

Tomato (*Solanum lycopersicum*) health components: from the seed to the consumer

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Abstract It is widely accepted that a healthy diet is an important factor in preventing chronic diseases, and in improving energy balance and weight management. Studies have shown strong inverse correlations between tomato consumption and the risk of certain types of cancer, cardiovascular diseases and age-related macular degeneration. Because tomato is the second-most important vegetable in the world after potato, this horticultural crop constitutes an excellent source of health-promoting compounds due to the balanced mixture of minerals and antioxidants including vitamins C and E, lycopene, β -carotene, lutein and flavonoids such as quercetin. Improvement in phytonutrients in tomatoes can be achieved by cultivar selection, environmental factors, agronomic practices, stage of ripeness at harvest, and appropriate handling and conditioning all

the way from the field to the consumer. The purpose of this paper is to review the recent literature of the main factors that can improve the nutritional quality of tomato and consequently their beneficial role in human diet. The importance of genotype selection and the optimization of environmental conditions (light, temperature, humidity, atmospheric CO₂ and air pollutants) for high nutritional value is outlined first, followed by the optimization of agricultural practices (soil properties, water quality, mineral nutrition, salinity, grafting, pruning, growing systems, growth promoters, maturity, and mechanical and pest injuries). The review concludes by identifying several prospects for future research such as modelling and genetic engineering of the nutritional value of tomato.

Keywords Antioxidants · Irrigation · Light · Mineral nutrition · Pigments · Phytonutrients · Salinity · Tomato · Temperature

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Introduction

It is widely accepted that a healthy diet is an important factor in preventing chronic diseases such as cancer, cardio-vascular and neuro-degenerative diseases, and in improving energy balance and weight management. In the scientific literature, studies have shown strong inverse correlations between tomato consumption and the risk of certain types of cancer,

cardiovascular diseases and age-related macular degeneration (Franceschi et al. 1994; Giovannucci et al. 1995; Levy et al. 1995; Ness and Powles 1997; Offord 1998; De Stefani et al. 2000; Grievink et al. 2000; Kotake-Nara et al. 2001; Landrum and Bone 2001; Levi et al. 2001; Rissanen et al. 2001; Gianetti et al. 2002; Giovannucci 2002; Giovannucci et al. 2002; Khachik et al. 2002; Muller et al. 2002; Sesso et al. 2003, 2004; Stahl and Sies 2005). From epidemiological studies, clinical trials and experiments on animals as well as in vitro studies, this protective effect has been mainly attributed to pro-vitamin A (Mayne 1996) and other carotenoids. Moreover, carotenoids are a major class of compounds providing precursors to essential vitamins and antioxidants. Because tomato is the second-most important vegetable in the world after potato, with an annual production of around 122.9 million tonnes of fresh weight (FW) (FAO 2005), this horticultural crop is the predominant source of carotenoids. From a total of around 40 carotenoids found in the human diet, only 25 are found in human blood due to selective uptake by the digestive tract. Of that number, 9–20 are derived from fresh and processed tomato; major ones being lycopene, α - and β -carotene, lutein, zeaxanthin and β -cryptoxanthin. Lycopene, which constitutes about 80–90% of the total carotenoid content of red-ripe tomatoes (Shi and Maguer 2000) is the most efficient antioxidant among carotenoids through its quenching activity of singlet oxygen and scavenging of peroxy radicals (Mortensen and Skibsted 1997; Sies and Stahl 1998). On the other hand, β -carotene, a potent dietary precursor of vitamin A (Olson 1989), accounts for around 7% of tomato carotenoid content (Nguyen and Schwartz 1999). Ascorbic acid (vitamin C), while being a most effective antioxidant in plants (Smirnoff 1996), is also an important phytochemical of tomato fruit. Except for some wild related genotypes (*L. chilense*, *L. hirsutum*, *L. cheesmanii*, *Solanum lycopersicoides*) or new commercial varieties recently developed (Jones et al. 2003), tomato (*Solanum lycopersicum*) fruits are not usually reported to contain anthocyanin. The limited caloric supply, relatively high fibre content, and provision of minerals, vitamins, and phenols such as flavonoids make the tomato fruit an excellent “functional food” providing additional physiological benefits as well as meeting basic nutritional requirements.

The aim of this chapter is to review the recent literature of the main factors that can improve the nutritional quality of tomato and consequently their beneficial role in human diet. The importance of genotype selection and the optimization of environmental conditions (light, temperature, humidity, atmospheric CO₂ and air pollutants) for high nutritional value will be outlined first, followed by the optimization of agricultural practices (soil properties, water quality, mineral nutrition, salinity, grafting, pruning, growing systems, growth promoters, maturity, and mechanical and pest injuries). The review will conclude by identifying several prospects for future research such as modelling and genetic engineering of the nutritional value of tomato.

