Identification of Melon Fruit Quality Quantitative Trait Loci Using Near-isogenic Lines

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ABSTRACT. A collection of melon (*Cucumis melo* L.) near-isogenic lines (NILs) derived from the cross between the Spanish *C. melo* cultivar Piel de Sapo (PS) and the exotic Korean accession Shongwan Charmi [SC (PI161375)], was used to study the genetic control of a large number of melon fruit quality traits, including morphological, external appearance, texture, flavor, and the overall differences between NILs and PS that might be detected by consumers with a triangle test. Heritability was significant for all the traits, being >0.5 for the whole area of the longitudinal section of the fruit, flesh proportion, skin lightness color, hue angle coordinate of flesh color, and flesh-extractable juice. NILs were classified by principal-component analysis. The first principal component (22% of the variation) was affected mostly by morphological traits, the second component (10%) was influenced by internal and external morphology pattern and color, and the third component (9%) was controlled mainly by flavor traits. An average of 5.6 quantitative trait loci (QTL) per trait were identified (range, between 1 and 12 QTL; 134 QTL in total). In most cases, allele effects with opposite actions were detected. A substantial number of QTL may be good candidates to introduce new quality attributes in modern melon cultivars.

According to cultivated area and production, melon fruit is the second vegetable crop in the world (Secretary of Agriculture, Fisheries and Food of Argentina, 2006). Melon cultivars display an enormous genetic diversity with respect to fruit quality traits, including morphological traits, skin and flesh color, skin texture, sugar levels, aroma, and climacteric and nonclimacteric ripening (Artés et al., 1993; Liu et al., 2004;

Monforte et al., 2005; Pardo et al., 2000; Seymour and McGlasson, 1993; Stepansky et al., 1999). Present-day regulations in the European Union and the United States are mostly based on tolerance to defects, absence of damage and decay, and morphological and appearance traits (Crisosto and Mitchell, 2002; E.U., 2001; Lester and Shellie, 2004; Shellie and Lester, 2004; USDA, 1967). However, regulations do not cover the several aspects of quality as understood by domestic and industrial users based on other objective and subjective traits (Crisosto and Mitchell, 2002; Kader, 2002). The definition of melon fruit quality is complex and varies depending on each particular melon cultivar and market, due to its morphological variability. For example, aroma and turning color are desirable traits for *C. melo* var. *cantalupensis* Naudin (Cantalupensis group) cultivars but undesirable for the ‘Piel de Sapo’-type melons [*C. melo* var. *inodorus* H. Jacq. (Inodorus group)]. Skin netting is a commercial harvest and quality index for some cultivars of the Inodorus group (such as PS-type) because consumers relate well-formed netting to an optimum stage of maturity (Ryall and Lipton, 1983; Seymour and McGlasson, 1993; Taha et al., 2003). The ground spot color (i.e., part of the fruit in contact with the soil) is used to define maturity in PS-type melons. Yellow or cream-yellow color means a ripe melon, and green to white ground spot color indicates that the PS-type melon is probably still unripe (Namesny, 1999). These traits

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make the external appearance another important factor taken into account by consumers at the purchase point because they tend to prefer shiny or glossy fruit (Fallik, et al., 2005; Kader, 2002).

The eating quality attributes of melon include a firm, juicy flesh texture, sugar, acids, and aromatic volatile compounds (Cantwell and Kasmire, 2002; Mutton et al., 1981), in addition to nutritionally valuable and health-promoting contents (Butz et al., 2005; Lester, 1997; Seymour and McGlasson, 1993). For example, juiciness is considered to be principal texture trait, but fruit with higher flesh firmness are usually less juicy (Harker et al., 2003). Juice pH is another important factor for fruit flavor (Holcroft and Kader, 1999).

However, the genetic control of most fruit quality traits is polygenic and largely unknown (Grandillo et al., 1999; Saliba-Colombani et al., 2001). Quantitative trait loci (QTL) analysis can be used to detect regions of the genome involved in such complex traits (Tanksley, 1993). Some QTL and major genes involved in melon fruit quality traits have been defined (Li et al., 2006; Monforte et al., 2004; Périn et al., 2002a, 2002b; Sinclair et al., 2006; Zalapa et al., 2007). However, these investigations have focused on a limited number of traits, mainly morphological ones (fruit size and shape), skin or flesh color, and yield components.

In the present work, we studied a collection of NILs developed from a cross between the Spanish cultivar Piel de Sapo and the Korean accession Shongwan Charmi to detect and map QTL involved in quality traits from commercial and consumer points of view. Each NIL carries marker-defined chromosome fragments from SC in the PS genetic background (Eduardo et al., 2005, 2007). The genome of these NILs is composed by >95% of the PS, and the rest comes from SC. The QTL analysis with NIL populations is also quite powerful, allowing detection of a larger number of QTL compared with other approaches (Eduardo et al., 2007; Eshed and Zamir, 1995). For example, using this NIL population, 10–15 QTL of morphological traits, four to five for ovary shape, external color, and flesh color (Eduardo et al., 2007), and 11 more related to physiological disorders, decay, and flavor loss (Fernández-Trujillo et al., 2007) have already been detected.

Because the number of traits was large, a principal-component analysis was also performed to identify the attributes that contribute most to the phenotypic variation and to classify the NILs into multivariate space (Fernández-Trujillo et al., 2005a). The basis of PCA consists on the compression of data to simplify a complex set of terms by expressing multiple variables (quality traits in this case) as components or variates, respectively.

Materials and Methods

PLANT MATERIAL. The set of 27 melon NILs derived from a cross between the Spanish ‘Piel de Sapo’ control genotype (Inodorus group) and the exotic Korean accession Shongwan Charmi [PI161375 (Conomon group)] used in this work was developed previously (Eduardo et al., 2005, 2007). The NILs had marked, defined introgressions from SC into the PS background, which covered most of the SC genome (Eduardo et al., 2007) and were coded with the prefix “SC.” The first number indicates the linkage group (LG), and a second one indicates the number of NIL within the LG. Further details are given in Eduardo et al. (2005, 2007).

EXPERIMENTAL DESIGN. The crop was cultivated in Casas de Santa Cruz (Torre Pacheco, Murcia, Spain), following the soil preparation, fertigation, plant protection, and other growing practices commonly used for melon cultivation in Mediterranean conditions. Field design was completely randomized with 10 replications of one plant per NIL, 50 replications for PS, and five plants of SC. The plantation had a grid of 2 m between rows and 1.4 m within rows (0.36 plants/m²), surrounded by a border of the commercial hybrid *C. melo* cultivar Nicolás F1 (Syngenta Seeds, El Ejido, Spain), a widely cultivated PS type, as the commercial hybrid reference. Melon seeds were planted on 7 Feb. 2004 and transplanted on 7 Apr. 2004 to a 50-m-long field divided into 12 rows that were covered with a 1.1-m-wide, 22.9- μ m-thick plastic mulch. NIL SC5-4 was not transplanted, due to germination problems, and only two replications of NILs SC4-3b and SC7-2 survived. Further details about this experiment have been reported previously (Eduardo et al., 2007; Fernández-Trujillo et al., 2005a, 2005b).

