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# Regulation of climacteric fruit ripening in melon, recent advances and future challenges

Marta Pujol[1,2*] and Jordi Garcia-Mas[1,2*]

[1]Centre for Research in Agricultural Genomics (CRAG) CSIC-IRTA-UAB-UB, Edifici CRAG, Campus UAB, 08193 Bellaterra, Barcelona, Spain.

[2]Institut de Recerca i Tecnologia Agroalimentàries (IRTA), Edifici CRAG, Campus UAB, 08193 Bellaterra, Barcelona, Spain.

Marta Pujol: marta.pujol@irta.cat

Jordi Garcia-Mas: jordi.garcia@irta.cat

*Corresponding authors:

Marta Pujol, marta.pujol@irta.cat, Phone: +34 935636600

Jordi Garcia-Mas, jordi.garcia@irta.cat, Phone: +34 935636600

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## Highlight

Recent findings demonstrate that the intensity of the climacteric response and the amount of ethylene production can be genetically modulated in melon.


## Abstract

Fruit ripening is a complex and highly regulated process where tomato and strawberry have been the model species classically used for studying climacteric and non-climacteric fleshy fruit ripening types, respectively. Melon has emerged as an alternative ripening model because climacteric and non-climacteric cultivars exist, which makes it possible to dissect the regulation of ripening using a genetic approach. Several QTLs that regulate climacteric fruit ripening have been identified to date, and their combination in both climacteric and non-climacteric genetic backgrounds resulted in lines with different ripening behaviors, demonstrating that the climacteric intensity can be genetically modulated. The review discusses our current knowledge of the physiological changes observed during melon climacteric fruit ripening as ethylene production, fruit abscission, chlorophyll degradation, firmness and aroma, as well as their complex genetic control. From pioneer experiments in which ethylene biosynthesis was silenced, to the recent genetic edition of ripening regulators, current data suggest that the climacteric response is determined by the interaction of several loci under quantitative inheritance. The exploitation of the rich genetic diversity of melon will enable the discovery of additional genes involved in the regulation of the climacteric response, ultimately leading to breeding aromatic melon fruits with extended shelf life.



**Keywords:** CRISPR, cucurbits, ethylene, fruit ripening, genetic regulation, melon, QTL, VOCs.


## Introduction

Ripening is the last stage of fleshy fruit development after fruit set and growth, involving several drastic physiological and biochemical changes that are regulated in a coordinated manner (Barry and Giovannoni, 2007; Li *et al.*,

2022a). These changes make the fruit suitable and attractive for animal consumption with the final goal of seed dispersal. The most common physiological changes related to fruit ripening are chlorophyll degradation, accumulation of pigments, acids, sugars and volatile compounds, softening and fruit abscission. Two types of fleshy fruit ripening have been defined, climacteric and non-climacteric (Paul *et al.*, 2012). In climacteric fruits, a burst of respiration and ethylene production initiate the ripening process, whereas abscisic acid (ABA) and other hormones as auxins and jasmonic acid are involved in regulating fruit ripening in non-climacteric fruits (Fan *et al.*, 2022; Li *et al.*, 2022b), where the burst of respiration and the ethylene production do not occur. It is widely accepted that plant hormones, transcription factors (TFs) and epigenetic modifications are the major regulators of fruit ripening (Fenn and Giovannoni, 2021; Li *et al.*, 2022a).

In climacteric fruits as tomato, the classic model fruit, ethylene is the main hormone that controls the initiation of fruit ripening. Ethylene is synthesized from methionine through the enzymes 1-aminocyclopropane-1-carboxylic acid synthase (ACS) and 1-aminocyclopropane-1-carboxylic acid oxidase (ACO). This pathway is tightly regulated by both negative and positive feedbacks, known as system 1 and system 2, respectively. In system 2, ethylene is produced in a positive feedback loop and triggers fruit ripening (Barry *et al.*, 2000). When ethylene binds to its receptor (ETR), the signal transduction pathway triggers the inactivation of the Constitutive Triple Response (CTR) protein. Consequently, the positive regulator Ethylene-Insensitive 2 (EIN2) is activated, which in turn stabilizes Ethylene-Insensitive3 (EIN3) and EIN3-like proteins (EILs) that promote the expression of ethylene response factor (ERF) family genes, which are responsible of transforming the signal into a cellular response through regulation of ripening-related genes that control color, firmness, flavor, shelf life and additional traits (Liu *et al.*, 2015a). A set of upstream TFs are known to regulate ethylene biosynthesis and response, among them *ripening-inhibitor* (*RIN*), *non-ripening* (*NOR*), *colorless non-ripening* (*CNR*), *Tomato Agamous 1* (*TAG1*), *Tomato Agamous-like 1* (*TAGL1*) and *Fruitfull 1* and *2* (*FUL1* and *FUL2*) (Li *et al.*, 2022a). Another layer of ripening control is at the epigenetic level through DNA methylation, histone

post-translational modifications and $N^6$-Methyladenosine mRNA modifications (Li *et al.*, 2022a). It has been suggested that epigenetic regulation through DNA methylation and H3K27me3 histone methylation may represent a developmental switch that prevents the initiation of ripening before seeds are mature (Liu *et al.*, 2015b; Lu *et al.*, 2018; Zhong *et al.*, 2013). Lu *et al.* (2018) recently suggested three major types of transcriptional feedback circuits controlling climacteric fruit ripening. The first one is present in eudicots that suffered recent whole-genome duplications (WGD) as tomato, apple and pear, and would involve *MADS* TFs as *RIN* and *TAGL1* in the transcriptional control of ripening. These *MADS* TFs possibly evolved after WGD through neofunctionalization of duplicated *MADS* that originally controlled floral organ identity. The second circuit, present in climacteric species as peach, papaya and melon, which did not suffer a WGD, would involve transcription factors derived from carpel senescence *NAC* TFs. The third circuit would imply both *NAC* and *MADS* TFs in a dual-loop circuit, which would be present in the climacteric monocot banana (Lu *et al.*, 2018).

Unlike climacteric ripening, non-climacteric ripening control is much less understood, and non-climacteric fruits as strawberry and grape have been exploited as model species. ABA is described as the major regulator that controls ripening in strawberry, which is produced by the receptacle cells at the white fruit stage (Bai *et al.*, 2020; Li *et al.*, 2022b). TFs, epigenetic modifications and other phytohormones such as IAA, gibberellins, ethylene or jasmonic acid are known to interact and modulate ABA biosynthesis and signaling (Li *et al.*, 2022c). MADS-box and NAC TF proteins, as in climacteric ripening, are also known to control strawberry fruit ripening. In grape, several studies have shown that both ABA and IAA hormones play a central role regulating its ripening, and brassinosteroids, ethylene, gibberellins or jasmonic acid, among other hormones, are also involved (Fan *et al*. 2022; Fortes *et al.* 2015; Khun *et al*. 2013). Therefore, in non-climacteric fruits, hormonal regulation of ripening seems to be governed by the interaction of several hormones under a synergistic effect, in contrast to climacteric fruits, where ethylene is the main hormone controlling fruit ripening initiation.

