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# Inheritance mode of fruit traits in melon: Heterosis for fruit shape and its correlation with genetic distance

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**Summary**

Fruit quality traits were studied in 12 exotic accessions and their hybrids with a "Piel de Sapo" inodorus melon cultivar. The genetic relationships among these genotypes were assessed with 16 microsatellite markers, which agreed with the classification of *Cucumis callosus*, *C. pubescens* and *C. trigonus* as accessions within *C. melo*. There were very large differences between all the exotic accessions and "Piel de Sapo" genotype for fruit traits. When the hybrids were analysed, three different situations regarding mid parent heterosis were found, depending on the trait: no heterosis (soluble solid concentration), highly variable, from negative to positive (fruit weight and fruit diameter) and general positive heterosis (ovary shape, fruit length and fruit shape). Best parent heterosis for fruit shape was also common among hybrids. A highly significant correlation ($r = 0.81$) was detected between fruit shape and fruit length heterosis, suggesting that fruit shape heterosis is caused mainly by the enlargement of the fruit longitudinally. A highly significant correlation ($r = 0.84$) between heterosis for fruit shape and genetic distance, as estimated with microsatellites, was also found. These results, together with the previously reported observation that melon fruit shape is polygenic and highly heritable, makes the genetics of melon fruit shape a suitable system for dissecting the genetic and molecular basis of heterosis.

*Abbreviations:* $H_{MP}$, mid parent heterosis; $H_{BP}$, best parent heterosis; OS, ovary shape; FW, fruit weight; FD, fruit diameter; FL, fruit length; FS, fruit shape; SSC, soluble solid concentration

## Introduction

Melon (*Cucumis melo* L.) is an economically important species of the Cucurbitaceae family. The origin of melon was in Africa, but the distribution of wild and cultivated melon types currently is worldwide (Pitrat et al., 2000). A high level of molecular and morphological variability in leaf, plant and fruit characters has been described within this species (Kirkbride, 1993; Stepansky et al., 1999; Monforte et al., 2003). *C. melo* has been sub-classified in two sub-species based on the hairiness of the ovary (Jeffrey, 1980): *C. melo* ssp. *melo* with pilose or lanate ovaries and *C. melo* ssp. *agrestis* with sericeous ovaries. This classification has been confirmed by molecular marker studies (Stepansky et al., 1999; Monforte et al., 2003). Most European and American cultivars are classified within *C. melo* ssp. *melo*, while East and South Asian cultivars generally belong to *C. melo* ssp. *agrestis*. Within ssp. *agrestis*, Indian melon germplasm has the highest levels of genetic variability (Akashi et al., 2002; Monforte et al., 2003), representing an important reservoir of genetic variability.

South and East Asian melons have been used as a source of resistance genes (Pitrat & Lecoq, 1980; Soria et al., 1996; Morales et al., 2002). However, their fruit quality parameters are inferior according to Occidental standards, and their potential for improving fruit quality of European and American cultivars has not been investigated thoroughly. Mining alleles from

exotic or unadapted germplasm capable of improving elite modern cultivars is feasible combining Quantitative Trait Loci (QTL) analysis and marker assisted selection (Tanksley & McCouch, 1997). These principles have already been applied to tomato (Monforte et al., 2001) and rice (Xiao et al., 1998).

The Mediterranean region is a major world producer of both Cantalupensis and Inodorus melon types. "Piel de Sapo" market class melons, within the Inodorus type, are particularly important in Spain and are becoming of interest in the United States (Schultheis et al., 2002). In the current report, hybrids between a "Piel de Sapo" line and an array of exotic accessions belonging to both *melo* and *agrestis* subspecies were evaluated to investigate the potential of exotic melon germplasm being incorporated in breeding programs for fruit quality, and to study the genetic basis of fruit quality traits in melon.

## Materials and methods

### *Plant material*

The 13 melon accessions studied are described in Table 1. Some of them showed within-accession variability as assessed by molecular markers (Monforte et al., 2003). To minimize the effect of that variability, parental and hybrid seed used in the current experiment came from a single plant after self-pollination or crossing with Piel de Sapo (PS) control genotype, respectively.