Fruit were harvested at commercial maturity according to the harvest indicators previously reported for PS and other melon cultivars (Alarcón et al., 2001; Cantwell and Kasmire, 2002; Fernández-Trujillo et al., 2005a, 2005b, 2007; Liu et al., 2004; Namesny, 1999), although not all of them are valid for the entire diversity of NILs assayed. Harvest indicators included fruit growth period from anthesis [32-d minimum and 50-d maximum, according to Alarcón et al. (2001)], fruit size, skin waxing appearance, loss of skin trichomes, development of abscission layer, yellow ring or scar at the peduncle (half to full slip), death of the first leaf beside the peduncle, fruit compactness, ground spot yellowing, netting development, characteristic skin color, and soluble solids content (SSC) that were monitored in previous trials [levels should be $\approx$ 12% SSC for PS and ‘Nicolás’ (Monforte et al., 2004)]. Only fruit with a minimum of 9% SSC were considered well mature and considered for the statistical analysis (Eduardo et al., 2007; Fernández-Trujillo et al., 2005b). Two to three fruit per plant were harvested and analyzed according to Fernández-Trujillo et al. (2005a, 2005b) as follows.

MORPHOLOGICAL TRAITS. Fruit convexity (the length from the stem-end to blossom-end of the fruit to the location of maximum equatorial center) was calculated from digital images taken of every fruit (Fernández-Trujillo et al., 2005b). The rate of convexity (1 = round-shaped fruit) was obtained at dividing fruit convexity by fruit length, and the results were recorded in percentages. The digital images of the longitudinal section of the fruit were used for determining whole fruit size, seed area, and flesh cavity (in cm²). The flesh proportion was also evaluated in the longitudinal section measured. Image analysis was performed according to conventional methodology (Russ, 1999; Young, 2001). Image background was modified from white-gray tones to uniform blue with Adobe Photoshop (CS 8.0.1 for Windows; Adobe Systems, Seattle, WA). The images were cleaned by digital retouching to obtain normalized images without spots using ImagePRO Plus software (Media Cybernetics, Silver Spring, MD). A calibrated square (in millimeters) at the bottom left of the original picture served as reference. To measure *X* and *Y* axes, a script was created to separate the blue ground color of the melon section. To suppress erroneous measurements, displacement of one of the axes was limited to five sexagesimal degrees compared with the overall vertical of the image. From here, two pairs of axes were obtained; one intersecting with the flesh and other with the rind, and the

average of the two verticals and horizontals gave the final result. The histogram of the color was corrected. A batch script programmed into the software automatically segmented the pictures into colors with the help of extended histograms. The different colors of the image correspond to skin and flesh area, the placental tissue containing the seeds, and the possible flesh defects in the sections. The contour plots were measured and the areas corrected according to the previous calibration using the direct pixel count option of the software. The area of each pixel was scaled according to the calibrated rule (≈ 14 pixels per centimeter), and the number of pixels multiplied by the area of one pixel equals the area in square centimeters. Finally, the possible regions with defects in the fruit were assigned manually to the formerly assigned areas, and the results were exported to an Excel database (Microsoft Corp., Redmond, WA).

Skin thickness was measured with a digital caliper and included the nonedible portion of the fruit. The percentage of thickness (i.e., edible flesh or skin) was calculated by dividing skin thickness or flesh thickness at the equatorial center, respectively, by the fruit diameter. Fruit density was calculated by the water displacement method, and results were recorded in kilograms per cubic meter (Fernández-Trujillo et al., 2005a, 2005b).

EXTERNAL APPEARANCE TRAITS. Skin netting was visually evaluated with a scale based on digital pictures (data not shown) and scored as follows: 0 = none; 1 = very slight; 2 = slight; 2.5 = slight to medium; 3 = moderate; 3.5 = moderate to heavy; 4 = heavy.

The classification into commercial categories was mostly based on a one to four range [extra, first, second, and noncommercial, respectively (Fig. 1A–D, top)] depending on the external fruit appearance (local immature areas, scars, or the peduncle such as bruising, etc.) according to E.U. (2001). The commercial evaluation can be interpreted in terms of “the higher the grade, the lower the category.” Extra category includes fruit without defects, first or second category includes maximum 5% or 5% to 10% area with defects, respectively, and noncommercial fruit have no sound peduncle area or >10% area with defects.

The melon fruit was cut longitudinally in halves. The half without the ground-spot was selected, and several semispherical sections of each half from the equatorial region of the fruit perpendicular to the peel obtained. Flesh cylinders (20 mm long and 15 mm in diameter) were trimmed from the middle of the

Fig. 1. **(Top)** Fruit from near-isogenic lines (NILs) of *Cucumis melo* at harvest showing different attributes, such as external appearance (A–D), skin netting (E–L), and skin ground spot associated by maturity and indicated by bottom line (M,N) compared with the parental line ‘Piel de Sapo’ (PS): (A) PS, (B) SC1-3d, (C) SC8-3, (D) SC8-4, (E) PS, (F) SC1-3d, (G) SC2-2a, (H) SC2-3d, (I) SC3-5ab, (J) SC8-3, (K) SC8-4, (L) parental Korean accession Shongwan Charmi [SC (PI161375)], (M) yellow ground spot of full mature PS fruit, and (N) green or white color of ground spot typical of a less mature PS fruit. Bold line is 10 cm for the pictures (A–D or E–L). **(Bottom)** Internal cavities in NILs of *Cucumis melo* fruit at harvest. (A) Line SC12-1ab with a more-developed internal cavity, (B) parental ‘Piel de Sapo’ line, and (C) parental Korean accession Shongwan Charmi [SC (PI161375)]. Bold line is 10 cm.

section, with an apple cork borer from the middle part of the flesh of one of the longitudinal sections of every fruit, according to recommendations of Paris et al. (2003). This tissue corresponds to hypodermal mesocarp, not to epidermal or seed integument tissues. Juice was squeezed with an aluminum Simplex-Super metal juicer (manufacturer unknown, Italy), using the cylinders obtained. Skin, ground spot (part of the fruit in contact with the soil), and flesh and juice color were measured in trichromatic coordinates and recorded in lightness, chroma, and hue angle (L^* , C^* , H^*), using C illuminant, 0° viewing, and a white plate as reference (Fernández-Trujillo et al., 2005b; Kabelka et al., 2004; Pardo et al., 2000).

