Fruit quality

Nadia Bertin

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INTRODUCTION

Quality of fleshy fruit is a complex trait including multiple variables. While the commercial quality relies mainly on external attractiveness (e.g. colour, shape, size), firmness and shelf-life, the organoleptic quality depends on physical (texture or firmness) and biochemical traits determining the overall taste and flavour. On the other hand, the health benefits rely on the composition in vitamins and antioxidant compounds (lycopene, β-carotene, ascorbic acid and polyphenol) as well as minerals (potassium, calcium, phosphorus, magnesium), whereas the sanitary quality is defined by residues of pesticides or other unhealthy compounds such as allergens, mycotoxins, antibiotics, environmental persistent pollutants and pathogenic microorganisms. In past decades, genetic improvement mainly favoured the producers and distributors, by derivation towards resistant productive cultivars and long-life products, whereas consumer preferences were generally overlooked. At the same time, yields have steadily increased by improvement of technical crop management in horticulture, so that intensive production systems launched on the market homogeneous, firm but tasteless products suitable for large distribution networks. Recently, the social demand for tasty, healthy fruits rich in vitamins and antioxidant compounds, but also for environmentally friendly production of fruits free of pesticides and residues, has given rise to new research concerning these traits. Meanwhile, fresh fruits have been recognized as a major source of vitamins and antioxidants and as important components of human diet and welfare on account of their nutritional value. Thus increasing their consumption became a worldwide priority, in particular to limit the risks of chronic diseases and nutritional deficiencies. Tomato also represents a major economic issue as it is the second highest vegetable (first fruit) consumed worldwide (Food & Agriculture Organization of the United Nations; see http://faostat.fao.org). This changing social and environmental context led to the search for new cultivars adapted to more sustainable modes of production and able to maintain yield and produce high quality fruits.

This chapter focuses on main quality traits from the consumer's point of view, which are fruit size or fresh weight, colour, taste, flavour, texture and nutritive value. Quality standards have been defined that give quantitative market values. However, there are as many quality standards as there are consumer types. A recent study (Causse *et al.*, 2010) revealed that preferences are quite homogeneous across European countries (The Netherlands, France and Italy) and that within each country two main factors discriminate the consumers of fresh tomatoes: the first is based on overall fruit flavour (aroma, juiciness, taste); the second is made up of textural components such as firmness, 'meltiness' and crunchiness.

Fruit quality is 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 programme and by environmental conditions (Génard *et al.*, 2007). Fruit taste, texture, overall flavour and nutritive value are mainly determined by the amount of dry matter and its composition in sugars, acids, cellulose and proteins, antioxidant compounds and minerals as well as by the ratio between sugars and acids and their dilution by water. At harvest, these traits are highly variable among fresh cultivated tomatoes: fruit fresh weight may vary 200-fold whereas the dry matter, sugar, acid or vitamin C contents may vary by four- to fivefold. After harvest, quality continues to evolve in relation to postharvest storage conditions and ripening stage at harvest. Despite increasing knowledge on the main metabolic pathway and molecular regulations occurring at plant and fruit levels, the improvement of fruit quality and the reconciliation of both yield and quality traits is still a challenge. Indeed, due to antagonistic relationships between fruit size and composition in sugars, the most tasty varieties are cherry or cocktail tomatoes, which represent only a minor part of the market, while the taste of large tomato fruit varieties is rather poor. In order to gain insight into the formation and variations of fruit quality in relation to genetic and environmental conditions, a preliminary step is to understand the processes underlying each trait and the development of integrative approaches to fruit quality to disentangle the complex network of interactions among these processes in response to external or internal stimuli. For this reason, in recent decades understanding fruit quality in relation to gene × environment × management (G×E×M) interactions and analysing correlations among yield and quality traits have been key objectives for fruit physiologists and ecophysiologists in view of crop management and cultivar adaptation to specific environments.

This chapter is divided into four parts. The first describes major quality traits of tomato fruit and the underlying processes. The second and third parts review some of the effects of environmental and genetic factors involved in quality variations. A few physiological disorders that may negatively impact the marketable yield are presented in the fourth part. Finally, an integrative approach for optimizing fruit quality is discussed in the last part.

QUALITY CHARACTERISTICS AND UNDERLYING PROCESSES

Fruit size and shape

Size and shape of tomato fruits are major traits of quality exhibiting a huge genetic variability (Tanksley, 2004). Fruit shape is determined mainly by the genetic make-up and it has been strongly diversified during breeding. Fruit size largely varies in response to G×E×M interactions. The increase in fruit volume results from the development of pericarp tissue, which generally accounts for more than two-thirds of total fruit weight (Ho, 1996). The increase in pericarp volume is achieved through two important processes: (i) the production of new cells, which is limited to a more or less short period (10–25 days after anthesis) of development; and (ii) cell expansion, which generally proceeds until start of maturation (Fig. 5.1). Although most of the fruit volume increase occurs during the expansion phase, several authors have provided evidence that final size is highly correlated to the number of cells determined early during the division phase (Fig. 5.2) (Bertin *et al.*, 2003). After cell division stops, the increase in tissue volume results from cell growth by increase in cytoplasmic volume and expansion through vacuolation, and from biophysical constraints related to epidermal extensibility (Thompson, 2001). Cell expansion is supported by the pressure of cell contents and constrained by cell wall properties (Cosgrove, 1997). The decrease in cell turgor and water potential resulting from cell wall relaxation and loosening enables water to enter the cell and to stimulate expansion (Lockhart, 1965). Water enters the fruit through xylem (15–20% of water influx) and phloem (75–80% of water influx) tissues following the stem-to-fruit gradient of water potential, which is generated by the gradient of osmotic potential between source and sink tissues, linking cell expansion to sugar metabolism and subcellular compartmentalization. Cessation of cell division and increase in cell size have been found to be closely linked to the switch of the complete mitotic cycle to an incomplete cycle without mitosis, so-called endoreduplication, which leads to polyploid cells in pericarp tissue where C-values range from 2C to 512C (Joubès and Chevalier, 2000). In tomato, large endoreduplicated cells are located in the mesocarp with DNA contents up to 256C (eight endocycles) or even 512C (nine endocycles) in cherry tomatoes as well as in large-fruit cultivars (Bertin *et al.*, 2007). The functional role of endoreduplication remains controversial. Among a large diversity of tomato lines, Cheniclet *et al.* (2005) reported a positive correlation between endoreduplication and cell size of pericarp tissues. By contrast, absence of correlation has been reported for mutants affected by the number of endocycles (Leiva-Neto *et al.*, 2004), in transgenic lines over-expressing a cell-cycle inhibitor (De Veylder *et al.*, 2001), or in response to changes in growth conditions affecting cell size (Bertin, 2005). Many theories have been developed to explain the link between cell size and nuclear size or DNA content, such as the

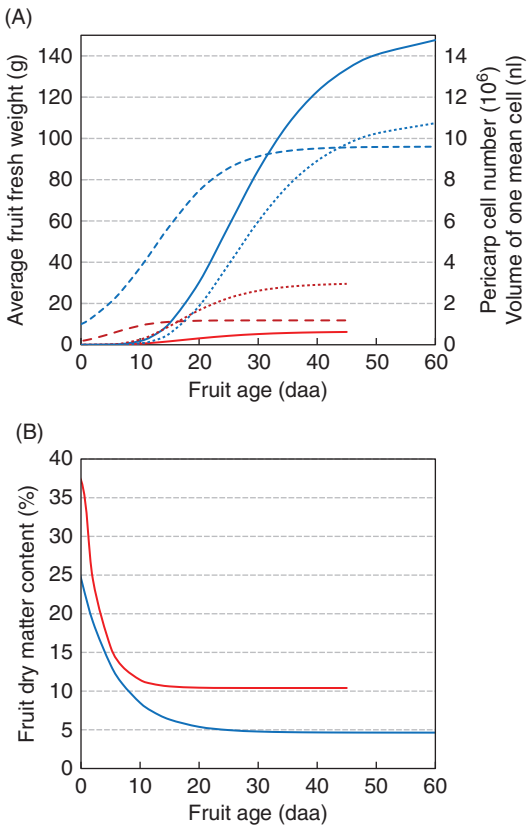

Fig. 5.1. Dynamics of (A) fruit fresh weight (solid lines), pericarp cell number (dashed lines) and mean cell volume (dotted lines) and (B) fruit dry matter content in cherry (red) and large-fruited (blue) tomatoes. The curves were fitted on several sets of experimental data. (N. Bertin, personal communication.)

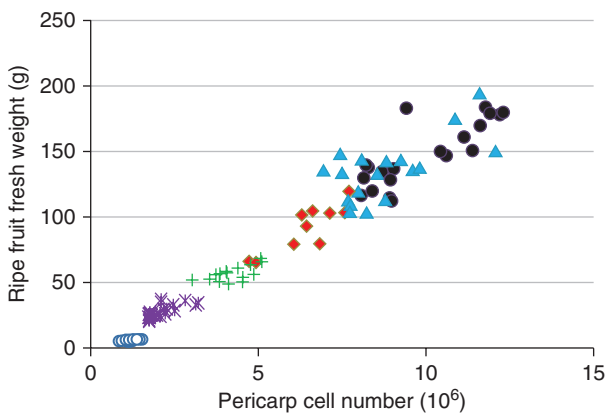

Fig. 5.2. Relationship observed at maturity between fruit fresh weight and cell number in a QTL-Nils population of tomato. Each point represents an individual fruit and each colour is a different genotype. (Bertin *et al.*, 2009; reprinted by permission of the Society for Experimental Biology.)

nuclear–cytoplasmic ratio theory, but the molecular basis of this correlation remains poorly understood (Chevalier *et al.*, 2011).

The onset of fruit ripening coincides with the rapid slowdown of cell expansion and the onset of intensive metabolic transformations. Tomato is a climacteric fruit and ripening is associated with ethylene production and cell respiration peaks in both attached and detached tomato fruits. As ripening progresses, fruit colour changes from green to red as chloroplasts are transformed into chromoplasts, chlorophyll is degraded and carotenoids accumulate. Fruit softening and textural changes occur as the fruit cell wall is partially disassembled by enzymes and the ripe flavour develops as specific volatiles increase and the sugar–acid balance alters (see below). Ethylene biosynthesis in pre-climacteric immature and mature-green tomato fruits and ripening climacteric tomato fruits is by the conventional pathway of methionine to SAM (shoot apical meristem) to ACC to ethylene (Abeles *et al.*, 1992). Exposure of mature-green fruit to endogenous levels of ethylene hastens the onset of the climacteric and ripening. Once the ethylene concentration within the fruit surpasses a 'threshold' level, it will promote its own biosynthesis (i.e. positive feedback) and autocatalytic ethylene production will cause a rapid increase in production and accumulation within the tissues (Abeles *et al.*, 1992). The atmosphere within a tomato fruit is effectively isolated from the surrounding atmosphere by an impermeable skin and cuticle; about 95% of gas exchange occurs through the stem scar. Therefore, once ethylene has started its positive feedback climacteric rise, few external treatments can modulate its synthesis. Reduced temperatures and lowered oxygen atmospheres slow overall metabolism but ripening will continue, albeit at a slower pace. However, certain inhibitors of ethylene action (e.g. 1-methylcyclopropane (1-MCP), ethanol vapours) appear to stop reversibly ethylene-enhanced fruit ripening at almost any stage of ripeness (Saltveit and Sharaf, 1992).

