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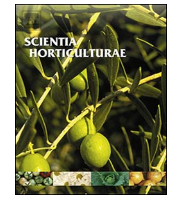

Review

Tomato quality as influenced by preharvest factors

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A R T I C L E I N F O

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A B S T R A C T

Tomato quality is a multi-faceted trait, involving many processes at the plant and fruit level, which depend on interactions between cultural practices, genetic and environmental factors. This review focusses on tomato quality as influenced by pre-harvest factors, and quality is defined from the consumer's point of view, *i.e.* through fruit size or fresh mass, colour, taste, flavour, texture and health value. Tomato is a model plant for biologist and the second fruit consumed worldwide. The mechanisms involved in tomato fruit quality have been extensively investigated by physiologists and geneticists, and the responses to climatic and cultural practices have been widely described. Yet, our ability to manage and improve fruit quality in a context of global change will rely on our capacity to integrate knowledge's and anticipate interactions among genotype, environment and cultural practices. The recent development of process-based models of fruit quality may help us for this challenging issue. Several models of tomato growth and quality are reviewed here, as well as their potential application for the design of ideotypes, *i.e.* conceptual plants that are expected to perform in specific environments.

1. Introduction

Whereas an overall increase in crop yield is required to feed the growing population, improving crop quality is a challenging and pending issue as the demand for premium quality has been increasingly affected by consumer's behaviour in recent years. Regarding horticultural crops, one difficulty arises from the lack of universal definition of quality integrating the various components, and from the gap that may exist between the quality, instrumentally measured at harvest and the one perceived by consumers after purchase and storage (Kyriacou and Rouphael, 2017). Tomato (*Solanum Lycopersicum*) is the second most important vegetable crop after potato (FAO Stat, 2015), and it is a model species for biologists, especially for those studying the quality and ripening of fleshy fruits. Quality is made of multiple traits, whose relative importance depends on stakeholders. Commercial quality mainly relies on external attractiveness (*e.g.* colour, form, size), firmness and shelf life; organoleptic quality depends on physical (texture or firmness) and biochemical traits (mainly the contents in sugars, acids and volatile compounds) determining the overall flavour. On the other hand, the health benefits rely on the composition in vitamins and phytonutrients (lycopene, β-carotene, ascorbate and polyphenol) as well as minerals (potassium, calcium, phosphorus, magnesium), whereas the sanitary quality is defined by the absence of residues of pesticides or other unhealthy compounds such as allergens, mycotoxins, antibiotics, environmental persistent pollutants and pathogenic microorganisms. Fruit quality is currently evaluated at harvest, but it is elaborated in the course of fruit development, resulting from many interacting growth processes and metabolic activities, which are regulated according to the fruit ontogenetic program and by environmental conditions (Ho, 1996, 2003). At harvest, main traits of quality are highly variable among fresh cultivated tomatoes: fruit fresh weight may vary 200-fold whereas the dry matter, sugar, acid or ascorbate contents may vary by 4- to 5-fold. Despite increasing knowledge's on metabolic pathways and molecular regulations occurring at the plant and fruit levels, the improvement of fruit quality and the reconciliation of yield and quality is still a challenge. Most tasteful varieties are cherry or cocktail tomatoes, while the taste of large tomato fruit varieties is rather poor, suggesting antagonistic relationships between fruit size and taste. For a long time, breeding has focused on yield and fruit shelf life (Bai and Lindhout, 2007) and, indeed, the yield of greenhouse tomato has double during the last decades, due to improvements of cultivars, climate control and crop management (de Gelder et al., 2012). In contrast, the quality of tomato has been overlooked for a long time, and breeding programs have integrated fruit taste and nutritional quality in respectively, the 1990s and the 2010s (Bai and Lindhout, 2007). Recent attempts to boost tomato consumption have focused on the diversification of the market, but they poorly impacted the global consumption. Yet, consumer's demand and acceptability encompass a large range of quality traits including environmental, sanitary and gustatory traits and health value and there is much interest in improving all the various aspects of fruit quality in order to meet this demand. At the same time, growers have to tackle new challenging constraints related to climate

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change. One of them is the development of innovative strategies to improve yield and quality in low-input production systems.

A preliminary step towards the understanding and management of fruit quality variations in relation to genetic and environmental conditions, is the identification of the processes underlying each trait; then the development of integrative approach will help to disentangle the complex network of interactions among these processes in response to external or internal stimuli (Martre et al., 2011). For this reason, in the last decades understanding fruit quality in relation to genetic × environment × management (G × E × M) interactions and analyzing correlations among yield and quality traits have been key objectives for fruit ecophysiologists in view of developing innovative strategies of crop management. In this respect, process-based models of fruit quality, which are mathematical representations of the main processes characterizing fruit functioning, have proved to be efficient tools to define relevant strategies and design ideotypes of plants adapted to specific environment or crop systems, *i.e.* genotypes capable of maintaining yield and producing high-quality fruits (Génard et al., 2007, 2016).

This review intends to provide novel insight into tomato fruit quality development with a specific focus on organoleptic quality and health value. We first describe major traits of quality and the underlying processes from fruit setting until ripening, *i.e* during the preharvest period. The second and third parts review some of the effects of environmental and genetic factors involved in quality variations. Then, process-based models of fruit quality and their application for the design of ideotypes are presented.