Selection of cultivars for high nutritional value

During the green agriculture revolution, breeding programs developed hybrid cultivars with a high yield potential per hectare, a uniform and pleasing appearance, disease tolerance, and long shelf life. Those cultivars had a high response to synthetic fertilizers and water supply, and plant development characteristics which lead to easy crop management and market distribution. This led to the development of a very small number of varieties available to large-scale markets without sufficient attention to the content of health-promoting compounds compared to wild type and heirloom fruits. Today, consumers are looking for healthy and tasty food. Consequently, even though the diversity of commercial tomato cultivars is still limited, the content of healthy compounds is becoming a crucial parameter for growers and tomato breeders. Seed companies are now offering different types of fruit (cherry, cocktail, grape, plum, round and salad) of different colours (green, red, yellow, orange, pink, purple, brown, black) with higher phytonutrients as well as some heirloom varieties. Plant-breeding programs are now using both traditional and molecular methods to enhance levels of lycopene and other carotenoids in tomatoes (Ronen et al. 2000; Thompson et al. 2000). Increased antioxidant levels through modification of the flavonoid biosynthetic pathway and other phenolic compounds have also been achieved (Muir et al. 2001; Tomas-Barberan and Espin 2001; Bovy et al. 2002; Verhoeven et al. 2002; Schijlen et al. 2004).

For example, purple-fruited tomatoes that contain high level of anthocyanins have been developed (Jones et al. 2003). Unfortunately, complete information about the nutritional value of wild or heirloom genotypes is scarce in the scientific literature.

Selection of small and highly coloured tomatoes (*high pigment* genes) by growers and market distribution chains optimizes fruit levels of carotenoids, flavonoids, and vitamin C, and consequently their nutritional value and health benefits. Smaller fruits have generally higher vitamin C content while the greater skin/volume ratio of cherry tomatoes may enhance their flavonol content, which is mainly found in the skin. In commercial and commonly-used varieties, processing genotypes have generally a higher content of carotenoids, followed by cherry, cluster and salad tomatoes (Davies and Hobson 1981; Leonardi et al. 2000a; Barrett and Anthon 2001; Dorais et al. 2001a; Dorais 2007). Within the most-utilised salad tomato varieties, however, lycopene content varies slightly (Dorais 2007). Recently, it was shown that the lycopene content of 40 tomato varieties was higher in cherry tomato types followed by cluster and round tomato types (Kuti and Konuru 2005). Interestingly, the selection of orange tomato fruits optimizes the nutritional value of the fruit as orange cultivars have a higher content of carotenoids and vitamin A than conventional red cultivars (Hart and Scott 1995), while yellow varieties have 10 times less lycopene content than red ones. A summary of cultivar, tomato type, and growing system effects on nutritional attributes is given in Table 1.

Optimizing environmental factors for high nutritional value

The two best-known environmental factors influencing the nutritional value of tomato are light and temperature. These may be closely related. Less conclusive studies are reported on the direct effect of high CO₂ and air humidity on phytonutrients. For field tomato crops, changes in nutritional value are often described in terms of variation in geographic location or season, which include interactions among several factors, making interpretation difficult. For example, higher altitudes reduce temperature but increase visible and UV light, which may increase the level of certain phytonutrients such as carotenoids

since their major function is to absorb light during photosynthesis and to protect cells against excessive light. On the other hand, carotenoids in the fruit of protected tomato crops were found to be higher at the end of the harvest period than at the first harvest in May (Auerswald et al. 1996). This could be partly due to differences in light but also to the poorer plant water status in older plants. Under water stress conditions, increase in abscisic acid may influence ethylene production, which has an effect on the concentration of carotenoids. However, the content of ascorbic acid in tomato fruit was found to be more dependent on cultivar than on seasonal changes (Shinohara et al. 1982). A summary of environmental effects on nutritional attributes is given in Table 2.

Light

Phytonutrients of tomato such as vitamin C, carotenoids and phenols are strongly affected by the intensity, duration, and quality of light. For example, several studies have shown that antioxidants such as vitamin C, lycopene, β -carotene and phenols increase with light intensity (McCollum 1954; Ju et al. 1999; Lee and Kader 2000; Merzlyak et al. 2002; Amiot et al. 2007). Linear relationships between anthocyanin accumulation and light intensity have also been reported (Ubi 2004). Although light is not essential for the synthesis of ascorbic acid, the amount and intensity of light during the growing season influences its content in the fruit because ascorbic acid is synthesized from sugars supplied through photosynthesis (Lee and Kader 2000). In fact, positive correlations were observed between fruit sugar content and vitamin C and lycopene content (Gautier et al. 2005). Similarly, even though the formation of carotenoids in ripening tomato fruit does not require induction by light, light plays a fundamental role in determining the content of carotenoids. On the other hand, the biosynthesis of anthocyanins in maturing fruit is a light-dependent process (Lancaster 1992) requiring a photomorphogenic signal mediated by photoreceptors. The involvement of either a UV-B photoreceptor, or phytochromes or cryptochromes has been suggested (Adamse et al. 1989; Kerckhoffs et al. 1992, 1997; Mol et al. 1996; Ninu et al. 1999; Giliberto et al. 2005). Light of sufficient energy is also important to promote photosynthetic production

Table 1 Effects of agricultural techniques on the nutritional value of fresh tomato fruits