Recently, melon has emerged as an alternative model for studying fruit ripening, as climacteric and non-climacteric melon types exist (Ezura and Owino, 2008; Pech *et al.*, 2008), making it possible to genetically dissect the regulation of fruit ripening. Crossing climacteric and non-climacteric melons generates climacteric ones, and accumulated data suggest that the genetic regulation of the climacteric trait in melon is complex (Pech *et al.*, 2008). Melon climacteric varieties of the *cantalupensis* group as 'Védrantais' show the typical burst of respiration and an increase of ethylene production observed in other climacteric species. Contrary, non-climacteric varieties, as 'Piel de Sapo' or 'Honeydew', belonging to the *inodorus* group, are not able to produce the peak of ethylene at the onset of ripening (Pratt *et al.*, 1977; Vegas *et al.*, 2013). The generation of *ACO1* antisense 'Védrantais' melon lines resulted in a reduction of ethylene production and provoked drastic effects in fruit ripening (Ayub *et al.*, 1996). Similarly, changes in the climacteric ripening phenotype were also observed in studies where ethylene production was compromised (Clendennen *et al.*, 1999; Nuñez-Palenius *et al.*, 2006; Silva *et al.*, 2004). Melons with suppressed ethylene production revealed that ethylene-dependent and ethylene-independent ripening pathways exist. Flesh color change due to carotenoid accumulation, sugar accumulation and a minor part of fruit softening are ethylene-independent processes, while a major part of softening, fruit abscission or the production of aromatic volatiles are ethylene-dependent (Pech *et al.*, 2008).

In this review, we will discuss the recent findings on the genetic regulation of climacteric ripening in melon. Controlling ethylene biosynthesis may be of great importance for extending fruit shelf life, improving shipping and storability, while maintaining fruit nutritional and organoleptic attributes. We will also discuss the possibility to modulate the climacteric intensity of melon fruit ripening by combining several recently characterized ripening-related QTLs, and the use of CRISP/Cas9 gene editing technology to improve new varieties.

## Phenotypic changes observed during melon climacteric ripening

During melon ripening fruit suffers several physicochemical changes as flesh and rind color change, sugar accumulation, fruit softening, ethylene and volatile

production and fruit abscission. All these traits can be expressed at different degrees or intensity, or even be absent depending on the cultivar and the type of ripening behavior. The most common melon cultivated types belong to the *cantaloupensis* (cantaloupe), *reticulatus* (muskmelon) and *inodorus* (honeydew) groups, which show a continuous spectrum of climacteric response and postharvest characteristics, suggesting that the classical dual classification into climacteric and non-climacteric types should be reconsidered. The absence of phenotypic indicators of melon ripening adds difficulty to the selection of uniformly ripe fruits during the harvest season. Melon types with extended or long shelf life (ESL or LSL) have slight ripening signals and do not abscise, often known as non-slip melons. Contrary, traditional shelf life (TSL) cultivars form an abscission layer and slip (Farcuh *et al.*, 2020). Therefore, the identification and measurement of different traits linked to ripening is of great importance at the scientific level and for transferring knowledge to melon growers and producers. In this review, we will focus only on the ethylene-dependent traits related to fruit ripening described by Pech *et al.* (2008), which are ethylene production, fruit abscission, chlorophyll degradation, firmness, and aroma (Figure 1). The accurate measurement of these traits has facilitated the mapping of several candidate genes related to climacteric ripening in this species.

Ethylene has an important role during ripening and an impact at postharvest, accelerating the decay of fruits and shortening their shelf life (Ayub *et al*., 1996; Pech *et al*., 2008). Therefore, it is of great importance to develop efficient methods for monitoring this gaseous hormone during ripening and storage. Detection and quantification of ethylene in melon-detached fruits has been performed using gas chromatography with a Flame Ionization Detector (GC-FID) (Moreno *et al.*, 2008; Obando-Ulloa *et al.*, 2008; Vegas *et al.*, 2013). Later, an improvement was performed to study ethylene production during fruit development *in planta* by enclosing fruits within a volatile collection chamber sealed temporarily to the stem to collect samples for GC, which is a non-destructive analytical method (Pereira *et al.*, 2017). In this case, the GC was coupled to a Mass Spectrometry (MS) detector to increase the sensitivity (GC-MS) (Pereira *et al.*, 2017; Pereira *et al.*, 2020). Electrochemical sensors are

also available to measure ethylene and have good sensitivity, however they lack robustness compared to GC analysis and are more frequently used to monitor ethylene in postharvest fruit management (Wang *et al.*, 2020). The complexity of analyzing a gaseous hormone represents a big challenge, and new methodologies combining non-destructive methods to detect and quantify ethylene in attached fruits during fruit development and ripening in a high throughput manner are still needed.

Another trait that has been widely evaluated as a signal of the onset of ripening or indicator of harvest time is fruit abscission (Beaulieu and Grimm, 2001). Abscission enables the detachment of the fruit by the enlargement, separation, and breakdown of cells in the abscission zone (AZ) (Corbacho *et al.*, 2013; Webster, 1975). This process is activated as a response to a developmental stage, hormone signal and environmental conditions; and in melon, it is differentially expressed depending on the ripening behavior of the cultivar. The regulatory gene network of AZ activation during melon ripening has been studied by Corbacho *et al.* (2013), showing the complexity of the process. Externally, the AZ activation in climacteric cultivars is visually observed as a crack or scar between the pedicel and the fruit, and depending on its extent, the fruit can be partially or completely detached of the plant (abscission). The easy observation of external signs of AZ activation has been used for gene mapping as a qualitative trait (presence or absence of abscission) (Dai *et al.*, 2022a; Pereira *et al.*, 2021; Perin *et al.*, 2002; Perpiñá *et al.*, 2016; Vegas *et al.*, 2013) or as a semi-quantitative trait in a scale from 0 (no sign of AZ activation) to 3 or 4 (fruit abscission) (Leida *et al.*, 2015; Pereira *et al.*, 2020; Santo Domingo *et al.*, 2022a; Santo Domingo *et al.*, 2022b). The abscission of ripe fruits has an impact on crop harvesting and production, even when present or absent, therefore, the study of its molecular and genetic determination is of great importance as a key trait for melon breeding.

External fruit color is a signal of ripeness and nutritional quality (Adaskaveg and Blanco-Ulate, 2023), being an important trait for fruit marketability. The major pigments accumulated in the melon rind are chlorophylls and carotenoids, but also flavonoids have been described; and the ratios of these compounds change during fruit ripening (Tadmor *et al.*, 2010). Rapid chlorophyll

degradation at the onset of fruit ripening, manifested by change in external visual color from green to yellow or degreening of the rind, is another trait to assess the ripening stage and to determine harvest time. It has been used as a qualitative trait (presence/absence) but also as an indicator of precocity of ripeness for mapping ripening-related QTLs in certain cultivars (Pereira *et al.*, 2021; Pereira *et al.*, 2020; Rios *et al.*, 2017; Santo Domingo *et al.*, 2022b; Vegas *et al.*, 2013). Nevertheless, the complexity and diversity of rind colors found in melon germplasm (Tadmor *et al.*, 2010), and their different behavior during fruit ripening makes it difficult to use this trait as a phenotype to study the onset of ripening, since both climacteric and non-climacteric cultivars can produce yellow or orange pigments at different stages of fruit development and ripening.

Fruit firmness or softening is another important quality trait that determines fruit shelf life, storability, transportation, and consumer acceptance, being texture a key trait in taste perception, together with aroma (Nishiyama *et al.*, 2007). Different factors contribute to fruit softening, as decrease in cell turgor, physiological changes in membranes, degradation of starch and cell-wall and apoplast modifications. However, the latter is considered as the main reason of texture changes in fruit ripening (Goulao and Oliveira, 2008). Highly climacteric varieties, such as cantaloupes, suffer a rapid decrease in firmness during ripening, and ethylene plays and important role in this process (Pech *et al.*, 2008). This phenotype can be determined by sensory evaluations, requiring a previously trained panel (Bianchi *et al.*, 2016; Farcuh *et al.*, 2020), and instrumentally with the use of a penetrometer (Moreno *et al.*, 2008; Nimmakayala *et al.*, 2016; Pereira *et al.*, 2020; Zhang *et al.*, 2022), or a Texture Analyzer (Farcuh *et al.*, 2020; Pan *et al.*, 2022).

