Mapping Fruit Susceptibility to Postharvest Physiological Disorders and Decay Using a Collection of Near-isogenic Lines of Melon

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**Abstract.** Melon (Cucumis melo L.) is a perishable fruit that requires refrigeration to extend its shelf life. Postharvest behavior differs substantially among melon varieties due to genetic differences. In this work, we use a collection of near-isogenic lines (NILs) derived from a cross between the Spanish cultivar Piel de Sapo (PS) and an exotic Korean accession ‘Shongwan Charmi’ [SC (PI161375)], each of them with a single introgressed region from SC into the PS background, to detect and map quantitative trait loci (QTLs) involved in postharvest life traits, such as total losses, water-soaking, necrosis of the placental tissue, chilling injury (CI), decay, fruit over-ripening, flesh browning, hollow flesh disorder, and flavor loss during storage. Fruit were examined at harvest and after 35 days at 8 °C. Three QTLs induced desirable quality traits; flv8.1 reduced the loss of fruit flavor after refrigeration, tl8.1 reduced total losses, and fus8.4 reduced the susceptibility to fusarium rot (Fusarium Link). Another 11 QTLs produced a detrimental effect on other quality traits. The NIL population was useful for dissecting complex, difficult-to-measure pre- and postharvest disorder traits of different degrees of development and for investigating flavor loss during storage. Further studies with the QTLs described herein will shed light on the genetic control of melon shelf life and help breeders who are interested in this fruit quality trait.

Cucumis melo is an annual diploid species that belongs to the Cucurbitaceae, one of the largest families in the world and important from a commercial point of view (Secretary of Agriculture, Fisheries and Food of Argentina, 2006). Most of the members of the family can be affected by several fruit disorders that negatively affect postharvest fruit quality and harm fruit shelf life (Blancard et al., 1995; Snowdon, 1991). The accessions with a good shelf life are mostly found within C. melo var. saccharinus Naud. and C. melo var. inodorus Naud. (Liu et al., 2004). According to these authors, the shelf life of melon fruit is correlated with flesh quality, abscission of the peduncle, development periods of plant and fruit, rapid yellowing of epidermis at maturity, the soluble solids content, and the color of the flesh and epidermis.

Melon disorders such as water-soaking (du Chatenet et al., 2000; Serrano et al., 2002) and over-ripening are also important problems for the fresh melon fruit market. Melon over-ripening symptoms are due to fruit senescence, when fruit exhibit disintegrated and waterlogged flesh, particularly close to the seed cavity and the placenta, unusually yellow, very soft flesh, and, in severe stages, the fruit split open at the blossom end (Rose et al., 1998). Melon water-soaking is a calcium-related disorder and is affected by crop management, lack of soil aeration, extreme differences between day and night temperatures, average soil temperatures below 15 °C, lack of calcium nutrition, and...
excessive irrigation in periods with high insolation, shading, or unbalanced fertilization (Cornillon et al., 2000; Madrid et al., 1997, 2001; Nishizawa et al., 1998, 2004a). The disorder symptoms include a glassy texture of the flesh and water exudation (a watercore disorder), accompanied by flavor degradation with a tendency to alcoholic fermentation, normal levels of flesh sugars, excessive softening, and increased polygalacturonase activity, intercellular spaces, and membrane permeability (du Chatenet et al., 2000; Madrid et al., 1997; Nishizawa et al., 2004b; Serrano et al., 2002). The water-soaking disorder is characterized by lower calcium concentration in the NaCl-soluble fraction of the mesocarp tissue of the ripe fruit from the basal hemisphere but not in tissue from the inner mesocarp of the distal hemisphere (Nishizawa et al., 2004a).

Chilling injury (CI) negatively affects fruit skin appearance and flesh flavor in most Cucurbitaceae species because most of them are sensitive to CI below 13 °C (Ben-Amor et al., 1999; Lipton, 1978; McCollum, 1990; Miccolis and Saltveit, 1995; Yang et al., 2003; Zong et al., 1995). Typical CI symptoms in melon and other members of the Cucurbitaceae are pitting and skin scald, lesions that are usually colonized in a few days by saprophytic or necrotrophic fungi such as Alternaria Nees or Cladosporium Link (Fernández-Trujillo and Martínez, 2006; Miccolis and Saltveit, 1995). Overall, both internal and external disorders are a serious obstacle to extending melon shelf life for exporting melons overseas.