### *Genetic relationships among genotypes*

The genetic relationships among the genotypes were estimated by analysing microsatellite marker variability. DNA was extracted from a mixture of leaves from ten individuals per accession using the method described by Garcia-Mas et al. (2000). The 16 microsatellite markers (CMACC146, CMAT141, CMAT35, CMCCA145, CMGA128, CMAG59, CMGA104, CMGA15, CMGT108, CMTA134b, CMTAA166, CMTC123, CMTC160, CSCCT57, CSGA57, CSAT425) used in the current study had been developed by Danin-Poleg et al. (2001). All microsatellites were amplified in a total volume of 15 $\mu$l of 1 $\times$ SSR buffer (20 mM $(NH_4)SO_4$, 75 mM Tris–HCl pH 8.8, 0.01% (v/v) Tween 20), 2 mM $MgCl_2$, 166 mM dNTPs, 2 pmol of each primer (one of them labelled with IRD-800) and 2 units of Taq DNA polymerase (PE Applied Biosystems). Cycling conditions were as follows: an initial cycle at 94 °C for 1 min followed by 35 cycles at 94 °C for 30 s, the appropriate annealing temperature for 30 s and 72 °C for 1 min and

*Table 1.* Melon (*Cucumis melo* L.) accessions examined in this study

| Plant designation | Code[a] | Accession no. | Subspecie[c] | Sex type[b] | Country of origin | Seed source[d] |
|---|---|---|---|---|---|---|
| Agrestis | AGR | | *agrestis* | m | India | CSIC |
| *C. callosus* | CAL | PI 435284 | | m | Iraq | NCRPIS |
| Ein Dor | EIN* | PI 385966 | *melo* | am | Israel | NCRPIS |
| Snake cucumber | FLEX* | PI 435288 | *melo* | m | Iraq | NCRPIS |
| Freeman Cucumber | FREE* | PI 420149 | *agrestis* | am | Japan | NCRPIS |
| Ginsen Makuwa | GIN* | PI 420176 | *agrestis* | am | Japan | NCRPIS |
| 2564 | INB* | PI 124112 | *agrestis* | m | India | NCRPIS |
| KLM-1683 | MAL | PI 536481 | *agrestis* | m | Maldives | NCRPIS |
| G 22841 | SEN* | PI 436532 | | am | Senegal | NCRPIS |
| Piel de sapo | PS | | *melo* | am | Spain | Semillas Fitó |
| *C. pubescens* | PUB | CUC48/1991 | | m | India | IPK |
| Songwhan Charmi | SON* | PI 161375 | *agrestis* | am | Korea | Semillas Fitó |
| *C. trigonus* | TRI | Ames 24297 | | m | Pakistán | NCRPIS |

[a]Codes marked with (*) are the same as those used by Silberstein et al. (1999) and Stepansky et al. (1999).
[b]Sex type: m, monoecious; am, andromonoecious.
[c]According to passport data or Monforte et al. (2003).
[d]Seed donors: NCRPIS: North Central Regional Plant Introduction Station (Ames, Iowa, USA); CSIC: La Mayora Research Station of Consejo Superior de Investigaciones Científicas (Málaga, Spain), Semillas Fitó S.A. (Barcelona, Spain); IPK: Institute of Plant Genetics and Crop Plant Research (Gatersleben, Germany).

a final cycle at 72 °C for 5 min. The annealing temperature was 51 °C for all microsatellite markers, except CMAG59 and CMGA104 were 45 °C was used. Five $\mu$l of loading buffer (95% formamide, 20 mM EDTA, 0.05% bromophenol blue, 0.05% xylene cyanol) were added to the PCR mix, samples were denatured at 100 °C for 10 min and 0.8 $\mu$l were loaded on to a LICOR IR$^2$ sequencer (Li-Cor Inc., Lincoln, Nebraska, USA) using 25 cm plates filled with 6% acrylamide gels in 1 × TBE (90 mM Tris-borate, 2 mM EDTA pH 8.0 and 7.5 M urea) buffer. Electrophoresis was performed at 1500 V, 35 mA and 31 W at 50 °C until the PCR products were visible. The molecular weight of each microsatellite band was estimated by comparing its migration on electrophoresis with the IRD-labelled STR molecular size marker (Li-Cor Inc., Lincoln, Nebraska, USA).