Aroma in melon is determined by the volatile organic compounds (VOCs) produced during ripening (Gonda *et al.*, 2016). The characteristic climacteric ‘melon aroma’, which is a fruity flavor caused predominantly by esters, can be easily detected by smelling the fruits, since an intense aroma is released at the onset of ripening. In contrast, non-climacteric melon types such as those belonging to the *inodorus* group have a different composition of VOCs, predominantly determined by aldehydes giving a green, cucumber-like aroma

non-detected by simple smelling the fruit. Therefore, high sensitivity methods are needed to decipher the complex VOCs composition during melon ripening and after storage. Gas chromatography-mass spectrometry-solid-phase microextraction (GC-MS-SPME) has been the analytical method most extensively used in melon aroma determination (Esteras *et al.*, 2020; Esteras *et al.*, 2018; Freilich *et al.*, 2015; Galpaz *et al.*, 2018; Lignou *et al.*, 2013; Majithia *et al.*, 2021; Mayobre *et al.*, 2021; Santo Domingo *et al.*, 2022a). The identification and quantification of different VOCs will facilitate the study of metabolic pathways and the discovery of genes underlying their biosynthesis.

The ability to efficiently phenotype as many traits as possible related to fruit ripening will facilitate to perform genetic analysis to get insights into this complex process, facilitating its modulation in melon breeding programs.

**Aroma production in melon fruit**

Aroma is the melon fruit trait that has been more intensively studied in past years. The production of melon VOCs is influenced by several factors such as the genetic architecture of the plant, environmental conditions, and post-harvest storage conditions (Wyllie *et al.*, 1994). Many studies have been conducted to identify and quantify the composition of VOCs in different varieties of melon in both flesh and rind tissues, since they determine the characteristic flavor of each cultivar and are key factors determining consumer acceptance (Esteras *et al.*, 2020; Esteras *et al.*, 2018; Freilich *et al.*, 2015; Galpaz *et al.*, 2018; Lignou *et al.*, 2013; Majithia *et al.*, 2021; Mayobre *et al.*, 2021; Obando-Ulloa *et al.*, 2010; Shi *et al.*, 2020). The high genetic variability existing in melon (Zhao *et al.*, 2019) is probably determining the high number of VOCs already identified: more than 300 VOCs within the species and more than 100 VOCs in a single cultivar (Gonda *et al.*, 2016). The most abundant volatile compounds in melon are esters, aldehydes and alcohols, but other minor volatiles are also present depending on the cultivars, such as benzoids, ketones, furans, lactones, monoterpenes, sesquiterpenes and apocarotenoids (Gonda *et al.*, 2016).

Even though understanding the genetic control of VOCs biosynthesis in melon is essential to improve fruit flavor, not many genes that control this process

have been identified yet. In melon fruit, VOCs are produced through three main biosynthetic pathways: from fatty acids, from amino acids or from terpenoids, all of them involving several enzymatic reactions (Gonda *et al.*, 2016).

In the VOCs biosynthetic pathway from fatty acids, lipoxygenases (LOXs) are the main enzymes involved in aldehyde production. In the melon genome, 18 *CmLOX*s candidate genes have been identified (Tang *et al.*, 2015; Zhang *et al.*, 2014). The unsaturated fatty acids oxidized by LOXs are then metabolized by hydroperoxide lyases (HPLs) to finally produce aldehydes, and the *CmHPL* CYP74C family has been identified in melon (Grechkin *et al.*, 2006; Tijet *et al.*, 2001). Aldehydes, apart from being the main VOCs produced in non-climacteric varieties, are precursors of alcohols, which are produced by alcohol dehydrogenase enzymes (ADHs). Two *ADH*s have been characterized, *CmADH1* (*MELO3C023685*, alcohol dehydrogenase medium chain zinc-binding type) and *CmADH2* (*MELO3C014897*, alcohol dehydrogenase short chain type), which have been described as ethylene-dependent since they are coexpressed during the ethylene peak production (Manriquez *et al.*, 2006). The final step of volatile biosynthesis from fatty acids is the esterification of alcohols, mediated by alcohol acyltransferases (AATs). Four *CmAATs* (*Cm-AAT1, Cm-AAT2, Cm-AAT3* and *Cm-AAT4*) have been characterized and were described as key steps in the production of the melon unique aroma, being strongly regulated by ethylene (El-Sharkawy *et al.*, 2005; Liu *et al.*, 2020; Yahyaoui *et al.*, 2002).

Aminotransferases (ATs) are the enzymes that produce aldehydes from amino acids, and two *AT* genes have been identified in melon, *CmArAT1* (*MELO3C025613*, aromatic amino acid aminotransferase) and *CmBCAT1* (*MELO3C010776*, branched-chain amino acid aminotransferase) (Gonda *et al.*, 2010). More recently, genes involved in the downstream pathway such as *CmCNL* (*MELO3C025110*, CoA ligase), and *CmBAMT* (*MELO3C003803*, S-adenosyl-L-methionine:benzoic acid carboxyl methyltransferase) have been reported (Gonda *et al.*, 2018).

Terpenoids are also an important source of volatiles in melon aroma, and include monoterpenes, sesquiterpenes and apocarotenoids. Two terpene synthases (TPS) have been identified, *CmTpsDul* (*MELO3C016595*,

sesquiterpene synthase) and *CmTpsNY* (*MELO3C016588*, sesquiterpene synthase), in two melon accessions, ‘Dulce’ and ‘Noy Yizre’el’, respectively (Portnoy *et al.*, 2008). Related to apocarotenoids, three phytoene synthases (*PSY*) (Saladie *et al.*, 2015), and the gene *CmCCD1* (*MELO3C023555*, carotene cleavage dioxygenase) were identified (Ibdah *et al.*, 2006; Vogel *et al.*, 2008).

Not all the VOCs produced by the fruit have the same impact on the melon flavor or are equally perceived during fruit consumption (Gonda *et al.*, 2016). Some studies have been performed to correlate the different compounds with their impact in flavor by using different methods. Kourkoutas *et al.* (2006) evaluated the VOCs composition and sensory attributes (aroma and taste) of three different cultivars of melon, ‘Cantaloupe’, ‘Galia’ and ‘Honeydew’, and described the main characteristics of each melon type. Lignou *et al.* (2014) compared two cantaloupe melons with different shelf life at different maturity stages for VOCs production and flavor and concluded the importance of harvesting the fruits at the maturity stage as well as the negative effect on VOCs and flavor of the long shelf life varieties because of a reduction of total volatiles, mainly esters. Bianchi *et al.* (2016) evaluated six commercial varieties with a trained sensory panel to compare and correlate flavor with fruit texture and other quality traits. Even though some studies have been performed, there is a significant amount of work to be done to fully understand the relationship between the biosynthesis of VOCs and the flavor perceived by the consumer in order to define an effective breeding program aimed to improve fruit flavor in melon. Therefore, the biosynthesis of VOCs in melon is an area of active research, and further advances in this field will help us to better understanding the biochemical processes and the genetics that underlie the production of VOCs and their impact in melon flavor.

Ripening behavior is crucial in the production of VOCs and has an important effect in the aroma profile. In general, climacteric varieties are highly aromatic, characterized by producing a high number of total VOCs, being esters the predominant ones. On the other hand, non-climacteric varieties have much lower levels of total VOCs, with aldehydes and alcohols as the predominant volatiles (Allwood *et al.*, 2014; Esteras *et al.*, 2018; Gonda *et al.*, 2010; Moing *et*

*al.*, 2020; Obando-Ulloa *et al.*, 2008; Shi *et al.*, 2020). Freilich *et al.* (2015) studied the association between aroma and ripening by analyzing metabolomic and transcriptomic data of a RIL population between 'Dulce' (ssp *melo, reticulatus* group) and PI 414723 (ssp *agrestis*, *momordica* group) and observed that the production of VOCs in melon is an ethylene dependent process. Later on, Mayobre *et al.* (2021) also demonstrated the involvement of climacteric ripening in the production of VOCs in a RIL population between the climacteric *cantalupensis* type 'Védrantais' and the non-climacteric *inodorus* type 'Piel de Sapo'.