Wild or exotic germplasm can be used to improve fruit yield and quality traits if selected genomic regions are introgressed into an elite genetic background (Tankersley and McCouch, 1997). Approaches to identify the quality trait loci (QTLs) responsible for low-temperature responses in the introgressed region of near-isogenic lines (NILs) of tomato (Solanum lycopersicon L.) have been conducted by Oyanedel et al. (2001). NILs of summer squash (Cucurbita pepo L.) containing gene B showed increased sensitivity to CI (McCollum, 1990). However, no information is available on melon NILs. A collection of NILs derived from a cross between the Spanish ‘Piel de Sapo’ control genotype (inodorus type) and the exotic Korean accession ‘Shongwan Charmi’ (PI161375) has recently been developed (Eduardo et al., 2005). The parental lines of this cross can be useful for studying melon disorders; Périn et al. (2002b) indicated that SC is useful for dissecting melon quality traits (including mealiness), and ‘Piel de Sapo’ F1 melon hybrids are sensitive to CI after long-term storage (Giambanco de Ena, 1997; Valdenegro et al., 2004, 2005). Cucumis melo from different cultivars of the ‘Piel de Sapo’ type can be stored at 6 to 9 °C and 85% to 90% relative humidity (RH) up to 16–20 d, but prolonging the storage results in CI (Giambanco de Ena, 1997; Valdenegro et al., 2005). Also, previous experience with melons from the C. melo var. inodorus group indicated that sensitivity to some disorders and senescence are strongly dependent on the cultivar, storage time, and temperature (Barreiro et al., 2000a; Giambanco de Ena, 1997; Miccolis and Saltveit, 1995; Valdenegro et al., 2004, 2005). For this reason, melon fruit of the NILs were tested for disorders at harvest or after postharvest refrigerated storage. Our hypothesis is that, in the NIL population, differences in the disorder symptoms are associated with the different introgressions coming from SC. The results were used to identify and map QTLs with a beneficial or detrimental effect on fruit quality, with less ambiguity than when other techniques are used.

Materials and Methods

Plant Material. A set of 27 NILs of C. melo derived from a cross between the Spanish melon cultivar PS and the exotic Korean accession SC were used. Most of the NILs had a single introgressed region from SC into the PS background covering the whole genome of the Korean accession (Eduardo et al., 2005, 2007). NILs were coded with the prefix “SC,” followed by a first number indicating the linkage group (LG) and a second number indicating the number of NIL within the LG, exactly the same nomenclature used by Eduardo et al. (2007).

Experimental design. Ten replications of one plant per NIL, 50 replications of one plant for the PS parental line, and five plants of SC were completely randomized in the field. The plantation had a grid with a distance of 2 m between rows and 1.4 m within rows (0.36 plants/m²), surrounded by a border of a commercial hybrid of C. melo cultivar Nicolás F1 (Syngenta Seeds, El Ejido, Spain), a widely cultivated ‘Piel de Sapo’ type which was used as reference for comparison purposes. Melon seeds were planted on 7 Feb. and transplanted on 7 Apr. to a field 50 m long divided into 12 rows that were covered by plastic mulch 1.1 m wide and 22.9 μm thick. Soil preparation, fertigation, plant protection, and other growing practices were those commonly used for melon cultivation in the Mediterranean conditions in Torre Pacheco (Murcia, Spain), a long-standing PS melon growing area. Further details about this experiment have previously been reported (Eduardo et al., 2007; Fernández-Trujillo et al., 2005a, 2005b).

Fruit were harvested at commercial maturity according to the indices previously reported for ‘Piel de Sapo’ melons (Fernández-Trujillo et al., 2005b). At least two fruit for each 23 replications of the control PS and at least five replications for eight NILs with introgressions in six LGs (SC2-2a, SC2-3d, SC4-4, SC5-2, SC8-3, SC8-4, SC9-3, and SC10-2) were harvested. Additional NILs with introgressions in seven LGs (SC1-4a, SC3-3, SC3-5ab, SC4-1hb, SC5-3, SC8-1, SC9-2a, and SC12-4hb) were also evaluated with three to five replications and five to 10 fruit per NIL depending on the availability of the fruit in the plot. Fruit were stored for 35 d at 8 °C ± 0.6 °C and 76% ± 4% RH, covered with plastic liners (Plásticos del Segura SL, Murcia, Spain) to reduce RH fluctuation in the atmosphere surrounding the fruit (air). The temperature and RH were selected according to recommendations from Giambanco de Ena (1997) and previous experiences on commercial storage of melon hybrids to induce CI without exacerbating decay (Valdenegro et al., 2005). After this time, fruit were examined for CI and other disorders, decay, loss of whole fruit finger texture, internal over-ripening, disorders, and flavor.

The physiological disorders at harvest, particularly over-ripening and water-soaking disorder, were examined (n = 7–10 replications of two fruits) in the above-mentioned NILs and in another not included in the refrigeration experiment (SC1-3d, SC6-4, SC7-4ab, SC9-1a, SC12-1ab). Observation of unexpected disorders at harvest (necrosis of the placental tissue, flesh browning and mealiness, skin greasiness, abnormal flavor, cork flesh browning, etc.) were also recorded and photographed.