Fruit texture

Texture is a main trait of quality determining the end-use value of fruits, whether intended for fresh market or for industrial processing. In the case of tomato, texture not only influences purchasing and consumer acceptance but also has a significant impact on whole organoleptic quality, shelf-life and transportability (Seymour *et al.*, 2002) and it strongly interferes with flavour and aroma perception (Causse *et al.*, 2003). Texture is a complex trait, implying several components such as firmness, 'meltiness', mealiness, juiciness or crunchiness (Harker *et al.*, 2002). It can be evaluated by sensory analysis (Szczesniak, 2002), or it can be objectively measured by instrumental methods, including mechanical measurements, magnetic resonance imaging, or sonic and ultrasonic techniques (Abbott, 1999). 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). These events are accompanied by the increased expression of numerous cell wall-degrading enzymes, including hydrolases, transglucosylases, lyases and other wall-loosening proteins such as expansins. However, fruit texture might be already determined during the fruit growth period (Chaïb *et al.*, 2007), involving various mechanisms. Several reports have examined the importance of fruit anatomical and histological properties (Barrett *et al.*, 1998). At the fruit scale, proportion and thickness of the different tissues are determinants for fruit texture (Bourne, 2002). At the tissue scale, the cellular structure is likely involved in fruit mechanical properties, such as firmness (Aurand *et al.*, 2012). Moreover, 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. A recent study (Aurand *et al.*, 2012) noted that tomato firmness and stiffness measured by puncture tests correlate with both morphological (locular number), histological (cell size) and biochemical (dry matter and soluble sugar content) fruit traits.

After harvest, texture evolves rapidly, while membrane and cell wall breakdown occurs in relation to turgor loss and to enzyme-orchestrated cell wall loosening. This evolution may critically threaten the distribution of the production, with dramatic economic consequences.

Fruit composition in 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 the 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% water and 5–10% dry matter, of which about 50% is represented by sugars and 15% by organic acids and amino acids (Fig. 5.3). The fruit structure and proportion of the different tissues may influence its taste, since jelly tissues contain more acid and less sugars than pericarp tissue. Metabolic pathways of sugar and acid syntheses and links between enzymatic activities and product accumulation in fruits have been well documented (~~recently~~ reviewed by Etienne *et al.*, 2013, for acids and by Beckles *et al.*, 2012, for sugars).

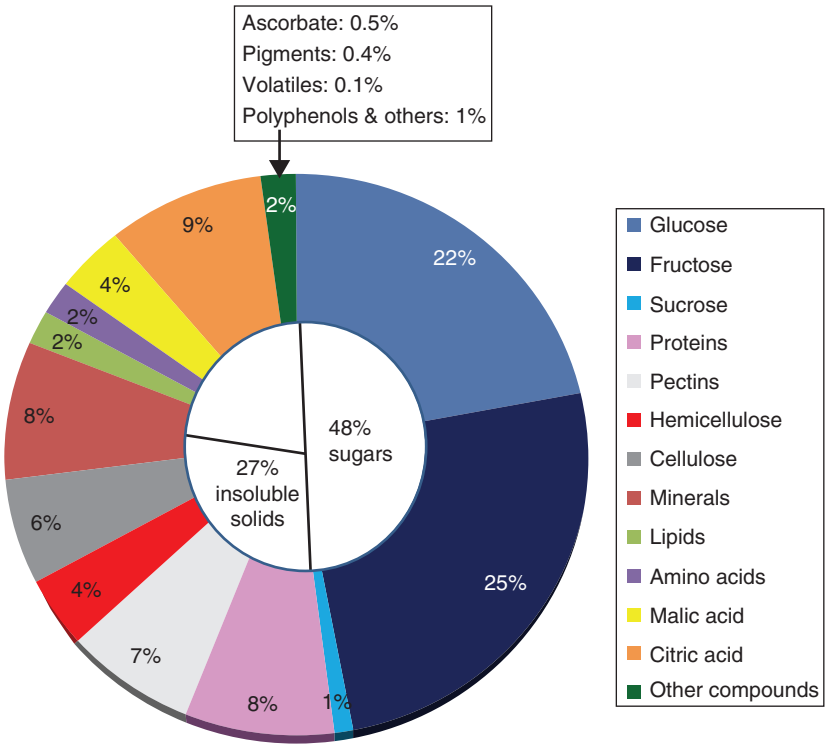

Fig. 5.3. Composition of tomato fruit dry matter, adapted from Davies and Hobson (1981) by permission of Taylor & Francis Ltd (http://www.tandfonline.com)

Tomato fruit shifts from partially photosynthetic to truly heterotrophic metabolism. Rare quantitative studies indicated that carbon fixed by the fruit itself contributes between 10% and 15% of that required for fruit growth (Tanaka *et al.*, 1974). Other studies based on transgenic lines or mutants confirmed that fruit photosynthesis is not necessary for fruit energy metabolism or development but suggested an important role for photosynthesis in the initiation of fruit development, or in properly timed seed development (Lytovchenko *et al.*, 2011). Thus most of the carbon required for growth is imported from leaves into fruit through the phloem tissues. Sucrose is the main form of carbon import in tomato fruit. It is either metabolized in the apoplast by a cell wall invertase or directly transported into fruit cells (Fig. 5.4). The transport occurs via symplastic (through the plasmodesmata) or apoplastic loading, involving hexose transporters. Although symplastic loading of sucrose is believed to predominate in young fruit, apoplastic loading has been suggested to occur throughout fruit development (Zanor *et al.*, 2009). Part of the imported carbon is consumed through respiration, providing energy for maintenance and structural growth, and

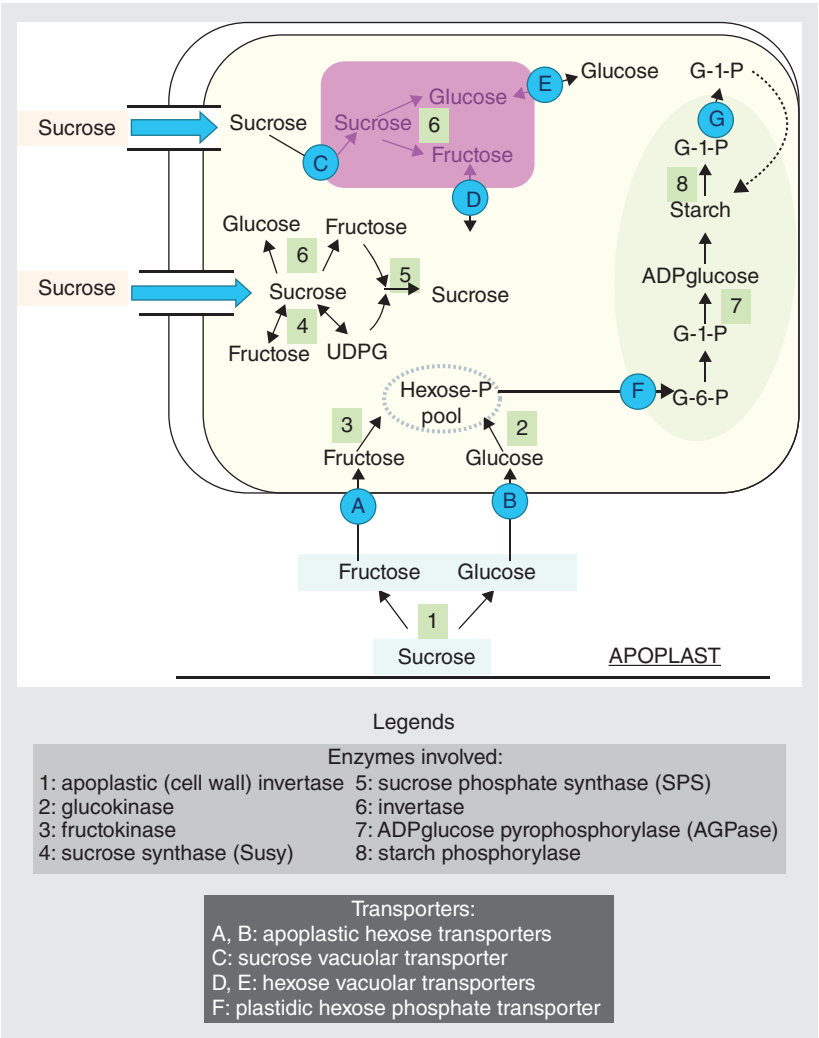

Fig. 5.4. Carbohydrate metabolism in developing tomato fruit. Sucrose may be imported directly via the symplast or may be inverted in the apoplast to hexoses, which are then imported into the cell. Both sucrose and hexoses may be stored in the vacuole. The flux of sucrose to starch occurs early in fruit development from anthesis to ~20–25 days post-anthesis (DPA). Here, sucrose metabolism via sucrose synthase and hexokinases dominates. Hexose phosphate intermediates are then imported into the plastid for the synthesis of starch. As the fruit ripens, Susy and hexokinase activity declines relative to invertase and the apoplastic import of hexose becomes more significant with storage of sugars in the vacuole. Starch biosynthesis is minimal and active degradation of the starch occurs, which may add to the sugar content available for storage. (Beckles *et al.*, 2012, reprint permission requested 25 July 2017.)

the rest is stored in different forms (mainly starch, sucrose, glucose, fructose). While the pools of hexoses increase until maturation, a transient pool of starch particularly located in the columella, the placenta and the inner and radial pericarp (Schaffer and Petreikov, 1997) is filled in the early phase of fruit expansion and peaks around ~~20–50~~ 40 days after anthesis (Fig. 5.5). Starch accumulated during this period is completely hydrolysed afterwards and maximum starch levels correlate well with final levels of soluble sugars (Ho, 2003). In the mature fruit, glucose and fructose are present at an approximately equimolar ratio (Davies and Hobson, 1981), while sucrose represents a small portion of the soluble sugars (generally less than 5%) in most commercial cultivars (Ho, 1996).

Malic and citric acids are the main organic acids accumulated in tomato fruit. They determine fleshy fruit acidity, as measured by titratable acidity and/or pH. The pH of tomato juice currently ranges between 4 and 4.5 but it does not correlate with acid content, which fluctuates over a much larger range. The perception of fruit acidity is due mainly to citric acid. Even though some organic acids are supplied by the sap, variations in fruit acidity primarily result from the metabolism of malate and citrate in the fruit itself (Fig. 5.6). Etienne *et al.* (2013) demonstrated that accumulation of malate and citrate is the result of complex interactions between metabolism and vacuolar storage. The first steps of acid synthesis, i.e. malate and oxaloacetate synthesis, take place in the cytosol and require the fixation of CO_2 on

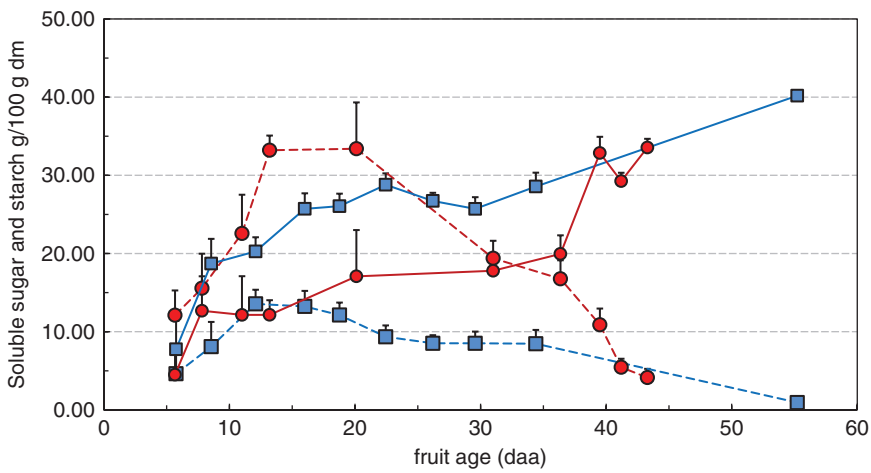

Fig. 5.5. Dry matter composition in total soluble sugars (solid lines) and starch (dotted lines) during development of cherry (red) and large-fruited (blue) tomato fruit. Vertical bars indicate 95% confidence intervals. (Adapted from Bertin *et al.*, 2009, by permission of the Society of Experimental Biology.)

