NFT and GY, and more consistent for PH, TGW and NGE.

Discussion

Heterogeneity between environments

The differences observed across environments for the measured traits could be attributed to environmental conditions and particularly to the climatic conditions of each environment (differences in rainfall, evaporative demand). In M97rain, the RILs presented the lowest GY, PH, DAB, NGE and NFT values. The highest values for DAB, GY and TGW were obtained in M97ir, the environment that had received the highest amount of water. In G96, the values of PH were the highest but this environment received more than 86% of the total rainfall during the vegetative-growth period (Table 1). M95 and G96 were subjected to a huge evaporative demand during the grain-filling period, more accentuated in G96, which could explained the low TGW values obtained for this environment compared to the other ones. For PH, the values were similar in M95 and M97ir even though the two environments received different amounts of wa-

ter and presented different R/ET ratios during the vegetative growth period. The differences between the two environments were then more pronounced during the grain-filling period, the plants having less water available in M95. The heterogeneity between all the environments considered have also influenced the number and location of QTLs. Indeed, numerous QTLs were identified in one particular environment such as a QTL on chromosome 7H nearby BCD1066 detected for HI only in M99rain (Table 4 and Fig. 1). However, seven QTLs were identified across several environments such as the QTL of chromosome 6H involved in the variation of plant height in all six environments. The use of markers associated to those QTLs consistent across environments are more confident and efficient for assisting selection because they were expressed whatever the conditions and represent all the environments studied. However, the identification of QTLs that seem specific to one Mediterranean environment characterised by particular climatic conditions could also be of interest for breeders. If environmental data could be used as cofactors in QTL identification models, these QTLs could indeed be used as diagnostic QTLs representative of the trait expression in this environment. This represents a new perspective in plant genetics.

Consistency of QTLs

Consistent QTLs over environments in the present study

Because of permutation-derived thresholds for SIM using MQTL, the primary QTLs detected with this software are those in which we have most confidence. QTLs found with MQTL analysis were at locations where QTLs were already identified in one or several environments separately (Table 5 and Fig. 1). This was particularly true for traits like TGW and PH. For example, the QTL consistent across environments for PH on chromosome 6H was found separately in each of the six environments. By contrast, 17 QTLs detected in only one environment were not significant with the multiple-environment QTL analysis. This was the case for the QTLs for NFT identified on chromosomes 3H and 4H in M95 and M97rain respectively. The new QTLs identified with MQTL were only secondary QTLs interacting with the environment: on chromosomes 2H (closest to Bmag0378) and 5H (closest to BCD298) for TGW, on chromosome 6H (closest to Bmac0316) for NFT and on chromosome 4H (closest to HVRCABG) for GY.

QTLs with main effects presented generally the most-consistent and greatest allele effects (Tables 5 and 6). As in Tinker et al. (1996), in some cases, only sCIM gave evidence for a QTL. sCIM can detect QTLs with smaller effects and, in most cases, the peaks were present with SIM but were not significant. This point was discussed by Tinker et al. (1996). Secondary QTLs detected by sCIM must be taken with care, particularly if cTS was not high, because of the impossibility to derive a threshold with sCIM (Tinker and Mather 1995a). However, even if it is difficult to appreciate the consistency of the QTLs presenting main effects or interaction with the environment only detected by sCIM, secondary QTLs are presented in this paper in order not to omit any putative QTLs that may be hidden by strong environmental heterogeneity between environments. Except for the primary QTL×E interaction identified for HD on chromosome 3H, all the QTLs interacting with environments were detected only by sCIM. Few primary QTLs with main effects also presented some QTL×E interaction. Tinker et al. (1996) suggested that some QTL×E interaction is always present.

Comparison with QTLs from other barley progenies

The analyses performed over environments support the presence of a QTL in the genetic background studied, but comparison with similar work in other progenies could reinforce their relevance in barley. The stability of QTLs across genetic backgrounds was tested by comparing QTLs obtained in the present study with QTLs previously identified in barley for the same traits. Numerous studies have been conducted for the identification of QTLs for GY and yield components, as well as the phenology and plant architecture in this species with various population backgrounds (2- and 6-row, spring or winter barleys) and structure (double-haploid, recombinant inbred line progenies) (Hayes et al. 1993; Pan et al. 1994; Backes et al. 1995; Thomas et al. 1995; Kjaer and Jensen, 1996; Tinker et al. 1996; Bezant et al. 1997; Qi et al. 1998; Yin et al. 1999; Zhu et al. 1999). Comparisons between the results of the present study to those already reported were obtained with the help of the genetic map of Qi et al. (1996) and the recent barley QTL summary of Hayes et al. (2000).

