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ORIGINAL PAPER

Detection of QTL for yield-related traits using recombinant inbred lines derived from exotic and elite US Western Shipping melon germplasm

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Abstract The inheritance of yield-related traits in melon (*Cucumis melo* L.; $2n = 2x = 24$) is poorly understood, and the mapping of quantitative trait loci (QTL) for such traits has not been reported. Therefore, a set of 81 recombinant inbred lines (RIL) was developed from a cross between the monoecious, highly branched line USDA 846-1 and a standard vining, andromonoecious cultivar, 'Top Mark'. The RIL, parental lines, and three control cultivars ('Esteem', 'Sol Dorado', and 'Hales Best Jumbo') were grown at Hancock, WI and El Centro, CA in 2002, and evaluated for primary branch number (PB), fruit number per plant (FN), fruit weight per plant (FW), average weight per fruit (AWF), and percentage of mature fruit per plot (PMF). A 190-point genetic map was constructed using 114 RAPD, 43 SSR, 32 AFLP markers, and one phenotypic trait. Fifteen linkage groups spanned 1,116 cM with a mean marker interval of 5.9 cM. A total of 37 QTL were detected in both locations (PB = 6, FN = 9, FW = 12, AWF = 5, and PMF = 5). QTL analyses revealed four location-independent factors for PB (*pb1.1*, *pb1.2*, *pb2.3*, and *pb10.5*), five for FN (*fn1.1*, *fn1.2*, *fn1.3*, *fn2.4*, and *fn8.8*), four for FW (*fw5.8*, *fw6.10*, *fw8.11*, and *fw8.12*), two for AWF (*awf1.3* and *awf8.5*), and one for PMF (*pmf10.4*). The significant ($P \leq 0.05$) positive phenotypic correlations observed among PB, FN, and FW, and negative phenotypic correlations between PB and AWF and between FN and AWF were consistent with the genomic locations and effects (negative vs. positive) of the QTL detected. Results indicate that genes resident in highly branched melon types have potential for increasing yield in US Western Shipping type germplasm via marker-assisted selection.

Keywords *Cucumis melo* · Best linear unbiased prediction (BLUP) · Best linear unbiased estimation (BLUE) · Composite interval mapping · Epistasis · Quantitative trait loci

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Introduction

Many economically important yield and quality traits are polygenetic, and thus their inheritance is complex (Lande and Thompson 1990). Generally, selection for yield has been difficult, and has relied on the estimation of genetic parameters (e.g., variance components, heritabilities, and least number of effective factors) for strategic planning and resource allocation (Comstock 1978; Dudley and Moll 1969). Such parameters have traditionally been estimated using complex statistically based biometrical methods (Comstock and Robinson

1948; Griffing 1956; Mather 1949). Although these methodologies estimate the average properties of genes or quantitative trait loci (QTL), they do not allow for the dissection and quantification of individual genetic effects (Kearsey and Pooni 1996).

QTL analysis provides an opportunity for the genetic dissection of economically important traits (Beavis 1998; Lande and Thompson 1990). In melon (*Cucumis melo* L; $2n = 2x = 24$), only Cucumber Mosaic Virus resistance (Dogimont et al. 2000), ethylene production during fruit maturation (Perin et al. 2002a), several melon fruit quality traits (Monforte et al. 2004; Perin et al. 2002b), resistance to *Fusarium oxysporum* (Perchepied et al. 2005a), and resistance to downy and powdery mildew (Perchepied et al. 2005b) have been the focus of QTL analysis. The scarcity of QTL mapping studies in melon is due to the fact that most linkage maps in this species have been constructed using F_2 and BC_1 populations that are not amendable for extensive QTL analysis (Baudracco-Arnas and Pitrat 1996; Danin-Poleg et al. 2002; Liou et al. 1998; Oliver et al. 2001; Silberstein et al. 2003; Wang et al. 1997). Recently, however maps have been developed from immortalized melon populations such as recombinant inbred lines (RIL) (Périn et al. 2002a, b, c) and double haploid lines (DHL) (Gonzalo et al. 2005).

Few studies have investigated the genetics of yield or traits involved in yield formation (Lippert and Legg 1972; Lippert and Hall 1982) in melon (hereafter referred as yield-related traits or factors). Recently, however, F_2, F_3, and BC_1 progeny originating from a relatively wide cross in melon (US Western Shipping × highly branched exotic germplasm) were used to determine the inheritance of eight yield-related traits (Zalapa 2005; Zalapa et al. 2006). If the predictive value of QTL controlling such traits could be defined, then the efficiency of plant selection for improved yield in melon might be enhanced by marker-assisted selection (MAS). Therefore, RIL originating from F_3 progeny examined by Zalapa (2005) were created and employed herein for the construction of a molecular map to identify and localize QTL associated with yield-related traits. This study provides a first step towards the development of high-yielding US Western Shipping melon germplasm with early concentrated fruit set using MAS.

Materials and methods

Plant material

Horticulturally unique germplasm was obtained by the US Department of Agriculture (USDA) and designated CR (received in 1995 from Mr. Claude Hope, Cartago, Costa Rica). This *C. melo* ssp. *agrestis* (Naud.) Pangalo accession is early flowering, monoecious, rapid growing, indeterminate, possesses standard size internodes, abundant branching (6–12 primary branches), and bears many small fruits (up to 100 fruits/plant) 3–6 cm in diameter (Staub et al. 2004; Zalapa 2005; Zalapa et al. 2006). The architectural type of CR is unique and distinct from vining (Rosa 1924), dwarf (Denna 1962; Mohr and Knavel 1966), and bird-nest (Paris et al. 1981 1982 1984) plant habits, and thus is designated herein as a "fractal" type (Fig. 1; Prusinkiewicz and Haran 1989) because of its highly branched radiant growth habit when compared to standard vining phenotypes (i.e., 'Top Mark'). CR was crossed to an F_1 plant derived from a cross between USDA line FMR#8 × line SC#6. A monoecious, early flowering plant from this mating was selected and self-pollinated to produce an S_4 inbred line designated USDA line 846-1 (Staub et al. 2004; Zalapa et al. 2004). The monoecious, highly branched fractal USDA 846-1 (P_1) line was crossed to 'Top Mark' (P_2), which is

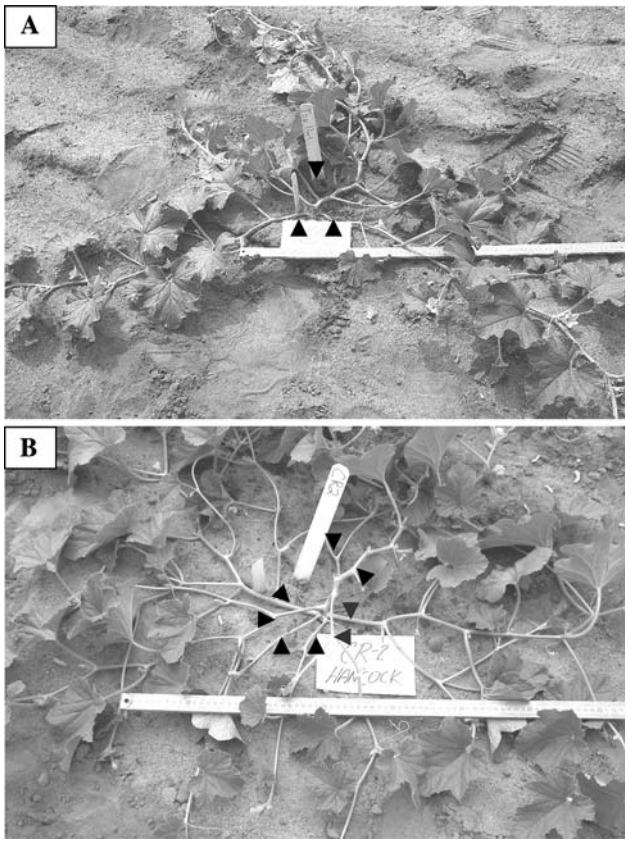

Fig. 1 Indeterminate melon (*Cucumis melo* L.) standard vining (*panel A* 'Top Mark' = 3 primary branches with sparse secondary and tertiary branching) and fractal (*panel B* CR-2 = 8 primary branches coupled with profuse secondary and tertiary branching) plant types

andromonoecious, possesses between two to four lateral branches, and produces a diffuse, distal fruiting setting habit typical of vining melon types. A single F_1 plant from this initial mating was self-pollinated to generate F_2 individuals, which were subsequently used in a single-seed descent procedure to produce 81 RILs (F_6).