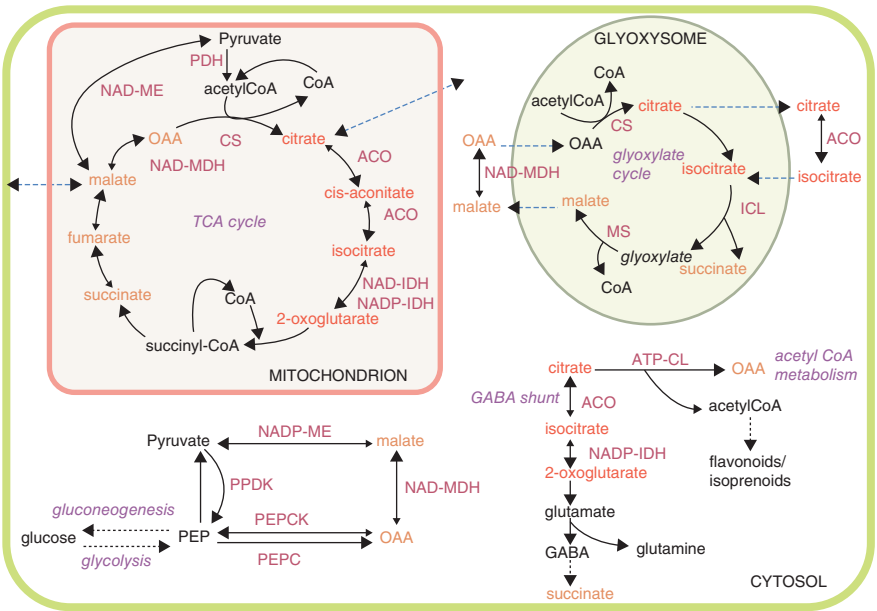

Fig. 5.6. Citrate and malate metabolic pathways in fruit mesocarp cells. Only the enzymes described in the source are shown. ACO, aconitase; ATP-CL, ATP-citrate lyase; CS, citrate synthase; ICL, isocitrate lyase; MS, malate synthase; NAD-MDH, NAD-malate dehydrogenase; NAD-ME, NAD-malic enzyme; NAD-IDH, NAD-isocitrate dehydrogenase; PDH, pyruvate dehydrogenase; PEPC, phosphoenolypyruvate carboxylase; PEPCK, phosphoenolpyruvate carboxykinase; PPDK, pyruvate orthophosphate dikinase. The probable direction of reversible reactions is indicated by the large arrow. Dashed blue arrows indicate malate and citrate transport. Names in orange are dicarboxylates and names in red are tricarboxylates. (Etienne *et al.*, 2013; reprinted by permission of the Society for Experimental Biology.)

a carbon skeleton derived from hexose catabolism. Both cytosolic pH and malate concentration play an important role in the regulation of malate synthesis (Etienne *et al.*, 2013). Then malate can be converted to citrate or to other tricarboxylates or dicarboxylates via several pathways in the mitochondria, leading to fruit acidity fluctuations. While acid synthesis and conversions through different pathways occur in different cell compartments (cytosol, mitochondria and glyoxysomes), large amounts of acids are accumulated mainly in the vacuole after transport through the tonoplast, which depends on both vacuolar pH and electric potential gradient across the tonoplast. Then, during fruit ripening, the cytosolic degradation of organic acids through the gluconeogenesis pathway promotes the accumulation of soluble sugars (Etienne *et al.*, 2013).

Fruit ascorbate (vitamin C)

Ascorbic acid or ascorbate (AsA) plays important roles in plants. For instance, it is involved in cell division and cell wall synthesis and in the interaction of plants with the environment, pathogens and oxidizing agents (Smirnoff, 2000). It is also an important micronutrient and an essential antioxidant in the human diet. In tomato, vitamin C exists in two water-soluble, biologically active forms: ascorbate (reduced form) and dehydroascorbic acid (oxidized form). Both forms are present in all cell compartments of tissues undergoing active growth and development, and the total amount of vitamin C ranges from 8 to 60 mg/100 g fresh weight among tomato species and cultivars (Table 5.1) (CTIFL, 2011). The biosynthesis pathway of AsA in plants and the numerous enzymes involved have been well described (L-galactose pathway) (Wheeler *et al.*, 1998). AsA is synthesized from D-glucose both in leaves and in fruits. Once synthesized, AsA can rapidly be oxidized, as result of its antioxidant function, and so the recycling pathway (reduction of the oxidized form) also plays an important role in maintaining AsA levels and redox status in plant cells (Massot *et al.*, 2013). Thus the AsA pool size in fruit results from its import (or the import of precursors) from leaves, its synthesis and recycling within the fruit and its export, as well as its degree of oxidation or degradation. During fruit development, fruit AsA content decreases during the periods of cell division and expansion, probably because of dilution effects, then increases during ripening concomitantly to the hexose content (Massot *et al.*, 2010). Many studies have found good correlations between fruit soluble sugar and AsA contents. However, recent works have demonstrated that AsA synthesis in tomato fruit is not limited by sugar content (Massot *et al.*, 2010) and that the *in situ* synthesis prevailes over AsA transport from leaves (Gautier *et al.*, 2009).

In the postharvest period, ascorbic acid content shows significant losses during storage but the content of vitamin C shows remarkable stability when expressed as the sum of ascorbic acid and dehydroascorbic acid. Moreover, it has been shown that mature-green and breaker fruits that have been ripened with ethylene lose less vitamin C by the time they reach the red-ripe stage than fruits allowed to ripen without added ethylene. However, both are lower than in fruits ripened on the plant. Interestingly, monodehydroascorbate reductase (MDHAR) activity plays an important role in the maintenance of ascorbate levels in fruit after chilling injury induced by storage below 10°C. Furthermore, under these conditions, an increased fruit MDHAR activity and a lower oxidation level of the fruit ascorbate pool are correlated with decreased loss of firmness (Stevens *et al.*, 2008).

Fruit carotenoids

Carotenoids are also of importance in the human diet due to their antioxidant properties (Dorais *et al.*, 2008). Besides their interest for humans, carotenoids

Table 5.1. Composition of different ripe tomatoes (Cantwell, 2010)

Tomato type	Fruit weight g	Red color, Hue	Soluble solids, %	Sugar, mg/mL	Titratable acidity, %	Vitamin C mg/100 g	Lycopene mg/kg
Campari	53.1	44.2	6.3	31.4	0.58	40.5	63.0
Cherry	20.3	45.5	4.2	28.9	0.31	54.0	84.6
Grape	5.0	51.3	5.6	29.5	0.51	47.1	49.1
Grape	6.2	41.7	4.2	39.6	0.35	61.7	98.0
Orange Cluster	111.5	71.5	4.6	26.1	0.33	29.2	4.2
Round Cluster	102.1	43.2	7.6	20.1	0.62	26.9	53.6
Round Cluster	119.8	44.6	3.8	15.3	0.44	26.0	44.8
Round Greenhouse	231.2	45.9	4.5	22.5	0.36	30.4	28.0
Round Greenhouse	179.4	47.7	4.7	25.0	0.44	20.4	42.5
Roma	94.8	42.1	4.3	24.0	0.27	22.8	46.4
Roma	84.5	45.2	6.2	20.2	0.67	24.3	44.4
Romanita	20.5	41.3	6.3	32.9	0.44	45.9	70.3
LSD.05	6.7	2.4	0.3	5.0	0.08	8.0	7.5

play fundamental biological roles in plants (for instance, in light harvesting in photosynthetic membranes, protection of the photosynthetic apparatus from excessive light energy, pigment-protein complexes in thylakoids, precursors of abscisic acid, and attractants to pollinators, thus involved in seed dispersal).

Carotenoids are C_{40} isoprenoid molecules formed in plastids, alongside the differentiation of chloroplasts into chromoplasts. Carotenoid accumulation is spatially and temporally regulated in the chloroplasts and chromoplasts of fruits and flowers. All carotenoids are synthesized from geranylgeranyl diphosphate (GGPP). Then isomerization, cyclization, hydrogenation and oxygenation events give rise to the chemical variability of carotenoids, whose accumulation results from the balance between synthesis and catabolism through enzymatic or non-enzymatic oxidative cleavage (review by Fanciullino *et al.*, 2014). The most abundant carotenoid in tomato fruit is lycopene, followed by phytoene, phytofluene, zeta-carotene, gamma-carotene, beta-carotene (precursor of vitamin A), neurosporene and lutein. Lycopene and β-carotene are the principal ripe fruit pigments of tomato responsible for fruit coloration, and lycopene represents about 80–90% of total carotenoid content of ripe fruit. In tomato, total carotenoid concentration increases between 10- and 50-fold during fruit ripening, with a concomitant decrease in chlorophyll (Fraser *et al.*, 1994). Reported contents in lycopene and β-carotene range from, respectively, 0.4 to 10 mg/100 g fresh weight and from 0.6 to 1.4 mg/100 g fresh weight (CTIFL, 2011) (Table 5.1). The primary mechanism that controls the increase in carotenoid content is based on the differential regulation of expression of genes encoding enzymes of the carotenoid biosynthetic pathway, such as the phytoene synthase and phytoene desaturase gene (Fraser *et al.*, 1994). The carotenoid biosynthetic pathway has been well described and several regulatory mechanisms have been suggested, including ethylene, light, availability of substrates and metabolic sequestration (Ronen *et al.*, 1999; Fanciullino *et al.*, 2014). However, carotenoid accumulation and activities of many enzymes involved in the biosynthesis do not correlate during fruit development.

The ability of the fruit to synthesize lycopene and β-carotene is almost the same for harvested mature-green fruits as it is for fruit ripening on the plant (Table 5.2). Exposure of harvested mature-green fruits to ethylene stimulates

Table 5.2. Composition of tomato fruit at different stages of ripeness. Fruit were harvested at the mature-green, breaker or red-ripe stage of ripeness (source: Cantwell, 2000).

Stage of ripeness	Soluble solids (%)	Reducing sugars (%)	pH	Titratable acidity (%)	β-carotene (μg/g)	Lycopene (μg/g)	Ascorbic acid (mg/100 g)
Mature-green	2.37	0.81	4.20	0.28	0.0	0.0	12.5
Breaker	2.42	0.85	4.17	0.39	0.40	0.52	18.0
Red-ripe	5.15	1.62	4.12	0.43	4.33	48.3	22.5

normal ripening with the synthesis and accumulation of lycopene and β-carotene, often to a greater extent than for harvested fruits left to ripen without ethylene stimulation (Saltveit, 1999).

