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Review

Physiological aspects of fruit ripening: The mitochondrial connection

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ABSTRACT

Fruit ripening is a genetically programmed process which leads to an assortment of physiological and metabolic changes that irreversibly alter its characteristics. Depending on the species, fruit maturation can be either climacteric or non-climacteric. In both cases there is a metabolic shift from normal development conditions toward the fully mature state, but climacteric fruit is characterized by a sharp increase in respiration. In non-climacteric fruit, that generally does not display this feature, respiration changes can be affected by processes related to postharvest storage. This review describes some of the many ways in which mitochondrial metabolism is implicated in this crucial reproductive stage, such as the connection between ethylene production and respiration rate, the involvement of alternative oxidase (AOX) and plant uncoupling mitochondrial protein (PUMP) during the ripening and the common alterations of this organelle in fruits affected by different stress conditions.

Contents

1. Fruit ripening

Fruit ripening is a genetically programmed, highly coordinated process of organ transformation from unripe to ripe stage, to yield an attractive edible fruit with an optimum blend of color, taste, aroma and texture (Brady, 1987). Sourness is generally attributed to proton release from organic molecules, while the anions of each acid such as citric, malic and tartaric, would contribute to a distinctive taste in oranges, apples and grapes, respectively. In general terms, fruits accumulate mainly organic acids during the first period of development, as an energy reserve. Organic acid and amino acid accumulation shifts toward sugar synthesis during the later stage of fruit development (Carrari et al., 2006; Deluc et al., 2007; Fait et al., 2008).

In the case of citrus, for example, sucrose is translocated to the fruits from the leaves throughout fruit development, and constitutes about 50% of the total soluble sugars. During the first half of fruit development, sucrose is hydrolyzed by cytosolic invertases or stored in the acidic vacuoles and hydrolyzed by vacuolar acidic invertases (Echeverria, 1992; Echeverria and Burns, 1990). Meanwhile, citrate begins to accumulate.

Citrate is synthesized in the mitochondrion but accumulates in the vacuole (Martinoia et al., 2007). Export from the mitochondrion is by counter exchange with other carboxylic acids. Therefore, the rate at which TCA intermediates (mainly malate and oxaloacetate, Etienne et al., 2013) are replenished will affect the rate of export of citrate.

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Uptake into the vacuole is ultimately dependent on the tonoplast membrane potential generated by the proton-pumping V-type ATPase but can occur as well by facilitated diffusion through the malate channel (for a review see Etienne et al. (2013)). Accumulation in the vacuole is a function of both the influx and efflux of citrate from this organelle (Shimada et al., 2006) and of subsequent metabolism by the cytosolic isoforms of aconitase and isocitrate dehydrogenase. Thus, the transport of citrate between the different subcellular compartments will influence its rate of accumulation (Shiratake and Martinoia, 2007).

During the second half of citrus fruit development, citrate declines, a trend associated with the activity of CsCit1, a H^+/citrate symporter. Moreover, an increased expression of genes associated with the TCA cycle and genes encoding enzymes mediating sugar accumulation was reported for this stage of development (Deluc et al., 2007). These observations together with the lower activity of the enzymes responsible for sucrose degradation (Katz et al., 2011) suggest that the rapid accumulation of sucrose through the late stages of fruit development is a contribution of the sugar uptake from the tree and *de novo* synthesis of this metabolite in citrus juice sac cells at expense of organic acids deassimilation.

As can be appreciated, metabolic changes along the fruit development involve many mitochondrial enzymatic activities and transporters, which underscores the crucial role of this organelle during fruit ripening. Ripening physiology has been classically defined as either 'climacteric' or 'non-climacteric'. Climacteric fruits show a sudden increase in respiration at the onset of ripening, usually in concert with increased production of the gaseous hormone ethylene. Whereas ethylene is typically necessary for climacteric ripening, non-climacteric fruits do not increase respiration at ripening and often have no requirement for ethylene to complete maturation.

However, these distinctions are not absolute, as closely related melon or Capsicum species can be both climacteric and non-climacteric (Ezura and Owino, 2008). Also, some so-called non-climacteric fruits display enhanced ripening phenotypes in response to exogenous ethylene. Nevertheless, increased ethylene synthesis at the onset of ripening is required for the normal ripening of many fruits (Barry and Giovannoni, 2007).

On the other hand, patterns of organic acid accumulation and degradation do not always match the classification of species as climacteric or non-climacteric, nor can be attributed to changes in overall respiration rates. For instance, some climacteric fruits, such as tomato, appear to utilize malate during the respiratory burst, while others such as banana, continue to accumulate malate throughout ripening, even at the climacteric stage (Sweetman et al., 2009). In this group of fruits, including mango, strawberry, kiwifruit and others, the conversion of starch into soluble sugars is the most important event during the ripening (Han and Kawabata, 2002; Moing et al., 2001).