2. Tomato quality characteristics

2.1. Fruit size and shape

Fruits size and shape are major traits of quality that drive consumer purchasing. Fruit shape is determined mainly by the genetic make-up and it has been strongly diversified during breeding. While fruit shape poorly depends on environment, fruit size largely varies in response to GxExM interactions. The increase in fruit volume results from the development of pericarp tissue, which is achieved through two important processes (Ho, 1996): the production of new cells which ceases about 10–25 days after anthesis (daa), and cell growth and expansion which generally proceeds until start of maturation (Fig. 1) and may be limited by the epidermal extensibility (Thompson, 2001). Although most of the fruit volume increase occurs during the expansion phase, several works evidenced that final size is highly correlated to the number of cells (Bertin et al., 2003). Cessation of cell division and increase in cell size are closely linked to the switch of the complete mitotic cycle to an

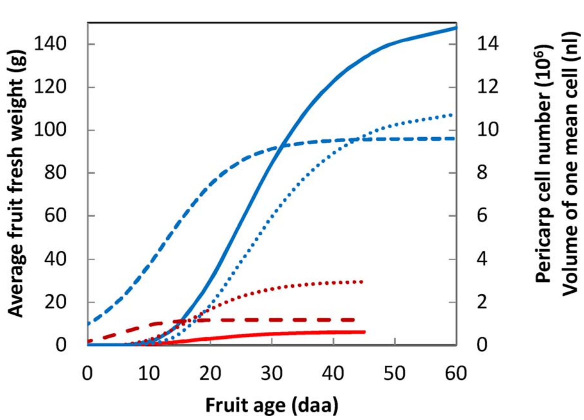

Fig. 1. Dynamics of fruit fresh weight (solid lines), pericarp cell number (dashed lines) and mean cell volume (dotted lines) of cherry (red) and large-fruited (blue) tomatoes. The curves were fitted on several sets of experimental data (adapted from Bertin et al., 2009). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

incomplete cycle without mitosis, so-called endoreduplication. Incomplete cell cycles lead to an increase in cell DNA content, up to 256C or even 512C (corresponding to respectively, 8 and 9 endocycles) in cherry tomatoes as well as in large-fruit-size cultivars (Bertin et al., 2007), which has been suggested to correlate with cell size (Chevalier et al., 2011). Cell expansion mainly results from the balance between water inflow through xylem and phloem, and outflow through transpiration and possibly water backflow to the plant through xylem. Water enters the fruit through xylem following the stem-to-fruit gradient of water potential, and through phloem tissues following the stem-to-fruit gradient of turgor pressure which is generated by the gradient of osmotic potential between source and sink tissues, linking cell expansion to sugar metabolism and subcellular compartmentalization (Ho, 1996).

2.2. Fruit texture

Texture may affect the end-use value of fruits, intended either for fresh market or for industrial processing. In case of tomato, texture strongly influences purchasing and consumer acceptance (Causse et al., 2010). It also interferes with flavour and aroma perception (Causse et al., 2003) and it significantly influences fruit shelf-life and transportability (Seymour et al., 2002). Texture implies several components such as firmness, meltiness, mealiness, juiciness or crunchiness (Harker et al., 2002), which can be evaluated by sensory analysis and objectively measured by mechanical methods, near-infrared spectroscopy or hyper-spectral imaging methods (reviewed by Chen and Opara, 2013). The most common mechanical methods are compression and puncture tests (Barrett et al., 2010), which mainly evaluate fruit or tissue firmness and elasticity, and usually correlate well with sensory evaluation (Causse et al., 2002).

Mechanisms underlying fruit texture are complex. Extensive work has focused on the molecular and biochemical mechanisms that lead to fruit softening during ripening, when the decline in fruit firmness coincides with the dissolution of the middle lamella, resulting in the reduction of intercellular adhesion, depolymerization and solubilization of hemicelluloses and pectic cell wall polysaccharides (Toivonen and Brummell, 2008). At the same time, numerous cell wall degrading enzymes are up-regulated, including hydrolases, transglucosylases, lyases and other wall loosening proteins such as expansins. However, fruit texture might be already determined during the fruit growth period (Chaib et al., 2007), involving various mechanisms (Barrett et al., 1998). Several works outlined the importance of fruit anatomical (locular number and thickness of the different tissues), histological (cell size) and biochemical (dry matter and soluble sugar content) traits (Bourne, 2002; Aurand et al., 2012). Cell turgor (Shackel et al., 1991), transport of solutes among cell compartments (Almeida and Huber, 1999), chemical and mechanical properties of cell walls (Rosales et al., 2009), cuticle structure and loss of water by transpiration (Saladié et al., 2007) also contribute to textural properties. After harvest, texture evolves rapidly, while membrane and cell wall breakdown occurs in relation to turgor loss and enzyme orchestrated cell wall loosening. Interestingly, on the contrary to other fruits like apple, there is no significant correlation between firmness measured at harvest and the relative loss of firmness during storage in tomato (Page et al., 2010; Aurand et al., 2012).

2.3. Fruit sugars and acids

Soluble sugars (glucose, fructose and sucrose) and organic acids (mainly malic and citric acids) are major osmotic compounds accumulated in tomato fruit. Both the absolute amounts and balance between sugars and acids are responsible for fruit sweetness and sourness, and contribute to their overall flavour (Davies and Hobson, 1981). Tomato fruit is made up of about 90–95% of water and 5–10% dry matter, of which about 50% is represented by sugars and 15% by