‘MAK-10’: A Long Shelf-life Charentais Breeding Line Developed by Introggression of a Genomic Region from Makuwa Melon

Gorka Perpiñán, Jaime Cebolla-Cornejo, and Cristina Esteras
Instituto de Conservación y Mejora de la Agrodiversidad Valenciana (COMAV), Universitat Politècnica de València (UPV), Camino de Vera 14, 46022 Valencia, Spain

Antonio J. Monforte
Instituto de Biología Molecular y Celular de Plantas (IBMCP), Consejo Superior de Investigaciones Científicas (CSIC), Universitat Politècnica de València (UPV), Camino de Vera s/n, 46022 Valencia, Spain

Bélén Picó¹
Instituto de Conservación y Mejora de la Agrodiversidad Valenciana (COMAV), Universitat Politècnica de València (UPV), Camino de Vera 14, 46022 Valencia, Spain

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¹Corresponding author. E-mail: mpicosi@lte.upv.es.
The melon breeding line ‘MAK-10’ was cultivated in the greenhouse facilities of the Fundación Cajamar in Paipata, in the spring-summer season in 2016 (from March to July). Plants were grown in substrate bags (70% coconut fiber and 30% coconut chips) and nutrients were provided through the irrigation system. Each plant was phenotyped for traits related to flowering (number of male and female flowers 15 and 30 after the opening of the first female flower, coded RefA15, RefF15, RefF30, and RefF30). The plants were self-pollinated, and the fruits were sequentially harvested at different stages after pollination (DAP), from 30 to 34, from 35 to 39, from 40 to 44, from 45 to 49, from 50 to 55, and >55 DAP. In addition, fruits of the two genotypes collected at 40–44 and at 50–55 DAP were stored in a chamber at room temperature and phenotyped at 5 and 10 d after harvesting (DAH), with the aim to study the postharvest behavior. All the fruits were phenotyped for the following traits with the methodology described by Perpiñá et al. (2016): fruit weight (FW), fruit length and diameter (FL and FD), cavity width (CW), flesh and rind thickness (Fth and Rth), FF, presence of AL, and netting occurrence (AL and NET), flesh color (FCHl, FCa, FCb), and soluble solids content (SSC). Sensory evaluation of the external aroma of the whole fruit was also performed, to determine if fruits have external aroma similar to that of VED were nonaromatic as MAK (AR).

A cross section of 5 cm was obtained from the equatorial plane of each fruit. This sample was used for the quantification of sugars (sucrose, glucose, and fructose) and organic acids (citric, malic, and glutamic) via capillary electrophoresis with the methodology described by Cebolla-Cornejo et al. (2012) with an Agilent 7100 system (Agilent Technologies, Waldbronn, Germany). Results were expressed in grams per kilogram of fresh weight. Sucrose equivalents were calculated by multiplying sucrose, glucose, and fructose contents by their relative sweetening power, 1, 0.74 and 1.73, respectively, and adding them up (Koehler and Kays, 1991).

### Description

‘MAK-10’ and VED do not differ in flowering time and fruit morphology. ‘MAK-10’ and VED did not show differences in a number of traits related to flowering time and fruit morphology. Both lines flowered the same week after transplanting and had similar number of male (RefA15 and RefF30) were 3.9 ± 0.57 and 6.95 ± 0.55 vs. 4.11 ± 0.25 and 7.10 ± 0.39 flowers, for ‘MAK-10’ and VED, respectively) and female (RefF15 and RefF30 were 2.66 ± 0.24 and 1.66 ± 0.34 vs. 2.21 ± 0.16 and 2.05 ± 0.18) flowers per plant, at 15 and 30 d after the opening of the first female flower.