Nei (1972) standard genetic distance was calculated for each pairwise genotype combination. The Neighbour-Joining (NJ) phylogenetic tree was calculated with the software MEGA 2.0 (Kumar et al., 2001).

*Greenhouse experiment and characters measured*

Ten plants of each exotic accession, 10 of each hybrid and 20 of PS were equally distributed in two rows and completely randomised individually within rows in the greenhouse. Plants were grown in Cultivator-40 sack containing organic substrate (Bures Professional SA, Vilablareis, Girona, Spain) with ferti-irragation (N:P:K ratio 1:0.45:1.97, 10 ppm of microelements, pH 6.0, conductivity 1.8 mS/cm) and 20–30% drainage. Flowers were hand pollinated, allowing the development of only one fruit per plant. The agronomic evaluation included the following traits: ovary shape (OS) calculated as the ratio between ovary length and ovary maximum diameter, fruit weight (FW) in grams, fruit length (FL) in centimetres, fruit diameter (FD), the maximum fruit diameter in centimetres, fruit shape (FS) as the ratio FL/FD, soluble solid concentration (SSC) measured from melon flesh crude extract as °Brix with a refractometer.

*Statistical analysis*

Means, standard deviations and other statistical analysis were performed with SAS for Windows release 8.01. Means of exotic genotypes were compared with a PS control by a Dunnett (1955) test. In the case of FS, the value for the FLEX genotype was so different compared with the rest of the genotypes that subtle differences between the exotic genotypes and PS were undetected. The FLEX genotype was then excluded from the Dunnett test.

Mid parent heterosis ($H_{MP}$) was calculated relative to the expected mid parent value as:

$$H_{MP} = 100\left[F_1 - \left(\frac{P + PS}{2}\right)\right] \Big/ MP$$

where $F_1$ is the mean of the hybrid, $P$ the mean of the exotic parent and PS the mean of the "Piel de Sapo" control genotype and MP the mid parent value (average between the two parents).

The statistical significance of $H_{MP}$ was studied by the contrast:

$$2F_1 - P - PS$$

To consider a contrast significant, the probability threshold was adjusted according to the Bonferroni correction to $p < 0.00069$ to obtain an overall Type I error of 5% (0.05/72 contrasts = 0.00069)

Best parent heterosis ($H_{BP}$) was calculated relative to the best parent as:

$$H_{BP} = 100(F_1 - B)/B$$

where $B$ is the highest mean value of the exotic parent or PS. The contrast $F_1 - B$ was considered statistically significant when $p < 0.00069$.

Correlations of $H_{MP}$ and $H_{BP}$ for different traits were also calculated (considered significant if $p < 0.003$, 0.05/15 tests = 0.003), as well as the correlations between $H_{MP}$, $H_{BP}$ and Nei's genetic distance (considered significant if $p < 0.004$, 0.05/12 tests = 0.004).

## Results and discussion

*Genetic relationships among melon accessions*

A mean of five alleles per microsatellite marker was detected in the genotypes tested, ranging from two to 10 alleles. The Neighbour-Joining tree of all the genotypes, based on Nei's genetic distance is given in Figure 1. The tree topology was similar to that obtained previously by Monforte et al. (2003), reflecting the division of *C. melo* into two subspecies: *C. melo* ssp. *melo* (represented by the genotypes PS, EIN, FLEX, and SEN), and *C. melo* ssp. *agrestis* (represented by the other genotypes). *C. trigonus* (TRI), *C.*

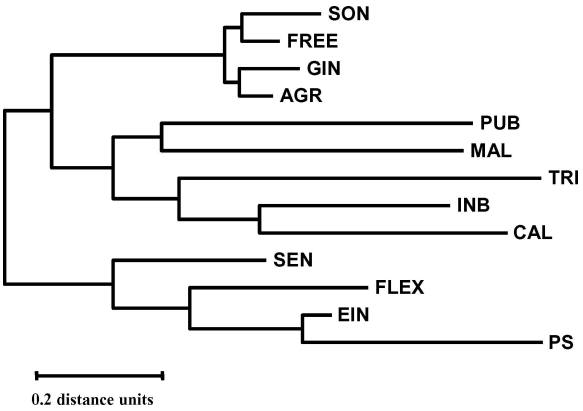


*Figure 1*. Neighbour-Joining tree of melon accessions based on Nei's genetic distance. Accession code is according to Table 1. The distance scale is indicated with a bar below the dendogram.