Experimental design

The two parental lines, 81 RIL, and three commercial cultivars, 'Esteem' (ES) and 'Sol Dorado' (SD) (Syngenta Seeds, Gilroy, CA), and 'Hales Best Jumbo' (HB) (Excel Seeds, Chattanooga, TN) were evaluated in 2002 at the University of Wisconsin (UW) experimental farm at Hancock, WI and at the University of California Desert Research and Extension Center, El Centro, CA. These cultivars were included in the analysis since they have historical significance (HB) or are industry standard plant types for the characters evaluated.

The experimental design at both locations was a randomized complete block design (RCBD) consisting of four blocks with 10 plants per plot. 'Esteem', 'Sol Dorado', and 'Hales Best Jumbo' were used as controls to provide a benchmark for yield-related traits and fruit maturation rate comparisons. In Wisconsin, 3-week old seedlings were transplanted (June 3rd to 5th) every 0.35 m within rows on 2 m centers (14,285 plants/ha; Hancock's average season temperature, May–August = 15°C and average relative humidity = 68%). Standard cultivation practices were followed according to UWEX (2001) for Hancock's Planefield loamy sand (Typic Udipsamment) soil. In California, seeds of each entry were sown singly on raised beds (Imperial silty clay Vertic Torrifluvents soil; plant density same as in Wisconsin) from August 21 to the 23 (average season temperature in El Centro, CA, August–November = 26°C and average relative humidity = 36%). Water and fertilizer was delivered through a drip line irrigation system following cultural practices for commercial melon production in the Imperial Valley growing region.

Data collection

Sex expression (presence of staminate and/or pistillate flower parts as conditioned by the *a* locus) was evaluated per plot for each RIL 30 days after transplanting in Wisconsin and 45 days after sowing in California. The number of primary branches (PB) for each plant was counted 30 days after transplant in Wisconsin, and 45 days after sowing in California to include all branches of more than 12.5 cm in length below the fourth node. Fruit number (FN) and fruit weight (FW; kg) data (fruit at least 7.5 cm in diameter) were collected per plant 80 days after transplanting in Wisconsin and 90 days after sowing in California. The average weight per fruit (AWF; kg) was calculated for each plant by dividing the total weight per plant by the total number of fruit per plant. The percentage of mature fruit (PMF) per plot was calculated by dividing the number of mature fruit in a plot (assessed by their fruit scar, color, aroma, netting, and flesh color) at the time of harvest by the total number of fruit in that plot, and then multiplying by 100.

Analysis of variance

Location data were initially combined to perform analyses of variance (ANOVA) using the *proc mixed covtest* method *type3* procedure of SAS (SAS 1999). Additionally, variance components were estimated employing restricted maximum likelihood (REML), and each variance estimate was tested for significance using the likelihood ratio statistic (Littell et al. 1996). The linear random-effects model for such analyses was the following: $Y = \mu + L + B(L) + F + L \times F + e$; where Y is the trait, μ is the common effect, L is the location effect, $B(L)$ is the block within location effect, F is the effect of the RIL, $L \times F$ is the location × RIL interaction effect, and e is the plot-to-plot variation within the RIL. Analyses of the RIL were also performed by location for all traits.

Best linear unbiased prediction (BLUP) has been used for QTL analysis in several plant species (Borevitz et al. 2002; Bernardo 1998; Jones et. al. 2002; de Leon et al. 2005). BLUPs, standard errors (SE), and confidence intervals (95%) (CIs) were estimated for each RIL family examined using the "solution" option of the model statement of the *proc mixed covtest* procedure (SAS 1999; Bernardo 1998). The two parental inbred lines (P_1 and P_2) and the control cultivars (ES, SD, and HB) were analyzed independently using a linear mixed-effects model. The parental lines and control cultivars were considered as fixed effects, and best linear unbiased estimation (BLUE) was estimated accordingly using the "solution" option of the model statement of the *proc mixed covtest* procedure (SAS 1999). The 95% CIs of RIL BLUPs and the BLUEs of the parental lines and control cultivars were used for comparisons of genotype performance. When the BLUE of the parental lines and/or control cultivars was outside the CI limit of the BLUP of the RIL, such genotypes were considered to be significantly ($P \leq 0.05$) different from each other (de Leon et al. 2005).

In order to assess whether G × E interactions were due to trait magnitude changes between locations or

changes in the direction of the response (i.e., RIL rank changes), Spearman (rank) correlation coefficients (r_s) were calculated using RIL data for each individual trait across locations according to Yan and Rajcan (2003). When the correlation coefficient between data across locations was $r_s \leq 0.5$, G × E interactions were considered more likely to be due to RIL rank changes, and when $r_s \geq 0.5$, G × E interactions were considered more likely to be due to trait magnitude changes between locations. In order to evaluate the reliability of RIL performance across traits and locations, the percentage of RIL performance concordance for each trait across locations was calculated for the top 20 performing families (i.e., % RIL that matched in top 20 in both locations).

Phenotypic correlations

Phenotypic correlations (r; $n = 81$) between pairs of traits were calculated by location using the *proc corr spearman* procedure of SAS (1999).

Estimation of heritabilities

The broad-sense heritabilities based on RIL BLUPs (h^2_{BF}) were calculated as $h^2_{BF} = (\sigma^2_F)/\sigma^2_{PF}$; where σ^2_F and σ^2_{PF} are the variance among RIL and phenotypic variance based on RIL BLUPs, respectively. The estimate of σ^2_{PF} was calculated as $\sigma^2_F + \sigma^2_{LxF/B} + \sigma^2_{E/BL}$; where B, L, σ^2_F, σ^2_{LxF} and σ^2_E refer to the number of blocks, the number of locations, the variance among RIL, the variance due to location × RIL interactions, and the plot-to-plot variation within RIL, respectively (Falconer and Mackay 1996). The standard error of broad-sense heritabilities based on RIL BLUPs were calculated as SE $(h^2_{BF}) = [\mathrm{Var}(\sigma^2_F)]^{1/2}/\sigma^2_{PF}$.

DNA analysis

Sample preparation and DNA extraction was according to Fazio et al. (2003a). A set of heritable random amplified polymorphic DNA (RAPD) primers found to be polymorphic in diverse melon accessions (López-Sesé and Staub 2001; Staub 2001) were used to assay the RIL population. Primers (10-mer) were obtained from Operon Technologies, Alameda, CA (OP) and the University of British Columbia, Vancouver, Canada (BC). All PCR solutions were purchased from Promega (Madison, WI), and PCR reaction preparation, thermocycling, and DNA electrophoresis was performed according to Horejsi et al. (1999). RAPD markers were scored as codominant markers if the parental lines and F_1 hybrid showed codominant segregation patterns, and a RIL with both bands absent (null) was not observed. Each marker was designated by the abbreviated company name, the name of RAPD primer plus the fragment size of PCR product (e.g., OPAR1-700).

Simple sequence repeat (SSR) markers from different sources (Danin-Poleg et al. 2001; Fazio et al. 2002; Gonzalo et al. 2005; Katzir et al. 1996) were evaluated for their potential value during map construction using the RIL population. SSR PCR reaction preparation was the same as for RAPD analysis. Thermocycling conditions were previously described by Danin-Poleg et al. (2001), Fazio et al. (2002), Gonzalo et al. (2005), and Katzir et al. (1996). Marker data analyses were performed both by gel electrophoresis (on 3.5% agarose gels) using an Applied Biosystems 3700 fluorescent sequencer (POP-6 and a 50 cm array) in conjunction with Gene Scan Analysis Software version 3.1 of Applied Biosystems (Foster City, CA). SSR markers that had the expected base pair length were labeled according to the marker designations given by the initial reference source. SSR markers that amplified only one parental genotype in both gel electrophoresis and GeneScan analyses were scored as dominant markers and designated (Do) plus the name of the original SSR primer pair combinations and the base pairs fragment size (e.g., DoTJ10-120).