### Table 1. Mean and standard error of fruit weight (FW), fruit length (FL), fruit diameter (FD), cavity width (CW), rind thickness (Rth), flesh thickness (Fth), flesh firmness (FF), presence/absence of abscission layer (AL), aroma (AR) and netting (NET), soluble solids content (SSC), and flesh color (parameters FCHl, FCa, FCb) in 'Vedrantais' (VED) and 'MAK-10' fruits collected at 30–34, 35–39, 40–44, 45–49, 50–55, and >55 d after pollination (DAP).

| DAP | Genotype | FW (g) | FL (mm) | FD (mm) | CW (%) | Fth (mm) | Rth (mm) | FF (kg cm⁻²) |
|-----|----------|--------|---------|---------|--------|----------|----------|------------|
| 30–34 | ‘MAK-10’ | 584.00 | 47.04 | 9.57 | 0.32 | 10.68 | 1.77 | 21.62 | 1.14 |
|       | VED      | 461.37 | 52.87 | 9.80 | 0.32 | 10.59 | 1.81 | 21.14 | 1.14 |
| 35–39 | ‘MAK-10’ | 406.33 | 25.78 | 9.83 | 0.23 | 9.80 | 2.38 | 49.38 | 2.46 |
|       | VED      | 580.00 | 103.24 | 9.46 | 0.40 | 10.52 | 0.67 | 50.47 | 4.16 |
| 40–44 | ‘MAK-10’ | 577.60 | 39.36 | 9.32 | 0.22 | 10.52 | 0.27 | 52.30 | 1.37 |
|       | VED      | 534.11 | 32.25 | 9.48 | 0.17 | 10.17 | 0.22 | 49.16 | 0.85 |
| 45–49 | ‘MAK-10’ | 576.25 | 27.57 | 8.70 | 0.17 | 10.10 | 0.17 | 50.36 | 2.72 |
|       | VED      | 498.00 | 32.99 | 9.04 | 0.25 | 9.99 | 0.21 | 48.18 | 1.18 |
| 50–55 | ‘MAK-10’ | 667.43 | 71.20 | 9.70 | 0.42 | 10.84 | 0.40 | 51.43* | 2.42 |
|       | VED      | 498.20 | 24.40 | 8.56 | 0.26 | 9.62 | 0.31 | 43.29* | 1.26 |
| >55  | ‘MAK-10’ | 492.00 | 106.00 | 8.75 | 0.15 | 10.4 | 0.60 | 45.88 | 2.75 |
|       | VED      | —-     | —-     | —-     | —-     | —-     | —-     | —-     | —-     |

### Description

‘MAK-10’ and VED fruits also did not differ in size and morphology during the ripening process, showing similar FW, FL, FD, CW, Fth and Rth, and netting at most DAP (Table 1). Therefore, despite the
early flowering, the small fruit size, the oval shape, and the thin and smooth rind of the MAK fruits (Perpiñá et al., 2016), the MAK introgression from chromosome 10 into the VED background of line ‘MAK-10’ did not alter these traits.

‘MAK-10’ differ from VED in the ripening process. One of the traits associated with the ripening process is FF. VED fruits presented a typical profile of FF evolution (Rose et al., 1998) with a continuous decrease of firmness (FF ranging from 6.60 ± 0.71 to 1.38 ± 0.32 kg·cm⁻² at 30–34 and 50–55 DAP, respectively) (Fig. 1). However, the firmness of ‘MAK-10’ fruits remained constant during the ripening process (FF of 4.40 ± 0.65 and 3.28 ± 0.36 kg·cm⁻² at 30–34 and 50–55 DAP).

VED fruits started to form the AL at 40–44 DAP and at 50–55 DAP most of the VED fruits had dropped from the plant and we could not harvest fruits after 55 DAP. ‘MAK-10’ fruits did not form AL during the whole ripening process (Table 1), and even after 55 DAP, the fruits remained attached to the plant.

The formation of the AL is an external signal of maturity of climacteric fruits and is associated with the occurrence of external aroma. VED fruits reached full maturity from 40 to 49 DAP, exhibiting at this time appropriated FF and SSC, based on commercial standards (FF from 3.57 ± 0.21 to 2.36 ± 0.33 kg·cm⁻² and SSC from 11.21 ± 0.62 to 13.08 ± 0.91 °Brix, at 40–44 and 45–49 DAP, respectively). VED fruits collected later, at 50–55 DAP were overripened, with very soft flesh (FF 1.38 ± 0.32 kg·cm⁻²). ‘MAK-10’ fruits collected at the VED ripening time (from 40 to 49 DAP) also met commercial requirements, although with a slight delay in the accumulation of SSC (FF from 4.42 ± 0.52 to 4.27 ± 0.33 kg·cm⁻² and SSC from 9.64 ± 1.14 to 13.65 ± 0.64 °Brix, at 40–44 and 45–49 DAP, respectively). At this time, ‘MAK-10’ fruits were netted with rinds turning to yellow, external signals of maturity that were also found in VED fruits. The fruits of ‘MAK-10’ collected after 50 DAP were not over ripe and still met commercial requirements for FF and SSC, even having SSC values higher than those of the VED fruits (SSC 12.76 ± 0.64 °Brix vs. 15.68 ± 0.32 °Brix, for VED and ‘MAK-10’, respectively).