	Cultivars	Tomato type		Growing systems				
		Processing vs. beef	Small/cherry vs. beef	Grafting	Soil type	Protected crops vs. field	Hydroponics vs. soil	Organic vs. conventional
Carotenoids	↑↓	↑	↑			↑↓*	=	
Lycopene	↑↓	↑	↑	=↑*		↑↓*		=↑
β-carotene	↑↓			↑*	↑↓			=↑
Lutein	↑↓							
Vitamins								
C	↑↓*		↑	↑*	↑↓	↑	↑	=↑
A	↑↓							
Phenols	↑↓							=↑
Anthocyanins	↑↓							
Flavonoids	↑↓		↑					
Flavonols	↑↓		↑					
Quercetin	↑↓							
Total mineral	=				↑↓			
N								↓
K							↑	
Ca				↑	↑↓		↑	=↑
Mg							↑	
Micro					↑↓			
Antioxidant activity	↑↓	↑	↑	=↑		↑↓*		=↑

= No effect; ↑ increased content; ↓ reduced content; Bold breeding and genetic engineering; * species/cultivars-dependent

of carbohydrates, which are the substrates for flavonoid biosynthesis via the shikimic acid and phenylpropanoid pathways. Formation of flavonol glycosides such as kaempferol and quercetin also requires light, but not all phenolic synthesis is responsive to light.

Light duration also affects phytonutrient levels. Even though light is not required for the ripening of tomato picked at the breaker stage, fruit exposed to an 8-h photoperiod failed to develop lycopene levels as high as those in 24-h-exposed fruit (Cox et al. 2003).

Lastly, light quality is an important determinant of fruit nutritional quality. Red light stimulates carotenoid accumulation in tomato, while far-red light stops the production of carotenoids such as lycopene, probably from fruit-localized phytochromes (Thomas and Jen 1975; Alba et al. 2000). In contrast, the content of vitamin C increased with infrared light exposure of 700–1,100 nm (Gautier et al. 2004). This response may be due to a combined effect of spectral

quality and fruit temperature, which affects sugar metabolism and consequently the vitamin C content (Gauthier et al. 2005). A positive effect of blue light on tomato phytonutrients is less conclusive (Jen 1974; Spalding and Cosgrove 1989; Parks et al. 2001; Ménard et al. 2006) due to variations among genotypes and in growing conditions. Nevertheless, during fruit ripening, increasing PAR and more precisely, blue light, increased the fruit content of lycopene and β-carotene (Gautier et al. 2004). For other plant species, blue light increased the ascorbic acid and anthocyanin fruit concentrations (Spalding and Cosgrove 1989; Parks et al. 2001; Lester 2006).

In contrast, under excessive solar radiation or UV-B radiation of only a few hours, photo-oxidative damage or photoinhibition may occur and reduce lycopene synthesis as well as vitamin C content of tomato fruit (Adegoye and Jolliffe 1987; Prohens et al. 2004). For example, Torres et al. (2006) observed, either with or without UV radiation, that tomato fruit exposed for 5-h to high solar irradiance

Table 2 Effects of environmental conditions on the nutritional attributes of fresh tomato fruits

	Light						Temperature		CO ₂	VPD	Pollutant
	PPFD	UV-B	B	R	FR	IF	Average	Δ			
Carotenoids	↑*↓♦	=↑*↓♦	↑*	↑	↓		↑↓*	↓	=		↓
Lycopene	↑↓♦	↓	↑		↓	=	=↑↓♦*	↓		↑	
β-carotene	↑		↑				=↑↓*				
Vitamins											
C	↑↓♦	↑*↓♦				↑	↓		=↑		↓
A									↑		
B-complex											↓
Phenols	↑	↑							↑*		↓
Antocyanins	↑	↑	↑	↑	↓						
Flavonoids	↑	=↑									↓
Kaempferol	↑	=									
Quercetin	↑	=									
Antioxidant activity		=↑↓*								↓	

= No effect; ↑ increased content; ↓ reduced content; * species/cultivars-dependent; ♦ under extreme conditions; PPFD, photosynthetic photon flux density (light wavelength between 400 and 700 nm); VPD, vapour pressure deficit

had 30% less ascorbic acid and 20% less dehydroascorbic acid in the fruit exocarp, suggesting a partial degradation of the entire ascorbate pool. They also observed a decrease in total carotenoids after 5-h of exposure, with a significant interaction between duration of exposure and intensity of UV radiation. For total ascorbate (ascorbic acid + dehydroascorbic acid), a similar negative effect of UV-B ambient radiation was observed for low (Esperanza) and high (DRW 5981) lycopene genotypes, while a positive effect on the high carotenoid and flavonoid genotype (HP1) was found (Giuntini et al. 2005). A UV-B-free environment increased the antioxidant activity and carotenoid content of Esperanza, while it reduced the carotenoid content of DRW 5981, and had no significant effect on HP1. For flavonoids, synthesis of different flavonoid classes might have different spectral sensitivity characteristics (Awad and Jager 2002). Even though the production of flavonoids and other phenylpropanoids may be stimulated to protect plant tissues from UV damage (Dixon and Palva 1995; Ubi 2004), natural UV radiation does not always affect flavonoid accumulation. Torres et al. (2006) found that tomato exocarp had no detectable changes in concentrations of flavonoids (quercetin, kaempferol, or naringenin enantiomers) as the duration of exposure increased. On the other hand, tomato fruits grown under tunnels and exposed to ambient

solar UV (290–400 nm) had ~20% higher phenolic acids (caffeic acid, *p*-coumaric and ferulic acid) and 10–16% higher total phenolic content than fruits grown under UV exclusion conditions (Luthria et al. 2006). As UV-B exerts very different effects on carotenoid content in fruits of different tomato genotypes (Giuntini et al. 2005), light conditions should be considered in the selection of varieties or lines.