Amplified fragment length polymorphism (AFLP) analysis was according to the methodologies described by Vos et al. (1995) and the AFLP protocol of Berres (http://www.ravel.zoology.wisc.edu/sgaap/AFLP_html/AFLP.htm) with the modifications described by Sun (2005) and Sun et al. (2006). AFLP markers were designated as specified by Vos et al. (1995), where designations were derived from the restriction enzymes used to produce the DNA fragments (i.e., *EcoRI* and *MseI*), their specific primer combinations, and the size of the polymorphic band given in base pairs (e.g., E19M47-74).

Linkage map construction

Prior to linkage analysis, segregation ratio distortion tests were performed in JoinMap 3.0 (Van Ooijen and Voorrips 2001) as assessments of predicted dominant and codominant marker ratios (1:1 for RIL). Markers with chi-square P-values greater than 0.01 were employed for linkage analysis (Marques et al. 1998; Vuylsteke et al. 1999) using MapMaker/EXP 3.0 (Lander et al. 1987). One hundred and ninety-eight markers and one phenotypic marker (a = andromonoecious) were used in linkage analysis from which 190 markers were assigned to 15 linkage groups (LG) using LOD thresholds of 5.0 (173 markers) and 3.0 (16 markers and the a locus) and a recombination frequency value of 0.35

(Fig. 2). The recombination fraction frequencies were converted to map distances using the Kosambi mapping function by employing the *centiMorgan function* command, and the *three point* command was utilized for multi-point analysis. For each linkage group, the *order* command with a LOD of 3.0 and five specified parameters was used to choose a seed order (order with the highest log-likelihood ratio) of highly informative markers. The remaining markers from each linkage group were manually added sequentially to the seed order using the *try* command. During each iteration, a marker with the most likely position was placed, and the map order was re-tested using the *ripple* command.

QTL mapping

Composite interval mapping (Zeng 1993, 1994) was performed for all traits using Windows QTL Cartographer 2.0 (Wang et al. 2004). A stepwise forward regression procedure employing a walking speed of 1 cM, a window size of 5 cM, and the inclusion of up to 15 maximum background marker loci were used to eliminate background effects inherent among linked multiple QTL. A QTL was declared significant when its LOD score was higher than the LOD threshold calculated using 1,000 permutations (Churchill and Doerge 1994; ≥2.8 LOD for all traits) for an experimental-wise (type I) error rate of $P = 0.05$ or when, in at least two locations, the LOD was higher than 2.5.

Two-dimensional genome scans for detection of epistatic interactions were performed by employing the Haley–Knott protocol (HK; Haley and Knott 1992) in R/qtl (Broman et al. 2003), which identifies putative epistatic interactions by calculating digenic joint and interaction LOD scores, but it does not provide estimates of genetic effects and associated phenotypic variation (R^2 %). The multi-point genotype probabilities for the HK analyses used in the two-QTL model were calculated using the *calc.genoprob* command with a step interval of step = 2 cM and an error probability of 0.01. The LOD thresholds for the two-QTL model analysis were determined by 1,000 permutations (≥6.0 LOD for all traits or when, in at least two locations, the LOD was higher than 5.0), which represent the range of the 95% quartile of 1,000 permutations.

Results

Analysis of variance

The RIL used in this study were phenotypically diverse in plant habit, fruit development, and maturity characteristics (Tables 1, 2, 3), and all phenotypic distributions were normally distributed (data not presented; Zalapa 2005). The *type3* analysis of variance and the likelihood ratio tests of the variance component analyses indicated the existence of significant differences ($P \leq 0.05$) among RIL for all traits. Similarly, variance component analyses revealed significant ($P \leq 0.05$) location and location × family interactions effects for all traits. Significant ($P \leq 0.01$) Spearman (rank) correlations (r_s) between environments indicated, however, that the interactions between family and environment for all traits were mainly due to changes in trait magnitude in the locations examined [r_s for locations (CA vs. WI) = 0.73 (PB), 0.59 (FN), 0,48 (FW), 0.74 (AWF), and 0.47 (PMF)]. Although, location × family interactions were significant for all traits, trait performance concordance for the top 20 highest performing families was relatively high (50–70 %; Tables 1, 2) for all traits, except for PMF (35 %). Given the significant location and/or genotype × location interactions detected for all traits, data are hereafter presented by location.

Parent and RIL data

Yield and fruiting characteristics of the USDA 846-1 (P_1), 'Top Mark' (P_2), 'Esteem' (ES), 'Sol Dorado' (SD), 'Hales Best Jumbo' (HB) varied dramatically. BLUPs (81 RIL overall) and BLUEs (P_1, P_2, and controls), and their associated SE, and CIs, for PB, FN, FW, AWF, and PMF are given by location in Table 3. For all traits at least one parent was significantly ($P \leq 0.05$) different than the average of the RIL population (BLUE vs. BLUP C.I. comparisons) indicating that the parental performance deviated from the population average (BLUP). Differences in performance were detected (BLUE vs. BLUP CIs comparisons) for all traits among highly branched fractal versus vining plant types (i.e., P_2/RIL and controls vs. P_1/RIL) at both locations. Individual RIL were observed that transgressed the performance of either parent or control cultivar for all traits (data not presented; Zalapa 2005). The BLUE of P_1 for PB, FN, and FW was consistently higher ($P \leq 0.05$) than the BLUE of P_2 and the BLUP of all RIL taken collectively, and the fruit development (i.e., FN, FW, and AWF) of P_1 was comparable to the control cultivars. While PB remained comparatively constant across locations (4.1, CA and 4.3, WI), FN (4.3, CA and 1.9, WI) and FW (1.9 kg, CA and 1.0 kg, WI) were higher in California than in Wisconsin. AWF was lower in California (0.48 kg) than in Wisconsin (0.56 kg).