*callosus* (CAL) and *C. pubescens* (PUB) were clustered among ssp. *agrestis* accessions. Some confusion exists in the taxonomy of the latter accessions in the genus *Cucumis*. Although they were initially described as different species, several authors have identified them as synonyms of *C. melo* (Puchalski et al., 1978; Parthasarathy & Sambandam, 1980; Kirkbride, 1993). It has been suggested that *C. trigonus* is a synonym of *C. callosus* (Chakravarthy, 1959). The dendogram depicted in Figure 1 supports the inclusion of these accessions within *C. melo*.

*Parent, hybrid evaluations and inheritance mode of fruit traits*

Table 2 shows the means and standard deviations of the studied traits in parent genotypes. Significant differences between the exotic cultivars and PS were observed for all characters with PS fruits being in general bigger and sweeter than the rest of the genotypes. FLEX was the only fruit significantly more elongated than PS when all the genotypes were included in the analysis. When FLEX was not considered, subtler differences between PS and the exotic accessions were significant. Fruits of exotic accessions ranged from rounder (TRI), to similar (EIN, GIN, SEN, SON) or more elongated (AGR, CAL, FREE, INB, MAL, PUB) than PS. In general, fruits from monoecious plants were more elongated than fruits from andromonoecious plants, although some exceptions were observed; TRI ovaries and fruits were round but the plant was monoecious (Tables 1 and 2). Stepansky et al. (1999) also observed that discrepancy between sex type and ovary shape in a few melon accessions. Ovary and fruit shape are under a complex genetic control, sex type may be one of the factors affecting these traits. A number of QTLs independent from the sex type have been described recently (Périn et al., 2002; Monforte et al., 2004). The discrepancies between fruit shape and sex type may be due to different allelic combinations at several of these QTLs.

*Table 2*. Means and standard deviations for the traits ovary shape, fruit weight, fruit length and fruit diameter, fruit shape and soluble solid concentration

| Genotype | Ovary shape | Fruit weight (g) | Fruit length (cm) | Fruit diameter (cm) | Fruit shape (FL/FD) | Soluble solid concentration (°Brix) |
|---|---|---|---|---|---|---|
| AGR | 2.83* ± 0.45 | 325.83* ± 125.17 | 10.23* ± 1.80 | 7.33* ± 0.76 | 1.39[b] ± 0.13 | 7.59* ± 0.80 |
| CAL | 2.14 ± 0.28 | 35.09* ± 5.52 | 4.88* ± 0.45 | 3.48* ± 0.12 | 1.41[b] ± 0.12 | 5.10* ± 1.23 |
| EIN | 2.05 ± 0.33 | 1153.75* ± 455.26 | 15.13 ± 2.66 | 11.81* ± 1.33 | 1.27 ± 0.10 | 9.22* ± 2.88 |
| FLEX | 5.39* ± 0.54 | 1142.2* ± 418.27 | 48.05* ± 9.49 | 8.45* ± 0.98 | 5.73[a] ± 1.19 | 3.57* ± 0.80 |
| FREE | 2.30 ± 0.16 | 410.44* ± 144.74 | 13.81 ± 2.56 | 8.18* ± 0.61 | 1.69[b] ± 0.27 | 4.16* ± 0.87 |
| GIN | 1.81 ± 0.11 | 283.56* ± 71.33 | 8.65* ± 0.82 | 7.69* ± 0.63 | 1.13 ± 0.07 | 10.49 ± 1.02 |
| INB | 2.16 ± 0.45 | 652.40* ± 195.40 | 16.00 ± 2.12 | 8.81* ± 1.02 | 1.78[b] ± 0.03 | 2.80* ± 0.59 |
| MAL | 2.42* ± 0.35 | 131.40* ± 75.81 | 7.93* ± 0.84 | 5.39* ± 0.44 | 1.47[b] ± 0.06 | 5.98* ± 1.15 |
| PUB | na | 97.50* ± 27.58 | 8.75* ± 1.06 | 4.75* ± 0.35 | 1.84[b] ± 0.09 | na |
| SEN | 1.82 ± 0.14 | 303.53* ± 178.80 | 8.86* ± 1.97 | 7.81* ± 1.33 | 1.14 ± 0.14 | 7.00* ± 1.70 |
| SON | 2.14 ± 0.21 | 661.57* ± 157.54 | 13.42 ± 1.16 | 10.3* ± 0.41 | 1.31 ± 0.10 | 8.12* ± 0.33 |
| TRI | 1.66 ± 0.32 | 39.15* ± 9.38 | 4.31* ± 0.45 | 3.95* ± 0.35 | 1.09[b] ± 0.10 | 8.90* ± 2.13 |
| PS | 1.93 ± 0.22 | 1515.90 ± 206.04 | 16.05 ± 1.39 | 13.05 ± 0.89 | 1.23 ± 0.11 | 11.28 ± 1.18 |