One of the main challenges related to aroma and ripening in melon breeding is the capacity to modify the ripening behavior without affecting the volatile content that determines fruit flavor. In general, climacteric varieties have short shelf life, such as cantaloupe melon types, which are highly appreciated by their unique aromatic flavor. It has been described that when developing long shelf life climacteric varieties, a decrease in flavor occurs, which negatively affects their marketability. Aubert and Bourger (2004) showed that long shelf life 'Charentais' melons reduced 2-30 fold the ester content, with a total VOCs reduction between 49-87 %. Lignou *et al.* (2014) also evaluated two types of 'Charentais' cantaloupe melons with different shelf life and concluded that those with long shelf life lacked fruity flavors and were less aromatic. Probably, the key factor is the relationship between ethylene production and VOCs biosynthesis. The ethylene and volatile production of a set of pyramided lines with ripening related QTLs in a non-climacteric background was evaluated by Santo Domingo *et al.* (2022a), and the results showed that once ethylene production is activated, total VOCs and ester production were increased, converting a low aromatic non-climacteric cultivar into a high aromatic one. Considering the accumulated findings in this field, we can assume that maintaining VOCs composition while increasing shelf life is a difficult task, however, by modulating ethylene production the biosynthesis of melon VOCs should be regulated. Therefore, there is a clear need to further study the genes related to VOCs biosynthesis and ethylene production in order to increase shelf life but still maintaining the production of the most important volatiles contributing to melon aroma.

## Genetic dissection of climacteric ripening in melon

In the last 20 years, several genetic studies have been conducted in order to understand the genetic control of fruit ripening in melon by comparing climacteric and non-climacteric accessions (Table 1). Some works have used recombinant inbred line (RIL) or introgression line (IL) populations for QTL analysis, and others performed association mapping using SNPs or whole genome sequencing. A few studies have obtained transgenic lines or CRISPR/Cas9 gene edited mutants to target genes related to ripening to elucidate their function.

A pioneer genetic study to decipher the genetic control of ripening between climacteric and non-climacteric melon cultivars was performed by Perin *et al.* (2002), using a RIL population composed of 144 individuals from the cross between the high climacteric cultivar 'Védrantais' and the non-climacteric Korean accession PI 161375 (Songwhan Charmi, ssp *agrestis*, *chinensis* group), and a second population of 64 RILs obtained by crossing 'Védrantais' with the Indian accession PI 414723 (ssp *agrestis*, *momordica* group). They observed a correlation between fruit abscission and ethylene production, being the climacteric phenotype dominant over the non-climacteric one, with absence of an ethylene peak and fruit abscission in non-climacteric fruits. Two redundant genes controlling ethylene-dependent fruit abscission and ethylene production, *Al-3* and *Al-4* , and four QTLs that modulated ethylene production (*eth1.1*, *eth2.1*, *eth3.1* and *eth11.1*) were identified (Perin *et al.*, 2002).

Later, Moreno *et al*. (2008) identified *eth3.5*, a QTL that induced climacteric ripening with increased respiration and ethylene production, in an IL collection obtained from two non-climacteric melon cultivars, 'Piel de Sapo' and PI 161375. They also reported five QTLs related to flesh firmness (*ff2.2*, *ff3.5*, *ff8.2*, *ff8.4* and *ff10.2*). This work showed the genetic complexity of ripening, since a climacteric phenotype was observed when combining two non-climacteric varieties. A second ripening-related QTL, *ETHQV6.3*, was characterized in the same IL population and the interaction between *eth3.5* (later named *ETHQB3.5*) and *ETHQV6.3* during fruit ripening was evaluated (Vegas *et al.*, 2013). An epistatic effect was observed when combining *ETHQB3.5* and *ETHQV6.3*, accelerating the climacteric response (ethylene

production, decrease in firmness and abscission layer activation) when the alleles of PI 161375 for both QTLs where introgressed in the 'Piel de Sapo' cultivar. Rios *et al.* (2017) performed a fine mapping of *ETHQV6.3* with the identification of the gene underlying *ETHQV6.3,* the *NAC* transcription factor *CmNAC-NOR* (*MELO03C016540*), a homologue of the tomato *NOR* gene. *CmNAC-NOR* has been the first cloned gene related to melon ripening, and recent results suggest that it is a key regulator of ripening in melon. To understand the function of *CmNAC-NOR*, Liu *et al.* (2022) performed CRISPR/Cas9 gene editing in the climacteric 'Védrantais' background. A knock-out mutant with a 1 bp deletion, causing a premature stop codon resulting in a truncated protein of 37 amino acids instead of 353, and a knock-down mutant with a 3 bp deletion causing the loss of a proline in the NAC domain were obtained. The knock-down mutant had a delay of 8-10 days of the onset of ripening, whereas the knock-out mutant did not ripe and showed no signs of ethylene and aroma production, resembling a non-climacteric cultivar. As previously described, no effects on flesh color (carotenoid content) or sugar content were observed in both *CmNAC-NOR* mutants. However, an unexpected phenotype was observed in the knock-out mutant, with a drastic effect on seed development. Another recent work in which CRISPR/Cas9 mutants of *CmNAC-NOR* were also obtained was reported by Wang *et al.* (2022) in the climacteric cultivar 'BYJH'. The authors showed that *CmNAC-NOR* regulates the expression of ethylene and ABA biosynthetic genes, as well as color and sugar biosynthetic genes. Some of their results do not completely agree with the data obtained by Liu *et al.* (2022), which could be attributed to the mutations being located in different domains of the CmNAC-NOR protein and thus having different effects. However, additional studies of these mutants are necessary to understand the mechanisms used by *CmNAC-NOR* to regulate climacteric ripening.

Leida *et al*. (2015) performed a genetic association study with 175 melon accessions in order to identify candidate genes involved in sugar accumulation and climacteric behavior, the later measured by activation of an abscission zone and loss of firmness. They observed the effect of intense selection for strictly climacteric or non-climacteric cultivars within ssp. *melo,* and a lower effect

449 within the ssp. *agrestis* cultivars, where a higher number of intermediate
450 ripening phenotypes were observed. Therefore, a high variability in ripening
451 behavior exists in melon, which offers the possibility to study the evolution of
452 this complex trait within the species. In this work, they observed a SNP located
453 in the coding region of *CmXTH5* (*MELO3C012004*) associated with fruit
454 abscission, which colocalizes with the previously described QTL *ff10.2* for fruit
455 firmness (Moreno *et al.*, 2008). Two other SNP associations for fruit abscission
456 and fruit firmness were also detected (Leida et al., 2015). Another genetic
457 association study was carried out by Nimmakayala *et al.* (2016) with 121
458 accessions belonging to different melon groups of worldwide distribution, and
459 also a biparental segregating population between 'MR1' (ssp. *agrestis,*
460 *momordica* group) and the western shipper cantaloupe 'Hale's Best Jumbo'
461 (ssp. *melo*, *cantalupensis* group). In this study, only fruit firmness was
462 evaluated, and QTLs, SNPs and candidate genes related to fruit softening were
463 identified on chromosomes 6, 8, 9, 11 and 12.