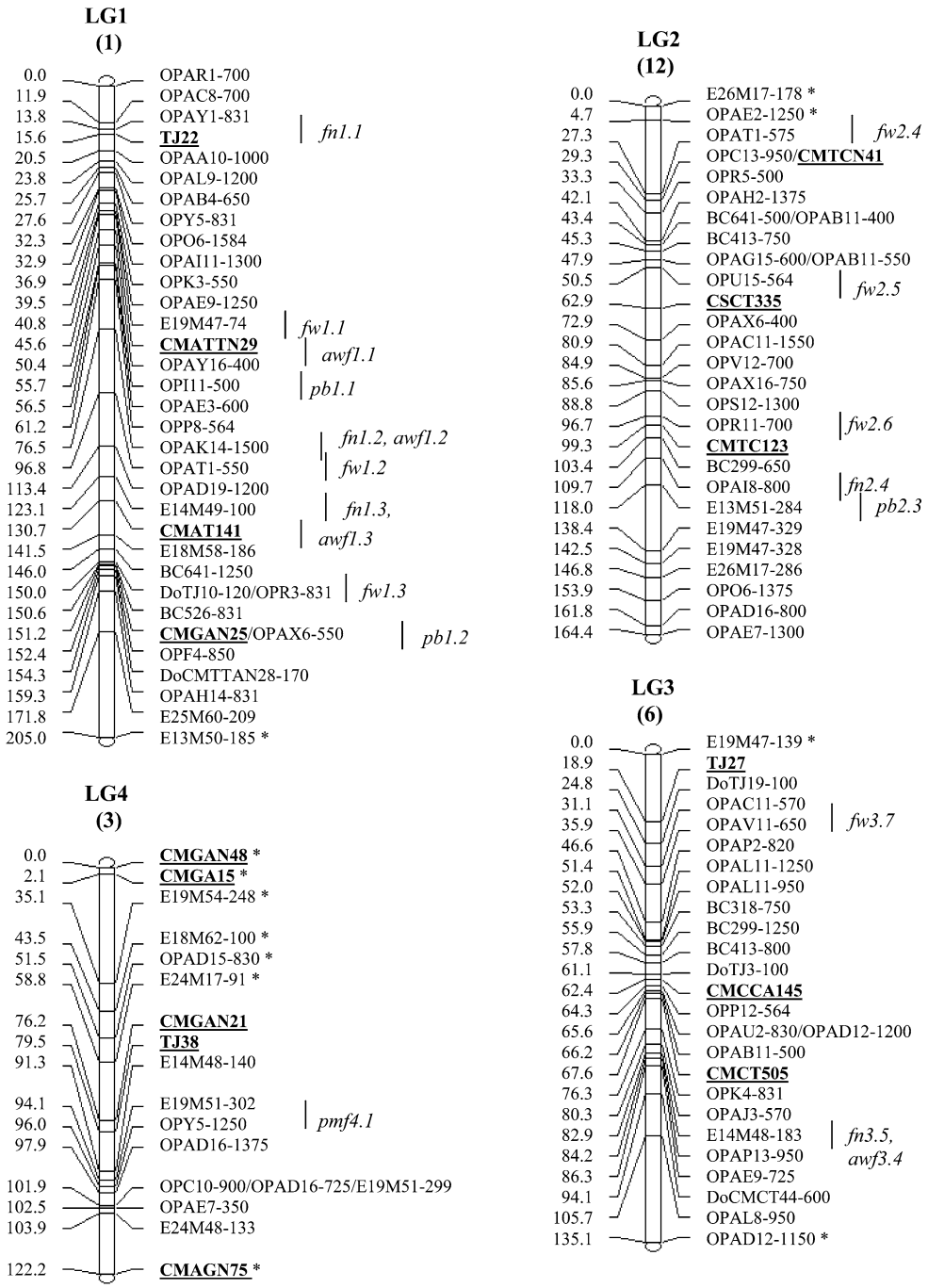

Fig. 2 Linkage map[1] and locations of quantitative trait loci associated with yield-related traits based on 81 melon (*Cucumis melo* L.) recombinant inbred lines derived from a cross of USDA 846-1 × 'Top Mark'. [1]Linkage groups designated LG followed by the linkage group number (e.g., LG1), and numbers inside parenthesis (1–12) correspond to linkage groups according to Oliver et al. (2001) and Gonzalo et al. (2005). *Underlined markers* are SSR markers from Katzir el al. (1996), Danin-Poleg et al. (2001), Fazio et al. (2002), Gonzalo et al. (2005), and Perin et al. (2002c)

Phenotypic correlations

Significant ($P \leq 0.05$) phenotypic correlations were detected between yield-related traits (Table 4). Primary branch was positively correlated with FN ($r = 0.27$, CA; $r = 0.55$, WI), FW ($r = 0.22$, CA; $r = 0.19$, WI), and PMF ($r = 0.23$, CA), and negatively correlated with AWF ($r = -0.32$, CA; $r = -0.32$, WI). Fruit number was positively correlated with FW ($r = 0.41$, WI) and negatively correlated with AWF ($r = -0.69$,

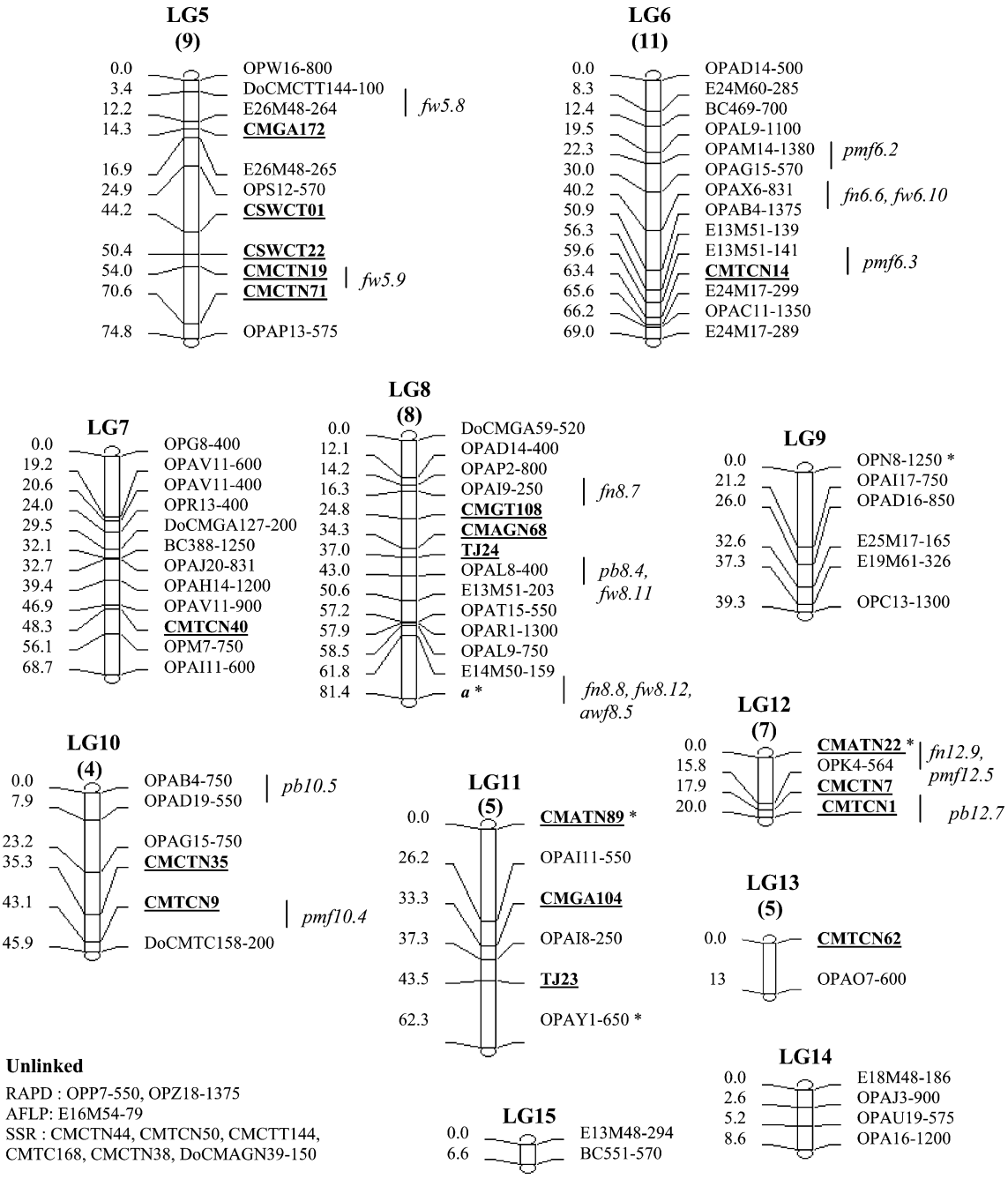

Fig. 2 continued

CA; $r = -0.51$, WI). Fruit weight was positively correlated with AWF ($r = 0.64$, CA; $r = 0.51$, WI) and PMF ($r = 0.43$, CA; $r = 0.42$, WI), and AWF was positively correlated with PMF ($r = 0.30$, WI).

Heritabilities estimates

Broad-sense heritabilities (h^2_B) for PB, FN, FW, AWF, and PMF ranged from 0.55 to 0.85 (Tables 1, 2).

Linkage analysis

Linkage analysis employing 199 markers (116 RAPD, 49 SSR, 33 AFLP, and one phenotypic marker) resulted in a genetic melon map consisting of 15 linkage groups (LG1 to LG15; 173 markers assigned at 5.0 LOD and 17 at 3.0 LOD; Fig. 2). This map spans 1,116 cM consisting of 190 markers (114 RAPD, 43 SSR, 32 AFLP, and *a* locus), and nine unlinked

Table 1 Analysis of variance, estimates of variance components, broad-sense heritabilities, and Spearman correlation (rank) coefficients (r_s) between locations for primary branch number, and fruit number and weight (kg) per plant based on 81 melon (*Cucumis melo* L.) recombinant inbred lines derived from a cross of USDA 846-1 (P_1) × 'Top Mark' (P_2) grown at El Centro, CA and Hancock, WI in 2002

Source of variation	Primary branch number (PB)		Fruit number per plant (FN)		Fruit weight per plant (kg; FW)	
	df	MS	*df*	MS	*df*	MS
Location [L]	1	7.88 n.s.	1	903.78**	1	133.58**
Block (Location) [B(L)]	6	4.35**	6	3.77**	6	0.86**
Family [F]	80	2.65**	80	4.71**	80	0.65**
Family × Location [F × L]	80	0.44**	80	1.39**	80	0.29**
Family × Block (Location) [F × B(L)]	478	0.27	472	0.35	472	0.07
Total	645		639		639	

