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Review

Climacteric fruit ripening: Ethylene-dependent and independent regulation of ripening pathways in melon fruit

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Abstract

Cantaloupe melons have a typical climacteric behaviour with ethylene playing a major role in the regulation of the ripening process and affecting the ripening rate. Crossing of Cantaloupe Charentais melon with a non-climacteric melon indicated that the climacteric character is genetically dominant and conferred by two duplicated loci only. However, other experiments made by crossing two non-climacteric melons have generated climacteric fruit, indicating that different and complex genetic regulation exists for the climacteric character. Suppression of ethylene production by antisense ACC oxidase RNA in Charentais melon has shown that, while many ripening pathways were regulated by ethylene (synthesis of aroma volatiles, respiratory climacteric and degreening of the rind), some were ethylene-independent (initiation of climacteric, sugar accumulation, loss of acidity and coloration of the pulp). Softening of the flesh comprised both ethylene-dependent and independent components that were correlated with differential regulation of cell wall degrading genes. These results indicate that climacteric (ethylene-dependent) and non-climacteric (ethylene-independent) regulation coexist during climacteric fruit ripening. In addition, ethylene-suppressed melons allowed demonstrating that the various ethylene-dependent events exhibited differential sensitivity to ethylene and that ethylene was promoting sensitivity to chilling injury. Throughout this review, the data generated with melon are compared with those obtained with tomato and other fruit.

Keywords: Antisense ACC oxidase melons; Genetics of the climacteric; Cell wall-degrading genes; Ethylene sensitivity; Aroma volatiles; Chilling injury

Contents

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1. Introduction

The plant hormone ethylene regulates a wide range of plant developmental processes and environmental responses [1,2]. One of the most studied examples of ethylene regulation is the ripening of climacteric fruit in which, contrary to non-climacteric fruit, the ripening process is accompanied by a peak of respiration and a concomitant burst of ethylene production [3–5]. The ethylene burst results from autocatalytic stimulation of ethylene synthesis. The discovery of the ethylene biosynthesis pathway [6] has been a crucial step in the isolation of the two main regulatory enzymes, ACC synthase and ACC oxidase and the encoding genes. Suppression of ethylene production by knocking-down the expression of ACC oxidase and ACC synthase has resulted in a strong inhibition of the ripening process [7–9]. Ethylene affects the expression of many ripening-related genes [10,11] but, although it has been less studied, ethylene-independent regulation also exists in climacteric fruit. Most of the recent studies on climacteric fruit ripening have been carried out using tomato as a model fruit due to the relatively small genome, well characterized developmental mutants, availability of genomic tools, ease of genetic transformation and relatively short life cycle. The melon, although possessing less favourable characteristics, has some advantages over the tomato in comprising climacteric and non-climacteric genotypes. In addition, melons in which ethylene production has been almost totally abolished through down-regulation of ethylene biosynthesis genes have been generated [12]. In these conditions, melon has proved useful for undertaking generic studies devoted at understanding the inheritance of the climacteric character and at discriminating between ethylene-dependent and independent regulation. This review is aimed at bringing together recent advances made using melon fruit on these two aspects and at comparing with data obtained with tomato and other fruit.

2. Ethylene and ripening rate

As mentioned earlier, the melon comprises climacteric and non-climacteric genotypes. Typical climacteric phenotypes with high ethylene production, such as *Cucumis melo* var *cantalupensis*, have a fast ripening rate and short shelf-life. Non-climacteric melon, such as *C. melo* var *inodorus*, unable to produce autocatalytic ethylene, generally have a slow ripening rate associated with a long shelf-life. Hybrids of the Charentais *cantalupensis* type with an un-characterized non-ripening Charentais genotype has led to the generation of mid or long shelf-life melons. The characteristics of the non-ripening parent lines and hybrids have not been studied in terms of ethylene biosynthesis or sensitivity. Data are available only for the production of aroma volatiles which are shown to be strongly reduced in long shelf-life varieties [13]. Nevertheless, by screening different cantaloupe melons, Zheng and Wolff [14], have found a correlation between ethylene production and post-harvest decay. In addition, using ACC oxidase (ACO) cDNAs probes, they were able to demonstrate that low ethylene production was associated with the presence of an RFLP ACO allele *Ao*, whereas high ethylene production was associated with the *Bo* allele in homozygous conditions [15].

In other fruit species, such as the apple, it has been established that low ethylene production was correlated with long storage life [16]. The amount of ethylene in ripening Fuji apples parallels the transcription level of the ripening-specific 1-aminocyclopropane-1-carboxylic acid synthase (*ACS*) gene, *MdACS1* [17]. An allele of this gene (*MdACS1-2*) contains an insertion of a retro-transposon-like sequence in the 5′-flanking region and is transcribed at a lower level than the wild type allele *MdACS1-1*. Cultivars that are homozygous for the *MdACS1-1* allele have a long storage life [18].

In the tomato, the *rin* mutation [19] that encodes a MADS box type transcription factor and regulates the ripening process confers ethylene insensitivity to the fruit [20] and has been used for generating long shelf-life commercial varieties. However, the *rin* gene has been shown to control ripening of both climacteric and non-climacteric fruit [21] indicating that it probably acts upstream of the climacteric switch.

3. Inheritance of the climacteric character

As emphasized above, the climacteric character represents an important determinant of the ripening rate and storability. Because genetically compatible climacteric and non-climacteric types of melon are available, it has been possible to study the inheritance of the climacteric character. Périn et al. [22] have generated a segregating population resulting from a cross between a typical climacteric type Charentais melon (*C. melo* var *cantalupensis* cv *Védrantais*) and a non-climacteric melon, Songwhan Charmi PI 161375 (*C. melo* var *chinensis*). By studying the segregation of the formation of the abscission layer (Al) of the peduncle and ethylene production, it was found that the climacteric character was controlled by two duplicated independent loci (*Al-3* and *Al-4*) and that the intensity of ethylene production was controlled by at least four quantitative trait loci (QTLs) localized in other genomic regions. None of the QTLs matched with known genes of the ethylene biosynthetic or transduction pathways. It was recently reported that some introgression lines generated from two non-climacteric melons, Piel de Sapo (var *inodorus*) and Songwhan Charmi PI 161375 (var *chinensis*) presented a climacteric character [23]. The QTLs associated with ethylene production and respiration rate in this work were not located at the same position with the *Al* loci described by Périn et al. [22]. Taking together, these data suggest that different and complex genetic regulation exists for the climacteric character.

Whatever the genetic control involved, crossing climacteric with non-climacteric melons generates climacteric melons. Crossing of long shelf-life honeydew melon (*C. melo* var *inodorus*) with cantaloupe Charentais type melon (*C. melo* var *cantalupensis*) gives hybrids of the climacteric type [24].