It is important to note that in addition to the effects of light on the plant, various factors such as weeds, mulches, plant population, leaf area index (LAI), shading screens, greenhouse or tunnel coverings that influence light interception by the tomato fruit will potentially influence fruit phytochemical content and its value in human nutrition.

Temperature

Temperature has a direct influence on plant metabolism and, thus, affects tomato fruit development and its nutritional value (Heuvelink and Dorais 2005; Dorais et al. 2001a). As carbon skeleton availability is required for the biosynthesis of certain phytonutrient compounds such as flavonoids and ascorbic acid, an increase in sugars through reduced respiration under lower temperatures may result in a higher level

of phytochemicals. Consequently, ascorbic acid generally declines with increasing temperature, while temperature regulation of carotenoids is crop specific. For tomato, lycopene synthesis is highest when the temperature ranges between 12 and 21°C. The optimum temperature depends on the genotype and interactions with environmental and cultural factors (Dorais et al. 2001a). On the other hand, Krumbein et al. (2006) recently observed an increase in the lycopene concentration of cherry and round type tomatoes when the temperature during the fruit ripening stage increased from 15 to 20.3°C in fall and from 18 to 22°C in spring. In agreement with Robertson et al. (1995) who found a maximum plateau of lycopene concentration between 18 and 26°C in cell suspension cultures, Krumbein et al. (2006) suggested that the optimal temperature for lycopene biosynthesis ranges between 20 and 24°C. Recently, Gauthier et al. (2005) showed that fruit load or fruit position on the truss altered the response of the fruit to temperature; lycopene content increased with higher fruit temperature under low fruit competition whereas it strongly decreased under high fruit-source ratio, especially for distal fruits. Higher fruit temperature also had a negative effect on β -carotene and vitamin C, independently of its effect on sugar metabolism, but dependent on assimilate competition. Temperatures below 10°C or higher than 30°C inhibit the development of lycopene (Tomes 1963; Koskitalo and Ormrod 1972). Hence, cool night temperatures for field tomato crops reduce fruit carotenoids. In contrast to lycopene, β -carotene of tomato is only slightly affected by high temperature, probably due to the conversion of lycopene into β -carotene under high temperature conditions. Nevertheless, cherry tomato fruits subjected to elevated temperatures and solar radiation showed increased lipid peroxidation and decreased content of carotenoids such as lycopene and β -carotene in the exocarp fractions, despite the fact that the oxidation of reduced ascorbate by ascorbate peroxidase increased under these conditions (Rosales et al. 2006). When fruit tomato surface temperatures averaged 46°C, Torres et al. (2006) detected thermoinhibition after 2.5-h of exposure. Similarly to photoinhibition, thermoinhibition could cause increases in cellular reactive oxygen species (ROS) flux and possible up-regulation of antioxidant systems to cope with the increased ROS (Torres et al. 2006). In greenhouse

crops, temperature patterns such as day/night temperature or temperature integration over several days may influence the phytonutrients of fruits. For example, Dorais (2007) found that the use of a low temperature pulse (12°C compared to 15°C, over a 2–4 h period) at the end of the photoperiod for a same 24-h average temperature (18.5°C) decreased the lycopene content of the fruit and their antioxidant activity. Consequently, the widespread use of a pre-night low temperature by greenhouse growers to control plant balance may affect the health qualities of fruit at harvest.

CO₂ and VPD

Despite the fact that carbon dioxide (CO₂) concentration in the atmosphere has increased dramatically during the last 150 years (270–367 $\mu\text{l l}^{-1}$; Watson et al. 1990, 375 $\mu\text{l l}^{-1}$ in 2007) due to fuel combustion, volcanic activity, urban development and intensification of industrial production (Manning and Tiedemann 1995; Romanova 2005), few scientific studies have been done on the influence of CO₂ air concentration on the nutritional value of tomatoes. Nevertheless, the beneficial effects of elevated CO₂ concentrations on biomass production of horticulture crops such as tomato is well known (Nederhoff 1994; Dorais et al. 2001a; Heuvelink and Dorais 2005). According to the source-sink balance hypothesis, there is a general trend towards increasing concentration of carbon-based secondary compounds in response to high CO₂ (Peñuelas and Estiarte 1998). The trend, however, has been shown for only some kinds of carbon-based secondary compounds such as soluble phenolics, and depends on the species and growing conditions. On the other hand, high atmospheric CO₂ concentration appears to reduce oxidative stresses in plants (Idso and Idso 2001), and consequently it has been found to reduce plant antioxidant concentrations. For tomatoes, even though CO₂ stimulated the production of vitamin A, there appears to be a small (7%) increase in vitamin C in fruit grown at three times the normal CO₂ concentration or no effect of CO₂ enrichment on vitamin C (Özçelik and Akilli 1999; Idso and Idso 2001; Idso et al. 2002). In addition, no effect of CO₂-enriched air (380 vs. 1,000 $\mu\text{l l}^{-1}$) on carotenoid content of cherry and round type greenhouse tomatoes has been

reported for plants grown under low or high salinity (Krumbein et al. 2006). Genotypic variation and interaction with other environmental growing conditions and cultural practices such as LAI often make interpretation rather difficult.