Fruit colour and appearance

During ripening, the most obvious external changes are associated with the loss of chlorophyll and the accumulation of lycopene, which first becomes apparent at the blossom end of the fruit and progresses toward the stem end. Therefore during ripening the fruit can be partially green and red. Once ripe, however, high-quality fruits have uniform red distributed over the entire surface of the fruit. Under proper conditions of temperature and humidity, tomato fruits progress through six well defined stages to the red-ripe stage (Fig. 5.7). These stages are: (1) mature-green, (2) breaker, (3) turning, (4) pink, (5) light-red and finally (6) red-ripe; and they are based almost entirely on the external colour change of the fruit from green to red (i.e. destruction of chlorophyll and synthesis of lycopene). At the mature-green stage (no external red coloration), fruits have reached about 80% of their final size and acquire the ability to continue to develop and ripen normally after harvest. While fruits of most cultivars change from a uniform green to red as they ripen, a few cultivars have fruits that turn yellow (reduced or incomplete synthesis of lycopene) or are variegated in colour.

Fruit polyphenols

Polyphenols are a widespread family of phytochemicals with diverse biological functions in plants, for instance in response to various biotic or abiotic stress factors. They are also bioactive health compounds involved in the prevention of cancer and cardiovascular diseases related to their potent antioxidant activity as well as hepatoprotective, hypoglycaemic and antiviral activities (Slimestad and Verheul, 2009). Polyphenols are mainly synthesized from the phenylalanine produced by the shikimic acid pathway. Tomatoes are an important source of phenolic compounds, mostly restricted to their skin and exocarp. About 50 compounds have been reported in fruit, among which phenolic acids, phenylpropanoids, coumarins and flavonoids play an important role in fruit quality (Slimestad and Verheul, 2009). Chlorogenic acids and flavonoids are the main polyphenols in tomato. According to the flavonoid database of the US Department of Agriculture (USDA) (Bhagwat *et al.*, 2014), red tomatoes contain on a year-average basis 15 mg flavonoids per kilogram of fresh weight (FW) but the total flavonoid content of different tomato types varies from 4 to 26 mg/100 g FW (Slimestad and Verheul, 2009). Naringenin (45%) is reported to be the main flavonoid, followed

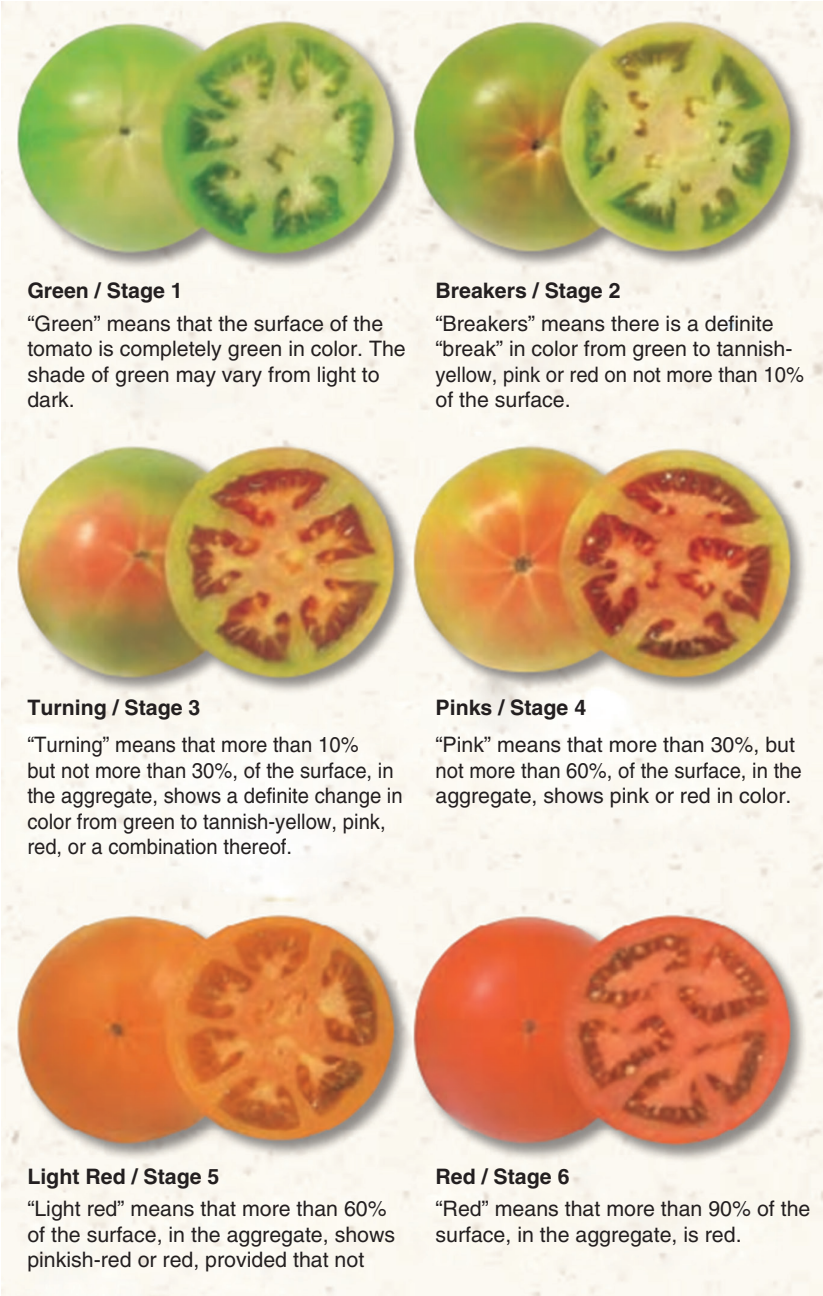

Fig. 5.7. Classification of fresh market tomatoes based on changes in external and internal colour and tissue softening (USDA Tomato Ripening Stages).

by quercetin (39%), myricetin (10%) and kaempferol (5%) (Slimestad and Verheul, 2009).

Fruit aroma and flavour

Flavour and aroma have often given rise to consumer complaints about the quality of tomato. Flavour results from complex interactions among sugars, acids and aroma volatile compounds (Baldwin *et al.*, 2008). The latter have been shown to affect human perception and preference with tomato fruit (Tieman *et al.*, 2012). Over 400 volatile compounds have been identified in fresh tomatoes, among which only 30 are present in concentrations over 1 ppb and thus have been long considered to contribute significantly to the perceptible flavour (Buttery, 1993) (Table 5.3). However, the presence of a molecule even at a relatively high level does not necessarily contribute to flavour or consumer liking. A study by Tieman *et al.* (2012) demonstrated that the near complete removal of the most abundant class of volatiles (C6 volatiles) in transgenic fruit, without affecting sugars, acids and other volatiles, impacts on flavour intensity but does not significantly impact on consumer preference. Thus odour thresholds alone are inadequate to predict the impact of particular volatiles on flavour. Moreover, the same authors demonstrated that aroma volatiles, such as geranial, make contributions to perceived sweetness independently of sugar concentration, suggesting a novel way to increase perception of sweetness. Volatile compounds are synthesized during ripening with a lesser contribution of the locular gel in the total production by the whole fruit (Maul *et al.*, 1998). Volatile components include acyclic, cyclic and heterocyclic hydrocarbons, alcohols, phenols, ethers, aldehydes, ketones, carboxylic acids, esters and lactones, as well as nitrogen, sulfur and halogen-containing compounds (reviewed by Lewinsohn *et al.*, 2001). The aroma of tomato is not directly related to the presence or absence of a single compound, but rather to synergism among components. (Z)-3-hexenal, hexanal, 1-octen-3-one, methional, 1-penten-3-one and 3-methylbutanal belong to the most odour-active aroma volatiles in fresh tomatoes (Krumbein and Auerswald, 1998) whereas the acyclic monoterpene alcohol, linalool, strongly influences the flavour of tomatoes (Buttery, 1993). Volatile compounds found in fruits are formed in different metabolic pathway (Klee *et al.*, 2013) and derived from fatty acids (e.g. *cis*-3-hexenol and *n*-hexanal), aliphatic amino acids (e.g. 2-isobutylthiazole and guaiacol), phenolic compounds (e.g. eugenol and methyl salicilate), or longer terpenoids such as β-carotene and lycopene (e.g. β-ionone and geranylacetone). Although the biosynthetic pathways have been well described, the enzymes and genes controlling the production of aroma compounds are poorly known.

Fruits harvested mature-green and improperly ripened or ripe fruits stored at chilling temperatures do not produce the characteristic volatiles associated with high-quality tomatoes (Saltveit, 1999).

Table 5.3. Volatiles emitted by ripe fruits of two tomato lines, *S. habrochaites* LA1777 and *S. lycopersicum* LA4024 (Mathieu *et al.,* 2009; reprinted by permission of the Society for Experimental Biology)).

Volatile	*S. habrochaites*	*S. lycopersicum*	Ratio
(ng g^{-1} FW h^{-1})	LA1777	LA4024	LA1777/LA4024
β-Damascenone	0.18±0.07	0.01±0.00	30.31
Methyl jasmonate	0.69±0.55	0.03±0.01	23.53
β-Ionone	0.31±0.21	0.03±0.00	12.00
2-Methylbutanal	12.53±1.54	2.56±0.42	4.90
cis-2-Penten-1-ol	2.68±1.31	0.64±0.09	4.15
Isobutyl acetate	11.14±4.07	2.71±0.47	4.11
Geranylacetone	10.04±4.58	2.65±0.65	3.78
Phenylacetaldehyde	1.03±0.29	0.28±0.09	3.69
2-Methylbutanol	46.96±22.95	14.99±2.99	3.13
Benzaldehyde	14.90±7.45	4.93±0.81	3.02
1-Penten-3-ol	10.78±3.61	3.64±0.28	2.96
1-Penten-3-one	2.00±0.81	0.68±0.11	2.93
Pentanal	12.78±4.42	5.07±0.36	2.52
Methylsalicylate	3.15±2.98	1.26±0.28	2.50
Methyl benzoate	4.00±2.00	1.61±0.49	2.48
cis-3-Hexenal	169.21±117.83	69.13±13.94	2.45
2-Methoxyphenol	2.39±1.26	1.01±0.31	2.36
trans-2-Hexenal	4.47±1.53	2.52±0.72	1.77
Methional	0.24±0.18	0.14±0.02	1.70
Geranial	0.37±0.28	0.23±0.07	1.65
cis-3-Hexen-1-ol	63.87±32.25	45.12±9.39	1.42
trans-2-Pentenal	0.81±0.50	1.14±0.16	0.72
Benzyl alcohol	0.27±0.15	0.43±0.11	0.63
2-Phenylethanol	0.24±0.04	0.42±0.15	0.58
Hexyl alcohol	20.02±16.24	36.08±13.02	0.56
3-Methylbutanol	15.74±6.04	34.80±5.91	0.45
Hexanal	54.12±27.38	120.18±14.58	0.45
1-Pentanol	2.21±1.42	4.98±1.07	0.44
1-Nitro-2-phenylethane	0.42±0.28	1.25±0.30	0.33
trans-2-Heptenal	0.20±0.10	0.84±0.23	0.24
2-Isobutylthiazole	0.48±0.29	5.05±0.75	0.09
Isovaleronitrile	0.61±0.33	6.90±1.80	0.09
6-Methyl-5-hepten-2-one	0.27±0.10	6.31±1.45	0.04

ENVIRONMENTAL CONTROL OF FRUIT QUALITY

A wealth of descriptive studies have outlined the effects of environmental factors (temperature, light, CO_2) or cultural management (fruit pruning, fertilization, water and saline stress) on quality traits. Environmental factors may

impact fruit quality through their effects on carbon fixation and distribution among sink organs, but through stress-induced osmotic and turgor regulations, and stimulation of antioxidant metabolism in the case of induced oxidative stress. Because in many studies fruit composition is often reported on a fresh weight basis, it is not clear whether the reported enhancement of quality is due to an actual stimulation of the biosynthetic capacity and/or to dilution/concentration effects associated with changes in fruit size and water content (Koricheva, 1999).