TEXTURE TRAITS. Whole fruit and flesh hardness were recorded in $N\cdot mm^{-1}$ after 1.75 mm of controlled deformation obtained by using a 1-kN cell charge (100-N cell for flesh measurements) mounted on a universal testing machine

(Fernández-Trujillo et al., 2005b; Mir et al., 2004). Flesh firmness measured the breaking force in Newtons of the above-mentioned flesh cylinders using a 4.6-mm-diameter probe. Flesh-extractable juice (in percent w/w) was measured according to Artés et al. (1999). Juice density was calculated by weighing 1 mL of juice at $20^\circ C$.

FLAVOR TRAITS. The soluble solids content (SSC) was measured with a hand refractometer (in percentage), as reported previously (Eduardo et al., 2007). The dry matter (in percent w/w) was calculated by subjecting 50–100 g of frozen flesh cylinders obtained as reported above to freeze-drying. Juice pH and titratable acidity [TA (in millimoles of H^+ per liter)] were calculated according to Fernández-Trujillo et al. (2005b), and the maturity index was calculated at dividing SSC by percentage of citric acid (Botía et al., 2005; Flores et al., 2001).

Table 1. Morphological and fruit quality traits related to external appearance in near-isogenic lines (NILs) of *Cucumis melo*, number of QTL with mean effects above or below the mean of the 'Piel de Sapo' control genotype (PS), and estimated heritability (h^2).

Genotype	Half fruit	Flesh proportion (%)	Skin netting (0–4 scale) ^v	Commercial			
	longitudinal surface area (cm ²)			category (1–3 scale) ^w	Extractable juice (%)	Skin thickness (mm)	Fruit convexity (mm)
SC1-3d	237.7	71.7*	4.0*	2.3	48.7	4.7	88.3
SC1-4a	193.1*	66.7*	2.1	2.4	46.7	4.7	89.8
SC2-2a	273.4	75.7	3.0*	2.4	58.2*	5.5	100.7
SC2-3d	316.3*	73.5*	2.8*	2.4	55.0	4.9	101.6
SC3-3	213.1*	73.0*	1.0	2.3	35.8*	4.5	86.6
SC3-5ab	237.8	77.1	0.2*	2.2	40.8*	4.2	91.0
SC4-1hb	243.2	80.7*	2.4	2.3	51.8	5.0	91.8
SC4-3b	138.7*	80.0	3.1	2.5	51.0	3.6	63.0*
SC4-4	154.2*	75.0	1.6	2.3	35.3*	4.3	75.7*
SC5-2	238.3	72.4*	2.0	2.3	54.2	4.5	84.2
SC5-3	296.9*	76.2	1.3	2.2	52.5	5.2	103.4*
SC6-4	267.7	73.8*	0.8	2.3	39.3*	4.6	81.6*
SC7-2	241.0	72.1*	1.4	2.0	47.3	4.6	97.5
SC7-4ab	175.3*	73.0*	1.2	2.7*	43.0*	4.3	79.5*
SC8-1	192.1*	73.5*	0.6	2.3	46.7	4.6	87.1
SC8-2	181.1*	75.6	2.0	2.6*	50.0	4.3	91.1
SC8-3	304.4*	75.3	2.7*	2.0	53.0	5.2	113.1*
SC8-4	188.0*	70.0*	0.3*	2.0	51.2	5.3	84.4
SC9-1a	309.1*	77.2	2.0	2.4	47.8	4.6	107.0*
SC9-2a	264.0	76.8	1.7	2.2	44.3	4.3	102.7*
SC9-3	249.0	73.0*	2.3	2.2	49.3	4.9	106.9*
SC10-2	187.0*	80.6*	1.5	2.4	32.1*	4.2	81.9
SC11-2hab	300.0*	82.5*	1.4	2.4	43.5*	4.6	111.5*
SC11-4d	316.2	75.0	2.2	2.6*	44.5	5.2	103.6*
SC12-1ab	252.0	67.2*	0.8	2.8	36.8*	4.7	92.4
SC12-4hb	254.3	73.6*	1.5	2.0	47.8	5.9*	100.6
PS	247.8	76.7	1.5	2.0	51.0	4.9	92.0
SC ^y	168.5	67.5	1.2	3.0	53.4	4.0	76.3
Nicolás ^x	350.1	75.1	3.8	1.8	52.5	7.3	118.5
QTL > PS	5	3	3	3	1	0	6
QTL < PS	7	11	2	0	7	1	3
h^2 (%)	0.81	0.73	0.41	0.06	0.51	0.16	0.60

^aNIL means ($n = 10$) followed by an asterisk were significantly different from the PS control genotype ($n = 50$) according to Dunnett's test ($P = 0.05$).

^yExotic accession Shongwan Charmi [SC (PI161375)].

^xCommercial hybrid cultivar of PS type.

^wScale definitions: 1 = extra (fruit with sound skin and peduncle cutting), 2 = first category (defects affecting <5% skin area), 3 = second category (5% to 10% skin area with defects), 4 = noncommercial fruit (no sound peduncle cutting or >10% skin with defects).

^vNetting scale based on digital images: 0 = none, 1 = very slight, 2 = slight, 3 = moderate, 3.5 = moderate to heavy, 4 = heavy.

TRIANGLE TEST. Triangle sensory test was performed according to Anzaldúa-Morales (1994). Trapezoidal pieces obtained from three representative melons with skin were offered to judges (13–18) on three different labeled dishes, containing two samples of the same NIL and one of PS at random. The judges determined whether at least one sample from the three presented differed from the other two.

STATISTICAL ANALYSIS. The statistical analysis and the estimation of the narrow-sense heritability (h^2) for all the quality traits evaluated were performed according to Eduardo et al. (2007). To study the effect of the SC introgressions, NIL mean values were compared with the control genotype PS using the Dunnet contrast (Dunnet, 1955) with type I error $\alpha \leq 0.05$. QTL were positioned within the SC introgression defined by molecular markers, assuming that there was only one QTL per introgression, and when two NILs with overlapping introgressions showed significant effects, the QTL was located in the overlapping region (Eduardo et al., 2007; Fernández-Trujillo et al., 2007). Thus, the total number of QTL detected for a given

trait must be considered as the minimum number of QTL because we cannot reject that the effect observed in one introgression could be due to two or more linked QTL.

The triangle test results were analyzed at $P = 0.05$, $P = 0.01$, or $P = 0.001$ according to Anzaldúa-Morales (1994). The lower the P , the greater the number of judges that found differences between the PS and the NIL tested.