Phenotypic evaluation. Typical symptoms of CI and associated decay by secondary infection of microorganisms were evaluated (Fernández-Trujillo and Martínez, 2006). The degree of skin CI was evaluated subjectively, and the whole
fruit was photographed on two opposite sides with a digital camera. Fruit were divided into five classes, depending on the skin or flesh area affected by the disorders: 0 = absent, 1 = very slight (0% to 5%), 2 = slight (5% to 10%), 3 = moderate (10% to 20%), and 4 = severe (>20%) (Fernández-Trujillo and Martínez, 2006; Miccisi and Saltveit, 1995). Moderately to severely injured fruit was considered to be unmarketable (noncommercial) because these disorders affected >10% of the epidermis or flesh surface in a double cut parallel to the longitudinal diameter.

The fruit affected by moderate or severe water-soaking disorder (glassy texture, glassiness, vitrescence, flesh translucency), loss of whole fruit finger texture, or internal over-ripening were also considered noncommercial and therefore included in total losses. A hedonic test after storage scored whole fruit hardness (finger texture) and flesh over-ripening according to the symptoms reported by Rose et al. (1998). A 1–5 scale was used to score fruit flavor based on Aguayo et al. (2007): 1 = poor, soft, insipid, and nonsweet; 2 = limit of acceptance with fair texture, slight sweet, and aromatic flavor or senescent aroma; 3 = medium, firm, balance between sweetness and flavor; 4 = very firm, juicy, good; 5 = firm, juicy, excellent. The index data of each disorder was calculated in each replication and recorded on a percent scale using the following formula:

\[
\text{Index} = \sum_{f=1}^{MaxG} G \cdot N_G \cdot \frac{MaxG}{MaxG} \times 100,
\]

where \( G \) = degree of the disorder or trait (0 to 4; 1 to 4; or 1 to 5), \( N_G \) = number of fruit showing the degree \( G \) of the disorder in each replication, and \( MaxG \) = maximum value of the degree scale (4 or 5). The index represents the extension of the disorder or the flavor intensity in a sample.

The presence of decay was recorded as a percentage of fruit affected per NIL and considered as losses according to Blancard et al. (1995). The fungi were recorded with digital pictures and identified by light microscopy (400× magnification). When only sterile mycelium appeared, melon fruit were subjected to additional storage (~1 week at 22 °C ± 2 °C with >90% RH) to facilitate the emergence of the conidiophores. In case of absence of conidiophores and conidia, techniques, such as cutting the mycelium, were applied to fungi growing in potato dextrose agar (PDA). Decay-causing fungi were identified up to genus level by using the manual of Barnett and Hunter (1999).

Total losses included unmarketable fruit that were affected by moderate-to-severe disorders or by any symptom of decay, but a low score for fruit flavor was not considered as loss. The NILs with over-ripening and water-soaking disorders after storage were used for analyzing the soluble solids content and sugars according to Aguayo et al. (2007). The juice squeezed at harvest was obtained from pulp of the middle mesocarp section between the epidermis and the seed cavity.

**Data Analysis.** Data were transformed into their respective arcsin or the arcsin for the square root to fit normal distribution when needed. Untransformed or transformed data were subjected to analysis of variance using JMP 5.1.2 (SAS Institute, Cary, NC). To study the effect of SC introgressions, mean NIL values were compared with the control genotype PS by the Dunnet contrast with the Type-I error \( \alpha = 0.05 \) calculated. NILs showing means significantly different from PS were assumed to harbor a QTL in their SC introgression. The number of QTLs was estimated and mapped in the melon genetic map according to Eduardo et al. (2007), assuming that there was only one QTL per introgression. When two NILs with overlapping introgressions showed significant effects, the QTL was considered to be located in the overlapping region.

**Results**

**Phenotypic analysis of the parental lines.** At harvest, PS showed few symptoms of flesh water-soaking or over-ripening (indices of 3.8% ± 1.4% and 4.3% ± 1.3%, respectively). PS was free from external or internal disorders or decay. The flavor index was in the range of 80–100%. After 35 d of storage at 8 °C, the same PS line could not be considered of commercial value because total losses were >10% (Table 1). The PS melons developed CI injury (usually colonized by *Alternaria* spp. and *Cladosporium* spp.) and, to a lesser extent, symptoms of over-ripening, loss of fruit flavor, or other rotting (*Fusarium* spp.) (Table 1). SC was very sensitive to mechanical damages, had a mealy flesh at harvest or after storage (data not shown), particularly at the full stage of maturity, and showed deep skin netting developed in the field; it also developed severe CI and associated decay after 3 weeks at 8 °C or longer (Fig. 1A, top; Table 1).

**Total losses.** The NIL SC8–1 showed lower total losses than the PS as a result of lower levels of CI and associated decay (Fig. 1, top). This effect was negatively compensated in the total losses by higher over-ripening symptoms (Table 1).