Even if several QTLs were found to be specific to one site or genetic background, several consistent segments emerged from this work. Spaner et al. (1999) confirmed the presence of a QTL found by Tinker et al. (1996) affecting grain yield, plant height and lodging severity on chromosome 7 (5HS) in a two-row double-haploid (DH) progeny from the cross Harrington×TR306 (H/TR). They also demonstrated that the effect of individual QTLs may be small and may vary among environments by studying 24 DH carrying Harrington alleles and 23 DH carrying TR306 alleles in eight environments of Western Canada. Concerning yield, one QTL was found for GY on the short arm of 5H near WG889 in the present study. This QTL could correspond to one QTL identified by Hayes et al. (1993) but did not seem to correspond to the one verified by Spaner et al. (1999) in 2-row barley, located at a more telomeric position. In a different genetic background, Romagosa et al. (1999) focused their efforts on four regions of the barley genome associated with differential genotypic expression for grain yield across environments from a study of the 6-row Steptoe×Morex (S/M) progeny (on chromosomes

2H, 3H, 6H and 5H). From the study of lines having alternative alleles at the putative markers, the QTL on chromosome 3 (3H) was the most important and consistent locus to determine GY across sites with the Steptoe allele being favourable. This QTL was also confirmed by Larson et al. (1996) in a backcross progeny from a cross between the same genotypes. In the present study, QTLs on chromosome 3H were also detected for several yield components such as NGE, TGW and HI nearby MWG582B (Table 5 and Fig. 1). However, these QTLs presented interaction with the environment in the Tadmor×Er/Apm genetic background. The QTL for NGE on chromosome 3H could, however, correspond to one QTL found by Bezant et al. (1997) for the same trait. This segment, together with one region of chromosome 6H nearby CDO497, controls grain yield in several studies (Hayes et al. 1993; Yin et al. 1999 for example). A consistent QTL for TGW was identified in our study in this area of chromosome 6H (Table 5 and Fig. 1). A secondary QTL for GY, identified on chromosome 4H closest to the locus HVRCABG, could correspond to a QTL identified by Kjaer and Jensen (1996) for the same trait. A QTL for TGW which mapped on the long arm of chromosome 6H (nearby BCD1) was also identified by Bezant et al. (1997). In the same segment, the authors also found a QTL for ear grain weight over 2 successive years. Comparing the two studies, a common QTL was also revealed for GY on 4HL for all environments (Table 5 and Fig. 1), the QTL found by Bezant et al. (1997) concerning plant- and plot-grain yields. Tinker et al. (1996) have identified a QTL with a main effect for GY in this area, as well as a QTL interacting with the environment for TGW. For the latter trait, a QTL interacting with the environment was also found in the present study. A QTL for NGE found in the same area was identified by Bezant et al. (1997). Another QTL interacting with the environment was common to this study and that of Tinker et al. (1996) for TGW. It was mapped on the long arm of chromosome 5H nearby *dhn1*. The other QTL (a secondary QTL) found for TGW on the same chromosome arm, but closest to BCD298, could correspond with the one identified by Bezant et al. (1997). Finally, the secondary QTL found for the same trait on chromosome 2H, near Bmag0378, could correspond to one QTL identified by Kjaer and Jensen (1996) and confirmed by Kicherer et al. (2000). It was impossible to compare QTLs for HI because no study reported QTLs for this trait.

The most consistent QTLs identified in the present study concerned plant height (PH). The one on chromosome 3H, near MWG582B, seemed not correspond to the *denso* dwarf gene mapped by Laurie et al. (1993); but, under Mediterranean conditions, Baum et al. (1996) also found a QTL near MWG577 in our segment of chromosome 3H. This QTL could also correspond to a QTL found by Qi et al. (1998). The QTL on chromosome 7H had already been detected by Tinker et al. (1996). Concerning HD, QTLs on chromosomes 7H (closest to WG380) and 2H may correspond with the ones found by Backes et al. (1995) and Hayes et al. (1993) respectively. The latter QTL was recently also detected by Kicherer et al. (2000). Finally, the QTL on chromosome 3H could correspond to one QTL identified by Pan et al. (1994), and the one on chromosome 5HL to one QTL identified by Bezant et al. (1997).

QTLs specific to the study, and differences between rainfed and irrigated conditions

QTLs only found in the present study could be specific to one environment or, when detected across environments, specific to the genetic background employed or to the Mediterranean conditions. The most confident QTLs without apparently any correspondance to other studies were mapped on chromosomes 1H and 6H (near CDO497) for TGW, on chromosome 6H for NFT and on chromosomes 2H and 6H for PH (Table 5 and Fig. 1). Out of these, only the QTL identified for PH by Baum et al. (1996), near MWG577 on chromosome 2H, could be attributed to the Mediterranean conditions. All the other QTLs were apparently already detected.