Genotype codes are according to Table 1. In the case of fruit shape, (a) indicates significantly different from PS using all genotypes and (b) significantly different from PS after removing FLEX from the analysis. na denotes data not available.

* Indicates that the mean is significantly different ($p < 0.05$) compared with the PS control genotype.

*Table 3.* Mid and best parent heterosis ($H_{MP}$ and $H_{BP}$, respectively) for the measured traits

| Genotype code of exotic parents | Ovary shape (OS) | | Fruit weight (FW) | | Fruit length (FL) | | Fruit diameter (FD) | | Fruit shape (FS) (FL/FD) | | Soluble solid concentration (SSC) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $H_{MP}$ | $H_{BP}$ | $H_{MP}$ | $H_{BP}$ | $H_{MP}$ | $H_{BP}$ | $H_{MP}$ | $H_{BP}$ | $H_{MP}$ | $H_{BP}$ | $H_{MP}$ | $H_{BP}$ |
| AGR | 41.80* | 19.26 | −0.97 | −39.84 | 29.77* | 6.24 | −0.95 | −22.68 | 28.99* | 21.81* | −11.10 | −25.65 |
| CAL | 23.25* | 17.10 | −55.78* | −77.38 | 18.58* | −22.67 | −11.13 | −43.71 | 28.09* | 20.34* | −7.47 | −33.23 |
| EIN | −11.57 | −14.19 | 0.67 | −11.36 | 6.27 | 3.23 | 0.55 | −4.21 | 5.80 | 4.07 | −2.02 | −10.99 |
| FLEX | 8.79 | −26.13 | 51.61* | 32.92 | 11.55 | −25.60 | 9.30 | −9.96 | −11.60 | −46.29 | na | na |
| FREE | 33.84* | 22.96* | 69.02* | 7.39 | 59.81* | 48.69* | 14.02* | −7.28 | 34.97* | 16.76* | −12.27 | −39.96 |
| GIN | 21.84* | 17.95 | −7.54 | −45.12 | 30.12* | 0.14 | −3.35 | −23.20 | 35.70* | 30.07* | 0.31 | −3.22 |
| INB | 30.48* | 23.40* | 3.51 | −25.97 | 16.50 | 16.34 | −0.33 | −16.56 | 14.09 | −3.34 | −13.02 | −45.72 |
| MAL | 38.07* | 24.01* | 40.59* | −23.61 | 74.08* | 30.03* | 16.56* | −17.66 | 43.52* | 31.97* | −46.59* | −59.15 |
| PUB | na | na | 4.69 | −44.29 | 67.37* | 29.32* | 2.67 | −29.98 | 48.33* | 23.87* | na | na |
| SEN | −1.50 | −4.30 | −36.67* | −62.00 | −7.88 | −28.51 | −7.47 | −26.05 | 0.50 | −3.16 | 15.13 | −6.72 |
| SON | 34.03* | 27.31* | 21.17* | −12.97 | 49.77* | 37.50* | 1.18 | −9.48 | 49.06* | 45.04* | 14.41 | −1.62 |
| TRI | 38.11* | 28.31* | −51.66* | −75.21 | 21.65* | −22.87 | −9.48 | −41.06 | 36.36* | 28.59* | −9.83 | −19.35 |
| Correlation H-Nei's distance | 0.90* | 0.86* | 0.16 | −0.20 | 0.78* | 0.54 | 0.27 | −0.22 | 0.84* | 0.70* | −0.59 | −0.45 |