Important traits of quality (size and composition) have been assessed mainly in response to water or salinity stress (Dorais *et al.*, 2001; Guichard *et al.*, 2001), partial root-drying (Zegbe *et al.*, 2006), assimilate partitioning and carbohydrate compartmentation in fruit (Ho, 1996; Prudent *et al.*, 2011) and fertilizers (Benard *et al.*, 2009). Generally, a moderate water or carbon stress promotes fruit quality through an increased accumulation of compounds involved in taste and health value (e.g. sugars and acids, aroma, vitamins, lycopene), but reduces fruit size and marketable yield (Ripoll *et al.*, 2014). Compromises between quality and yield need to be found by manipulating the fruit environment to alter relevant physiological processes such as carbon metabolism and water relations. For instance, it has been demonstrated that both water content and chemical composition of tomato fruits can be manipulated by water and salt stresses with small loss of yield (Ehret and Ho, 1986; Dorais *et al.*, 2001), especially if moderate stress is imposed during the mid to late stages of fruit development (Mizrahi *et al.*, 1988; Ripoll *et al.*, 2016). Under high electrical conductivity (EC), fruit size is inversely related to EC while the fruit dry matter content linearly increases with EC at a rate that depends on cultivars, environmental factors, composition of the nutrient solution and crop management (Dorais *et al.*, 2001).

Most of the aroma and health-promoting compounds accumulated in tomato are regulated by environmental factors, in particular light and temperature (reviewed by Dorais *et al.*, 2008; Poiroux-Gonord *et al.*, 2010; Fanciullino *et al.*, 2014). Low temperatures (above 10°C) during the growth period are generally favourable to the accumulation of ascorbic acid, phenolic compounds and carotenoids, whereas temperatures above 26°C decrease lycopene and β-carotene but promote rutin and caffeic acid derivatives (Gautier *et al.*, 2008). Generally, good exposure or high light intensity is a positive factor for the accumulation of ascorbic acid, lycopene, β-carotene and phenolic compounds in tomatoes (Gautier *et al.*, 2008; Truffault *et al.*, 2015). For instance, seasonal variations in vitamin C levels have been described in relation to light intensity variations and sugar content, and fruits harvested during summer contain 8–50% more vitamin C compared with fruits harvested during early spring (Massot *et al.*, 2010). Fruit shading experiments have shown that AsA accumulation is not limited by leaf photosynthesis or sugar substrate but strongly depends on the fruit irradiance itself (Gautier *et al.*, 2008; Massot *et al.*, 2010). Moreover, the red to far-red ratio, which increases fourfold in pericarp tissues

during ripening, stimulates lycopene accumulation. This red-light-induced lycopene accumulation is regulated by fruit-localized phytochromes ~~independently of ethylene biosynthesis~~ (Alba *et al.*, 2000).

The effects of drought and high salinity on the accumulation of vitamins and secondary metabolites are more complex and conflicting results have been reported (review by Poiroux-Gonord *et al.*, 2010; Ripoll *et al.*, 2014). This is due to the fact that environmental factors may have indirect effects related to photosynthesis and carbon allocation (precursor availability) and/or direct effects on their biosynthesis. For instance, drought stress may be regarded as a negative factor for the synthesis of secondary metabolites because it limits photosynthesis; but, on the other hand, water (or other abiotic factor) stress may exacerbate photo-oxidative stress, thus providing a positive stimulus for their synthesis, probably involving signals transmitted from leaves to fruits (Poiroux-Gonord *et al.*, 2010). High salinity has global positive effects on ascorbic acid, lycopene and β-carotene (Frary *et al.*, 2010), with strong genotype × environment (G×E) interactions (Gautier *et al.*, 2009), whereas conflicting responses with regard to phenolic compounds are reported.

Nitrogen depletion lessens the accumulation of phenolic compounds alongside a slight increase in ascorbic acid concentration (Bénard *et al.*, 2009).

The environmental control of tomato fruit texture has been mainly investigated in the postharvest period, while the effects of environmental factors during fruit development have been more rarely reported (Sams, 1999; Rosales *et al.*, 2009). Generally, tomato firmness (physical component of texture) decreases in summer, which is empirically attributed to high temperature and high vapour pressure deficit. Regarding the mineral nutrition, high EC and high magnesium (Mg) supply increase fruit firmness in summer production, while high calcium (Ca) supply reduces fruit firmness (Hao and Papadopoulous, 2003). The latter authors suggested that high EC and high Mg might increase fruit tissue rigidity, whereas high Ca might increase only tissue plasticity. Water deficit also induces significant variations in fruit firmness with contrasting effects (Ripoll *et al.*, 2014). A moderate water deficit decreases firmness measured by compression test but increases firmness measured by puncture test, which correlates well with firmness and crunchiness assessed by sensory evaluation. Contrasting effects reported in the literature likely result from different methods of texture evaluation, different stress intensity, strong G×E interactions and from the complex interactions among the numerous processes involved in final fruit texture.

In the postharvest period, the effects of temperature storage and atmospheric composition on fruit quality have been primarily investigated. In particular, low temperatures, used by retailers or consumers to extend fruit shelf-life, may trigger physiological disorders and loss of quality. The optimum storage temperature differs with the stage at which fruits are harvested, due to different influences on the enzymatic activity (reviewed by Passam *et al.*, 2007). It also depends on varieties. For instance, long or extended shelf-life varieties

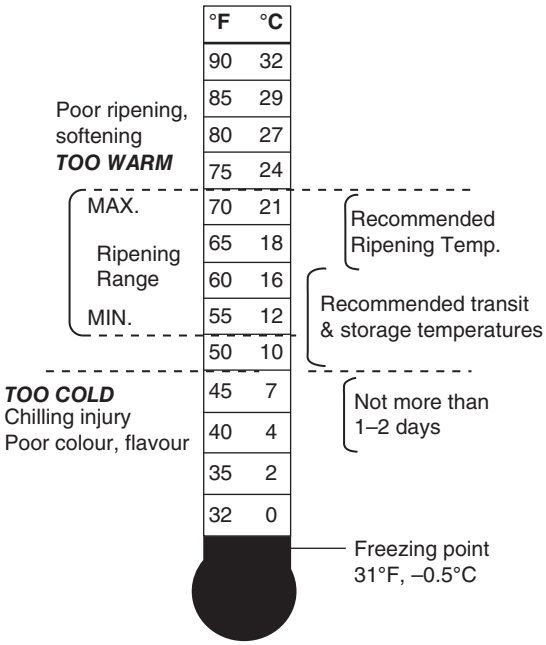

Fig. 5.8. Recommended temperature for tomato fruit storage (Cantwell, 2010).

may not be able to attain full red colour if harvested too early (Cantwell, 2010). Although fully ripe tomatoes may be held at 2–5°C for a few days prior to consumption (not longer, since colour loss and softening may occur), fruits that are mature-green or at the turning or breaking stage should not be subjected to temperatures lower than 12°C, to avoid chilling injury and relative symptoms such as rubbery texture, watery flesh and irregular ripening (Fig. 5.8) (Stevens *et al.*, 2008; Cantwell, 2010). Fruits stored at 5°C were rated by sensory analysis as significantly lower in ripe aroma (attributed to a loss of the principal volatile components), sweetness and tomato flavour, and significantly higher in sourness, compared with those stored at 20°C (Passam *et al.*, 2007). Although low temperatures during storage lower the lycopene content of fruit (twice less after 10 days storage at 7°C compared with 15°C or 25°C) even when harvested at a mature-red stage, they do not necessarily reduce the total antioxidant capacity related to phenolics and ascorbate over a limited period (Passam *et al.*, 2007).

GENETIC CONTROL OF FRUIT QUALITY

Major components of tomato fruit quality, such as fruit size, appearance, firmness and shelf-life, are quantitative traits that have continuous variation in segregating populations (Causse *et al.*, 2002). They have been tremendously

modified by breeding during the past 50 years, leading to a large diversity in size, shape and colour. For instance, domestication has increased fruit size up to 500-fold in cultivated species. On the contrary, the genetic improvement of organoleptic quality or health value has been considered only recently. The genetic control of interesting traits of quality relies either on a few natural mutations with tremendous effects or on the accumulation of numerous quantitative trait loci (QTLs) and genes with small individual effects. The multi-genic control of most traits of fruit quality, the co-localization of QTLs/genes with contrary effects, and the interactions among QTLs/genes and with the environment or cultural practices put a damper on the fast genetic improvement of tomato quality (Causse *et al.*, 2011). For instance, the antagonistic relationship between fruit size and taste represents a locking point for breeders. As a result, cherry tomatoes have the best flavour and higher contents in sugar and acids than large-fruited genotypes (Causse *et al.*, 2011). Although very few QTLs have been identified at the molecular levels, great advances are expected in the coming years by manipulating the components of tomato, thanks to progressing knowledge of the underlying genes, the release of the tomato genome sequence and the recent advances in sequencing and genotyping methods that allow identification of important genes and loci through analyses based on single nucleotide polymorphism (SNP) such as QTL mapping and genome-wide association study (GWAS) (Zsögon *et al.*, 2017). Many genetic engineering approaches have been already developed to modify the expression of genes controlling quality attributes, especially during ripening (e.g. for improving the taste, sugar-to-acid ratios, aroma and carotenoid levels in tomato) (Lewinsohn *et al.*, 2001; Guo *et al.*, 2012), but the use of genetic transformations for commercial purposes is highly regulated. On the other hand, the natural genetic variability within or among tomato species offers great potential for creating new improved varieties (Lin *et al.*, 2014). Until now, most genetic studies on QTL detection have been performed on populations derived from interspecific crosses between wild species and processing tomatoes. Numerous QTLs for fruit weight, shape, sugar and acid contents, firmness, volatiles and sensory attributes have been detected (reviewed in Labate *et al.*, 2007, and in Causse *et al.*, 2011). The introduction of five major regions bearing QTLs of quality has been successfully realized (Lecomte *et al.*, 2004) and fruit quality could be improved with favourable effects provided by cherry tomato (Causse *et al.*, 2002). Yet, interactions between genes or QTLs and environmental conditions should be considered (Albert *et al.*, 2015). Major mutations and genes for improving tomato fruit quality have been reported by Causse *et al.* (2011) (Table 5.4).