**CI.** CI symptoms (skin scald and pitting) developed on the fruit netting and were later colonized by *Alternaria* spp. or *Cladosporium* spp., generally growing together at 8 °C. Very slight or slight pitting resulted in slight skin depressing. On the surface of the fruit with moderate or severe CI, the skin was usually visibly affected by decay. SC developed slight CI after 1 week and moderate CI after 2 weeks (Fig. 1A, top), while PS showed no skin CI symptoms even before 3 weeks at 8 °C.

**Decay.** The main rots that developed after 1 month of storage at 8 °C in the population were *Alternaria* spp., *Cladosporium* spp., *Stemphylium* spp. Wallr., and *Fusarium* spp. These necrotrophic fungi mainly developed on scald and pitting incited by CI (Fig. 1A, top). In some NILs, the above-mentioned fungi developed in cracks and CI associated with skin netting and in the peduncle. *Alternaria* spp. and *Cladosporium* spp. were frequently isolated together from small skin CI lesions. SC fruit was severely affected by decay after 4 weeks at 8 °C (98% with alternaria rot and 15% with cladosporium rot). NILs did not significantly differ from PS in their susceptibility to alternaria rot or cladosporium rots (overall 46% ± 9% and 29% ± 10%, mean ± st, respectively). Rarely, both rots developed internally with mycelium. *Cladosporium* spp. was occasionally isolated from small spots with corky flesh browning. Botrytis rot incited by *Botrytis* spp. Pers. developed rarely (only NIL SC8–3 with 6% fruit) but was normally associated with the necrotrophic fungi mentioned above. The percentages of fruit affected by stemblyphium rot and fusarium rot were low in our experiment (Fig. 2D). *Fusarium* spp. were also located on fruit skin rather than only in the peduncle and was frequently associated with alternaria rot. SC8–4 showed a higher incidence of *Stemphylium* spp. (mostly located in the peduncle) but a lower incidence of fusarium rot than PS (Table 1). *Aspergillus* spp. Link, particularly, showed typical reddish stain on the fruit skin but only in nonrefrigerated fruit stored at 20 °C (data not shown).
Table 1. Physiological disorder indices and decay and total losses of interest for locating QTLs in the near-isogenic lines of *Cucumis melo* after 30–35 d at 8 °C. 

| Line     | Rep (no.) | Nf (no./line) | CI index* (%) | St (%) fruit | Fus (%) fruit | NPT (%) fruit | FT (%) | OR (%) | WSD (%) | Total losses (%) fruit | Flavor index (%) |
|----------|-----------|---------------|--------------|-------------|--------------|--------------|--------|--------|---------|-----------------------|------------------|
| SC1-4a   | 5         | 7             | 73           | 10          | 0            | 0            | 35     | 5      | 0       | 100                   | 56*               |
| SC2-2a   | 6         | 12            | 58           | 0           | 11           | 0            | 19     | 25     | 0       | 80                    | 37               |
| SC2-3d   | 6         | 14            | 38           | 0           | 26           | 43*          | 16     | 19     | 2       | 53                    | 28               |
| SC3-3    | 6         | 10            | 35           | 0           | 0            | 0            | 7      | 11     | 6       | 83                    | 36               |
| SC3-5ab  | 4         | 10            | 79           | 0           | 0            | 0            | 11     | 16     | 0       | 100                   | 60               |
| SC4-1hb  | 5         | 5             | 25           | 0           | 0            | 0            | 5      | 5      | 0       | 100                   | 40               |
| SC4-4    | 8         | 17            | 41           | 2           | 4            | 0            | 9      | 38*    | 0       | 94                    | 35               |
| SC5-2    | 9         | 16            | 62           | 2           | 4            | 0            | 24*    | 8      | 1       | 87                    | 29               |
| SC5-3    | 5         | 8             | 31           | 0           | 20           | 0            | 30*    | 46*    | 0       | 60                    | 33               |
| SC6-4    | 2         | 5             | 4            | 0           | 0            | 0            | 0      | 0      | 0       | 75                    | 25               |
| SC7-4ab  | 4         | 6             | 47           | 0           | 25           | 0            | 6      | 34     | 0       | 75                    | 20*              |
| SC8-1    | 4         | 5             | 17           | 0           | 0            | 0            | 13     | 47*    | 0       | 13*                   | 43               |
| SC8-3    | 8         | 19            | 71           | 6           | 6            | 0            | 28     | 38     | 0       | 92                    | 28               |
| SC8-4    | 10        | 50            | 43           | 10*         | 2*           | 0            | 8      | 13     | 12      | 73                    | 31               |
| SC9-2a   | 6         | 7             | 27           | 0           | 8            | 76*          | 4      | 0      | 0       | 50                    | 32               |
| SC9-3    | 7         | 12            | 41           | 0           | 0            | 0            | 0      | 7      | 6       | 86                    | 30               |
| SC10-2   | 5         | 13            | 54           | 0           | 10           | 0            | 5      | 3      | 22      | 93                    | 27               |
| SC12-4hb | 3         | 11            | 55           | 11          | 11           | 0            | 13     | 26     | 0       | 89                    | 55               |
| PS mean ± SD | 23  | 31            | 60 ± 5       | 0           | 6 ± 5        | 0            | 6 ± 3  | 11 ± 4 | 0       | 90 ± 5                | 45 ± 3           |
| SC        | 5         | 40            | 78           | 0           | 3            | 70           | 21     | 1      | 5       | 100                   | 30               |
| Nicolás  | 7         | 17            | 66           | 6           | 24           | 0            | 7      | 2      | 0       | 94                    | 53               |