Source of variation	Variance component	Percent of total [a]	Variance component	Percent of total	Variance component	Percent of total
Location [L]	0.01 ± 0.04 n.s.	1.6	2.82 ± 4.01 n.s.	72.5	0.42 ± 0.59 n.s.	69.6
Block (Location) [B(L)]	0.05 ± 0.03 n.s.	7.8	0.04 ± 0.03 n.s.	1.1	0.01 ± 0.01 n.s	1.7
Family [F]	0.28 ± 0.05**	42.7	0.42 ± 0.10**	10.7	0.05 ± 0.01**	7.6
Family × Location [F × L]	0.04 ± 0.02**	6.5	0.26 ± 0.06**	6.8	0.06 ± 0.01**	9.5
Family × Block (Location) [F × B(L)]	0.27 ± 0.02**	41.4	0.35 ± 0.02**	8.9	0.07 ± 0.00**	11.7
Total	0.65	100.0	3.89	100.0	0.60	100.0
h^2_{BF}	0.84 ± 0.15		0.70 ± 0.17		0.55 ± 0.19	
r_s	0.73**		0.59**		0.48**	
Top 20 RIL concordance (%) [b]	70		50		55	

df degrees of freedom, *MS* mean squares

*,**, n.s. indicates that the effect is significant at $P \leq 0.05$, $P \leq 0.01$, and not significant, respectively

[a] Percent of variance component contribution to the total variance

[b] Top 20 RIL (%) = RIL performance concordance (i.e., % RIL that matched in top 20 in both locations)

markers (six SSR, two RAPD, and one AFLP). While the mean marker interval was 5.9 cM, the largest interval between any two markers was 33.2 cM (E25M60-209 and E13M50-185; LG1). Four relatively small linkage groups were identified spanning 20 (LG12), 13 (LG13), 9 (LG14), and 7 (LG15) cM. Eleven linkage groups, LG1 to LG11, spanned 205, 164, 135, 122, 75, 69, 69, 81, 39, 46, and 62 cM, respectively.

Two RAPD markers (OPP7-550 and OPZ18-1375) remained unlinked and 114 were distributed in 15 linkage groups with four possessing codominant markers (OPAT1-550, LG1; OPAB4-1375, LG6; OPA16-850, LG9; OPAI8-250, LG11; Fig. 2). Similarly, one AFLP remained unlinked, and 32 were evenly distributed in 10 linkage groups. Thirty-seven SSR primer pairs amplified a single polymorphic codominant locus, two (CMCTN44 and CMCTT144) amplified one codominant and one dominant polymorphic loci each, and eight (TJ3, TJ19, TJ10, CMGA59, CMTTAN28, CMGA127, CMTC158, and CMAGN39) amplified one dominant polymorphic loci each. Thus, a total of 39 codominant and ten dominant polymorphic SSR loci were used for linkage analysis. The molecular weight of the 39 codominant SSR loci were within the expected range previously described (Danin-Poleg et al. 2001; Fazio et al. 2002; Gonzalo et al. 2005; Katzir et al. 1996), and the ten dominant SSR markers were confirmed by gel electrophoresis and GeneScan analyses. Thirty-four of the codominant markers were distributed in twelve linkage groups (LG1 = 4, LG2 = 3; LG3 = 3, LG4 = 5, LG5 = 5, LG6 = 1, LG7 = 1, LG8 = 3, LG10 = 2, LG11 = 3, LG12 = 3, and LG13 = 1), and five were unlinked (CMCTN44, CMTCN50, CMCTT144, CMTC168, and CMCTN38).

QTL mapping

Thirty-seven QTL were detected in both locations (PB = 6, FN = 9, FW = 12, AWF = 5, and PMF = 5; Table 5), and were distributed across 9 linkage groups (LG1 = 11, LG2 = 5, LG3 = 3, LG4 = 1, LG5 = 2, LG6 = 4, LG8 = 6, LG10 = 2, and LG12 = 3). Sixteen (43%) of these QTL were detected consistently across locations. Four QTL were consistently detected for PB (*pb1.1*, *pb1.2*, *pb2.3*, and *pb10.5*), five for FN (*fn1.1*, *fn1.2, fn1.3*, *fn2.4* and *fn8.8*), four for FW (*fw5.8*, *fw6.10*, *fw8.11*, and *fw8.12*), and two for AWF (*awf1.3* and *awf8.5*). While, the proportion of the phenotypic variance explained by single QTL (R^2) ranged from

Table 2 Analysis of variance, estimates of variance components, broad-sense heritabilities, and Spearman correlation (rank) coefficients (r_s) between locations for average weight per fruit (kg) and percentage mature fruit per plot based on 81 melon (*Cucumis melo* L.) recombinant inbred lines derived from a cross of USDA 846-1 (P_1) × 'Top Mark' (P_2) grown at El Centro, CA and Hancock, WI in 2002

Source of variation	Average weight per fruit (kg; AWF)		Percentage mature fruit per plot (PMF)	
	df	MS	*df*	MS
Location [L]	1	1.06**	1	83437.00**
Block (Location) [B(L)]	6	0.01*	6	1641.88**
Family [F]	80	0.18**	80	1039.76**
Family × Location [F × L]	80	0.03**	80	369.40**
Family × Block (Location) [F × B(L)]	472	0.01	472	138.90
Total	639		639	

Source of variation	Variance component	Percent of total[a]	Variance component	Percent of total
Location [L]	0.0032 ± 0.0047 n.s.	9.6	254.11 ± 367.60 n.s.	45.9
Block (Location) [B(L)]	0.0001 ± 0.0001 n.s.	0.2	18.66 ± 11.77 n.s.	3.4
Family [F]	0.0190 ± 0.0036**	56.6	84.31 ± 21.96**	15.2
Family × Location [F × L]	0.0052 ± 0.0011*	15.5	58.16 ± 14.88**	10.5
Family × Block (Location) [F × B(L)]	0.0061 ± 0.0004**	18.1	138.82 ± 9.01**	25.1
Total	0.0336	100.0	554.06	100.0
h^2_{BF}	0.85 ± 0.16		0.64 ± 0.16	
r_s	0.74**		0.47**	
Top 20 RIL concordance (%)[5]	70		35	

df degrees of freedom, *MS* mean squares

*,**, n.s. indicates that the effect is significant at $P \leq 0.05$, $P \leq 0.01$, and not significant, respectively

[a] Percent of variance component contribution to the total variance

[b] Top 20 RIL (%) = RIL performance concordance (i.e., % RIL that matched in top 20 in both locations)

Table 3 Best linear unbiased estimates (BLUE) of melon (*Cucumis melo* L.) line USDA 846-1 (P_1), 'Top Mark' (P_2), 'Esteem' (ES), 'Sol Dorado' (SD), and 'Hales Best Jumbo' (HB), and best linear unbiased predictions (BLUP) of a population of 81 recombinant inbred lines from a cross of $P_1 \times P_2$, and confidence intervals (CI) for five yield-related traits based on plants grown at Hancock, Wisconsin and El Centro, CA in 2002

Trait	BLUE					BLUP	CI (95%)	
	P_1	P_2	ES	SD	HB	±SE	Lower	Upper
Hancock								
Primary branch number (PB)	5.33*	3.45*	4.25 n.s.	3.75*	3.63*	4.30 ± 0.11	3.96	4.64
Fruit number/plant (FN)	2.33*	2.13 n.s.	1.78 n.s.	2.40*	1.78 n.s.	1.92 ± 0.0	1.64	2.20
Fruit weight/plant (kg; FW)	1.35*	1.22*	1.62*	1.38*	1.66*	1.01 ± 0.03	0.90	1.12
Average weight/fruit (kg; AWF)	0.58 n.s.	0.58 n.s.	0.93*	0.60 n.s.	0.93*	0.56 ± 0.02	0.50	0.62
Percentage of mature fruit/plot (PMF)	88.75*	87.50*	88.75*	76.25*	92.50*	60.06 ± 2.01	53.67	66.46
El Centro								
Primary branch number (PB)	5.70*	3.58*	2.96*	3.23*	3.10*	4.08 ± 0.15	3.59	4.57
Fruit number/plant (FN)	5.55*	3.86 n.s.	4.27 n.s.	3.47 n.s.	2.62 n.s.	4.30 ± 0.18	3.72	4.88
Fruit weight/plant (kg; FW)	2.55*	2.00 n.s.	2.94*	2.41*	2.14 n.s.	1.93 ± 0.08	1.66	2.19
Average weight/fruit (kg; AWF)	0.47 n.s.	0.52 n.s.	0.74*	0.70*	0.81*	0.48 ± 0.02	0.42	0.53
Percentage of mature fruit/plot (PMF)	87.50 n.s.	88.75 n.s.	92.50 n.s.	100.00*	97.52*	82.86 ± 3.11	72.96	92.77