Genotype codes are according to Table 1. The bottom row indicates the correlation between heterosis and Nei's distance (*$p < 0.004$). na denotes data not available.

(*Significantly higher than mid or best parent, $p < 0.00069$) in the melon hybrids of "Piel de Sapo" and exotic melons.

The inheritance mode differed with traits and genotypes (Table 3). No significant heterosis was detected for SSC, except in the one case of MAL × PS hybrid, indicating an additive gene action for this trait. Mid parent heterosis ($H_{MP}$) for FW was observed in seven of the hybrids, the direction being negative in three of them and positive in the remaining four. Thus, $H_{MP}$ for FW seemed to be highly specific to the cross. A similar pattern was observed for FD $H_{MP}$, although the magnitude was lower, being significant only in a few cases. The traits OS, FL and FS gave highly significant positive $H_{MP}$ in most hybrids. $H_{BP}$ was observed only in these latter traits. Heterosis for these three traits was detected independent of the sex type of the exotic parent, suggesting that sex type has little or not influence on fruit shape heterosis. In summary, three different situations of heterosis were found, depending on the trait: no heterosis (SSC), highly variable (FW and FD) and generally positive heterosis (OS, FL and FS).

Correlations of heterosis between the different traits were also investigated (Table 4), giving only a few significant ones. The significant high correlation between FW and FD $H_{MP}$ ($r = 0.95$) and $H_{BP}$ ($r = 0.89$) suggested that FW and FD were different measurements of the same trait: fruit size. Similarly, the correlation between OS and FS heterosis supports the hypothesis that melon fruit shape is determined prior to anthesis (Périn et al., 2002). The significant

*Table 4.* Correlations of mid and best parent heterosis ($H_{MP}$ and $H_{BP}$) between the different traits (*$p < 0.003$). Trait abbreviations are according to Table 3

| | $H_{MP}$ correlations | | | | | $H_{BP}$ correlations | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | OS | FW | FL | FD | FS | OS | FW | FL | FD | FS |
| FW | 0.13 | | | | | −0.43 | | | | |
| FL | 0.70 | 0.53 | | | | 0.51 | 0.39 | | | |
| FD | 0.18 | 0.95* | 0.63 | | | −0.35 | 0.89* | 0.50 | | |
| FS | 0.77 | 0.02 | 0.81* | 0.09 | | 0.82* | −0.48 | 0.48 | −0.28 | |
| SSC | −0.47 | −0.36 | −0.60 | −0.60 | −0.33 | −0.39 | −0.19 | −0.35 | 0.01 | 0.12 |

correlation between FS and FL $H_{MP}$ ($r = 0.81$) and the lack of correlation with FD $H_{MP}$ ($r = 0.09$) suggested that FS $H_{MP}$ was caused mainly by the longitudinal enlargement of the fruit.

Heterosis for FS has been reported previously in melon hybrids (Abadia et al., 1985; Kitroongruang et al., 1992; Périn et al., 2002), supporting that heterosis for this trait may be common in melon. The same authors suggest that additive gene action for SSC is very common in melon hybrids (Abadia et al., 1985; Kitroongruang et al., 1992; Zhihua, 1995), in agreement with our results. Finally, these authors also reported heterosis for FW. This feature was not consistently detected by our analyses, indicating that heterosis for this character is cross-specific.