*The SD following the mean is only included for the ‘Piel de Sapo’ parental line (PS); Rep = replications, Nf = total number of fruit, CI = chilling injury, St = stemphylium rot, Fus = fusarium rot, FT = loss of whole fruit finger texture, OR = flesh over-ripening, WSD = water-soaking disorder, NPT = necrosis of the placental tissue. Means with * were significantly different compared with the PS according to Dunnett test at P ≤ 0.05.

†Fruit of the Korean accession ‘Shongwan Charmi’ [SC (PI161375)] were examined after 4 weeks at 8 °C.

‡Commercial hybrid cultivar of the ‘Piel de Sapo’ type.

Index= \[ \sum_{i=1}^{MaxG} G_{Ni} \times 100 \]; G = score of the disorder (0 to 4; 1 to 4; or 1 to 5); N\_G = number of fruit showing the degree of the disorder; Max\_G = maximum score (4 or 5) multiplied by the sum of each replicate.

†Disorder index depending on the scores of the percentage of skin or flesh area affected: 0 = absent, 1 = very slight (0% to 5%), 2 = slight (5% to 10%), 3 = moderate (10% to 20%), 4 = severe (>20%).

††Flavor index obtained from the following scores: 1 = poor, 2 = limit of acceptance, 3 = medium, 4 = good, 5 = excellent.

**Necrosis of the placental tissue.** This disorder was manifested by a corky dry weight of seeds and placental tissue and usually started in the apex of the placental tissue before spreading to the nearby seeds and flesh (Fig. 1, bottom). *Cladosporium* spp., *Acremonium* spp. Link, *Stemphylium* spp., and *Alternaria* spp. were isolated from the necrotic tissue in <50% of the samples studied. These fungi were more probably a secondary fungal infection rather than the cause of the necrosis. The disorder was more frequent in mature fruit. The NILs SC2-3d and SC9-2a (n = 17 fruit) showed necrosis in 76% and 83% of fruit at harvest, respectively, while in SC2-2a (n = 15) 27% of the fruit were affected. The necrosis also occurred at harvest in mature SC fruit (Fig. 1E, bottom), and rarely occurred (slight symptoms <5% fruit affected) in other NILs located in six LGs (SC1-3d, SC1-4a, SC 4-1hb, SC5-3, SC9-1a, SC10-2, and SC 11-2hab). The disorder was confirmed in different degrees of severity after storage in NILs SC9-2a and SC2-3d (60% and 100% fruit affected, respectively; Table 1). Consequently, additional QTLs with a lower quantitative effect could be affecting the onset of the disorder.

**Fruit over-ripening.** Flesh over-ripening disorder was particularly important close to the seed cavity and the placenta, though fruit rarely split open at the blossom end. The NILs SC5-2 and SC5-3 shared a QTL responsible for loss of whole fruit finger texture (Table 1), indicating possible flesh softening surrounding the seed cavity. The NILs SC4-4, SC5-3, and SC8-1 showed more pronounced symptoms of flesh over-ripening than PS (Table 1; Fig. 2B). Over-ripening indices evaluated at harvest were only higher in NIL SC10-2 than in PS (21.8% vs. 16.4% ± 1.3%, respectively). In summary, only NIL SC5-3 showed symptoms of over-maturity, both external and internal (Fig. 2B).

**Water-soaking disorder.** The disorder started in vessels that feed the placental fruit tissue and developed through peripheral mesocarp tissue to give the flesh a translucent aspect and dark-brown color (Fig. 2E). NILs SC8-4 and SC10-2 also showed more symptoms of flesh spots or bitter pit as a manifestation of a water-soaking disorder (ranging from 12.5% to 22.5%; Fig. 2A and C). The same symptoms were observed in the flesh spots of mature or over-ripe SC fruit (data not shown).