Fruit size and shape

Many QTLs of fruit mass have been detected. Six of them explain more than 20% of the phenotypic variance (Grandillo *et al.*, 1999), among which fw2.2

Table 5.4. Major mutations and genes for improving tomato fruit quality (reprinted from Causse *et al.* 2011, by permission of John Wiley & Sons)

Quality trait	Mutation	Phenotype	Chromosome	Activity	Reference
Size and shape	*Fw2.2 (QTL)*	Fruit weight	2	Transcription factor	Cong & Tanksley, 2006
	fas (fasciated)	Fruit shape	11	Transcription factor	Cong *et al.*, 2008
	o (ovate)	Fruit shape	2	Transcription factor	Liu *et al.*, 2002
	SUN	Fruit shape	7	IQD protein	Xiao *et al.*, 2000
Sugar content	*Lin5*	Increased sugar content	9	Cell wall Invertase	Fridman *et al.*, 2000
Vitamin C	*Vtc9.1*	Higher vitamin C	9	MDHAR	Stevens *et al.*, 2008
Shelf life	*Rin*	inhibited ripening (semi-dominant)	5	MADS-box transcription factor	Vrebalov *et al.*, 2002
	nor (non ripening)	inhibited ripening (semi-dominant)	10	transcription factor	Moore *et al.*, 2002
	Nr (Never-ripe)	inhibited ripening (dominant)	9	C_2H_4 receptor	Wilkinson *et al.*, 1995
	Cnr (Colorless non-ripening)	inhibited ripening (dominant)	2	Epigenetic control	Thompson *et al.*, 1999; Seymour *et al.*, 2002
Color	*B* (Beta)	yellow fruits	6	Lycopene cyclase	Ronen *et al.*, 2000
	og (old gold-crimson)	higher lycopene content	6	Lycopene cyclase	Ronen *et al.*, 2000
	Del (Delta)	orange fruits	12	Lycopene cyclase	Ronen *et al.*, 1999
	r (yellow flesh)	yellow fruits	3	Phytoene synthase	Fray & Grierson, 1993
	t (tangerine)	orange fruits	10	Carotenoid isomerase	Isaacson *et al.*, 2002
	hp-2 (high pigment)	higher lycopene content	12	DETI homolog	Mustilli *et al.*, 1999
	hp-1 (high pigment)	higher lycopene content	2	DDBI light signaling	Liu *et al.*, 2004
	Dg (dark green)	higher lycopene content	12	DETI homolog; allelic to hp1	Levin *et al.*, 2003
	y	uncolored epidermis	1	MYB transcription factor	Adato *et al.*, 2009

controls 30% of fruit size variations and is involved in the control of cell division in the pre-anthesis period. Among 13 QTLs that contributed to fruit mass enlargement during the improvement of modern tomato cultivars, five are located at the distal end of the long arm of chromosome 2 (fw2.2, lcn2.1, fw2.1, fw2.3 and lcn2.2), whereas five others related to fruit mass (fw1.1, fw5.2, fw7.2, fw12.1 and lcn12.1) likely contributed to the enlargement of tomato fruits during domestication of wild species (Lin *et al.*, 2014).

Three major QTLs for fruit shape have been identified on chromosomes 2, 7 and 8 and two major QTLs for locule number: fasciated (*fas*) and locule number (*lc* or *lcn2.1*) are located on chromosomes 11 and 2, respectively. Other QTLs such as OVATE and SUN modify fruit shape more specifically, as they are responsible for elongated fruit shape (reviewed in Causse *et al.*, 2011).

Fruit texture

Forty-six QTLs controlling texture as assessed by touching (30 QTLs), by mechanical measurement (11 QTLs) and by sensory evaluation (five QTLs) were reported in several populations, with a few main clusters on chromosomes 1, 2, 4, 5, 9, 10 and 11 (Causse *et al.*, 2002; Labate *et al.*, 2007). At the molecular level, most studies on texture have focused on the molecular mechanisms that lead to fruit softening during ripening and on the characterization of mutants affected in ripening-related genes; for instance, the ripening inhibitor (*rin*) gene, non-ripening (*nor*) gene, delayed-fruit deterioration (*DFD*) gene or colourless non-ripening (*Cnr*) gene (Seymour *et al.*, 2002; Giovannoni, 2004; Saladié *et al.*, 2007). On chromosomes 2, 5 and 10 the firmness QTL co-localized with the genes *rin*, *nor* and *Cnr*. Interestingly, the divergence between firm processing tomatoes and soft fresh tomatoes resides in SNPs located on chromosome 5 in a region where a major QTL for firmness has been detected (Lin *et al.*, 2014). However, no key determinants of fruit texture have been clearly identified, due to the high number of processes involved, including processes unrelated to cell wall loosening (Saladié *et al.*, 2007; Aurand *et al.*, 2012).

Fruit composition in sugar and acids

Increasing fruit sugar content is one main objective of breeding programmes focusing on organoleptic quality. This is particularly true for tomato, as domestication has led to a loss of flavour, despite abundant literature and knowledge on the physiological and genetic factors controlling the main steps of sugar and acid metabolisms in tomato (Beckles *et al.*, 2012; Etienne *et al.*, 2013). The number of regions bearing QTLs for sugar and acid contents obtained in different populations is very high (Labate *et al.*, 2007), likely because of the high number of processes involved and strong G×E interactions (Prudent *et al.*,

2009; Albert *et al.*, 2016). For instance, among 56 regions (95 QTLs) bearing QTLs for sugar content (or Brix), about 28 regions were found in several populations (the wild allele mostly increasing the trait) (Labate *et al.*, 2007). Only a few regions are common to sugars and acids (Sauvage *et al.*, 2014) while frequent collocations between sugars and fruit weight with opposite allelic effects have been detected (Grandillo *et al.*, 1999; Prudent *et al.*, 2009). At the molecular level, a high number (more than 60) of candidate genes involved in carbon metabolism have been identified (Causse *et al.*, 2011). Among them, a few genes encoding major enzymes of sugar metabolism affect the final fruit sugar content. For instance, *Lin5*, encoding the apoplastic invertase, is involved in the control of total soluble sugar content due to an increase capacity to uptake the phloem unloaded sucrose (Baxter *et al.*, 2005) and would explain a QTL for soluble compounds on chromosome 9 (Sauvage *et al.*, 2014). On chromosome 10, a QTL controlling fructose content contains two cell wall invertase genes *Lin6* and *Lin8* (Albert *et al.*, 2016). Similarly, *AgpL1*, *AgpL2*, *AgpL3* and *AgpS1* regulate the AGPase activity and starch synthesis during the expansion stage of fruit development, which constitutes a reservoir contributing to higher soluble sugar content at the ripe stage (Causse *et al.*, 2011).

Fruit composition in health-promoting phytochemicals

Metabolic engineering of plants to produce novel compounds or to improve the production of existing compounds is possible by over-expressing one or more specific genes coding for enzymes that control key steps of the known biosynthetic pathways.

Several QTLs for fruit ascorbic acid have been identified in different populations with a range of phenotypic variation from 6 to 50 mg/100 g fresh weight (Stevens *et al.*, 2007; Ruggieri *et al.*, 2014). The ascorbic acid concentration in cells depends on its biosynthesis, recycling and degradation. Thus, efficient ways to manipulate ascorbic acid content might be achieved via regulatory genes of the synthesis or via the up-regulation of recycling. Two main genes, both on chromosome 9, co-localized with QTL for fruit ascorbic acid: *MDHAR* (monodehydroascorbate reductase) involved in the recycling and *GME* (GDP-mannose epimerase) involved in the synthesis of ascorbic acid (Stevens *et al.*, 2007, 2008; Sauvage *et al.*, 2014).

Several mutants of different genes of the carotenoid biosynthesis pathway have been identified (reviewed in Liu *et al.*, 2003). For instance, the *yellow-flesh* (*r*) mutant corresponds to a loss of the phytoene synthase gene resulting in the absence of lycopene. Another single dominant gene, *Del*, encoding a lycopene ε-cyclase, changes the fruit colour to orange in the tomato mutant *Delta* as a result of accumulation of δ-carotene at the expense of lycopene (Ronen *et al.*, 1999). Similarly *Beta* (*B*) is a partially dominant, single-locus mutation that causes an orange color in the fully ripened fruit because of

the accumulation of β-carotene at the expense of lycopene. In the wild type, β-carotene constitutes 5–10% of total fruit carotenoids, whereas in *Beta* it is 45–50% and can exceed 90% (Ronen *et al.*, 2000). The existence of *r*, *B* and *Del* in wild tomato species suggests a hypothetical scenario for the evolution of fruit color in tomato (Ronen *et al.*, 2000). Other genes are involved in the carotenoid and other antioxidant contents. For instance, the *high pigment* (*hp*) mutant, a light-signalling gene not involved in the carotenoid biosynthesis pathway, also affects the carotenoids, flavonoids, ascorbic acid and sucrose contents in leaves and fruits (reviewed in Poiroux-Gonord *et al.*, 2013, and in Causse *et al.*, 2011). However, only a few candidate genes involved in the carotenoid biosynthesis pathway co-localize with colour QTL, indicating a complex regulation (Causse *et al.*, 2003; Liu *et al.*, 2003).

Concerning aroma formation, the complexity of the multiple biosynthetic pathways contributing to volatile composition has discouraged tomato breeders and there are relatively few examples of genetic improvement enhancing the profile or quantity of tomato fruit volatiles (Lewhinson *et al.*, 2001; Tieman *et al.*, 2012). However, a few recent studies identified important loci that control aroma in tomato. Thirty QTLs spread over the genome (except on chromosomes 8 and 9) and affecting 24 different volatile compounds were mapped in a population of introgression lines derived from a cross between the cultivated tomato *Solanum lycopersicum* and its wild relative, *Solanum habrochaites* (Mathieu *et al.*, 2009). In a *Solanum pennellii* introgression line (IL) population, 25 loci were identified that significantly alter one or more of 23 different volatiles (Tieman *et al.*, 2006). More recently a GWAS analysis on 28 main volatiles outlined significant associations on chromosomes 2 and 4 where previous QTLs have been identified (Zhang *et al.*, 2015). Genes regulating the output of volatile synthesis pathways and associated with flavour-imparting volatiles in tomato have been reviewed by Klee and Tieman (2013). Moreover, a large natural diversity in volatile composition was reported in Heirloom populations of tomato (Table 5.5) which could be exploited with molecular-assisted breeding techniques (Tieman *et al.*, 2012).

FRUIT PHYSIOLOGICAL DISORDERS

A number of disorders affect the quality of fresh market tomato fruit and reduce the marketable yield. These disorders result from a combination of environmental, production or handling procedures, or are genetic in origin. A few of them are represented in Fig. 5.9.

Blossom-end rot

This disorder (BER) is associated with a local calcium deficiency in the distal fruit tissue, resulting from a misbalance between calcium supply/transport and

Table 5.5. Observed variations in flavour volatiles within *S. Lycopersicum* Heirloom varieties ((Reprinted from Current Biology, 22(11), Tieman *et al.,* The chemical interactions underlying tomato flavor preferences, 1035-1039, Copyright (2012), with permission from Elsevier).