SE standard error of the estimate

* Significantly different ($P \leq 0.05$) from the average of the RIL when values were outside the CI limit of the RIL population BLUPs; n.s. The BLUEs of the a parental line, their hybrid, and/or 'Hales Best Jumbo' considered not significantly different ($P \geq 0.05$) from the average of the RIL when values were within the C.I. limit of the RIL population BLUPs

4% (*fn1.1*) to 43% (*awf8.5*), major QTL ($R^2 \geq 20\%$) were detected for PB (*pb1.1*), FN (*fn2.4*), FW (*fw5.8*), and AWF (*awf8.5*). The direction of additive effects of QTL was consistent across locations, and both parental lines contributed horticulturally desirable alleles for all traits. Line USDA 846-1 contributed alleles that were

Table 4 Phenotypic correlations among yield components in 81 melon (*Cucumis melo* L.) recombinant inbred lines (RIL) derived from a cross between USDA 846-1 (P_1) and "Top-Mark" (P_2) evaluated at Hancock, Wisconsin (above diagonal) and El Centro, CA (below diagonal) in 2002

Trait	Primary branch number (PB)	Fruit number per plant (FN)	Fruit weight per plant (kg; FW)	Average weight per fruit (kg; AWF)	Percentage of mature fruit per plot (PMF)
PB	–	0.55***	0.19*	−0.32***	0.13 n.s.
FN	0.27***	–	0.41***	−0.51***	0.40***
FW	0.22*	0.04 n.s.	–	0.51***	0.42***
AWF	−0.32***	−0.69***	0.64***	–	0.03 n.s.
PMF	0.23*	0.00 n.s	0.43***	0.30***	–

n.s., *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, and 0.001

associated with higher values (i.e., improved performance) for most the traits examined (*pb1.1*, *pb1.2*, *pb12.7*, *fn1.1*, *fn1.2, fn1.3*, *fn2.4, fn8.7, fw2.5, fw2.6, fw5.9, fw8.12, awf3.4, awf8.5*, and *pmf10.4*).

Two-dimensional epistasis genome scans

The presence of over 100 pairs of putative QTL possessing joint-QTL epistatic and interaction-QTL epistatic effects were detected (data not presented; Zalapa 2005). For traits for which additive effects are important (Zalapa 2005; Zalapa et al. 2006), only joint-QTL epistatic effects were detected, whereas when traits were conditioned by non-additive effects both joint/interaction-QTL epistatic effects were identified (Table 6). A number of QTL interactions were consistent across environments (5–12 per trait) of which some of the most interesting are presented in Table 6.

Discussion

Empirical estimates of genetic parameters of yield-related traits in melon are scarce (Lippert and Legg 1972; Lippert and Hall 1982), and their inheritance is complex (Zalapa et al. 2006). Thus, breeding to increase yield in melon will likely require the implementation of complicated phenotypic selection strategies. These strategies might be augmented by QTL analysis of yield-related traits to facilitate MAS for the introgression of horticulturally preferred alleles into elite lines. This is the first report of QTL mapping analysis for yield-related traits in melon where correlative and putative epistatic effects are identified and estimated. Thus, it represents the initial steps required for the implementation of MAS for the introgression of a unique, fractal growth habit (Fig. 1) into commercial germplasm.

A saturated melon genetic map has been estimated to have a total length of 1,500–2,000 cM distributed across 12 linkage groups (Baudracco-Arnas and Pitrat 1996; Perin et al. 2000). However, most published melon maps define more linkage groups than the basic chromosome number for this species (Baudracco-Arnas and Pitrat 1996; Danin-Poleg et al. 2002; Liou et al. 1998; Silberstein et al. 2003; Wang et al. 1997). We describe a relatively unsaturated 190-point linkage map consisting of a preponderance of dominant markers (~60%). Although the use of RAPD markers in genetic analysis has disadvantages (Staub 1996a, b; Staub et al. 2007), the markers mapped herein segregated predictably in a diverse array of F_2 populations (Staub 2001) and have proven valuable in diversity analyses (López-Sesé and Staub 2001; López-Sesé et al. 2002 2003). Moreover, their map placement was based on relatively stringent mapping criteria (linkage assignment at 5.0 LOD for 109 out of 114 markers), and they are currently being converted to SCAR markers.

Dominant marker maps tend to over-estimate the total linkage group length (particularly for F_2 and BC progenies), even in RIL populations where map length is often comparatively shorter than other mapping populations (Mackay 2001; Perin et al. 2000; Staub et al. 1996a). In order to provide useful information about the quality of the RIL population used herein, 39 codominant SSR loci were employed to estimate residual heterozygosity, which mirrored theoretical expectations (average ~4.0%; data not presented). Nevertheless, increasing the experimental population size and continued incorporation of additional markers (preferably codominant markers at <5 cM) will be necessary in this mapping population to reduce sample variance (i.e., detect rare recombination events) and increase map saturation (Liu 1998a,b). Deployment of such strategies will likely allow for a reduction in linkage group length, and the merging of small linkage groups defined in the map presented herein (Fig. 2), resulting in a characterization of the expected 12 linkage groups (Danin-Poleg et al. 2000).

The addition of SSR markers common to other maps has allowed for syntenic comparisons between

Table 5 Linkage group (LG) positions of quantitative trait loci (QTL) along with their associated logarithm of odds (LOD), percentage of phenotypic variation (R^2), and additive effect for yield components based on a population of 81 recombinant inbred lines derived from a cross of melon (*Cucumis melo* L.) line USDA 846-1 × 'Top Mark' evaluated in El Centro, CA and Hancock, WI in 2002

Trait	Linkage group	QTL[a]	Trial location	Position (cM)	Nearest marker locus[b]	LOD	R^2 (%)	Additive effect[c]
PB	LG1	*pb1.1*	WI	56	OPI11-500	5.02	0.09	0.31
	LG1	*pb1.1*	CA	57	OPAE3-600	8.84	0.2	0.25
	LG1	*pb1.2*	CA	151	CMGAN25	6.13	0.13	0.2
	LG1	*pb1.2*	WI	152	OPF4-850	7.43	0.14	0.2
	LG2	*pb2.3*	WI	123	E13M51-284	6.56	0.18	−0.27
	LG2	*pb2.3*	CA	126	E13M51-284	2.56	0.08	−0.16
	LG8	*pb8.4*	WI	43	OPAL8-400	3.22	0.05	−0.13
	LG10	*pb10.5*	CA	0	OPAB4-750	2.88	0.06	−0.13
	LG10	*pb10.5*	WI	5	OPAD19-550	3.16	0.06	−0.13
	LG12	*pb12.6*	CA	20	CMCTN1	3.86	0.08	0.15
Total R^2 (%)	CA 0.55	WI 0.52						
FN	LG1	*fn1.1*	CA	12	OPAC8-700	3.09	0.04	0.24
	LG1	*fn1.1*	WI	17	TJ22	6.12	0.09	0.18
	LG1	*fn1.2*	WI	70	OPAK14-1500	2.62	0.05	0.13
	LG1	*fn1.2*	CA	70	OPAK14-1500	2.83	0.06	0.28
	LG1	*fn1.3*	WI	122	E14M49-100	9.92	0.17	0.22
	LG1	*fn1.3*	CA	123	E14M49-100	7.80	0.12	0.45
FN	LG2	*fn2.4*	WI	103	BC299-650	3.56	0.05	0.19
	LG2	*fn2.4*	CA	110	OPAI8-800	11.86	0.21	0.55
	LG3	*fn3.5*	WI	83	E14M48-183	4.56	0.06	−0.13
	LG6	*fn6.6*	WI	30	OPAG15-570	3.18	0.04	−0.11
	LG8	*fn8.7*	WI	18	OPAI9-250	3.52	0.07	0.59
	LG8	*fn8.8*	WI	81	*a*	6.60	0.10	−0.18
	LG8	*fn8.8*	CA	81	*a*	9.60	0.16	−0.45
	LG12	*fn12.9*	WI	0	CMATN22	4.53	0.06	−0.13
Total R^2 (%)	CA 0.59	WI 0.69						
FW	LG1	*fw1.1*	CA	41	E19M47-74	5.02	0.06	−0.12
	LG1	*fw1.2*	WI	94	OPAT1-550	3.59	0.07	−0.06
	LG1	*fw1.3*	CA	150	OPR3-831	4.23	0.07	−0.12
	LG2	*fw2.4*	WI	27	OPAT1-575	4.68	0.07	−0.06
	LG2	*fw2.5*	WI	52	OPU15-564	3.91	0.07	0.07
	LG2	*fw2.6*	CA	96	OPR11-700	9.52	0.15	0.42
	LG3	*fw3.7*	WI	36	OPAV11-650	7.92	0.14	−0.16
	LG5	*fw5.8*	WI	4	DoCMCTT144-100	5.16	0.09	−0.07
	LG5	*fw5.8*	CA	12	E26M48-264	12.53	0.20	−0.18
	LG5	*fw5.9*	WI	71	CMCTN71	3.68	0.06	0.05
FW	LG6	*fw6.10*	WI	30	OPAG15-570	4.04	0.06	−0.06
	LG6	*fw6.10*	CA	36	OPAX6-831	5.40	0.08	−0.11
	LG8	*fw8.11*	WI	43	OPAL8-400	6.55	0.11	−0.09
	LG8	*fw8.11*	CA	43	OPAL8-400	4.56	0.06	−0.10
	LG8	*fw8.12*	WI	67	E14M50-159	4.29	0.11	0.09
	LG8	*fw8.12*	CA	81	*a*	8.82	0.14	0.16
Total R^2 (%)	CA 0.76	WI 0.78						
AWF	LG1	*awf1.1*	CA	47	OPAY16-400	7.23	0.17	−0.06
	LG1	*awf1.2*	WI	60	OPP8-564	5.49	0.11	−0.06
	LG1	*awf1.3*	CA	127	CMAT141	6.38	0.14	−0.06
	LG1	*awf1.3*	WI	131	CMAT141	8.82	0.18	−0.07
	LG3	*awf3.4*	WI	83	E14M48-183	3.88	0.07	0.08
	LG8	*awf8.5*	WI	79	*a*	8.36	0.18	0.07
	LG8	*awf8.5*	CA	81	*a*	14.88	0.43	0.1
Total R^2 (%)	CA 0.74	WI 0.54						
PMF	LG4	*pmf4.1*	CA	96	OPY5-1250	3.44	0.08	−2.69
	LG6	*pmf6.2*	CA	22	OPAM14-1380	4.02	0.1	−2.99
	LG6	*pmf6.3*	WI	60	E13M51-141	4.55	0.12	−4.74
	LG10	*pmf10.4*	WI	45	DoCMTC158-200	4.63	0.13	6.67