The principal-component analysis (PCA) and the calculation of the pairwise correlations (Pearson product moment correlations) were conducted using JMP software (version 5.1.2; SAS Institute, Cary, NC). The variables were the traits described above, except skin L^* , juice C^* , and H^* due to missing data, and variables that have been reported in other works: SSC, fruit weight, fruit length, fruit diameter, fruit shape (Eduardo et al., 2007), flesh hardness or flesh firmness (E. Moreno, J. Obando, N. Dos-Santos, J.P. Fernández-Trujillo, A.J. Monforte, and J. García-Mas, unpublished data). The first three PCA axes were studied. The first principal component (PC1) represents the greatest amount of variation resulting from a combination of all

Table 2. Color trichromatic coordinates analyzed in different parts of fruit and in juice of near-isogenic lines (NILs) of *Cucumis melo*, number of QTL with mean effects above or below the mean of the ‘Piel de Sapo’ control genotype (PS), and estimated heritability (h^2).

Genotype	Skin ground						Flesh			Juice		
	Skin			spot			L^*	C^*	H^* (°)	L^*	C^*	H^* (°)
	L^*	C^*	H^* (°)	L^*	C^*	H^* (°)						
SC1-3d	49.0*	23.9	103.5	61.4	34.5*	101.5	67.0	16.4*	111.7*	26.8	1.8*	123.1
SC1-4a	46.4*	26.4	104.3	60.5*	42.4	100.6	71.0	12.3	108.1*	27.1	1.0	132.6
SC2-2a	46.2*	22.3	104.1	63.9	43.4	99.5	71.5	12.7	107.2	26.9	1.0	128.3
SC2-3d	45.1*	23.2	104.3	65.4	43.1	101.0	71.0	13.6	106.5	27.1	1.0	128.8
SC3-3	47.6*	32.0*	105.5	64.6	49.3	102.0	73.2*	15.4*	107.3	28.0*	1.6*	133.3
SC3-5ab	48.4*	31.8*	107.4*	68.4	55.6	101.0	71.0	16.0*	105.4	27.6	1.6*	120.9*
SC4-1hb	43.0	24.1	102.7	58.4*	41.6	101.0	67.7	12.6	107.3*	27.2	1.1	130.3
SC4-3b	48.8*	25.6	99.4	58.3	34.7	96.2	70.6	13.9	105.2	27.2	1.1	121.6
SC4-4	42.8	27.5	104.1	58.9*	46.6	100.8	67.8	13.1	107.6*	27.5	1.3*	128.4
SC5-2	46.3*	27.5	103.9	64.8	49.7	98.4	70.8	11.7	108.0*	27.5	0.8	138.3
SC5-3	42.6	25.7	102.4	61.5	47.6	100.1	67.7	12.8	106.4	27.1	1.0	129.2
SC6-4	40.0	25.2	108.5*	66.5	59.1*	98.8	72.9*	13.2	107.3	27.4	1.1	134.5
SC7-2	42.8	22.2	106.1	61.9	42.0	106.0	69.5	14.1	106.5	27.2	1.3	124.3
SC7-4ab	46.8*	24.6	105.0	58.9*	35.5*	102.0	64.2*	14.0	109.1*	27.4	1.4*	124.1
SC8-1	38.5*	23.1	104.7	56.7*	49.0	95.3	72.0*	14.0	105.3	27.2	1.1	128.4
SC8-2	37.7*	19.2*	103.2	55.9*	42.7	98.4	70.7	14.0	105.4	27.2	1.0	125.0
SC8-3	44.2	26.6	101.5	62.6	44.4	97.5	66.1*	14.6	111.0*	27.1	1.9*	123.4
SC8-4	49.7*	32.6*	101.5	64.5	55.0	95.7	67.5	24.0	111.4*	27.0	1.9*	123.8
SC9-1a	42.2	23.9	106.4*	66.3	46.0	100.6	69.5	13.4	107.0	27.2	1.1	128.3
SC9-2a	42.0	27.4	103.4	60.5*	47.7	102.1	72.7*	13.1	104.6	27.4	1.1	131.4
SC9-3	41.2	22.6	104.4	61.0*	47.0	101.0	70.3	12.5	106.2	27.2	0.9*	130.0
SC10-2	41.6	14.3*	110.4*	63.2	29.8*	108.2*	70.0	13.7	108.7*	27.3	1.3*	127.1
SC11-2hab	40.7	24.5	104.7	58.6*	42.3	103.2	71.7	13.0	106.0	27.6	0.9	135.7
SC11-4d	45.0*	23.5	105.5	62.2	37.6*	102.8	67.8	12.6	107.3	27.0	1.1	123.6
SC12-1ab	40.0	23.8	106.0*	58.2*	46.0	104.3*	73.1*	12.6	106.5	27.5	0.9	139.1
SC12-4hb	42.3	27.1	103.3	63.1	51.8	99.1	68.2	13.4	108.4*	27.0	1.3*	129.1
PS	41.6	25.1	102.8	62.0	49.8	98.8	69.2	12.6	105.8	27.0	1.0	131.5
SC ^y	54.7	21.8	113.5	58.8	31.0	105.8	69.2	36.5	114.6	27.5	5.7	120.6
Nicolás ^x	41.3	20.3	102.0	65.0	49.2	93.2	68.2	11.6	106.5	26.0	0.9	130.0
QTL > PS	8	2	5	0	1	2	5	2	8	1	7	0
QTLs < PS	1	2	0	8	4	0	2	0	0	0	1	1
h^2 (%)	0.52	0.47	0.22	0.22	0.42	0.22	0.45	0.25	0.51	0.11	0.29	0.16

^yNIL means ($n = 10$) followed by an asterisk were significantly different from the PS control genotype ($n = 50$) according to Dunnett's test ($P = 0.05$).

^xExotic accession Shongwan Charmi [SC (PI161375)].

*Commercial hybrid cultivar of PS type.

of the variables. The second principal component (PC2) represents the next greatest source of variation, and so on. Traits with eigenvectors >0.20 were considered the most significant contributors to each PC. Finally, NILs PC mean values were compared with PS PC mean values by Dunnett's contrast.

Results

PHENOTYPIC ANALYSIS OF THE PARENTAL LINES. Fruit from PS were larger than SC and oval in shape, with white flesh, light yellow juice, green skin, a typical yellow skin spot in contact with the soil, a sparse spot pattern, very slight to slight skin netting, high SSC, moderate extractable juice (51% w/w), firm flesh texture, and fruit and juice density values of 805 ± 90 and 1045 kg·m⁻³, respectively (Tables 1–3; Fig. 1A,E,F; data not shown) with a slight development of skin netting. At harvest, PS flesh showed few symptoms of water-soaking disorder but was free from external or internal disorders or decay, which classified them as first category fruit (2 grade units).

On the other hand, SC showed pear-shaped fruit (smaller than PS also in whole fruit area and flesh proportion), non-uniform green skin with a typical spot pattern and white ground spot color, very slight skin netting, green flesh (orange beside the placenta) and green juice color, second commercial category (3 grade units), slightly higher extractable juice and fruit density (888 ± 24 kg·m⁻³), but lower flesh firmness, juice density, TA, and maturity index than PS, and thin and delicate skin (Tables 1–3; Figs. 1L and bottom 1C; data not shown).