**Sugar content in fruit affected by over-ripening or water-soaking disorder.** The NILs SC4-4 and SC5-3 did not differ from PS with respect to sugar content, but SC8-1 had lower glucose content (109 vs. 203 µmol g⁻¹ FW in SC8-1 and PS, respectively) and SC10-2 had lower sucrose content (272 µmol g⁻¹ FW). The NILs SC8-4 and SC10-2, with their more severe water-soaking disorder, showed lower sucrose contents than PS (164 µmol g⁻¹ FW in SC8-4, 272 µmol g⁻¹ FW in SC10-2,
and 380 μmol·g⁻¹ FW in PS). Additionally, SC8-4 had a lower glucose content than PS (92 vs. 203 μmol·g⁻¹ FW).

**Flesh Browning.** The disorder was absent or, when present, usually severe and was located a few millimeters below the skin and extended up to 75% of the cross section of the flesh (Fig. 2D), especially in fully mature fruit (data not shown). *Cladosporium* spp. were also identified in two of the four samples subjected to PDA culture. The NIL SC6–4 showed 24% flesh browning index at harvest (37% fruit affected, n = 19 fruit), a disorder that was absent in PS. This symptom was not a water-soaking disorder, which reached values of 3.8% ± 1.4% at harvest in PS and the color was never brown. After refrigeration, the flesh browning index was 38% (60% fruit affected, n = 5 fruit).

**Hollow Flesh Disorder.** The disorder was characterized by hollows randomly distributed in the mesocarp of the melon (Fig. 2F–I). The percentage of fruit affected by this disorder was low (10% in SC3-5ab, 4% in SC8-4, 8% in SC9-3, and 6% in PS). The affected fruit seemed to have a certain wateriness of the seed cavity and what looked like a few seeds germinating (Fig. 2F–I), which is a typical symptom of senescence (G.E. Lester, personal communication).
FLAVOR AFTER STORAGE. SC1-4a presented better flavor after storage than PS (Table 1). Line SC7-4ab had worse flavor scores than PS (Table 1), due to a particular ripening behavior. SC7-4ab had small fruit with hard flesh but sometimes showing over-ripening in the seed cavity (Fig. 2J). A few fruit of line SC3-5ab also had a very different flavor from PS and were similar to C. melo cultivar Amarillo.

OTHER DISORDERS AT HARVEST. Such disorders are not mapped in Fig. 3. The disorders only appeared in a few NILs and included dry or mealy flesh (SC8-4, SC12-1ab), skin greasiness (SC2-2a, SC2-3d); fruit cracking or deep furrows in netted melons (SC, SC2-2a, SC2-3d); fruit with off- or nontypical flavor (SC1-3d, SC8-4); and fruit with unusual ripening behavior (SC7-4ab; Fig. 2J). Fruit with off-flavor were sometimes associated with slight internal decay, as in the case of SC8-4.

MAPPING QTLs. Overall, the QTLs were identified in 10 of the 12 LGs of the genetic map of melon, with the exception of LGs III and XII (Fig. 3). Three of the QTLs had a beneficial effect on the quality traits. One QTL (tl8.1) reduced total losses, while three increased flesh over-ripening (ovr4.4, ovr5.3, ovr8.1). One QTL increased loss of whole fruit finger texture (ft5.3), and two more induced water-soaking (wsd8.4 and wsd10.2). The wsd10.2 QTL was probably associated with late ripening. Another QTL increased flesh browning (fb6.4). One QTL decreased the susceptibility to fusarium rot (fus8.4) but probably the same QTL increased the susceptibility to stemphylium rot (st8.4). One QTL improved overall fruit flavor after refrigeration (flv1.4), while another reduced fruit flavor after refrigeration (flv7.4). Two principal QTLs (nec2.3, nec9.2) were associated with necrosis of the placental tissue, while another six QTLs, which showed minor effects (nec1.3, nec1.4, nec4.1, nec5.3, nec10.2, and nec11.2), should be carefully studied.

Discussion

Overall, the NILs have proved their usefulness for dissecting beneficial postharvest traits. Among these traits, for practical purposes those involved in reduction of total losses and fusarium rot or in improved fruit flavor after storage are important. These three traits are important components of commercial fruit quality and consumer acceptance (Kader, 2003). Genetic factors, independent or not of ethylene control, are critical during fruit development and ripening (Guis et al., 1997). These NILs showed nonclimacteric behavior. However, they showed differential sensitivity to several disorders, confirming the apparent independence on the climacteric behavior during ripening and...
the susceptibility to the disorders. This independence was outlined by du Chatenet et al. (2000) for water-soaking and Miccolis and Saltveit (1991, 1995) for the postharvest loss of firmness in *C. melo* var. *inodorus* melons. The same may be true for placental necrosis. The differential sensitivity of the NILs to total losses or over-ripening opens up different possibilities. For example, new *C. melo* cultivars with extended shelf life or better performance for refrigerated transport or quarantine cold treatments can be developed.