Table 5 continued

Trait	Linkage group	QTL[a]	Trial location	Position (cM)	Nearest marker locus[b]	LOD	R^2 (%)	Additive effect[c]
	LG10	*pmf10.4*	CA	43	CMTCN9	2.98	0.07	2.36
	LG12	*pmf12.5*	WI	0	CMATN22	4.93	0.13	−4.68
Total R^2 (%)	CA 0.25	WI 0.38						

PB primary branch number, *FN* fruit number/plot, *FW* fruit weight/plot, *AWF* average weight/fruit, *PMF* percentage of mature fruit/plot

[a] QTL designated by abbreviated trait name, linkage group number, and QTL number

[b] Nearest marker to peak of the detected QTL

[c] Additive effect as obtained from a composite interval mapping (CIM) model resident in QTL cartographer (Wang et al. 2004)

Table 6 Epistasis detected among yield components QTL in melon (*Cucumis melo* L.) as estimated from the analysis of recombinant inbred lines (RIL) derived from a cross between USDA 846-1 and "Top Mark" evaluated at Hancock, Wisconsin and El Centro, CA in 2002

Digenic epistasis			LOD scores[a]		
Trait	Site	Position (LG:cM)[b]	Joint	Interaction	Nearest markers
PB	WI	LG1:154/LG8:42	10.67	n.s.[c]	LG1:CMGAN25/LG8:OPAL8-400
	CA	LG1:156/LG8:42	8.42	n.s.	LG1:OPF4-850/LG8:OPAL8-400
FN	WI	LG2:98/LG8:78	6.7	n.s.	LG2:CMTC123/LG8: *a*
	CA	LG2:98/LG8:80	9.00	n.s.	LG2:CMTC123/LG8: *a*
FW	WI	LG2:30/LG10:0	7.15	n.s.	LG2:CMTCN41/LG10:OPAB4-750
	CA	LG2:30/LG10:8	7.23	6.31	LG2:CMTCN41/LG10: OPAD19-550
AWF	WI	LG1:82/LG8:80	12.21	8.6	LG1:OPAK14-1500/LG8: *a*
	CA	LG1:84/LG8:80	11.62	8.1	LG1:OPAK14-1500/LG8: *a*
PMF	WI	LG4:94/LG6:68	9.46	6.2	LG4:OPY5-1250/LG6:OPCA11-1350
	CA	LG4:74/LG6:48	7.07	6.17	LG4:CMGAN21/LG6:OPAB4-1375

PB primary branch number, *FN* fruit weight/plot, *FW* fruit weight/plot, *AWF* average weight/fruit, *PMF* percentage of mature fruit/plot

[a] LOD scores of effects (Jnt = joint QTL effect and Int = interaction QTL effect) detected by two-QTL analysis model resident in R/qtl (Broman et al. 2003)

[b] Linkage groups (LG) depicted in Fig. 2 and associated with digenic joint/interaction effects and effects given by linkage group and cM position

[c] n.s. indicates value was below threshold LOD

narrow- and broad-based maps in *Cucumis* (Staub et al. 2007; Danin-Poleg et al. 2000). Recently, Gonzalo et al. (2005) constructed a genetic map based on double haploid lines, ('Songwhan Charmi' × 'Pinyonet Piel de Sapo') consisting of 327 loci (226 RFLP, 97 SSR, and 3 SNP), distributed over 12 linkage groups, spanning 1,021 cM. Because SSR provide common anchor points for syntenic analysis (Danin-Poleg et al. 2000 2001; Katzir et al. 1996), the Gonzalo et al. (2005) genetic map has been proposed as a possible bridge with other melon maps containing common SSR markers. Périn et al. (2002c), in fact, showed the potential utility of SSR markers in this regard. Common SSR markers were therefore used to cross-identify ten linkage groups identified herein (Fig. 2) with equivalent linkage groups reported by Gonzalo et al. (2005). Twenty-eight SSR markers (LG1 = 2, LG2 = 3, LG3 = 3, LG4 = 3, LG5 = 1, LG8 = 3, LG10 = 2, LG11 and LG13 = 3, and LG12 = 3) were shared with the Gonzalo et al. (2005) map. These markers along with the *a* locus were highly conserved and comparisons of map distance between common markers were, for the most part, in agreement with other melon genetic maps (Danin-Poleg et al. 2000, 2002; Gonzalo et al 2005, Perin et al. 2002c; Silberstein et al. 2003). Although, anchor SSR in at least two linkage groups were lacking and some linkages were only partial (e.g., LG12), the collinear order of common markers indicates that merging of these maps is possible. This would allow for comparative QTL mapping analyses in this species when other yield component studies become available (Monforte et al. 2004). The collinearity of these linkage maps is indicative of the validity of the map presented herein and its potential broad application to melon breeding.

A genetic map's utility in plant breeding is dependent on its degree of saturation, composition (marker types), and QTL consistency (over locations, popula-

tions and generations) (Staub et al. 1996b; Francia et al. 2005). An understanding of the effects of environment on QTL and trait expression is particularly important during MAS implementation (Zhuang et al. 1997; Bezant et al. 1997; Dijkhuizen and Staub 2003; Sun et al. 2006). There were, in fact, dramatic location effects reported herein (e.g., for FN and FW), but RIL performance rankings (i.e., as evidenced by environment rank correlations and Top 20 RIL concordance %) were, in the main, consistent over environments for all traits, except for PMF (Tables 1, 2, 3). Environmental conditions (e.g., soil type and climatic conditions) contributed dramatically to plant vegetative growth where plants in California grew more rapidly (~2×) and larger (~1 m vs. ~3 m in diameter) than plants in Wisconsin (by visual inspection), thus allowing the formation of a secondary fruiting cycle in California (Rosa 1924). Despite location effects on the traits studied, 16 environmentally independent QTL (43%; PB = 4, FN = 5, FW = 4, AWF = 2, and PMF = 1) were identified. The most consistently high performing RIL families across locations were PB = RIL 36, 122, and 149; FN = RIL 28, 63, 104; FW = RIL 9, 15, and 32; AWF = RIL 15, 49, 89, PMF RIL 9, 12, and 58 and RIL 32, 122, 104, and 113 were the most consistent high performing families across locations and traits (data not presented; Zalapa 2005).