464 A transcriptomic analysis conducted between climacteric and non-climacteric
465 melon varieties confirmed the complexity of ripening behavior (Saladié *et al.*,
466 2015). Differential expression between climacteric and non-climacteric varieties
467 was observed for ethylene biosynthesis and signaling related genes such as
468 *CmACS1* (*MELO3C021182*), *CmACS5* (*MELO3C010779*), *CmACO1*
469 (*MELO3C014437*) and *CmATH* (*MELO3C026738*), which were highly
470 expressed in climacteric varieties, probably due to ethylene peak production at
471 the onset of ripening. Several genes related to fruit firmness were also strongly
472 up-regulated in 'Védrantais' than in 'Piel de Sapo' such as polygalacturonases
473 (*CmPG*), glucan endo-1,3-β-glucosidases (*CmGLU*) and β-d-xylosidases
474 (*CmXYL*), since fruit softening is more pronounced in climacteric melon types.
475 Moreover, many transcription factors were differentially expressed between
476 climacteric and non-climacteric varieties, suggesting that there are different
477 transcriptional regulatory networks depending on ripening behavior.

478 Two QTLs on chromosomes 7 and 10 (*MAK7-2* and *MAK10-1*) that delayed
479 ripening, increased firmness and decreased aroma were identified when the
480 'Ginsen makuwa' (PI 420176, ssp *agrestis*, *makuwa* group) alleles were
481 introgressed in the 'Védrantais' background (Perpiñá *et al.*, 2016). The MAK-10

introgression line, containing *MAK10-1*, lacked fruit abscission and was described as an interesting material for breeding long shelf life Charentais melons (Perpiñá *et al.*, 2017). A fruit abscission QTL on chromosome 10, *mfa10.1*, which colocalized with *MAK10-1*, was identified in a $F_{2:3}$ population between two thin-skinned melon lines with different ripening behavior (M2-10 and ZT00091) (Dai *et al.*, 2022a; Dai *et al.*, 2022b). *mfa10.1* has been fine mapped to an interval of 35 Kb, and *CmARM14* (*MELO3C012406*) has been proposed as the candidate gene, even though it has not been functionally validated. In the same population, two other QTLs related with flesh firmness were detected on chromosomes 2 (*ff2.1*) and 5 (*ff5.1*) (Dai *et al*., 2022b).

Another advance in the study of the genetic control of fruit ripening was obtained by Pereira *et al.* (2018, 2020), who revealed the existence of a major QTL on chromosome 8, *ETHQV8.1*, governing climacteric ripening, and other minor QTLs scattered across the genome modulating the climacteric response. This study was performed with a RIL population between 'Védrantais' and 'Piel de Sapo'. *ETHQV8.1* was also identified in a genome-wide association study (GWAS) with 211 accessions of the ssp. *melo* (Pereira et al., 2020). After a fine mapping strategy, among 14 genes contained within the genetic interval, three genes were considered as the best candidates for *ETHQV8.1*: an ethylene-responsive transcription factor *ERF024* (*MELO3C024520*), a serine/threonine kinase CTR1-like (*MELO3C024518*), and a protein *ROS1* (*MELO3C024516*). CRISPR/Cas9 mediated loss-of function mutants were obtained for the negative regulator of ripening *CTR1-like* and for the putative DNA demethylase *ROS1* in the 'Védrantais' background (Giordano *et al.*, 2022). Both mutations advanced ethylene production and ripening compared to the wild-type control, confirming their involvement in melon ripening. However, none of them seems to be the candidate gene underlying *ETHQV8.1* because of the observed phenotypes, and more work is needed to decipher the identity of this major regulator of fruit ripening located on chromosome 8. Interestingly, *ETHQV8.1* is located in a similar genomic interval than *Al-3*, however the very low resolution of the genetic map used by Perin *et al.* (2002) does not allow to conclude that both are the same QTL.

514 The role of *ETHQV6.3* (*CmNAC-NOR*) and *ETHQV8.1* in climacteric ripening
515 has been recently validated in two reciprocal IL collections between 'Védrantais'
516 and 'Piel de Sapo' (Pereira *et al.*, 2021; Santo Domingo *et al.*, 2022b). The 34
517 lines of the IL collection in the 'Védrantais' genetic background were all
518 climacteric, with aroma production and evident fruit abscission activation.
519 However, some ILs presented a delayed ripening or a less intense climacteric
520 phenotype when compared to the 'Védrantais' parental line. Most of the QTLs
521 were located on chromosomes 6 and 8, colocalizing with the previously
522 described *CmNAC-NOR* and *ETHQV8.1*, and other QTLs for chlorophyll
523 degradation, aroma production or earliness of ripening were detected on
524 chromosomes 2 and 11. Interestingly, 'Piel de Sapo' alleles on chromosome 11
525 advanced some ripening traits (Pereira *et al.*, 2021). On the other hand, most of
526 the lines from the IL collection in the 'Piel de Sapo' background were non-
527 climacteric, without production of aroma or fruit abscission. Nevertheless, some
528 ILs showed mild climacteric symptoms, confirming the segregation for ripening
529 behavior in the IL population. The most important detected QTLs were in
530 accordance with the reciprocal IL collection, being located on chromosomes 6
531 (*CmNAC-NOR*) and 8 (*ETHQV8.1*) for most of the ripening traits evaluated.

532 The importance of *ETHQB3.5* and *ETHQV8.1* was confirmed lately in a RIL
533 population between the climacteric 'Dulce' (ssp *melo*, *reticulatus* group) and the
534 non-climacteric 'Tam Dew' (ssp *melo*, *inodorus* group) cultivars (Oren *et al.*,
535 2022). Two major QTLs were found for ethylene production, *EtE3.3* and *EtE8.2*,
536 which colocalized with the previously described *ETHQB3.5* (Moreno *et al.*,
537 2008) and *ETHQV8.1* (Pereira *et al.*, 2020), respectively. Some candidate
538 genes were proposed based on genomic variations and transcript levels within
539 the *EtE3.3* interval: a WRKY family transcription factor *MELO3C011432* and a
540 transducin/WD40 repeat-like superfamily protein *MELO3C011365*. For *EtE8.2,*
541 a transmembrane protein putative gene, *MELO3C007661* was suggested.
542 However, none of these putative candidate genes has been validated. QTLs for
543 fruit firmness were also identified on chromosomes 2, 3 and 8. Concerning
544 *ETHQB3.5*, a recent report has used ILs containing overlapping introgressions
545 from PI 161375 in the 'Piel de Sapo' background in order to decipher the
546 underlying genes and their effect on volatile compound production (Dos-Santos

547 *et al.*, 2023). However, the candidate gene underlying *ETHQB3.5* remains
548 unknown.

549 In summary, even though many reports have tried to elucidate the genes
550 controlling the genetic complexity of climacteric ripening in melon during the last
551 20 years, only one master regulator has been identified and validated on
552 chromosome 6, *CmNAC-NOR* (*MELO03C016540*). Other major QTLs have
553 been identified for fruit abscission, ethylene production and climacteric ripening,
554 as *ETHQB3.5* on chromosome 3 (Dos-Santos *et al.*, 2023; Moreno *et al.*, 2008;
555 Oren *et al.*, 2022; Vegas *et al.*, 2013), *ETHQV8.1* on chromosome 8 (Oren *et*
556 *al.*, 2022; Pereira *et al.*, 2021; Pereira *et al.*, 2020; Perin *et al.*, 2002; Santo
557 Domingo *et al.*, 2022b), and *MAK10-1* on chromosome 10 (Dai *et al.*, 2022a;
558 Leida *et al.*, 2015; Perpiñá *et al.*, 2016). Interestingly, only the above-mentioned
559 four QTLs on chromosomes 3, 6, 8 and 10 were identified using different
560 mapping populations derived from several melon cultivars, suggesting that a
561 reduced number of genes control fruit ripening in melon. However, further work
562 is needed in order to determine the underlying genes of these QTLs and
563 elucidate their function and possible interactions.