TRAIT HERITABILITY. Whole fruit longitudinal section area, flesh proportion, extractable juice, and two color coordinates

(skin *L** and flesh *H**) were the only quality traits with *h*² values >0.5 (Tables 1 and 2). The *h*² values between 0.3 and 0.5 were found for skin netting, flesh hardness (Table 1; data not shown), skin *C** and ground *C** color, flesh *L** color, and TA (Tables 1–3), while the rest of the traits showed *h*² values <0.3 (Tables 1–3).

Morphological traits

WHOLE-FRUIT LONGITUDINAL SECTION AREA, FLESH PROPORTION, AND FRUIT DENSITY. PS fruit showed a whole-fruit area of ≈248 cm². Five NILs showed 20% to 28% higher whole fruit area than PS, while nine NILs showed a lower area than PS (–14% to –38%) (Table 1). Three NILs increased the flesh proportion of PS (76.7%) by 5.6% to 8%, and 11 NILs decreased it by –3% to –14% (Table 1). The latter phenotypes were due to an increase in the internal cavity of around 50.5 to 77.7 mm in the NILs, including free space, the placental tissue, and the seeds, compared with PS (57.2 mm) (Fig. 1, bottom). No significant differences in fruit density among NILs and PS were found.

External appearance traits

COMMERCIAL APPEARANCE AND SKIN NETTING. Three NILs were graded with higher appearance scores than PS (second class category; Table 1; Fig. 1A–D). Four NIL fruit were classified with a moderate netting (values ≈3 units), and two NIL fruit showed absence of this trait (near 0 units; Table 1; Fig. 1E–L).

TEXTURE TRAITS AND SKIN THICKNESS. The whole fruit hardness of PS was ≈36 N·mm⁻¹, which was reduced by 22% to 36% in the fruit of four NILs (data not shown). This trait can also be influenced by the nonedible portion of the fruit

Fig. 2. Ideogram showing the location of fruit quality trait loci, located by the means of near-isogenic lines on the melon genetic map. Linkage groups (LG) are depicted at the top according to Gonzalo et al. (2005), using the Périn et al. (2002a) nomenclature for the LG. For each trait, the estimated position of the QTL is indicated by a shadowed area and is colored black when the SC allele [SC = Shongwan Charmi (PI161375)] allele increased the trait or gray when it decreased the trait. For LG VI, the QTL position is broken because the introgression had a double recombination, and the genomic region around the marker MC224 did not have introgression from SC. Due to that fact, we could not rule out if the QTL was located on the right or the left of the double recombination.

measured as skin thickness (4.2–5.5 mm in NILs vs. 4.9 mm in PS; Table 1).

SKIN COLOR. Eleven NILs showed 8% to 19% higher skin L^* values than PS (42.6 units), indicating a lighter color than PS. On the other hand, two NILs showed lower skin L^* values than PS (Table 2). Three NILs produced more intense colors (25% greater C^* values) than PS, and two NILs a less intense skin color ($\approx 23\%$ and 43% lower C^* values) (Table 2). Finally, five NILs showed 3% to 7% higher hue angles ($H^* = 103^\circ$), indicating a greener skin color, probably due to higher contents of chlorophyll. Taking together the data from the three color components, the minimum number of QTL for skin color was 13 (Fig. 2).

GROUND SPOT COLOR. Ten NILs had darker ground spots than the PS (2% to 10% higher L^* units; Table 2). Only NIL SC6-4 showed a more intense color (19% higher C^* values) than PS, while four NILs showed less intense colors (Table 2; Fig. 1M,N). For the true color or H^* of the PS, H^* ground color was $\approx 99^\circ$, and two NILs showed 6% to 10% higher values, which were associated with less mature color than PS (Table 2). Considering all three color components, a total of 12 QTL for ground color were detected (Fig. 2).

FLESH COLOR. Two NILs had darker flesh colors than the 69 units of the PS (4% to 7% lower L^* values than PS), while five NILs showed lighter colors (4% to 5% higher L^* values than PS) (Table 2). Three NILs showed more intense colors than PS (higher C^* values; Table 2). PS flesh had a true color defined by an H^* value of $\approx 106^\circ$. Ten NILs showed 1.4% to 5.3% higher H^* (greener flesh color) than PS (Table 2). Considering the three color components, 16 QTL defined this character (Fig. 2).

JUICE COLOR. Only the juice of NIL SC3-3 was lighter than that of PS (L^* 3.7% higher; Table 2). The PS showed 0.95 unit of C^* , while 10 NILs increased the value by 33% to 100% and one decreased it (Table 2). Finally, the H^* juice of PS was around 132° , which was reduced by 8% in one NIL (Table 2). Considering the three color components, 10 QTL defined this character (Fig. 2).

Flavor traits

EXTRACTABLE JUICE, DRY MATTER, AND JUICE DENSITY. Only fruit from NIL SC2-2a were juicier than PS (extractable juice increased by 14%). Extractable juice was reduced by 14% to 37% in eight NILs (Table 3). The dry matter in PS fruit was 12.4%. Seven NILs showed between 2% and 3% lower dry matter. Three NILs showed a lower juice density than PS (Table 3).

JUICE pH, TITRATABLE ACIDITY, AND MATURITY INDEX. Only SC10-2 showed 4.3% higher pH units than PS, while SC8-4 showed a lower value (-3%) (Table 3). The TA of PS was reduced by 27% in NIL SC10-2 and was increased in NILs SC3-3 and SC6-4 by $\approx 21\%$ (Table 3). Eleven NILs showed lower maturity indices than PS (from -15% to -32% ; Table 3).

TRIANGLE TEST. No significant differences compared with PS were obtained in four NILs (SC1-4a, SC5-2, SC5-3, SC8-1), but significant differences were found in the rest of the NILs: the NIL SC9-5 at $P = 0.05$; five NILs at $P = 0.01$ (SC3-3, SC9-1a, SC2-2a, SC4-1hb, SC4-3b); and the other 16 NILs reported in Table 1 at $P < 0.001$. These NILs contained differences in one or more traits demanded by melon consumers, such as fruit appearance, flesh color, flesh texture, taste and aroma, or the overall quality perceived in the triangle test.

QTL MAPPING. A large number of QTL involved in fruit quality traits, in most cases showing alleles with opposite effects, have been mapped (Fig. 2) and reported as the

Table 3. Mean quality traits associated with flavor analyzed in juice extracted from fruit of near-isogenic lines (NILs) of *Cucumis melo*, number of QTL with the mean effect above or below the 'Piel de Sapo' (PS) control genotype, and estimated heritability (h^2).