Air humidity, generally expressed by the vapour pressure deficit (VPD), greatly influences the plant water status and consequently plant transpiration and the transport of nutrient elements. For many species, increasing air humidity in the range of 0.5–2.0 kPa has either little effect or increases photosynthesis (Heuvelink and Dorais 2005). Even though it is well known that VPD influences the external quality of fruits due to the development of physiological disorders (Dorais et al. 2001a), little is known about its effect on fruit health-promoting compounds. Some authors (Leonardi et al. 2000b; Dorais et al. 2001a) found that greenhouse tomato fruit had a more intense colouration when plants were grown under a high VPD, which suggests a higher lycopene concentration possibly due to a sub-optimal plant water status. It is also possible that a reduction in the net accumulation of water in fruit subjected to high VPD (Guichard et al. 1999) may concentrate health promoting phytochemicals in the fruit.

Air quality and contaminants

One of the physiological processes that can alter or reduce the nutritional quality and the antioxidant activity of plant products is oxidative stress (Rosales et al. 2006). For example, air pollutants (dust, ozone, sulphur dioxide, nitrous oxide, nitrite-N and ammonia) decrease ascorbic acid, carotenoids and B-complex vitamins in many fruits mainly due to their oxidative damage to fruit DNA, proteins, synthesizing enzymes and membranes (Lester 2006). Ozone can alter secondary metabolites such as flavonoids or other phenolic compounds, through changes in the activity of phenylalanine ammoniylase (PAL) and thus the status and productivity of the whole phenylpropanoid pathway (Manning and Tiedemann 1995). Carbon allocation in plants may also be affected by O₃ via effects on photosynthesis and modification of the canopy structure, and hence the environment around the fruit, which may indirectly affect their nutritional value. The effect of air contaminants produced by

volatilization of pesticides under elevated temperature on health-promoting compounds is another aspect that has not been extensively investigated in tomato fruit.

Another potential source of contaminants is biosolids from municipal sewage sludge or industrial wastes which may be used in some countries as fertiliser for horticultural crops such as tomatoes. Little scientific literature is available on the overall effect of biosolid contaminants (lead, cadmium, mercury, hormone, antibiotic, persistent organic compounds) on tomato health-promoting compounds. Soils often have pesticide residues that can be translocated to the fruit (Gonzalez et al. 2005). Despite increasing concerns about fruit and vegetable pesticide residues by consumers, little is known about their direct effects on disease-preventing molecules in plants.

Optimizing agronomic practices for high nutritional value

Similar to the other factors discussed, agronomic practices have a significant influence on the nutritional and health-promoting molecules of tomatoes (Tables 1, 3). Numerous studies have been conducted with tomato on the influence of water management, mineral nutrients, growing systems, plant management, and appropriate stage of fruit ripening on antioxidants and other compounds of value in human health. Except for special cases, only recent studies will be presented in the following section, as earlier reports have already been reviewed by several authors (Davies and Hobson 1981; Hobson 1988; Thakur et al. 1996; Dorais et al. 2001a; Dumas et al. 2003; Collins et al. 2006; Lester 2006; Dorais 2007).

Irrigation management and salinity

Water deficit and poor water quality are the main factors limiting worldwide crop productivity and food quality in terms of nutritional value and food safety. Pathogens present in irrigation water can contaminate tomato fruit and increase potential risk for human infection, e.g. by gastroenteritis and hepatitis A. The quality of water recommended for irrigation of crops frequently consumed raw (e.g. fresh tomatoes) is

Table 3 Effects of cultural practices on the nutritional value of fresh tomato fruits

↑↓	Minerals				Soil pH	Irrigation	Salinity	Growth promoters	Maturity	Injuries
	N	P	K	Micro						
Carotenoids	↓		↑			↓	↑↓♦		↑	
Lycopene	↓	↑	↑			↓	=↑*↓♦	↑	↑	
β-carotene	↓		=↑	↑	↑		=↑	↑	=↑*	
Lutein							=↑			
Vitamins						↓				
C	↓♦	↑	↑	↑	↓	↓	=↑	↑	=↑*	↓
A										
B-complex	↑	↑		↑						
α-tocopherol							=↑		↑	
Phenols	↓						↑		↓	↑
Antocyanins		↑								
Flavonoids		↑								
Flavonols	=↓									
Total minerals						↓				
N	↑						↓			
K			↑				↓			
P							↓			
Mg							↓			
Micro				↑	↓Fe ↓Zn		↓			
Antioxidant activity						↓	↑		↑	

= No effect; ↑ increased content; ↓ reduced content; * species-dependent; ♦ under extreme conditions

often higher than that for processed crops, and the costs associated with treating poor-quality water (filtration, chlorination, peroxide, ozonation, exposure to UV light, heat) for drip or surface irrigation and post-harvest washing of fruit must be considered (Steele and Odumeru 2004). Moreover, the long-term effects of water chlorination, which is the most commonly-used and least expensive method of water disinfection, on tomato health-promoting compounds are not well-documented. It is well known that chlorine can react with organic matter in treated water to yield potential carcinogens (Suslow 1997).