Differences in flesh properties were further studied by analyzing sugar and acid profiles in both lines during the ripening process. Both showed the typical profile of sugar evolution (Burger et al., 2006; Zhang et al., 2016), with the hexoses content, fructose and glucose, being almost constant during the ripening process and sucrose accumulation bursting during the last phase of ripening (Fig. 2). The differences between ‘MAK-10’ and VED resided in the higher sugar content of the IL, starting at 45–49 DAP and at 50 to 55 DAP for hexoses and sucrose levels, respectively. Consequently, sucrose equivalents, a variable directly linked with sweetness perception was considerably higher in ‘MAK-10’ by the end of the ripening process. Apart from the higher sugar content observed in ‘MAK-10’, this line exhibited a delay in the profile of sugar accumulation (Fig. 2). For example, VED tended to decrease hexoses content from 40–44 DAP, whereas this decrease started later (from 45 to 49 DAP) in ‘MAK-10’. Similarly, the sucrose burst was delayed in ‘MAK-10’ (occurring from 35–39 to 45–49 in VED and from 45–49 to 50–55 in ‘MAK-10’).

The different performance in sugar accumulation did not apply to organic acid accumulation, as little differences could be found in the evolution of citric, malic, and glutamic acids between ‘MAK-10’ and VED (Fig. 3). In both lines, citric acid content more than doubled that of malic acid, whereas glutamic acid accumulated mainly at the end of the ripening process.
The delayed ripening of 'MAK-10' could also be observed as a delay of flesh color change (Table 1). Fruits harvested at the immature state (30–34 DAP) still had green to yellow flesh color, whereas VED fruits were already light orange (FCa: –4.95 ± 0.76 and 4.4 ± 1.4; FCb: 19.58 ± 0.34 and 21.7 ± 0.48, for MAK-10 and VED, respectively) (Fig. 4). Despite this delay in color change, 'MAK-10' fruits did not differ from VED fruits at maturity (40–49 DAP) and even retained better flesh color when collected later at 50–55 DAP (FCa: 10.92 ± 0.46 vs. 6.84 ± 0.78, for 'MAK-10' and VED, respectively).

'MAK-10' and VED differ in the postharvest behavior. Despite the FF of 'MAK-10' fruits being constant while the fruits remained attached to the plant (Fig. 1), during storage it decreased slowly (Table 2), as it has been previously reported for Makuwa melons (Zhang et al., 2015). Nevertheless, 'MAK-10' fruits harvested at 40–44 DAP maintained a significantly higher FF than VED at 10 DAH (2.05 ± 0.05 vs. 1.10 ± 0.12...
kg·cm⁻²). Similarly, ‘MAK-10’ fruits harvested at 50–55 DAP were firmer than VED fruits at 5 DAH (1.45 ± 0.05 vs. 0.90 ± 0.10 kg·cm⁻²). In this case, VED fruits could not be analyzed at 10 DAH because they were already rotten.

A decrease in SSC was observed during room storage (Table 2), more rapid in VED fruits at 40–44 DAP (13.3 ± 0.8 and 9.8 ± 0.9 °Brix, at 5 and 10 DAH, respectively) than in ‘MAK-10’ fruits (14.00 ± 0.96 and 13.15 ± 0.15 °Brix, respectively). ‘MAK-10’ fruits collected at 50–55 DAP also had a stable Brix degree after 5 and 10 DAH (14.60 ± 0.20 and 14.90 ± 0.70 °Brix, respectively). These results do not disagree with those of Zhang et al. (2015), who described an initial increase in SSC in postharvest Makuwa fruits, reaching a maximum after 7 d of storage followed by a slow decrease.