564

565 **Modulation of the melon climacteric intensity**

566 It is important to understand the interactions between QTLs controlling
567 climacteric ripening in order to explore if it would be possible to modulate the
568 climacteric intensity by combining the effect of several QTLs, as it is exemplified
569 in Figure 2. The climacteric alleles of the above-mentioned QTLs *ETHQB3.5*,
570 *ETHQV6.3* and *ETHQV8.1* were recently introgressed in the non- climacteric
571 background of 'Piel de Sapo' (Santo Domingo *et al.*, 2022a). The three QTLs
572 produced a climacteric response in 'Piel de Sapo' independently, with some
573 production of ethylene and mild climacteric symptoms. *ETHQV6.3* advanced the
574 ethylene production and the ethylene peak, *ETHQB3.5* produced a narrowing of
575 the ethylene peak by decreasing the days from the start of the ethylene
576 production to its maximum production, and *ETHQV8.1* showed a weaker effect
577 compared to the other two QTLs, although it had an important role in enhancing
578 the response in combination with them. By combining these three QTLs, melons
579 with different degrees of climacteric response were obtained, demonstrating

that it is possible to control the amount and the time of the ethylene production and convert a non-climacteric phenotype into an extremely climacteric line, without affecting other quality traits as weight, soluble solid content and firmness (Santo Domingo *et al.*, 2022a).

The non-climacteric 'Piel de Sapo' allele of *ETHQV8.1* has also been introgressed in the climacteric background of 'Védrantais', producing a delay and a decrease in the ethylene peak (Pereira *et al.*, 2020). The ripening QTL *MAK10-1*, identified in the melon accession 'Ginsen makuwa' (MAK) was introgressed into 'Védrantais' to generate the MAK-10 breeding line, which also showed delayed ripening (Perpiñá *et al.*, 2016). These findings suggest that pyramiding the non-climacteric alleles of ripening QTLs in a climacteric background would also lead to the modulation of the climacteric response and an increase of the fruit shelf life.

## Conclusions and future perspectives

The genetic dissection of the control of climacteric ripening in melon has provided useful knowledge of this complex biological process. While several minor QTLs involved in ripening-related traits are distributed across the genome, four major QTLs have been identified as being involved in controlling fruit ripening. However, of these four major QTLs, only the gene underlying *ETHQV6.3*, the TF *CmNAC-NOR* (*MELO03C016540*), has been identified (Liu *et al.*, 2022; Rios *et al.*, 2017). Further work is needed to identify the genes underlying *ETHQB3.*5, *ETHQV8.*1 and *MAK10*-1 in order to understand their molecular function and interactions. Additionally, the exploitation of the rich genetic variability in melon may reveal new QTLs involved in fruit ripening regulation. Melon has been classified in 19 horticultural groups belonging to two subspecies (ssp. *agrestis* and ssp. *melo*) Pitrat (2017). Both climacteric and non-climacteric horticultural groups have been reported, some of them with intermediate behavior as Ameri and Cantalupensis, suggesting that natural variation for ripening behavior exists and could be exploited (Supplementary Table 1).

611 It has been demonstrated that the degree of climacteric response can be
612 genetically modulated in melon. Pyramiding the climacteric alleles of ripening
613 QTLs in the non-climacteric 'Piel de Sapo' background showed different
614 intensities of climacteric ripening. The line containing the climacteric alleles of
615 *ETHQB3.*5, *ETHQV6.3* and *ETHQV8.1* produced highly climacteric fruits that
616 produced early fruit abscission 28 days after pollination (DAP), while the control
617 climacteric line 'Védrantais' abscised at 36 DAP. In addition, individual non-
618 climacteric alleles of *ETHQV8.1* and *MAK10-1* in the 'Védrantais' climacteric
619 background delayed fruit ripening. Once the genes underlying all major QTLs
620 are identified, their natural variability in germplasm collections may provide new
621 alleles that may be used to fine-tune the ripening behavior. Moreover,
622 CRISPR/Cas9 gene editing of *ETHQV6.3* produced the line *nor-3* with delayed
623 ripening, confirming that gene editing is an effective tool for crop improvement
624 capable of producing additional ripening phenotypes that may be used to
625 extend fruit shelf life in breeding programs. However, it remains to be tested if
626 the organoleptic quality of these lines with altered ripening behavior is similar to
627 the original climacteric variety 'Védrantais'.

628 In tomato, non-climacteric cultivars are not available, making the modulation of
629 the climacteric intensity difficult. On the contrary, in melon we can exploit
630 natural and induced variability for breeding long shelf life varieties by comparing
631 the effect of allelic variation in genes such as *CmNAC-NOR* on ripening
632 behavior and shelf life. This turns melon into an attractive model to complement
633 the knowledge acquired in other model species to understand the control of fruit
634 ripening.

635 In view of our current knowledge about ripening regulation in melon, several
636 interesting questions arise. Would it be possible to generate climacteric lines in
637 non-climacteric close relatives as cucumber and watermelon by overexpressing
638 *CmNAC-NOR*, similarly to the climacteric 'Piel de Sapo' line containing an
639 introgression of *ETHQV6.3*? Another relevant direction would be to investigate
640 the ripening behavior of the undomesticated melon ancestor and understanding
641 how both ripening types evolved in this species.

642 The identification of new genes and their interactions will shed light into the
643 regulation of ripening, which is one of the most important traits related to melon

644 breeding. By using and combining all the information described in this review,
645 together with future findings and the use of gene editing technologies, it may be
646 possible to fine-tune the climacteric behavior and develop high quality long shelf
647 life varieties adapted to a more sustainable agriculture.

648

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653

654 **Conflict of interest**

655 The authors declare that they have no conflict of interest.

656

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663 **Data availability**

664 This review contains no new experimental data.

665 **References**

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## Tables

666 Table 1: List of QTLs and SNPs associated to climacteric ripening traits.

| QTL | Chr | Trait | Source | Reference |
|---|---|---|---|---|
| *Al-3* | 8 | ABS, ETH | RIL collection from 'Védrantais' x PI 161375 | Périn *et al.*, 2002 |
| *Al-4* | 9 | ABS, ETH | | |
| *eth1.1* | 1 | ETH | | |
| *eth2.1* | 2 | ETH | | |
| *eth3.1* | 3 | ETH | | |
| *eth11.1* | 11 | ETH | | |
| *ff2.2* | 2 | FIR | IL collection from 'Piel de Sapo' x PI 161375 | Moreno *et al.*, 2008 |
| *ff3.5* | 3 | FIR | | |
| *ff8.2* | 8 | FIR | | |
| *ff8.4* | 8 | FIR | | |
| *ff10.2* | 10 | FIR | | |
| *ETHQB3.5* | 3 | ETH, ABS, FIR | IL collection from 'Piel de Sapo' x PI 161375 | Moreno *et al.*, 2008; Vegas *et al.*, 2013 |
| *CmNAC-NOR (ETHQV6.3)* | 6 | ETH, ABS | IL collection from 'Piel de Sapo' x PI 161375 | Vegas *et al.*, 2013; Rios *et al.*, 2017 |
| SNP_CmXTH5 | 10 | ABS | GWAS 175 *C. melo* accessions | Leida *et al.*, 2015 |
| SNP_MLO65044.1 | 12 | ABS | | |
| SNP_PSI_41-B07 | 11 | FIR | | |
| GWAS SNP associations | 6,8,9,11,12 | FIR | GWAS 120 *C. melo* accessions and biparental F2 population from MR-1 x 'Hale's Best Jumbo' | Nimmakayala *et al.*, 2016 |