Genotype	Dry matter (%)	Juice density (kg·m ⁻³)	pH	Titratable acidity [mmol H ⁺ ·L ⁻¹]	Maturity index (% soluble solids/% citric acid)
SC1-3d	11.7	1042.9	5.8	14.1	116.6
SC1-4a	11.3	1041.6	5.8	14.2	117.6
SC2-2a	11.2	1041.1	5.8	13.9	119.5
SC2-3d	10.8*	1041.4	5.7	12.7	118.2
SC3-3	10.9*	1037.0	5.6	17.2*	90.0*
SC3-5ab	12.2	1040.3	5.8	16.4	102.4*
SC4-1hb	12.1	1047.4	5.7	14.9	114.3
SC4-3b	11.5	1035.5	5.8	13.7	123.1
SC4-4	11.6	1041.8	5.6	15.7	100.4*
SC5-2	11*	1037.1	5.7	13.2	123.8
SC5-3	13.2	1039.3	5.8	15.6	113.8
SC6-4	10.4*	1034.8	5.6	16.9*	86.7*
SC7-2	10.9	1046.5	5.8	12.6	120.1
SC7-4ab	12.5	1045.5	5.8	14.2	124.7
SC8-1	11.6	1041.2	5.7	16.0	106.2*
SC8-2	10*	1031.9*	5.7	15.3	93.1*
SC8-3	11.8	1043.6	5.6	16.2	106.2*
SC8-4	11.3	1036.6	5.6*	15.3	100.8*
SC9-1a	11.2	1042.0	5.7	12.3	127.5
SC9-2a	11.3	1041.9	5.7	14.5	102.4*
SC9-3	11.9	1042.0	5.7	15.3	107.7*
SC10-2	9.9*	1029.4*	6.0*	10.3*	124.5
SC11-2hab	11.5	1039.2	5.8	15.0	117.4
SC11-4d	11.6	1041.4	5.7	13.6	122.0
SC12-1ab	10.5*	1031.6*	5.7	13.6	106.0*
SC12-4hb	11.7	1041.0	5.7	13.8	116.0
PS	12.4	1045.0	5.8	14.1	127.2
SC ^y	14.6	1021.5	5.6	7.4	69.5
Nicolás*	15.5	1045.7	5.8	16.9	125.8
QTL > PS	0	0	1	2	0
QTL < PS	7	3	1	1	8
h^2 (%)	0.19	0.06	0.12	0.33	0.30

*NIL means ($n = 10$) followed by an asterisk were significantly different from the PS control genotype ($n = 50$) according to Dunnett's test ($P = 0.05$).

^yExotic accession Shongwan Charmi [SC (PI161375)].

*Commercial hybrid cultivar of PS type.

minimum number of QTL for these traits (Tables 1–3). In summary, 134 QTL were detected (52 for morphological and external appearance traits, 69 for color traits, and 23 for flavor traits). Practically every genome region covered by the SC introgressions has been associated with at least one QTL, most of them with two or more (average of 3.5 QTL per genomic region). LG X was associated with the higher number of QTL (13; Fig. 2).

CORRELATION AMONG TRAITS. The Table 4 depicts the correlation coefficients among the studied traits. Most of the correlations were low. The exceptions include some expected ones as between morphological traits, for example, fruit area and flesh area ($r = 0.97$), or dry matter and SSC. More interesting were the correlations between skin netting with extractable juice and TA and maturity index.

PRINCIPAL-COMPONENT ANALYSIS. The first three PCs contributed to a total of 41% of total variance. PC1, representing 22% of the variation, was most affected by fruit weight, fruit length, fruit diameter, flesh thickness, flesh area, dry matter, fruit convexity, and fruit area, that is, traits involved mainly in the final dimensions of the fruit. PC2, representing 10% of the variation, was affected mostly by fruit shape, skin color, and flesh proportion, that is, internal and external morphology pattern and color. The third component, representing 9% of the variation, was affected mostly by SSC, flesh hardness, flesh color, extractable juice, TA, and dry matter, which were involved in miscellaneous quality traits, particularly the flavor traits.

Figure 3 depicts a plot of PC1 and PC2. PS fruit were located in an area around the center of the axis, slightly biased

Table 4. Pearson product moment correlations coefficients found in the multivariate analysis among all the traits evaluated in the fruit of the near-isogenic lines of melon; all correlations with absolute values >0.18 were significant at $P \leq 0.01$.

	Stem- end to blossom- end length	Equatorial center diam	LD	Fruit wt	Fruit density	Whole fruit longitudinal section area	Whole fruit longitudinal section flesh area	Flesh proportion	Skin netting	Commercial category	Whole fruit hardness	Flesh firmness	Skin thickness	
Convexity														
Stem-end to blossom-end length (<i>L</i>)	0.65													
Equatorial center diam (<i>D</i>)	0.34	0.31												
LD	0.30	0.65	-0.48											
Fruit wt	0.58	0.67	0.87	-0.08										
Fruit density	0.31	0.34	0.34	0.02	0.45									
Whole fruit longitudinal section area	0.75	0.55	0.58	0.02	0.69	0.34								
Flesh area	0.74	0.56	0.54	0.07	0.67	0.37	0.97							
Flesh proportion	0.20	0.20	0.01	0.21	0.13	0.22	0.20	0.42						
Skin netting	0.28	0.34	0.26	0.10	0.37	0.13	0.30	0.30	0.14					
Commercial category	-0.10	-0.13	-0.20	0.08	-0.27	-0.06	-0.11	-0.08	0.08	0.05				
Whole fruit hardness	0.32	0.45	0.30	0.16	0.44	0.25	0.32	0.33	0.14	0.20	-0.14			
Flesh firmness	-0.01	0.12	0.08	0.06	0.03	0.05	-0.05	-0.04	0.01	-0.24	-0.02	0.24		
Skin thickness	0.16	0.15	0.22	-0.03	0.20	0.07	0.24	0.22	-0.02	0.16	-0.03	-0.04	-0.20	
<i>L</i> * skin	-0.12	-0.10	-0.07	-0.03	-0.16	-0.13	-0.08	-0.11	-0.19	0.18	0.11	-0.04	0.11	0.01
<i>C</i> * skin	-0.07	-0.17	-0.02	-0.14	-0.12	-0.04	-0.07	-0.10	-0.22	-0.26	-0.15	-0.04	0.12	-0.08
<i>H</i> * skin	-0.06	-0.07	0.11	-0.12	0.00	0.04	0.04	0.03	-0.01	-0.37	0.16	-0.03	0.35	-0.03
<i>L</i> * ground	0.04	0.02	0.09	-0.07	0.10	0.06	0.19	0.17	-0.04	-0.05	-0.13	-0.10	0.06	0.03
<i>C</i> * ground	0.00	-0.20	0.05	-0.25	0.01	0.001	0.03	-0.01	-0.18	-0.40	-0.33	-0.23	-0.08	-0.04
<i>H</i> * ground	0.11	0.21	0.14	0.08	0.18	0.06	0.12	0.13	0.08	-0.01	0.10	0.33	0.31	-0.06
<i>L</i> * flesh	-0.02	-0.08	0.09	-0.13	0.00	-0.07	0.02	0.00	-0.09	-0.29	-0.02	-0.27	0.17	-0.24
<i>C</i> * flesh	-0.17	-0.16	-0.28	0.13	-0.31	-0.15	-0.20	-0.18	0.04	-0.26	0.19	-0.16	0.27	-0.05
<i>H</i> * flesh	-0.14	0.03	-0.02	0.02	-0.03	-0.01	-0.08	-0.10	-0.11	0.12	0.16	0.13	0.23	0.08
<i>L</i> * juice	-0.05	0.01	-0.02	0.05	-0.03	0.08	-0.07	-0.05	0.03	-0.27	0.00	0.05	0.36	-0.18
<i>C</i> * juice	-0.22	-0.23	-0.31	0.05	-0.34	-0.08	-0.27	-0.25	-0.01	-0.27	0.08	-0.14	0.23	-0.12
<i>H</i> * juice	0.09	0.17	0.30	-0.08	0.27	0.14	0.14	0.12	-0.04	-0.06	-0.04	0.22	0.23	0.04
Extractable juice	0.25	0.20	0.10	0.08	0.19	0.03	0.27	0.25	0.00	0.47	-0.11	-0.03	-0.41	0.23
SSC	0.16	-0.04	0.07	-0.08	0.08	0.08	0.05	0.09	0.10	0.24	-0.05	-0.03	-0.22	0.19
Dry matter	0.15	-0.02	0.03	-0.05	0.06	0.08	0.04	0.05	0.01	0.21	-0.02	-0.07	-0.21	0.15
Juice density	0.18	0.02	0.13	-0.06	0.10	0.09	0.07	0.08	0.04	0.22	-0.04	0.06	-0.05	0.19
pH	-0.01	-0.03	-0.07	0.08	-0.11	-0.004	-0.04	-0.01	0.13	0.00	0.11	-0.06	0.14	-0.01
TA	0.03	-0.11	0.05	-0.09	0.06	0.003	-0.05	-0.04	-0.01	0.02	-0.10	-0.07	-0.21	0.08
Maturity index	0.10	0.11	0.06	0.02	0.05	0.09	0.13	0.14	0.07	0.17	0.02	0.04	0.05	0.09