The onset of postharvest quality and the development of disorders in melons are dependent on many preharvest factors, such as solar radiation (Lipton et al., 1987), soil fertilization (Lester and Grusak, 1999; Lester et al., 2005), and pre- and postharvest environmental factors (temperature, relative humidity, etc.) (Lester and Stein, 1993). The NILs in our experiment were grown in the same plot and conditions. Therefore, only minor differences in harvest date or differences in morphological or physiological changes typical of melons during ripening (Eduardo et al., 2007; Miccolis and Saltveit, 1991) could have affected the severity of the disorders.

The CI symptoms reported in the NILs studied generally agree with those found at 7.5 °C in bitter-melon (*Momordica charantia* L.), such as decay, pitting, and discoloration, as reported by Zong et al. (1995) and Valdenegro et al. (2004, 2005). The dominance of necrotrophic fungi *Alternaria* spp. and *Cladosporium* spp. associated with CI in our population

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Fig. 3. Location of the QTLs involved in disorders analyzed in fruit inspected at harvest or after 35 d at 8 °C on the melon genetic map. The map shows the skeleton from Gonzalo et al. (2005); on right of the linkage groups (LG) is shown the set of markers used to characterize the collection of near-isogenic lines (NILs) (Eduardo et al., 2005). Numbers indicate the position (in cM) of the marker on the LG, and on the left are shown the QTLs, with a bar indicating the extent of the introgression of the NIL that shows the effect. Underlined QTLs had beneficial effects on the trait.

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agrees with Snowdon (1991) and confirms the prevalence of CI in limiting fruit shelf life. For long-term storage, skin netting, which is a genetically determined character (Liu et al., 2004), was a critical factor that exacerbated CI and associated decay. Apparently, cultivars with skin netting are more prone to cracking. However, skin netting is also much appreciated as a quality index for consumers of PS melons. Therefore a compromise between both traits should be used in developing cultivars for long-term storage.

Ethylene production during the last ripening stages in melon results in shorter shelf life due to increased levels of postharvest decay (Zheng and Wolff, 2000). However, SC8-4, which exhibited increased stemphylium rot and reduced levels of fusarium rots, showed no significant differences in ethylene production at harvest compared with PS (data not shown). Fusarium rot was scarce and mostly in the peduncle, confirming previous results, (Snowdon, 1991). Fusarium spp. were not specific to CI because they also grew in fruit stored at 10 or 20 °C (data not shown). Stemphylium and fusarium rot QTLs in SC8-4 were probably the same, suggesting a certain competition between the two fungi in certain genetic backgrounds. This competition would affect fruit abscission or interaction among internal disorders, such as water-soaking spots (Fig. 2A), over-ripening, or stem-end mold. The role of calcium supply to the fruit during storage and the onset of senescence could be strongly influencing this QTL (Lester and Grusak, 1999).

The water-soaking symptoms observed in PS agree with those reported by du Chatenet et al. (2000) and Madriz et al. (1997, 2001). However, fermented (vinaigre-like) flavors were not detected. Nishizawa et al. (2004b) demonstrated that water-soaking mesocarp tissue does not result from increased alcoholic fermentation. Water-soaking disorder has been related in C. melo var. cantalupensis Naud. fruit to the accumulation of dry matter close to the placental tissue and to the lack of calcium in this zone (Cornillon et al., 2000; du Chatenet et al., 2000). Line SC8-4 is a green flesh line (Fig. 2A) that shows increased stemphylium rot at the peduncle but lower fusarium rot. NIL SC8-4 also had a slight incidence of hollow flesh disorder and much higher flavor loss during storage compared with PS. This latter fact was partly explained by water-soaking and sometimes by dry fruit texture (Fig. 1A, top). As occurs in C. melo var. cantalupensis (Cornillon et al., 2000), this disorder is difficult to study because it depends on the calcium gradient within the fruit, and nondestructive methods are not available. However, it is well known that water-soaking disorder is genetically determined in C. melo (Sánchez et al., 1997). A calmodulin-binding protein (CaM-BP) is absent in water-soaked but not in sound mature tissues, so it has been proposed as a marker for water-soaking disorder (du Chatenet et al., 2000). The corresponding gene of this protein could be a good candidate gene if it would map in the introgression of SC8-4.

The development of translucency symptoms in water-soaking disorder has been correlated with the sugar consumption by fruit to obtain energy to maintain metabolic activity. This hypothesis may be applicable to fresh-cut melon, particularly when processed in cylinders (Aguayo et al., 2004). At first sight, NILs both SC8-4 and SC10-2 showed low soluble solids concentration (Eduardo et al., 2007), supporting the previous hypothesis. However, other NILs showed lower soluble solids concentration than the PS (Eduardo et al., 2007) but no water-soaking disorder. Consequently, the lower soluble solids content in SC8-4 and SC10-2 could not be associated with water-soaking, in agreement with Nishizawa et al. (1998). These NILs may well harbor two independent linked QTLs controlling those traits.