VED and ‘MAK-10’ fruits differed in the postharvest evolution of hexoses content (Table 3), which presented a more accentuated decrease in VED than in ‘MAK-10’ fruits. This decrease, which specially affected glucose content, was consistent with the anticipation of hexoses decrease during the ripening process observed in VED fruits attached to plants. These differences were more marked in fruits harvested at 40–44 DAP (a harvesting time closer to commercial maturity of VED melons). Sucrose content increased during storage in both genotypes in fruits harvested at 40–44 DAP, more in VED than in ‘MAK-10’, consistently with the delay in sucrose burst previously observed in ‘MAK-10’ fruits at harvest (Fig. 2). In fruits harvested at 50–55 DAP, a similar slight decrease in sucrose content was observed for both genotypes during postharvest. Despite this reduction, the sucrose content in ‘MAK-10’ during postharvest was nearly twice that of the VED fruits (65.1–73.4 vs. 29.3–34.2 g·kg⁻¹ in ‘MAK-10’ and VED fruits stored 5 and 10 DAH, respectively).

These changes in sugar content resulted in a higher loss of sucrose equivalents in VED than in ‘MAK-10’, which was more pronounced in fruits harvested at 40–44 DAP (Table 3). Consequently, fruits of ‘MAK-10’ showed higher sucrose equivalents levels, which remained more stable during postharvest storage, and they had a higher potential in terms of sweetness perception. Previous studies with Makuwa melons have also reported reductions in hexoses and increase in sucrose contents during the postharvest storage (Liu et al., 2012).

Regarding the acid profile, citric acid slightly decreased in a similar way in both lines; whereas a different evolution was observed in glutamic and malic acid, mainly in fruits harvested at 40–44 DAP. Both acids increased in VED fruits during storage, but decreased or remained stable in ‘MAK-10’ fruits.

Conclusions

Our results indicate that the introgression from ‘Ginsen makuwa’ carried by ‘MAK-10’ clearly affects the ripening process, delaying flesh softening, flesh color change, and sugar accumulation, and preventing the formation of the AL and external volatiles emission in whole fruits. However, apart from the lack of AL and external aroma, the characteristics of the ‘MAK-10’ fruits at commercial maturity (40–49 DAP) are similar to that of the VED fruits. The ‘MAK-10’ line has the additional advantage that the fruits maintain commercial value for longer attached to the plant and have higher sugar content. This property could be used to extend the harvesting period. ‘MAK-10’ fruits also retain FF, sweetness, and have less variation of the organic acid profile for longer duration during room storage, which could be useful to extend the shelf life of Charentais melons. Despite the lack of external aroma, that could be a limitation for its use in specific markets, such as that of Cantaloupe Charentais, the flesh of ‘MAK-10’ fruits is aromatic. We did not find apparent differences in their internal aroma with VED fruits during fruit characterization. A quantitative analysis of flesh volatiles is being conducted to characterize the aromatic profile of this breeding line.

The Makuwa introgression of ‘MAK-10’ is located at chromosome 10. Therefore, the two genes, AL-3 and Al-4, reported to prevent the formation of AL by Perin et al. (2002) are not involved in this phenotype. This region contains two genes (MELO3C012390, annotated as NAC/NAM transcription factor, and MELO3C012332, annotated as a HD-Zip homeobox transcription factor) related with the ethylene transcriptional regulation (Rios et al., 2017; Saladie et al., 2015). These genes are good candidates to be involved in the observed ripening delay. This ripening delay may also account for the observed differences in sugar content between VED and ‘MAK-10’. Differences in sugar content in melon fruits can be due to differences in sugar accumulation and/or in sugar metabolism. In general, the increase in sucrose level is associated with a gradual decline in inveratase activity and an increase in sucrose phosphate synthase activity, although contributions of additional enzymes have also been proposed. Several studies indicate that gene expression is reprogramed during the onset of ripening. According to Saladie et al. (2015), there exist differences between climacteric and nonclimacteric varieties in the expression of genes related to sugar metabolism.