^zSSC = soluble solids content; TA = titratable acidity.

^yMaturity index = SC ÷ percent citric acid.

toward positive values of PC1; only two NILs (SC8-3 and SC11-4d, located in the right-hand side of the plot) showed a higher PC1 value than PS, whereas nine NILs (SC3-3, SC4-4, SC5-2, SC7-4ab, SC8-2, SC8-1, SC8-4, and SC10-2, located in the left area) showed a lower PC1 value. Five NILs (SC6-4, SC3-3 SC3-5ab, SC8-4, and SC12-1ab, located in the upper area) showed higher PC2 than PS and three NILs (SC7-4-ab, SC8-3, and SC12-1ab, located in the lower area) lower PC2. Figure 3B depicts a plot of the PC1 and PC3. PS fruit were located mainly in positive values of the PC1 and PC3, in the upper right quadrant. Seven NILs (SC2-3d, SC7-2, SC9-1a, SC9-2a, SC10-2, SC11-4d, and SC12-1ab, located preferentially in negative values of PC3) showed lower PC3 than PS. NILs SC10-2 and SC12-1ab showed significant differences with PS in all three PC axes, whereas NILs SC3-3, SC7-4ab, SC8-2, SC8-4, and SC11-4d showed significant differences in two of the PCs.

Discussion

The genetic control of a large number of complex fruit quality traits has been analyzed for the first time using a collection of NILs. Heritability was significant in all cases, confirming that the current melon NIL population has sufficient genetic variability for these traits to be studied. Some traits showed high h^2 , which is associated with a strong response to selection (Falconer and Mackay, 1996). A large number of QTL was detected, even in traits with low heritability, demonstrating the power of this population to dissect complex traits. Some of the QTL are highlighted, but not all of them, due to space constraints for individual discussions.

With respect to external appearance traits, detection of QTL for skin netting confirms that this trait is genetically determined (Liu et al., 2004) and amenable to breeding to satisfy consumer preferences (Ryall and Lipton, 1983; Seymour and McGlasson,

Skin color coordinates			Skin ground color coordinates			Flesh color coordinates			Juice color coordinates			Extractable juice	SSC ^z	Dry matter	Juice density	pH	TA ^z	Maturity index ^y
L*	C*	H*	L*	C*	H*	L*	C*	H*	L*	C*	H*							
0.57																		
-0.09	-0.15																	
0.33	0.30	0.09																
-0.08	0.45	-0.05	0.51															
-0.06	-0.16	0.36	-0.24	-0.56														
-0.16	0.05	0.33	0.10	0.21	0.05													
0.18	0.12	0.31	0.05	-0.04	-0.04	0.21												
0.35	0.09	0.05	0.05	-0.29	0.17	-0.26	0.14											
-0.11	0.11	0.24	0.08	0.16	0.07	0.32	0.18	0.02										
0.27	0.21	0.20	0.03	-0.03	-0.04	-0.03	0.69	0.27	-0.01									
-0.15	0.01	0.09	-0.02	0.10	0.18	0.27	-0.16	-0.06	0.48	-0.47								
0.11	-0.01	-0.47	0.06	0.06	-0.31	-0.27	-0.32	-0.04	-0.25	-0.37	-0.08							
0.10	0.05	-0.30	-0.04	0.04	-0.31	-0.34	-0.08	-0.14	-0.13	-0.06	-0.11	0.26						
0.14	0.08	-0.32	0.00	0.07	-0.34	-0.32	-0.02	-0.10	-0.19	0.08	-0.21	0.20	0.83					
0.17	0.10	-0.14	0.02	0.00	-0.15	-0.24	-0.02	-0.07	-0.05	0.00	0.03	0.19	0.42	0.35				
-0.02	-0.15	-0.03	0.00	-0.21	0.06	-0.01	0.08	0.00	-0.01	0.07	-0.18	-0.08	0.03	0.00	-0.06			
0.01	0.23	-0.09	-0.06	0.22	-0.19	0.05	0.14	-0.19	0.10	-0.01	0.14	0.00	0.38	0.37	0.20	-0.40		
0.07	-0.19	-0.08	0.12	-0.14	-0.09	-0.23	-0.19	0.08	-0.16	-0.09	-0.15	0.18	0.35	0.23	0.08	0.43	-0.68

Fig. 3. Plots of the three first principal components (PC) of the quality traits analyzed in near-isogenic lines (NILs) of *Cucumis melo* fruit at harvest. (A) Principal-component axes PC1 and PC2. To simplify the plot, only the NILs significantly different from the parental line 'Piel de Sapo' (PS) and the PS itself are plotted. (B) PC1 and PC3. Only NILs significantly different from PS for PC3, and the PS itself, are plotted.