Neither QTL ovr4.4, ovr5.3, or ovr8.1, which induced over-ripening symptoms, nor QTL f5.3, which induced loss of whole fruit finger texture, was related to those that reduced the sugar content. The QTL ovr8.1 that induced over-ripening could be associated with t18.1 that reduced total losses. In fact, fruit with an advanced stage of maturity are usually less susceptible to CI and associated decay (Lipton, 1978). In fact, Valdenegro et al. (2004) found that the susceptibility to CI in a PS hybrid could be reduced by externally applying ethylene, but this treatment induced internal over-ripening. The symptoms of over-ripening in SC10-2 were probably due to the difficulties to ascertain the right maturity at harvest in this line. SC10-2 presented a delay in average harvest date of >1 week compared with the PS line. Perhaps these were the reasons behind the higher over-ripening index at harvest (21.8%) compared with levels after storage (3%).

Necrosis of the placental tissue is a disorder new to melon (Eduardo et al., 2007) but previously reported in tomato (Blancard, 1994). Environmental or maturity effects, together with a possible minor contribution from the interaction of both with QTLs located in LGII, LGX, and other LGs cannot be ruled out, due to the minor incidence of necrosis in other NILs.

Hollow flesh disorder has not previously been described in melons. The symptoms of this disorder resemble the pillowy fruit disorder of cucumber (Cucumis sativus L.) fruit (Staub, 2002; Staub et al., 1987), but without the water-soaking and subsequent flesh browning. Pillowy fruit disorder is related with calcium deficiency, which in cucumber and watermelon [Citrullus lanatus (Thunb.) Matsum. and Nakai] has been associated with environmental and postharvest stress (Navazio and Staub, 1994). Hollow flesh is more probably a disorder related with senescence, perhaps brought on by an insufficient calcium supply during fruit formation, and the consequent expression of the disorder in fully mature fruit (G.E. Lester, personal communication). In cucumbers, the pillowy fruit disorder can be altered a certain degree during storage (Thomas and Staub, 1992), although the limited extent of hollow flesh disorder observed in our experiment did not enable us to try this in melon.

NILs SC2-2a and SC2-3d probably shared a QTL that exacerbates skin greasiness. The development of skin greasiness in ‘Jonagold’ apple [Malus ×domestica (Borkh.) Mansf.] has been associated with the presence of the secondary alcohol nonacosan-10-ol (Veraverbeke et al., 2001).

The mealy flesh QTL me-2 has been reported in melons (Périn et al., 2002a) and similar QTLs in tomato (Causse et al., 2001). The study of NILs with a mealy flesh or which show high flavor loss during refrigeration could be a straightforward approach to studying disorders occurring in fruit from the Rosaceae {apple, peach [Prunus persica (L.) Batsch]} or in tomato (Barreiro et al., 2000b; Causse et al., 2001).

**Implications for the future.** Physiological disorders are complex quality traits and new ones appear, particularly with the development of new cultivars or the introduction of new crops. The disorders reported in melon are similar to those found in other species from the Cucurbitaceae or other families. The QTLs detected in melon NILs have the potential to help us understand the genetic factors involved in new or existing fruit disorders, such as CI or hollow flesh disorder, and the
lower flavor life compared with postharvest appearance, which is very common in modern cultivars (Kader, 2003).

The number of markers used to screen the NILs is still limited (Eduardo et al., 2005, 2007). Consequently, some genomic regions are not well covered (e.g., top of LG I and VII; gaps of >45 cM between markers for LG II, IV, and IX). This, not only implies that some regions of the donor genome might not be represented in the set of NILs analyzed but also that some of the NILs that are supposed to contain a single donor introgression, could indeed contain multiple donor introgressions. Moreover, also in the case of the NILs that are known to contain additional donor regions (e.g., SC1-4a, or SC3-5ab), some of the QTL identified could be due to the presence of the additional donor introgressions (Eduardo et al., 2005). The NILs containing introgressions in LGs III and XII apparently do not contain QTLs associated with disorders, and SC3-5ab and SC12-1b in particular must be studied carefully in future experiments.

In summary, 14 QTLs were involved in several disorders. Three QTLs had positive effects on fruit quality, while 11 QTLs had a detrimental effect (not including hollow flesh disorders, the five minor QTLs of placental necrosis, or other minor disorders at harvest). The QTLs t18.1, f16s.4, and f14v.1 that reduce total losses, CI, fusarium rot, and flavor loss after storage, respectively, could be implemented in breeding programs. The goal for the future would be developing new varieties suitable for long-term storage with improved flavor and reduced susceptibility to decay and other disorders. Further studies with the QTLs described above will shed light on the genetic control of melon shelf life and help breeders interested in this fruit quality trait.

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