	High	Low	Fold Difference	Median
1-penten-3-one	9.37	0.17	55	1.18
isovaleronitrile	68.45	0.58	117	7.63
trans-2-pentenal	5.16	0.31	17	1.23
trans-2-heptenal	2.71	0.09	30	0.42
isovaleraldehude	51.08	1.55	33	8.59
3-methyl-1-butanol	184.46	3.20	58	27.26
methional	1.616	0.012	137	0.07
isovaleric acid	0.953	0.004	262	0.09
2-isobutylthiazole	63.61	0.37	174	8.34
6-methyl-5-hepten-2-one	20.07	0.17	120	3.38
β-ionone	0.396	0.008	47	0.05
phenylacetaldehyde	1.90	0.00	654	0.24
geranylacetone	28.96	0.03	1,095	1.22
2-phenylethanol	5.269	0.002	3,142	0.05
isobutyl acetate	11.93	0.14	85	1.67
cis-3-hexen-1-ol	124.15	10.00	12	40.00
1-nitro-2-phenylethane	2.59	0.02	149	0.25
trans,trans-2,4-decadienal	0.30	0.00	211	0.02
2-methylbutanal	14.66	1.14	13	3.47
hexyl alcohol	84.03	0.99	85	13.86
guaiacol	8.09	0.03	290	0.77
hexanal	381.05	15.55	25	88.65
1-octen-3-one	0.312	0.017	18	0.07
cis-3-hexenal	399.66	8.29	48	71.09
methylsalicylate	14.16	0.00	3,354	0.40
trans-2-hexenal	48.01	0.39	123	3.54
β-damascenone	0.1733	0.0020	86	0.01
2-methyl-1-butanol	115.69	1.93	60	15.08

Volatile emissions were measured as ng/g fresh weight/hr.

requirement for growth, especially during the phase of rapid fruit expansion, which is the most sensitive period (Ho and White, 2005). Symptoms occur first in the internal part of the fruit and then extend to the external tissues. The blossom end of a green fruit develops a water-soaked area near the blossom scar. The area dries, turns brown as a consequence of cell death, and there is subsequent leakage of cell contents into the extracellular space. High temperature, light, vapour pressure deficit (i.e. low humidity) and salinity, irregular watering, plant vigour, high nitrogen fertilization and root pruning are conducive factors. The sensitivity is genotype-dependent. For instance, large-fruit

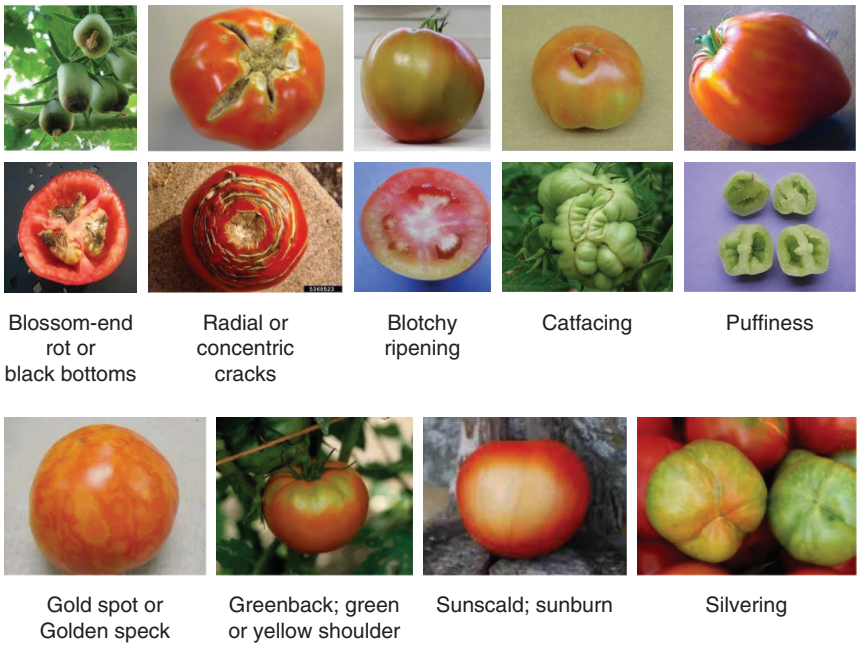

Fig. 5.9. Illustrations of main tomato disorders that impact negatively on marketable yield.

or plum tomatoes are much more sensitive than cherry or wild tomatoes. The incident of blossom-end rot increases significantly when the concentration of calcium in the fruit falls below 0.08% (dry weight) while the disorder seldom occurs at levels above 0.12% and spraying Ca directly on to young fruits is recommended for the prevention of BER (Ho and White, 2005).

Cracking and russeting

Cracking occurs when the internal expansion is faster than the expansion of the epidermis and so the epidermis splits. Concentric cracks can develop around the stem end of the fruit, and/or radial cracks can develop that extend from the stem to the blossom end. Cracking can occur at all stages of fruit growth, but as the fruit matures they become more susceptible, especially as colour develops. A rapid influx of water and solutes and reduced strength and elasticity of the tomato skin and pericarp wall contribute to the occurrence and severity of cracking. This disorder is not only unsightly but breaks in the epidermis also increase water loss and the entry of pathogens. Cracking can be minimized by the uniform application of water to avoid periods of water stress, adequate calcium nutrition and the selection of crack-resistant cultivars. Cracking and

splitting are inherited tendencies and cultivars differ greatly in susceptibility. The development of numerous very fine cracks is another disorder, known as russeting or micro-cracks. Unlike cracking where the cracks extend several millimetres into the pericarp, russeting is the development of numerous fine cracks in the tomato skin. Microbial infection is not a significant problem but water loss is increased and visual appearance decreased (reviewed in Dorais *et al.*, 2004).

Blotchy ripening

Blotchy ripening leads to uneven ripening with hard grey to yellow patches, usually near the calyx end of the fruit, retaining chlorophyll and not accumulating sufficient lycopene to produce a normal red fruit. Blotchy areas contain less nitrogenous compounds, organic acids, starch, sugars and dry matter (Yahia and Brecht, 2012). Early and mid-season greenhouse crops are particularly susceptible. The cause of this physiological disorder and its relationship to 'grey wall' is not well understood. Improper plant nutrition (e.g. potassium and/or boron deficiency and high nitrogen levels, which promote excessive growth), insect feeding and environmental stresses (e.g. chilling, temperature above 30°C, low light intensity or high soil moisture) may contribute to the occurrence of this disorder (Yahia and Brecht, 2012).

Catfacing

Catfacing is a generic term used to describe a tomato fruit that has a gross deformity. In this case the differential growth of the various locules produces a convoluted shape in contrast to the smooth shape of most fruits. Symptoms of catfacing also include corky brown scarring, cracks and uneven ripening. Large-fruited tomatoes with high number of locules (more than five) are more prone to this problem than small-fruit varieties. Critical flower development or pollination may be responsible for this problem. Moreover, low temperature and light intensity during flowering and fruit set may exacerbate the occurrence of catfacing (CTIFL, 2011; Yahia and Brecht, 2012).

Puffiness

Puffy fruits are flat-sided or angular fruits in which one or more seed cavities (i.e. locules) are empty of some or all tissue. Puffiness is also known as boxiness or hollowness. It may be impossible to detect light puffiness until the fruit is cut and open cavities are observed between the seed gel area and the outer wall. Puffy fruits are less dense than good ones and so they can be separated by

flotation in water. Growing conditions (too low or too high temperatures, high N, low light) that cause improper pollination, fertilization or seed development and genotype contribute to the occurrence of this disorder. Distal fruits of the inflorescence are more frequently affected (CTIFL, 2011; Yahia and Brecht, 2012).

Gold spot

Gold spot is described as yellow or white flecks distributed all over the fruit surface, and more especially near the calyx and shoulder of the fruit. The number can vary from a few to many. Flecks develop as small irregular-shaped green spots on the surface of immature fruit and turn gold as the fruit ripens. Gold spot is due to calcium oxalate crystals resulting from an excess of calcium. The disorder depends on genetic and environmental factors. Plum, Roma and saladette tomato types appear to be more susceptible than round tomatoes. The abundance of gold spot is increased by high humidity and high Ca fertilization (CTIFL, 2011; Yahia and Brecht, 2012).

Green shoulder

In this case the shoulders of a ripening fruit near the calyx remain green due to a high chlorophyll content, while the rest of the fruit turns red. While generally undesirable, this condition is actually preferred by consumers in some countries. Incorporating the 'uniform ripening' gene can eliminate this disorder in susceptible cultivars. Predisposing factors include exposure to excessive heat, high salinity and an inadequate supply of potash and phosphate fertilization (CTIFL, 2011; Yahia and Brecht, 2012).

Sunscald

Sunscald can be described as a yellow, hard area, usually on the shoulder of the fruit, which occurs when tissue temperature rises above 30°C and prevents the synthesis of red pigments and the softening of flesh. Fruit temperatures above 40°C are lethal and the exposed tissue will die, turn white, dry out and form a flat parchment-like covering over the affected area. Green fruits are more sensitive to solar injury than ripe ones. Damage usually occurs when fruits are suddenly exposed to sunlight, for instance after an over-pruning of leaves. Indeed, direct sunlight may increase the temperature of exposed fruit tissue by 10°C or more above ambient air temperatures. Plant architecture that shades the fruit during growth and bin covers that shade the harvested fruit during transport to packing facilities are the most effective ways to reduce sunscald (CTIFL, 2011; Yahia and Brecht, 2012).

Silvering

Silvering is represented by silver-green streaks that turn yellow as the fruit ripens. They are due to abnormal tissue development but the actual causes are unknown. Symptoms are more frequent in early crops with short day-periods or in case of thermal shocks (low temperature) (CTIFL, 2011).

OPTIMIZING FRUIT QUALITY THROUGH MODELLING APPROACH

As previously discussed, all the major traits of quality result from complex interactions and regulation loops among numerous processes, regulated at the plant and fruit levels. These processes are controlled by interactions between genetic, environmental and management (G×E×M) factors and the qualities of a given genotype under contrasted environments are hardly predictable. Significant variations in all quantitative traits of quality have been reported in response to G×E×M interactions (Causse *et al.*, 2003; Bertin *et al.*, 2009; Prudent *et al.*, 2009). A multi-site experiment including 42 tomato genotypes revealed as much as 211% change in performance of some genotypes in a particular location. Lycopene was found to be most influenced by the environment, whereas total acidity was the least influenced (Panthee *et al.*, 2012). Such interactions are difficult for breeders and producers to handle and multi-site tests are necessary for developing varieties that will perform consistently well across multiple environments. However, exploring all G×E×M combinations by experiments is an endless task. An alternative approach relies on the development of process-based simulation models (PBSMs) (Bertin *et al.*, 2010; Kromdijk *et al.*, 2014; Bertin and Génard, 2018). Indeed PBSMs allow complex traits, such as quality, to be unravelled by simulating interactions among the various components or processes that underlie the trait of interest. Moreover, G×E×M interactions are emergent properties of simulation models, i.e. unexpected properties generated by complex interconnections between subsystem components and biological processes. In this perspective, bottom-up (based on mechanistic knowledge of underlying processes), top-down (statistical regression to establish links between data and phenotype), or middle-out (combination of bottom-up and top-down) modelling approaches have been developed (Génard *et al.*, 2007; Yin and Struik, 2010) (Fig. 5.10). In these models, the so-called component traits are characterized in terms of model parameters, which instead of the complex trait itself may subsequently be linked to underlying genetic variations (Fig. 5.11).