The differences between the rainfed and the irrigated environments in M97 and M99 were mostly attributable to the difference in water availability. Even though the water supplies for the irrigated environments were not very important (Table 1), the trait values and some QTLs were different between the two water treatments within each site (Tables 2 and 4). These differences were more pronounced in M97, probably because of the different climatic events but also because of the repartition of the water supply along the growth cycle that was more progressive in M97 compared to M99 (Table 2). These events were certainly concerned with the origin of the difference in the number of QTLs between each rainfed and each irrigated environment. For example, for PH, five QTLs were detected in M97ir and two QTLs in M97rain leading to a total of seven QTLs for M97. In M99, three QTLs were identified in the rainfed, compared to one QTL in the irrigated, conditions leading to a total of four QTLs in this environment for the same trait. These differences in the number of QTLs also depended on the trait considered. Indeed, conversely to PH, more QTLs were obtained in M99 for TGW compared to M97, particularly for the rainfed conditions. Such comparisons between the positions of QTLs identified for different water regimes applied during the growth cycle were also performed in corn by Ribaut et al. (1997), and these authors have also noticed some inconsistencies of the QTL positions across water regimes.

The analysis with MQTL performed for the two environments of M97, where the difference in terms of plant water availability between the rainfed and the irrigated environment was more pronounced, have also allowed us to identify QTLs that could be independent of differences in water availability and QTLs interacting with water availability (Table 6 and Fig. 2). For PH, four of the five QTLs identified with this analysis seemed not to

be dependent on the water conditions (Table 6). Otherwise, these QTLs were already detected in one or several environments (Tables 4 and 5). This was not the case with the fifth QTL mapped on chromosome 4H and interacting with water conditions. The same was observed with NGE and NFT with one QTL consistent over the water conditions and another QTL depending on water conditions. However, for NFT, the cTS of the QTL interacting with E was particularly low and must be considered with care. The QTLs found for HI, DAB and HD in M97 did not interact with water conditions. Nevertheless for HD, M97rain and M97ir values were not significantly different (Table 2). For TGW, even though no significant differences were noticed between the two water conditions, one QTL was identified as presenting an interaction with water conditions on chromosome 2H. This QTL was located in the same area of the QTL interacting with the water conditions for NGE. Otherwise, the QTL found for TGW was already identified for the rainfed conditions in M99. Finally, the three QTLs identified for GY over M97rain and M97ir were previously found in one or several environments but one of them, on chromosome 4H nearby HVRCABG, seemed to be influenced by the water conditions.

Most studies on the identification of QTLs for agronomic traits in barley were made in genotypes grown in Northern environmental conditions and studied together with malt quality. The Tadmor×Er/Apm progeny used in the present work originated from the Mediterranean basin and was dedicated to the evaluation of yield under Mediterranean conditions. The Mediterranean basin conditions contrast with those of Northern Europe and America because of different sowing dates, higher light intensity, temperatures and evaporative demand, and lower rainfalls, all of which are erratically distributed (Loss and Siddique 1994). The QTLs detected in this study were compared to the ones obtained in previous work and, even if experiments based on rows do not properly represent field conditions, a part of these QTLs were already identified. When this is the case, QTLs detected in the present work are still of interest for cereal barley breeders in the Mediterranean basin. Few QTLs could, however, be specific to the present study. The results reported here must be considered as a first step in the identification of QTLs for agronomic performance in this genetic background under Mediterranean conditions. The present study is a starting point and, in order to reinforce the validity of the detected QTLs, complementary plot experiments with the same genetic background as well as with other Mediterranean barley progenies are underway in different countries of North Africa, broadening the spectrum of the Mediterranean conditions. These experiments will allow us to more-precisely evaluate the QTL×E interactions, to confirm the consistency of QTLs found in this study and to identify QTLs for yield stability in barley in the Mediterranean basin (Forster et al. 2000). The difficulty to have stable QTLs for yield underlines the fact that the improvement of yield in Mediterranean conditions will probably come through a combination of stable QTLs involved in the expression of traits significantly correlated with yield. Comparisons between QTLs for agronomic traits and yield stability, and QTLs for adaptive traits such as osmotic adjustment, relative water content or carbon isotope discrimination, could all be conducted. This will give a more mechanistic approach of drought tolerance conciliating physiological and agronomic aspects, and will help to define genomic targets for drought tolerance improvement.

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