1993; Taha et al., 2003). Development of melon netting is also linked with harboring enteric bacteria (Castillo et al., 2004; Richards and Beuchat, 2005). This suberized net tissue is also a preventive factor against pre- and postharvest mechanical injury (Keren-Keiserman et al., 2004), but it can increase the risk of chilling injury (CI) and associated decay during melon storage (Fernández-Trujillo et al., 2007). QTL for the commercial category have also been detected but showed poor correlation with other quality traits (Table 4).

Most QTL for extractable juice showed negative effects on the trait. SC contains at least the allele of the gene *me-2* responsible for melon mealiness at harvest (Périn et al., 2002b) and, therefore, low extractable juice values. The fact that a large number of QTL has been detected for this trait suggests that lower extractable juice (or juiciness) values may not necessarily

indicate mealiness at harvest as observed by Artés et al. (1999) in peach [*Prunus persica* (L.) Batsch].

Consumers usually relate the color change that accompanies maturation in many fruit to internal characteristics (Lester and Shellie, 1992; Pardo et al., 2000). Analysis of the true color H^* coordinate quantitatively revealed two QTL in common with those previously reported qualitatively for green-flesh NILs (SC8-3, SC8-4, and SC1-3d), light green flesh NILs (SC7-2 and SC7-4ab), or yellow to light orange NILs (SC3-3 and SC3-5ab) (Eduardo et al., 2007). This characteristic can be attributed to the combination of high chlorophyll contents and low concentration of carotenoids in plastids (Lester, 1997; Seymour and McGlasson, 1993). Detection of QTL for ground spot color may also be useful in breeding, as this trait is considered a reliable harvest index in the PS type.

Dry matter can be used not only as a quality index but also as a harvest indicator of the organic constituents in the fruit (Holcroft and Kader, 1999; Toldam-Andersen and Hansen, 1997). In this report, the correlation coefficients between dry matter and SSC ($r = 0.82$; Table 4) and between dry matter and TA ($r = 0.37$; Table 4) indicate the contribution of sugars and to a lesser extent organic acids to fruit total biomass in melons. No relation was found between dry matter and the fruit size evaluated by fruit area ($r = 0.04$) or other morphological traits (Table 4).

Generally, juice density shows a correlation with the concentration of dry matter (Assis et al., 2006; Magerramov, 2006). However, in the present, work low correlations

were found between melon juice density and other traits, such as extractable juice ($r = 0.19$), SSC ($r = 0.42$), TA ($r = 0.20$), or dry matter ($r = 0.37$) (Table 4).

Titrateable acidity is considered a melon harvest index because it is well correlated with fruit flavor and can be used to ensure an adequate concentration of fruit organic acids that decrease during ripening (Albuquerque et al., 2006; Fernie et al., 2006; Flores et al., 2001; Saliba-Colombani et al., 2001). The maturity index has also been used to monitor melon ripening (Flores et al., 2001). However, no correlation was found between this index and skin netting (Table 4). Additionally, the poor correlations between SSC or extractable juice and netting (Table 4) do not support the association between a well-formed netting and an optimum stage of maturity (Ryall and Lipton, 1983). On the other hand, juice pH of the NIL melon collection was under the control of two opposite QTL and perhaps more QTL.

Sweet cultivars of melon, including PS types, are characterized by a low organic acid content (Fernie et al., 2006). The two apparently independent QTL detected for TA opens up the opportunity for designing new cultivars with distinctive tastes, as suggested by Burger et al. (2003).

The PCA allowed identification of major components of genetic variation (Brewer et al., 2007; Langlade et al., 2005). The two first PC were most affected by morphological traits, indicating that the effects of the genes involved in these traits are relatively strong in this population (i.e., this NIL population is especially suitable for the genetic dissection of a large number of morphological traits). Complex fruit quality traits contributed mainly to PC3, indicating that there is enough genetic variability within this population for these traits to be genetically dissected. The PCA was also useful to group the NILs in a multivariate space, showing which NILs are different in a large number of quality traits. Six NILs (SC3-3, SC7-4ab, SC8-2, SC8-4, SC10-2, SC11-4d, and SC12-1ab) were significantly different from PS in at least two PC. Thus, these NILs contain the QTL that have more important effects on several quality traits. Due to the genetic resolution of the present NIL population, we cannot distinguish whether these multiple effects are due to pleiotropy at a single QTL or multiple linked QTL. The fact that most of the quality traits were not correlated indicates a physiological and genetic independence among them. Thus, the multiple effects observed in several introgressions most likely would be caused by QTL linkage rather than pleiotropic effects and a single QTL.

IMPLICATIONS FOR THE FUTURE. QTL of perceived consumer differences located in LGs III to V and X to XII (Fig. 2) were deduced from NILs showing the lowest probabilities in the triangular test compared with PS. Consequently more consumers recognized the NILs with introgressions in these LGs as different from PS. These LGs could be the best for targeting QTL to develop new cultivars with differential values that would appeal to consumers.

Melon consumers have a wide range of interests, depending on the segment of the agribusiness and agri-food chain analyzed (Kader, 2002; Shewfelt, 1999). From the total number of QTL detected in the population, 12 of them (e.g., skin netting, flesh color, flesh proportion, extractable juice or TA) can have clear beneficial effects on traits preferred by consumers, as was revealed in the triangle test, and the rest can be used in one direction or another, depending on the targeted uses.

From the perspective of plant breeding companies and the fresh market, QTL improving skin lightness, flesh color, extractable juice, the area of the longitudinal section of the whole fruit, fruit netting appearance, and skin color are probably the most important ones for designing new cultivars. For the juice or flesh processing industry, including fresh-cut, melon flesh drying, and drinks and liquor production, QTL for extractable juice alone or in combination with the above-mentioned fruit morphological QTL will be important, depending on the particular uses (Eduardo et al., 2005). QTL that increase flesh area or diminish seed cavity size can also help in automatic processing and to produce melon puree cremogenate. A higher flesh proportion is an indication of more edible flesh, requires less labor cost, and improves productivity for fresh-cut or canning processing (in cubes, trapezes, flesh, and juices), their derivatives such as liquors, and transportation efficiency.

Reduction in fruit juiciness may be desirable for flesh melon ball production in syrup or in fruit juice or in new canning products in the market.

The fresh-cut industry will also benefit from higher flesh area, because designing nonclimacteric cultivars with similar postharvest behavior but different color is better than mixing green-flesh climacteric cultivars, such as 'Galia', and non-climacteric ones. Overall, the QTL detected give more flexibility to breeding companies, in cooperation with industry, to design cultivars for specific purposes, focusing on individual consumer interests or differentiating melon products in the marketplace.

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