Precise irrigation scheduling to optimize water supply to the plant is also important for maximizing tomato nutritional value. To achieve this optimal water management, several parameters should be considered: (1) soil or growing media properties, (2) environmental growing conditions, (3) crop growth characteristics specific to the cultivar, and (4) the health compounds of interest. Soil chemical (e.g. ion exchange capacity, redox conditions, pH), physical

(e.g. air porosity, available water, hydraulic conductivity and relative gas diffusivity), and biological (e.g. activity of microorganisms, mineralization rate) properties influence the water and mineral uptake by plants and consequently the nutritional value of tomato. In the more ionic exchangeable soils such as clay, the higher mineral concentrations can have a significant effect on fruit vitamin and mineral concentrations. Thus, tomatoes produced on clay have higher ascorbic acid content than on sand (El Mahmoodi et al. 1966). Crop rotation will affect soil physical and chemical characteristics such as pH (Mozafar 1994) over time and also influence tomato nutritional content. Since Fe and Zn constitute important micronutrients for human health, high soil pH negatively affects their uptake by plants and subsequent content in edible plant organs. Similarly, the use of irrigation water with a high amount of bicarbonate inhibits uptake and translocation of some micronutrients. On the other hand, Ca uptake is impaired in soils showing Al toxicity (Frossard et al.

2000). Soil pH may also change under sub-irrigation due to an increased amount of nitrifying bacteria in the lower part of the substrate and a high ammonium concentration. In general, plants grown at low pH have low carotene concentrations whereas plants grown at high pH have low ascorbic acid concentrations (Lester 2006). Even though there is little literature on the influence of soil microbial populations on phytonutrients of tomato, their effects can be considerable (Bourn and Prescott 2002).

The nutritional quality of tomatoes may be affected by the amount of water applied, regardless of fertilizer management, and their irrigation system. For example, heavy rainfall may reduce the oxygen concentration in the soil, and indirectly affect the nutritional value of fruit. Depending on the production system, irrigation water is generally provided by surface and subsurface irrigation, sprinkler irrigation or micro-irrigation (Locascio 2005). Given the scarcity of high quality water in many parts of the world, deficit irrigation can constitute a sustainable tool for water conservation and reduction of leaching into ground water, as well as a plant management tool to improve the nutritional value of tomato fruit. Depending on cultivar, low soil water tension generally decreased the vitamin C content of the fruit (Rudich et al. 1977). For example, drip irrigation increased the tomato ascorbic acid content compared to surface irrigation due to a reduced amount of water available to the fruit (Mahajan and Singh 2006). On a fresh weight basis, sub-irrigation in soilless culture did not change the vitamin C content of tomato compared to a conventional drip system, even though a higher EC was found in upper and lower parts of the growing media (Santamaria et al. 2003). When expressed on a dry weight basis, however, vitamin C content increased as the percentage of dry fruit matter increased with successive harvests, and it was always greater with sub-irrigation than with drip irrigation. In general, increasing the water supply increased tomato fruit yield but reduced fruit quality attributes due to high fruit water content (Dorais et al. 2001a). Consequently, on a fresh weight basis, vitamin, mineral and carotenoid contents were generally lower under higher water supply (Matsuzoe et al. 1998; Zushi and Matsuzoe 1998), although not all health compounds responded to soil moisture variation. Conversely, under low water supply, increase in abscisic acid may influence ethylene

production, and hence the concentration of carotenoids. In soilless culture, however, higher plant water availability provided by a water reservoir and a capillary system did not reduce the lycopene content or the antioxidant activity compared to tomato plants grown either on rockwool or sawdust and irrigated according to solar radiation, even though higher yield was obtained with an increase in water availability (Dorais 2007). However, Dorais (2007) also found that lycopene content of fruit from plants grown in sawdust:peat at low levels of moisture stress was less than that of fruit grown on rockwool and irrigated according to solar radiation. Antioxidant activity was not affected by irrigation treatment.

Even though salinization is generally accompanied by a decrease in yield, the use of salinized water in many areas around the world increased health-promoting molecules in tomato and its nutritional value (Dorais et al. 2001b). Because high salinity in the root zone impairs water uptake, the increase in health-promoting molecules may have been first related to a water stress and a concentration effect. Moderate stress, however, may activate physiological antioxidant responses (Smirnoff 1995; Gomez et al. 1999) and thereby improve carotenoid levels and antioxidant activity in tomato fruit. More specifically, lycopene concentration may increase with moderate salinity due to an up-regulation of gene encoding enzymes involved in the key steps of lycopene biosynthesis, while inhibition may result under higher salinity, resulting in reduced lycopene content. However, the nutritional quality threshold varies depending on cultivar and growing conditions as well as on targeted phytonutrients. For example, under moderate salinity where greenhouse crop fruit yield was not reduced, adding NaCl to the nutrient solution to improve flavour did not affect phytonutrients such as antioxidant vitamins (ascorbic acid, α -tocopherol), carotenoids (lycopene and lutein), or flavonoids (quercetin) (Shi et al. 2002). However, when salinity was varied during the day according to solar radiation, fruit α -tocopherol and lycopene contents increased and ascorbic acid and β -carotene content decreased. An increase in salinity by 45% with NaCl or NaCl/KCl (1:1) did not change lycopene content, but it decreased β -carotene and vitamin C content and increased lutein concentration by 79% (Dorais et al. 2000). With different tomato cultivars and growing conditions, however, Wu et al. (2004) observed a