| | | | | |
|---|---|---|---|---|
| *MAK7-2* | 7 | ABS, FIR, ARO | IL collection from 'Védrantais' x 'Ginsen makuwa' | Perpiñá *et al.*, 2016 |
| *MAK10-1* | 10 | ABS, FIR, ARO | | |
| *ETHQV8.1* | 8 | ETH, FIR, ABS, ARO | RIL collection from 'Védrantais' x 'Piel de Sapo' | Pereira *et al.*, 2020 |
| Several QTLs related to climacteric ripening | 2,3,5,6,7,10,11 | ETH, FIR, ABS, ARO | | |
| PS6.2, PS8.2 | 6,8 | ABS | Two recirpocal IL collections from 'Piel de Sapo' x 'Védrantai's and 'Védrantais' x 'Piel de Sapo' | Pereira *et al.*, 2021; Santo Domingo *et al.*, 2022b |
| PS6.2, PS8.2, PS11.3 | 6,8,11 | ARO | | |
| PS2.1, PS4.1, PS8.2, PS8.3, PS12.2, PS12.3 | 2,4,8,12 | FIR | | |
| VED6.3, VED8.1, VED8.2, VED8.3 | 6,8 | ABS, ARO | | |
| VED2.2, VED2.3, VED8.2, VED8.3, VED11.2 | 2,8,11 | FIR | | |
| *EtE3.3, EtE8.2* | 3,8 | ETH | RIL collection from 'Dulce' x 'Tam Dew' | Oren *et al.*, 2022 |
| *RF2.1, RF3.1, RF3.2, RF8.2, FF8.3, FF5.1, FF2.1* | 2,3,5,8 | FIR | | |
| *mfa10.1* | 10 | ABS | F2 population from 'M2-10' x 'ZT00091' | Dai *et al.*, 2022a; Dai *et al.*, 2022b |
| *ff2.1, ff5.1* | 2,5 | FIR | | |

667 * Fruit abscission: ABS; ethylene production: ETH; flesh firmness: FIR; aroma: ARO.

## Supplementary Tables

**Supplementary Table 1:** Ripening traits across melon horticultural groups.

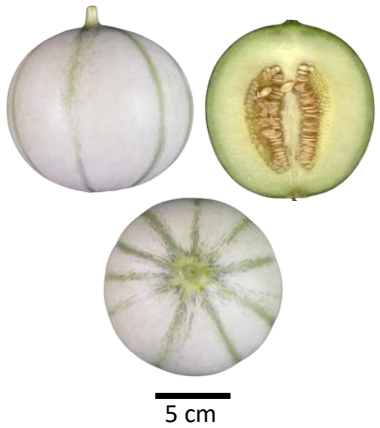
## Figure legends

**Figure 1**: Climacteric and non-climacteric ripening in melon. Representation of ethylene, volatile organic compounds (VOCs) production and fruit ripening in a high climacteric cantaloupe melon and a non-climacteric *inodorus* melon. At the onset of ripening, climacteric fruits produce a peak of ethylene and an increase of respiration. Almost simultaneously, a great amount of diverse VOCs is synthetized, the abscission zone is activated, and flesh firmness decreases rapidly. In contrast, non-climacteric fruits do not produce ethylene, do not increase respiration, VOCs production is lower and less diverse, there is no fruit abscission and the decrease in firmness occurs slowly compared to climacteric melons. Fruit pictures correspond to 'Védrantais' (top) and 'Piel de Sapo' (bottom) cultivars. Scale bar represents 5 cm.

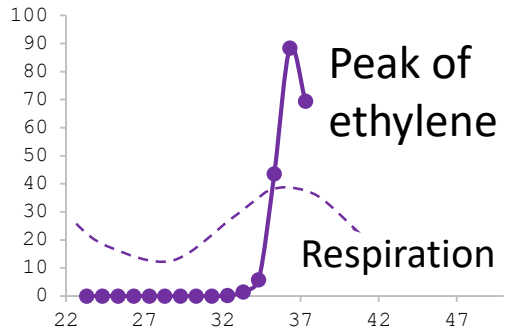
**Figure 2**: Modulation of melon ripening and shelf life through ethylene production. This chart represents the behavior of ethylene production in time until maturity (days after pollination) when combining four different major QTLs related to ripening (*ETHQB3.5, ETHQV6.3, ETHQV8.1 and MAK10-1*) in different genetic backgrounds: 'Védrantais' (VED, purple), 'Piel de Sapo' (PS, green), 'Songwhan Charmi' PI 161375 (SC, orange) and 'Ginsen makuwa' (MAK, blue). Arrows represent the introgression of a QTL, and their color represents the genetic background (allele) of the donor. Introgression lines are coded by the number of QTLs introgressed, followed by 'Q', the donor line, and the chromosome where the QTL is derived (1QSC3, 1QSC6, 1QVED8, 1QPS8, 1QMAK10, 2QSC3SC6, 2QSC3VED8, 2QSC6VED8 and 3QSC3SC6VED8). CRISPRCas9 edited lines in the VED background are represented in red color, with the name of the edited gene: *ros1* (knock-out of the *ROS1* gene), *ctr1* (knock-out of the *CTR1* gene), *nor-1* (knock-out of the *NAC-NOR* gene) and *nor-3* (knock-down of the *NAC-NOR* gene). The ethylene production was retrieved from Santo Domingo *et al.* (2022a), Liu *et al.* (2022) and Giordano *et al.* (2022). Scale bar represents 5 cm.

CLIMACTERIC CANTALOUPE MELON

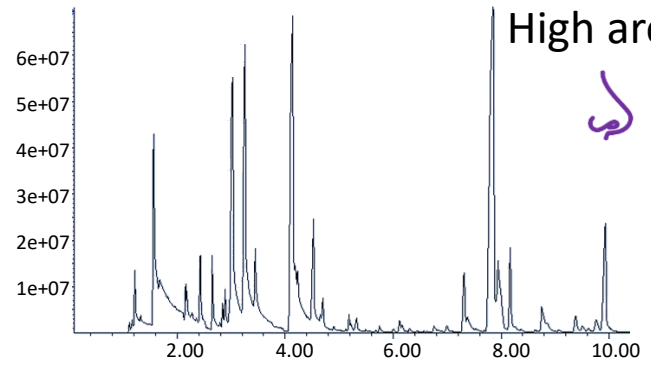
BEFORE RIPENING
15 days after pollination