Table 2. Mean and standard error of flesh firmness (FF) and soluble solids content (SSC) in fruits collected at 40–44 D after pollination (DAP) and at 50–55 DAP conserved at room temperature 5/10 d after harvesting (DAH).

| DAP + DAH | Genotype | FF (kg·cm⁻²) | SSC (°Brix) |
|-----------|----------|-------------|-------------|
| 40–44 DAP + 5 DAH | 'Vedrantais' (VED) | Mean: 0.60 a | SE: 0.10 | Mean: 2.50 b | SE: 1.00 |
| 40–44 DAP + 10 DAH | 'MAK-10' | Mean: 0.90 a | SE: 0.12 | Mean: 1.45 b | SE: 0.05 |
| 50–55 DAP + 5 DAH | 'Vedrantais' (VED) | Mean: — | SE: — | Mean: 1.00 | SE: 0.00 |
| 50–55 DAP + 10 DAH | 'MAK-10' | Mean: 1.00 a | SE: 0.10 | Mean: 14.00 a | SE: 0.96 |

Six fruits of each DAP, DAH, and genotype were phenotyped except for VED fruits at 50–55 DAP + 10 DAH (rotten fruits were not analyzed). Mean values in a row (for each harvesting date) followed by the same letter are not significantly different based on the least significant difference test (P ≤ 0.05) between ‘MAK-10’ and VED.

Table 3. Relative percentage of gain and loss of sugar compounds (fructose, glucose, sucrose, and sucrose equivalents) and acid compounds (citric, malic, and glutamic) of ‘MAK-10’ and ‘Vedrantais’ (VED) fruits harvested at different days after pollination (DAP) (40–44 and 50–55) and different days after pollination (DAH) (5 and 10) in comparison with fruits harvested at the same DAP without storage.

| DAP + DAH | Genotype | % Fructose | % Glucose | % Sucrose | % Sucrose eq | % Citric | % Malic | % Glutamic |
|-----------|----------|------------|-----------|-----------|--------------|----------|---------|-----------|
| 40–44 + 5 | 'MAK-10' | 0.00 a | -25.92 | 85.43 | -6.97 | -15.21 | -25.00 | 0.00 |
| 40–44 + 10 | 'Vedrantais' (VED) | Mean: -1.60 a | SE: -47.00 | Mean: 193.42 | SE: -13.66 | Mean: -26.19 | Mean: 83.33 | Mean: 750.00 |
| 50–55 + 5 | 'MAK-10' | 15.23 | 11.85 | -8.09 | 14.22 | -17.39 | -33.33 | -100.00 |
| 50–55 + 10 | 'Vedrantais' (VED) | Mean: -53.20 a | SE: -58.06 | Mean: 91.22 | SE: -54.50 | Mean: -4.76 | Mean: 50.00 | Mean: 300.00 |

Six sugars and organic acid compounds were quantified with the methodology described by Cebolla-Cornejo et al. (2012). Six fruits were analyzed for each genotype and DAP + DAH.
suggesting that they may be potential determinants of sucrose content and postharvest stability of sucrose levels in fruit. After the autocatalytic ethylene synthesis, the sucrose levels are stable in the flesh of VED melons (from 45 to 49 d on), whereas sucrose levels continue rising in ‘MAK-10’. Fruits of both genotypes were collected from plants at 50–55 d (all still attached to the plant). However, whereas VED fruits had already started the climacteric ripening process that can stabilize sucrose content, ‘MAK-10’ fruits lacked the autocatalytic ethylene synthesis and continued accumulating sucrose. In addition, the presence in the introgression of MAK alleles of genes involved in sugar metabolism can contribute to this differential sucrose accumulation behavior. In the introgressed, genomic region also maps MELO3C012320, a Sucrose-P phosphate 2 (CmSPP2) involved in sugar metabolism (Leida et al., 2015). This gene is a good candidate for future studies on this phenotype. Despite Makuwa melons being not as sweet as VED melons, MAK genes can have a different behavior when introgressed in a different genetic background. There are many examples of this type of masked variation when using ILs (Perpiñá et al., 2016).

In conclusion, ‘MAK-10’ provides fruits with long shelf life, stable flesh firmness, and high sugar content that can be suitable especially for melon markets other than Cantaloupe Charentais.

**Availability**

Small samples of ‘MAK-10’ seeds are available for research purposes, they can be obtained by written request to the author (mpicosi@btc.upv.es).

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