34–85% increase in lycopene content on a fresh weight basis when salinity was increased from 2.4 to 4.5 mS cm⁻¹. De Pascale et al. (2001) observed that the optimum total carotenoids and lycopene content (on a fresh and dry weight basis) was reached when salinity was 4.0–4.4 mS cm⁻¹ (0.25% NaCl), while ascorbic acid content increased with salinity up to 15.7 mS cm⁻¹. Carotene did not change with salinity. Similar results for β -carotene were found by other authors (Petersen et al. 1998; Krauss et al. 2006). Lipophilic and hydrophilic antioxidant activities both increase with increasing salinity (De Pascale 2001). However, even though increasing salinity (3–10 mS cm⁻¹) increased vitamin C ($\times 1.10$), lycopene ($\times 1.35$), β -carotene ($\times 1.23$) and phenols ($\times 1.21$) on a fresh weight basis, Krauss et al. (2006) observed no significant differences when expressed on a tomato fruit dry weight basis. Similarly, on a dry weight basis, D'Amico et al. (2003) did not find any effect of seawater up to 14 mS cm⁻¹ on total ascorbate concentration in green and red tomatoes. However, when they evaluated the antioxidant capability by measuring the reduced/oxidized ratios of the major antioxidants they observed a higher reduced pool of ascorbate at 14 mS cm⁻¹. On the other hand, Petersen et al. (1998) observed a decrease in vitamin C concentration on a dry weight basis when the salinity increased (3–9 mS cm⁻¹). Furthermore, salinity treatment of non-tolerant cultivars may also reduce leaf area of tomato plants, modifying the light and temperature conditions of the fruit, and thereby indirectly influencing the phytonutrient content. This genotype-dependent plant response may partly explain different results and thresholds reported in the literature. Salinity also changed mineral uptake profiles (Ehret and Plant 1999). For example, increasing water salinity from 0.5 to 15.7 mS cm⁻¹ with NaCl decreased P, K, Mg and Zn fruit concentrations due to ion competition with Na and Cl (De Pascale et al. 2001), which is undesirable. On the other hand, salinity decreased fruit nitrate content, which is desirable for food processing and human health (De Pascale et al. 2001).

Mineral nutrition

The effect of minerals on phytonutrients and nutritional value of tomato depends on the specific

mineral, the mineral form, the plant genotype, and any possible interactions with environmental conditions and agronomic practices. In general, even though moderate application of N increases yield, N fertilizers decrease the concentration of vitamin C and carotenoids, while K fertilization has the opposite effect. Secondary plant metabolites which lack N in their structure such as lycopene, β -carotene, phenolics and flavonols are favoured under N-limiting conditions although photosynthetic activity is not simultaneously reduced, whereas nitrogen-containing compounds are favoured when N is readily available and not limiting to growth. Phosphorous may increase the level of some phytochemicals like ascorbic acid, anthocyanins, flavonoids and lycopene, although interactions with climatic factors and growing season may occur (Bruulsema et al. 2004; Lester 2006), while boron availability affects phenolic content (McClure 1975). According to Mozafar (1994), ascorbic acid increases with increasing levels of P, K, Mn, B, Mo, Cu, Co and Zn, while β -carotene increases with increasing levels of K, Mg, Mn, B, Cu and Zn, and B-complex vitamins increase with increasing levels of N, P and B (Lester 2006).

The negative effects of N may also be due to canopy structural changes, as excessive application of N increases the LAI of the crop, resulting in fruit shading. Nitrogen applied as ammonium leads to an acidification of the rhizosphere and enhances the uptake of Fe, Zn and Ca by the plant, and consequently affects the nutrients of the edible part (Frossard et al. 2000). In contrast, the general use of NO₃ as a N-source for tomato crops leads to an alkalization of the rhizosphere, and reduces the Fe, Zn, P and Ca plant uptake. Increasing the rate of N fertilizer (0, 150, 300 and 600 kg ha⁻¹) decreased vitamin C concentration in tomato fruit by 18–28%, but the decrease was least when N was applied as nitrate or compost compared to ammonium (Montagu and Goh 1990). Fruit concentrations of P, K, Mg, Cu and Zn decreased when urea was used as the N source compared to ammonium and nitrate forms. Although different N sources generated only minor differences in the carotenoid concentration of tomato fruit, phytoene and phytofluene (essential precursors of carotenoids) increased when calcium nitrate was used as the N source, and the increase in ascorbic acid was higher when ammonium was used as the N source (Montagu and Goh 1990). Even though N deficiency

increased flavonol content of tomato leaves, no difference was observed in the fruit. Phosphorous deficiency had the reverse effect, with no change in leaf flavonol content and an increase in fruit flavonols, but only in the early stages of ripening (Stewart et al. 2001). Increasing K up to 8 mM increased carotenoids and lycopene concentrations of tomato (Trudel and Ozburn 1971). For phytoene and phytofluene, 2 mM K in the nutrient solution seems to have been the critical level beyond which changes in K had no effect. In the same study, β -carotene and γ -carotene were not influenced by K levels, while Lester (2006) reported that ascorbic acid and β -carotene increased in fruits and vegetables with increasing levels of K, Mn, B, Cu, and Zn.