Recently reported melon maps (Gonzalo et al. 2005; Périn et al. 2002c) possess more and higher-quality markers (e.g., SSR and AFLP) than the map presented herein. However, relatively unsaturated melon maps have been used successfully to detect nine QTL for resistance to *Fusarium oxysporum* (map consisting of 16 linkage groups and 641 cM; Perchepied et al. 2005a), and 11 QTL for resistance to downy and powdery mildew (map consisting of 36 linkage groups and 1,150 cM; Perchepied et al. 2005b). Moreover, a map possessing equivalent structure (i.e., marker density, proportion of dominant markers) and the same yield-related QTL as our map has proven useful in MAS of yield component traits in cucumber (Fazio et al. 2003b; Fan et al. 2006).

The number of yield-related trait QTL identified herein was likely underestimated due the relatively small size of the population used (81 RIL), the unsaturated nature of the map, and/or to the low heritabilities of some traits (FW and PMF; Tables 1, 2) (Beavis 1998; Melchinger et al. 1998; Utz et al. 2000). Likewise, analyses performed herein were not able to dissect closely linked QTL and/or detect QTL possessing small effects. Nevertheless, these QTL analyses recapitulated the hypothesized quantitative nature of the yield-related traits examined (Zalapa et al. 2006). Furthermore, this QTL mapping effort corroborated the empirical estimates of number of genomic regions affecting PB (~4), and provided a more accurate estimate of the number genes affecting FN, FW, AWF, and PMF than previously reported by Zalapa et al. (2006).

Increasing primary branch number has been shown to increase yield potential in cucumber (*C. sativus* L.; Fazio et al. 2003b; Fan et al. 2006) and can theoretically increase total yield in melon (Hughes et al. 1983; Nerson et al. 1983; Paris et al. 1985). The empirical data (i.e., BLUEs and BLUPs) presented herein (Table 3) provide evidence that highly branched, fractal melon types are capable of producing higher fruit number and weight per plant than standard vining types. For example, although the fractal line USDA 846-1 has not been intensely selected for high yield, it performed equal to/or better than 'Top Mark' and the three commercial cultivars examined (Table 3). In fact, fractal plant types usually produced significantly higher fruit numbers and in some cases higher fruit weight than vining types. Moreover, fractal plant types usually produced higher early, basally concentrated yield compared with vining plant types at both locations. Source–sink relation differences among plant types (i.e., fractal vs. vining; Hughes et al. 1983; Kubicki 1962; Kultur et al. 2001; McGlasson and Pratt 1963) likely contribute to higher photosynthetic capacities in fractal genotypes which could, in turn, be selected to produce higher total yield. This source/sink-based hypothesis is in agreement with the correlative relationships detected between PB and FN and FW observed herein (Table 4). Such correlations are consistent with those previously reported in diverse melon populations (Abdalla and Aboul-Nasr 2002; Kultur et al. 2001; Lippert and Hall 1982; Taha et al. 2003). In our map, five PB QTL (*pb1.1*, *pb1.2*, *pb2.3*, *pb8.4*, and *pb12.7*) were in close proximity to QTL for FN (*fn1.2*, *fn1.3*, *fn2.4, fn8.7, fn8.8*, and *fn12.9*) and FW (*fw1.1, fw1.2, fw1.3, fw2.6*, *fw8.11*, and *fw8.12*). Linkage Group 1 (LG1) is particularly interesting in this regard since positive additive effects contributed by USDA 846-1 were detected in two QTL for PB (*pb1.1* and *pb1.2*, $R^2 = 33\%$ CA) which were in close proximity to three QTL for FN (*fn1.2, Fn1.2*, and *fn1.3*; $R^2 = 31\%$ WI). Given the relatively high heritability of the 3–4 loci conditioning PB (Table 1; also Zalapa et al. 2006) and the fact that four QTL (*pb1.1*, *pb1.2*, *pb2.3*, and *pb10.5*) were consistently identified across locations accounting for up to 47% of the associated phenotypic variance of this trait, PB is an attractive candidate trait for MAS-augmented yield improvement in melon.

Genes can interact to influence the expression of yield and quality traits in cucurbit species (Serquen et al. 1997; Fazio et al. 2003a). For example, Perin et al.

(2002a) indicate that the *a* locus (controlling monoecious/andromonoecious female flower formation) has dramatic effects on fruit shape (LG II, *fs2.2*, LOD 5.46, $R^2 = 0.52$) and length (LG II, *fl2.1*, LOD 5.05, $R^2 = 0.47$). In the present study, clusters of yield-related QTL were identified (Fig. 2) that might be attributed to linkage and/or pleiotropy. For example, given their position on LG1, it is likely that the action of QTL *fn1.1, pb1.2*, and *fw1.3* are independent from the action of *pb1.1, fw1.1*, and *awf1.1* and from *fn1.2, fn1.3*, *fw1.2, awf1.2*, and *awf1.3*. Similarly, the *a* locus likely has pleiotropic effects on fruit number (*fn8.8*, LOD 9.6, $R^2 = 0.16$) and weight (*fw8.12*, LOD 8.82, $R^2 = 0.14$) and average weight per fruit (*awf8.5*, LOD 14.88, $R^2 = 0.43$; Tables 5; Fig. 2; LG8). Epistatic interaction effects were also detected between the *a* locus and map positions in Linkage Groups 1 and 2 associated with QTL for FN and AWF (Fig. 2; Table 6).

In general, monoecious female flowering is associated with elongated fruit whereas round fruit is associated with andromonoecious female flowering (Perin et al. 2002a). However, in our cross both parents possessed round fruit, but 'Top Mark' (andromonoecious) by USDA 846-1 (monoecious) offspring segregated widely for fruit shape. Fruit production (number, size, total weight) in these RIL is, in part, dependant on fruit shape and fruit size (i.e., average weight per fruit). Since CR1 (the exotic progenitor of USDA 846-1) produces many small, pyrifrom-shaped fruit (pear-shaped), it is likely that USDA 846-1, possesses genes for fruit shape and fruit length that co-segregate with the *a* locus and other fruit development genes (Perin et al. 2002a). Thus, the *a* locus (along with other complex gene interactions) is likely involved in mediating fruit development in our population through complementary pleiotropic effects of fruit shape (Perin et al. 2002a) and average weight per fruit (Tables 5, 6), which in turn condition total fruit yield. Additional studies (i.e., fine mapping) will be necessary to determine whether the effects of the *a* locus on fruit yield are due to pleiotropy and/or linkage between loci (Falconer and Mackay 1996).

The detection of epistatic interactions for yield-related traits reported herein confirms empirical findings regarding significant epistatic effects for most of the traits examined as obtained from generation means analyses (Table 6; Zalapa 2005; Zalapa et al. 2006). Knowledge leading to the application of breeding strategies that incorporate such epistatic interactions between and among traits (e.g. fruit number and weight) will increase the effectiveness of MAS for melon yield improvement (Serquen et al. 1997; Fan et al. 2006; Fazio et al. 2003a).

Given the negative correlations between fruit number per plant and average fruit weight, the development of fractal genotypes capable of supporting three to four early maturing fruit while simultaneously maintaining commercially acceptable fruit size (0.7–1.2 kg) may be challenging. Nevertheless, two QTL associated with FN (*fn1.1*, LG1; $R^2 = 9\%$ and *fn2.4*, LG2, $R^2 = 21\%$) and a QTL associated with AWF at the *a* locus (*awf8.5*; LG8; $R^2 = 43\%$) contribute independent effects, and therefore could be used during MAS-augmented phenotypic selection to increase fruit number while maintaining commercially acceptable fruit size. Such multi-trait selection strategies have been successful in cucumber MAS (Fan et al. 2006). The increase of unique alleles controlling important traits such as branching and fruit number and the strategic alignment with earliness, fruit yield, fruit concentration, and maturity characteristics in this melon population could be accomplished using a simple biparental recurrent selection scheme aided by MAS using the molecular markers associated with environmentally independent QTL described herein.

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