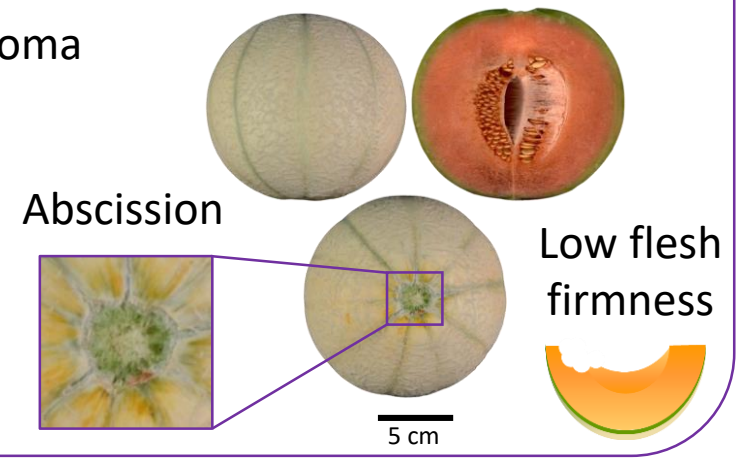

ETHYLENE PRODUCTION




VOCs PRODUCTION



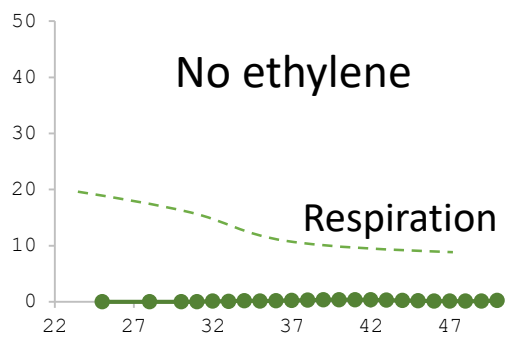

AFTER RIPENING
At harvest



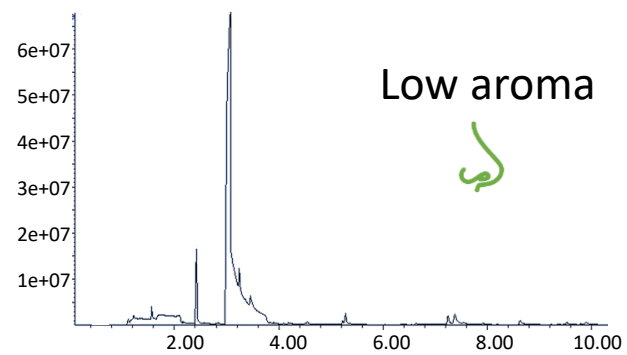

NON-CLIMACTERIC INODORUS MELON

BEFORE RIPENING
15 days after pollination


ETHYLENE PRODUCTION




VOCs PRODUCTION




AFTER RIPENING
At harvest

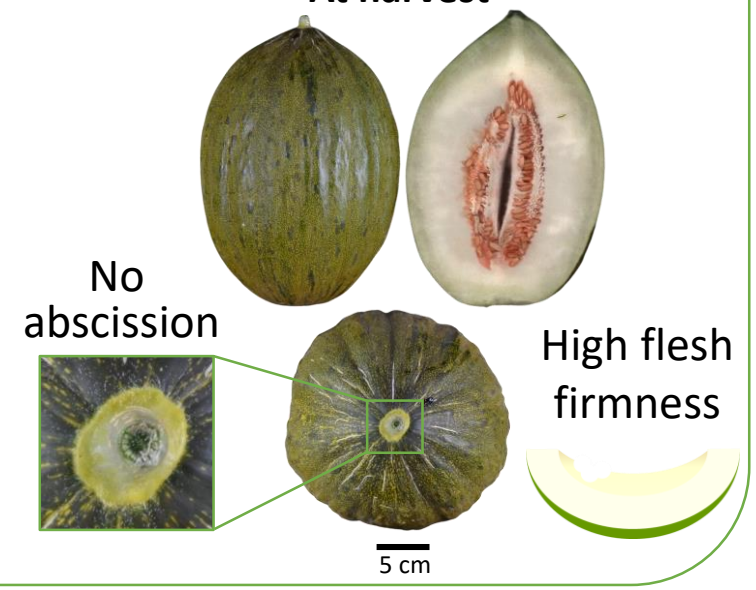
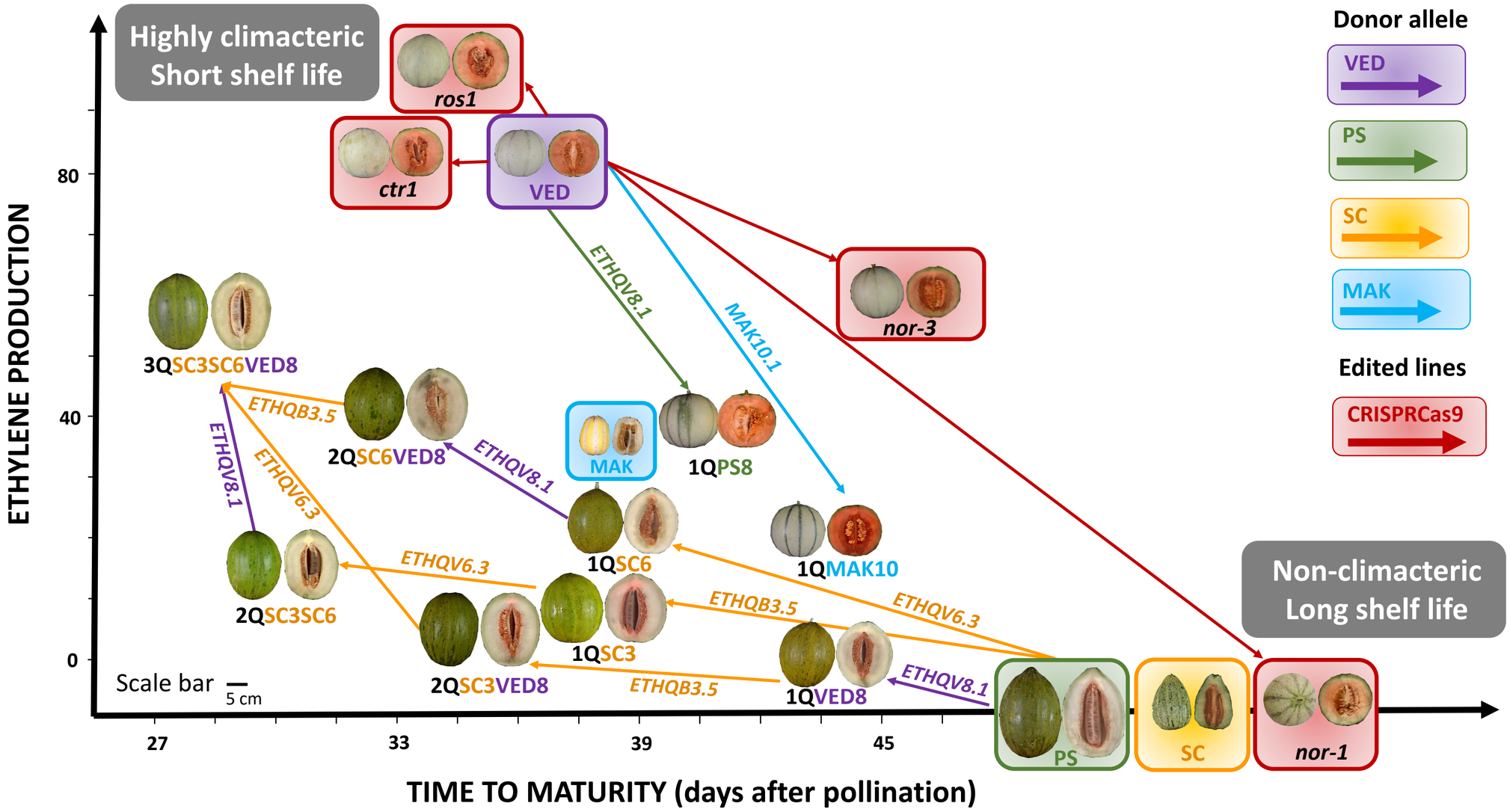



**Figure 1**: Climacteric and non-climacteric ripening in melon. Representation of ethylene, volatile organic compounds (VOCs) production and fruit ripening in a high climacteric cantaloupe melon and a non-climacteric *inodorus* melon. At the onset of ripening, climacteric fruits produce a peak of ethylene and an increase of respiration. Almost simultaneously, a great amount of diverse VOCs is synthetized, the abscission zone is activated, and flesh firmness decreases rapidly. In contrast, non-climacteric fruits do not produce ethylene, do not increase the respiration, VOCs production is lower and less diverse, there is no fruit abscission and the decrease in firmness occurs slowly compared to climacteric melons. Fruit pictures correspond to ‘Védrantais’ (top) and ‘Piel de Sapo’ (bottom) cultivars. Scale bar represents 5 cm.

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