Several predictive models of the processes involved in the quality of fruit have been developed ~~in the past decade or so~~ (Martre *et al.*, 2011). Concerning tomato growth, we can report a model of cell division and endoreduplication (Bertin *et al.*, 2007) and a model of cell expansion related to carbon and water

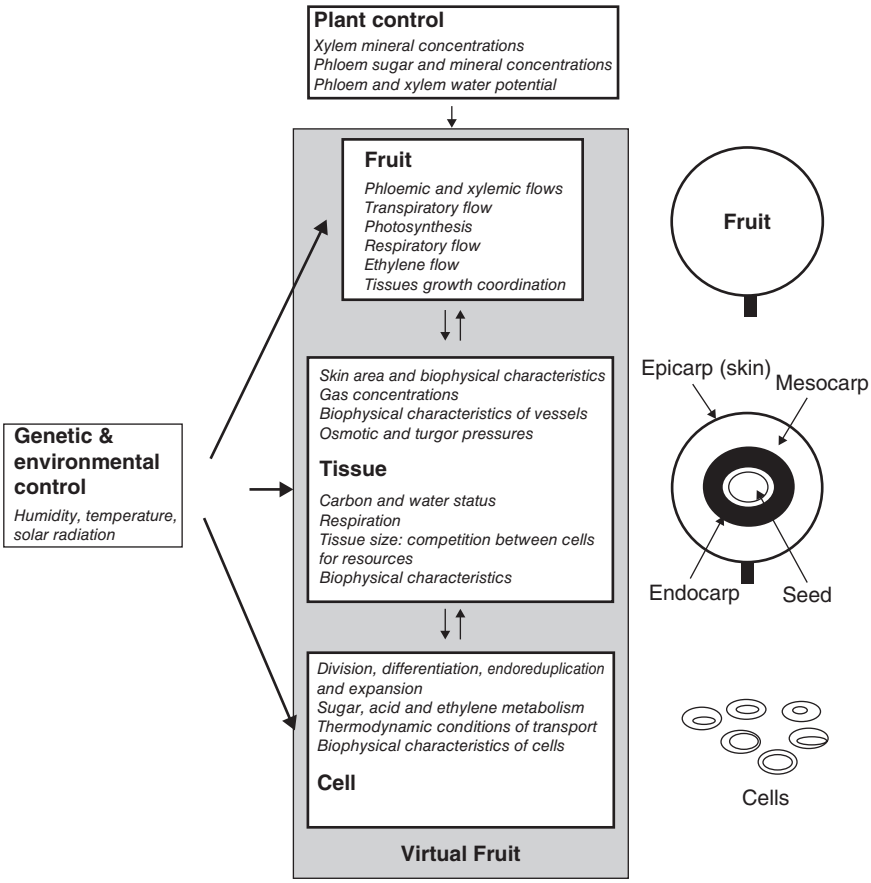

Fig. 5.10. Schematic presentation of the virtual fruit model organization in levels and objects (right). For each level, constraints on the lower level are given in the lower part of the box and initiating conditions are given in the upper part of the box. (Génard *et al.*, 2007; reprinted by permission of the Society for Experimental Biology.)

fluxes (Liu *et al.*, 2007). Concerning fruit composition, rare models of sugar and acid metabolism have been developed for peach (Génard *et al.*, 2003; Lobit *et al.*, 2003, 2006). These models could be easily transferred to tomato, taking account of species-dependent control of sugar and acid metabolisms. Several PBSMs that predict fruit quality as a function of the environment or crop management are now available. The next important steps to progress in this field will be: (i) the integration of the sub-models to consider the complex interactions and feedback regulations across the various organizational levels (Fig. 5.10); and (ii) the coverage of the genetic and molecular control on the modelled processes.

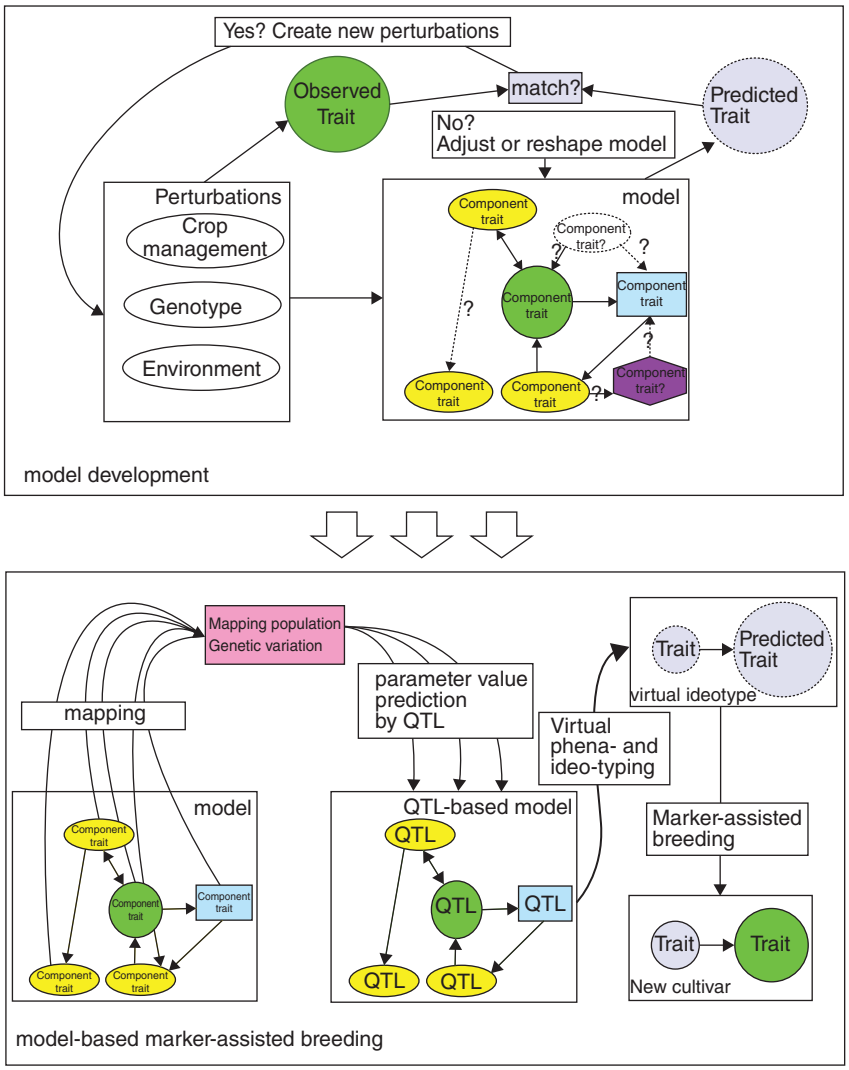

Fig. 5.11. Scheme of recommended workflow to use the combination of physiological modelling and breeding based on molecular markers. First, model development takes place by decomposing complex traits into components (characterized in terms of model parameters). To find reliable values for these model parameters, various perturbations are applied and the resulting data are used to evaluate or calibrate the model. Next, sensitivity analysis is applied to find influential component traits, which are selected for mapping on to marker-defined chromosomal regions. These model parameter values can subsequently be predicted by means of the identified correlations with one or various QTLs. The resulting QTL-based version of the model allows prediction of phenotypic traits based on QTLs and as such can also predict performance of novel QTL

Current fruit models have been developed either at cell or at organ level (one big cell model) (Génard *et al.*, 2007). Actually, the cell level is likely to be the elementary level for mechanistic modelling of fruit which will further allow linking of the fruit model with cellular models describing complex metabolic pathways and molecular regulatory networks. Therefore, modelling the way in which cell division and expansion progress together is crucial to understanding the emergence of specific morphological traits (Baldazzi *et al.*, 2012). Recently, models integrating cell division, cell expansion and DNA endoreduplication in the tomato fruit have been proposed (Fanwoua *et al.*, 2013; Baldazzi *et al.*, 2017). At a higher scale of integration, the virtual tomato model has been connected to a plant model describing water and carbon fluxes in the plant architecture, and the induced gradients of water potential and phloem sap concentration in carbon within the plant (Baldazzi *et al.*, 2013). Such integrated models centred on the fruit open new perspectives to integrate information on the molecular control of fruit cellular processes into the fruit model and to analyse the effects of G×E×M interactions on fruit quality. Yet the prediction of other traits of quality including the accumulation of healthy compounds such as vitamins and carotenoids still needs some developments.

Covering the genetic control in plant and fruit models is still far from satisfactory, despite promising approaches (Bertin *et al.*, 2010). Model parameters are considered as either generic parameters when they do not vary among genotypes, or as genotypic parameters (also called genetic coefficients) when they are genotype-dependent. Each set of gene or allele combination is represented by a set of parameters and the phenotype can then be simulated *in silico* under various environmental and management conditions. This implies that model parameters are usually specific to one genotype, restricting the validity range of the model itself. To overcome this limitation, the values of the genotypic parameters have to be predicted depending on combinations of QTLs (QTL-based models), alleles or genes (gene-based models) involved in the process that is modelled. Until now only a few genotypic parameters (i.e. allelic variants) have been advantageously introduced into simulation models. Regarding fruit quality, a QTL-based model of peach quality (Quilot *et al.*, 2005) and a model of tomato sugar composition (Prudent *et al.*, 2011) have been proposed. The model-based approach has clear benefits over traditional QTL mapping,

Fig. 5.11. Continued.
combinations or different growth environments or management practices, i.e. virtual phenotyping. This procedure can be used to derive virtual ideotypes, which can be realized by means of marker-assisted breeding. In this way, trait improvement can be reached in a fast and efficient way; namely, more QTLs are identified; QTLs are likely to be more robust, and when the environment is known, it is more straightforward to identify which markers will give the largest trait improvement. (Kromdjik *et al.*, 2014; reprinted by permission of the Society for Experimental Biology.)

since more QTLs are usually identified that tend to be more stable and the importance of which can be ranked under varying conditions. However, its wider implementation is hampered by the lack of genetic information on the traits and processes simulated by models, and also by the low degree of functionality of current PBSMs, which should be further refined in order to bind model parameters and physiological components. An important issue of simulating G×E×M interactions is the design of ideotypes or QTL/gene combinations relevant to optimizing fruit growth and quality under specific conditions by multi-criteria optimization methods (Quilot-Turion *et al.*, 2012; Génard *et al.*, 2016; Constantinescu *et al.*, 2016), adding genetic constraints to account for pleiotropic and linkage effects (Quilot-Turion *et al.*, 2016).

CONCLUSION

The various components of tomato quality are involved in many plant biological functions as well as being essential for a healthy and hedonic human diet. Thus improving fruit quality as a whole is a top priority. The increasing knowledge of the genetic and molecular controls of many traits of quality, the development of high-throughput methods for plant and fruit phenotyping under varying environments and the development of integrative approaches to unravel G×E×M interactions should rapidly contribute to this objective. Interestingly, most of the chemical components that contribute to the health value of fruits are also involved in plant adaptation and defence against stress. Thus, meeting the social demand for high-quality fruits is likely to be favourable in facing the urgent need to reduce inputs of water, fertilizers and pesticides in intensive production systems. Yet, finding viable compromises between yield and quality remains a challenge. In tomato this should be facilitated by the large genetic resources, such as near-isogenic lines, mutants, transgenics and mapping populations presenting interesting variability in size and composition of fruit.

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