Regarding mitochondrial participation in each type of system, the higher respiration rate in climacteric fruits seems to be specifically regulated by ethylene, as will be discussed below. The close functional relationship between increased respiratory activity and intracellular repair has led to the suggestion (Romani, 1974) that the respiratory climacteric may represent an attempt, ultimately futile, to repair and compensate for the effects of incipient senescence. At the climacteric peak, the normal homeostatic reactions or, at least, the respiratory component, will have reached its upper limit and any further injury will not elicit an additional respiratory response.

In this way, rather than being either the metabolic force propelling senescence toward death or simply an unexplained adjunct activity, the respiratory climacteric may represent a final, concerted, homeostatic response.

2. Regulation of the respiratory climacteric

The gaseous plant hormone ethylene has been identified as the major compound that initiates and controls ripening in climacteric fruit, and its biosynthesis in plant tissues has been extensively studied (Argueso et al., 2007; Srivastava and Handa, 2005). The biochemical features of the ethylene biosynthesis pathway in higher plants are well defined and are summarized in Fig. 1. Briefly, ethylene is synthesized from methionine in three steps: (1) conversion of methionine to S-adenosyl-L-methionine (SAM) catalyzed by the enzyme SAM synthetase, (2) formation of 1-aminocyclopropane-1-carboxylic acid (ACC) from SAM via ACC synthase (ACS) activity, and (3) the conversion of ACC to ethylene, which is catalyzed by ACC oxidase (ACO). The formation of ACC also leads to the production of 5′-methylthioadenosine (MTA), which is recycled via the methionine or Yang cycle to yield a new molecule of methionine. Increased respiration provides the ATP required for the methionine cycle and can lead to high rates of ethylene production without high levels of intracellular methionine.

Two systems of ethylene production have been defined in plants. System-1 represents basal ethylene in unripe fruit and vegetative tissues and is regulated in an autoinhibitory manner, whereas system-2 operates during the ripening of climacteric fruit and flower senescence and is autocatalytic (Yokotani et al., 2009).

ACS and ACO are encoded by multigene families in higher plants, and these are transcriptionally regulated along development and ripening. In tomato, for instance, some isoforms are specifically expressed in green fruit that are in a system 1 mode of ethylene synthesis, while others only are present in mature fruits (Barry et al., 1996; Barry et al., 2000). Although numerous transcription factors acting on ethylene synthesis have been identified, the physiologic and molecular pathways that operate to initiate the transition from a system 1 to a system 2 mode of ethylene synthesis remain incompletely defined. Interestingly, it was reported that a high concentration of indole-3-acetic acid (IAA) is required to generate a large amount of ethylene by system 2 in peaches (Tatsuki et al., 2013), suggesting that ethylene biosynthesis transition may be also regulated by auxin (Fig. 2). Small but significant increases in ethylene synthesis and an associated increase in respiration rate have also been detected in non-climacteric fruits like grape berries, citrus fruits and red ripe strawberry fruits (Chervin et al., 2004; Iannetta et al., 2006; Katz et al., 2004). However, the timing of this ripening-related increase in ethylene production is distinct from the patterns of ethylene production typically associated with the ripening of climacteric fruits. In strawberry, for example, the ethylene increase observed was not detected until 24 h after the fruits had developed full red pigmentation. In contrast, while mature citrus fruits do not exhibit an increased ethylene production associated with ripening, harvested immature fruits produce high levels of ethylene that can be further stimulated by ethylene and propylene treatments and inhibited by 1-MCP, indicating the autocatalytic nature of this phenomenon (Katz et al., 2004).

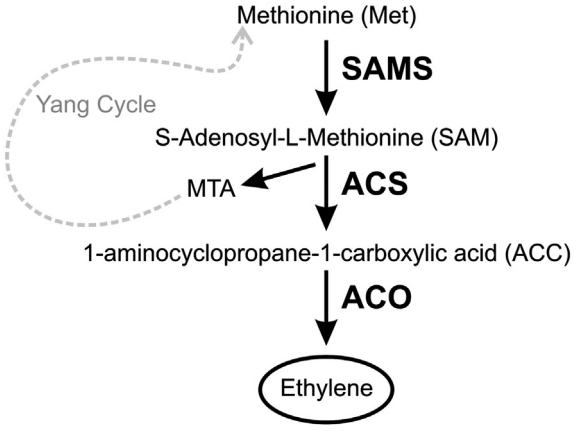

Fig. 1. Representation of ethylene biosynthesis from methionine. The main enzymes are: SAMS, S-Adenosyl-L-methionine synthetase; ACS, 1-aminocyclopropane-1-carboxylic acid synthase, ACO: 1-aminocyclopropane-1-carboxylic acid oxidase. MTA is 5′-methylthioadenosine, another product of the ACS reaction from which methionine is regenerated by the Yang cycle.

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