The genetic basis of heterosis has been a subject of debate since the beginning of the last century. Several hypotheses have been proposed to explain this phenomenon: overdominance at a single locus (Schull, 1908), dominance complementation and/or pseudo-overdominance (Bruce, 1910), and epistatic interactions (Allard, 1996). Recent advances in the identification and estimation of genetic effects at single Quantitative Trait Loci (QTL) have given insights into the genetic basis of heterosis. Some studies suggest that main effect QTLs, with overdominance/pseudo-overdominance or dominance complementation are the major genetic bases of heterosis (Stuber et al., 1992; Xiao et al., 1995; Lu et al., 2003), whereas other studies suggest that two-locus or higher order epistasis are involved (Li et al., 1997, 2001; Yu et al., 1997; Monforte & Tanksley, 2000; Hua et al., 2002, 2003). This apparent contradiction may be due to multiple non-exclusive reasons such as biased estimation of QTL effects (Melchinger et al., 1998), specificity of heterosis for each cross/trait/environment combination (Monforte et al., 1997; this report), low power to detect QTL × QTL epistatic interactions (Tanksley, 1993).

To the best of our knowledge, there are only two studies reporting estimates of the genetic effects of QTLs involved in melon fruit shape: Périn et al. (2002) and Monforte et al. (2004). Dominance effects at QTLs could be estimated only in one $F_2$ population, showing that addition is the most common gene action with FS QTLs (Monforte et al., 2004). However, important transgressive segregations were observed for this trait in populations of two recombinant inbred lines (Périn et al., 2002) and one double haploid line (Monforte et al., 2004) in several independent experiments. Together, these results suggest that heterosis for melon fruit shape can be produced by additive allelic complementation and epistatic interactions without the need for overdominance effects.

The recent development of a genomic library of melon introgression lines (Eduardo et al., 2003) will allow the unbiased estimation of single QTL effects, and, together with the advances in cloning genes involved in fruit shape (Liu et al., 2002; Van der Knaap et al., 2002), will provide the basic tools to elucidate the genetic and molecular basis of heterosis for fruit shape in melon hybrids.

### *Correlation between fruit shape heterosis and genetic distance*

Both types of heterosis ($H_{MP}$ and $H_{BP}$) for FS were common in hybrids between PS and accessions belonging to ssp. *agrestis*. Heterosis was also common for the traits FL and OS (Table 3). Significant correlation ($p < 0.004$) was observed between Nei's distance and fruit shape heterosis ($r = 0.84$ for $H_{MP}$ and $r = 0.7$ for $H_{BP}$), as well as OS and FL (Table 3).

Correlation between genetic distance and heterosis has been investigated in order to use information on genetic diversity to identify superior hybrids. Early reports suggested that genetic distance based on molecular markers between parents might be a good predictor of hybrid performance (Ali et al., 1995; Xiao et al., 1996; Zhang et al., 1994), however, recent reports have shown that the correlation may not be significant enough to be used as predictor of hybrid performance (Cheres et al., 2000; Manjarrez-Sandoval et al., 1997; Jordan et al., 2003) or may not be significant at all (Chowdari et al., 1998; Cerna et al., 1997). The correlation observed in the current report is higher than in the previous reports in different species, indicating that genetic distance might be a good predictor of heterosis for melon fruit shape. In the current report, melon accessions were crossed with a unique PS cultivar, further work is necessary to assess whether the correlation between genetic distance and heterosis for FS can be considered widespread in all melon germplasm or if it is specific to the current crosses.

### *Melon fruit shape as an alternative system to study the genetic basis of heterosis*

Most of the studies on heterosis have been carried out in cereals focusing mainly on yield. Yield is a very complex trait, controlled by multiple genes, with low heritability and high genotype by environment interaction, which make it difficult to obtain unbiased estimates of

single QTL effects. To minimize these problems, some authors propose the use of yield component traits with higher heritability instead of yield *per se* (Hua et al., 2002). On the other hand, recent studies have demonstrated that melon fruit shape is under highly heritable polygenic control (Périn et al., 2002; Monforte et al., 2004). Therefore, the study of melon fruit shape could be an appropriate system for the genetic dissection of heterosis and the study of the basis of the correlation between genetic distance and heterosis.

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