Because minerals essential for human health are not always easily taken up by the plant from the soil and then translocated to the fruit, the application of fertilisers directly to fruits may be highly efficient. For instance, Ca and B foliar spray applications on 40-day-old fruits to reduce tomato cracking increased the fruit B concentration by two times and the Ca concentration by 1.5 times compared to control fruits (Dorais et al. 2004). It has also been reported that 0.1–0.3% Ca spray applications to shoots increased the lycopene (by up to four times) and vitamin C (by up to 1.49 times) content of tomato (Subbiah and Perumal 1990). This finding is in agreement with other results reporting a positive relationship between the Ca and vitamin C levels in tomato fruit grown under various environments (Bangerth 1976; Premuzic et al. 1998). In contrast, increasing Ca concentration in the nutrient solution of hydroponically-grown plants decreased the carotene and lycopene content due to the decrease in K uptake that occurred because of cation competition (Paiva et al. 1998). The uptake by plants of nutrients that are beneficial for human health such as Fe, Zn and Ca, is also influenced by root architecture, the presence of mycorrhizal fungi, and by root physiology (cited in Frossard et al. 2000).

Organic and synthetic fertilizers

Despite the nutritional value debate on organic vs. conventionally-grown fruits (Woese et al. 1997; Brandt and Mølgaard 2001; Bourn and Prescott 2002), because of the limited number of long term rigorous controlled studies, there is no direct

evidence that organic and conventional tomatoes differ in concentrations of various nutrients, except for the nitrate content of organic products which tends to be lower than in conventionally-grown products (Woese et al. 1997; Brandt and Mølgaard 2001; Bourn and Prescott 2002). The heterogeneity of soil properties and activity among organic farms, variability between organic and conventional farms in terms of varieties, differing environmental conditions and agricultural practices often contribute to inconclusive findings. The use of resistant rootstocks in organic farming may also increase the content of defence-related secondary metabolites in organic tomato compared to conventionally-grown fruit. For instance, the higher concentration of Ca and vitamin C of tomato grown on organic soil and irrigated only with water compared to hydroponically-grown fruit produced with complete nutrient solution, was due to a reduced level of cations such as Na, Mg, K, resulting in reduced foliage development in the organic crop, and consequently higher ambient light levels on the fruit (Premuzic et al. 1998). Recently, Dorais (2007) observed that organically-grown tomato had a slightly higher lycopene content on a fresh weight basis compared to fruit from hydroponically-grown plants in rockwool due to lower LAI and soil matric potential. Higher levels of lycopene and other antioxidants (β -carotene, vitamin C, chlorogenic acid, rutin and naringenin) were also found in organically-grown tomato compared to conventionally produced fruit (Caris-Veyrat et al. 2004). In a study conducted on 10 organic and conventional farms in central and southern Taiwan, however, Lumpkin (2005) observed no significant differences between organic and conventional farming methods for the main tomato phytochemicals, which included β -carotene, lycopene, ascorbic acid, total phenolics and antioxidant activity. However, high heterogeneity among farm trials may have masked any effects. Although there is no clear effect of organic growing conditions on fruit nutritional value, organically-grown foods have lower pesticide residues (Baker et al. 2002; Bourn and Prescott 2002).

Grafting and pruning

The use of grafting for tomato production has increased in recent years because rootstocks improve

tolerance to pathogens, poor water quality, overly-wet soils, drought and soil micronutrient toxicity. Grafting can also increase tolerance to low-temperature, enhance water and nutrient uptake, increase plant vigour, extend the duration of harvest time, and reduce physiological disorders related to fruit quality. For tree fruits, antioxidant activity, anthocyanin and total phenolic content of the fruit are dependent on rootstock types and cultivars and may determine the mineral composition of the fruit (Walker 1986; Sorce et al. 2002; Ubi 2004; Giorgi et al. 2005; Scalzo et al. 2005). For tomato fruit, depending on the grafted cultivar, ascorbic acid of grafted plants grown under 30 and 60 mM NaCl increased compared to ungrafted plants, while grafting increased the lycopene and β -carotene content of fruit grown under all salinity treatments (Fernandez-Garcia et al. 2004). For beef type tomato, however, the lycopene content and the antioxidant activity of fruit from grafted and non-grafted plants were not affected by grafting, while Ca concentration and water uptake of grafted plants was higher than in non-grafted plants (Dorais et al., unpublished). Similarly, depending on cultivar and the level of salinity, increases in ascorbic acid, lycopene and β -carotene content per unit of fruit dry weight of grafted plants may or may not be observed (Fernandez-Garcia et al. 2004). Furthermore the effect of grafting may vary according to the number of grafted tomato stems per rootstock plant.

Cultural practices such as pruning and thinning determine the crop load and fruit size, which can influence the nutritional composition of fruit (Lee and Kader 2000). By adjusting the number of leaves per plant or per fruit, leaf pruning can also affect the phytonutrient content of fruit, since leaves provide carbohydrates for secondary metabolites, and act as a light filter absorbing the red light and transmitting far-red light to the bottom or inside the canopy, affecting carotenoid and anthocyanin synthesis of shaded fruit.

Production systems

Mulch materials in tomato crops may have an indirect influence on fruit phytonutrients via their effect on weed control, reduction of nutrient losses, improvement of the soil hydrothermal regimes, and light quality that is reflected to the plants. Similarly,

covering materials for greenhouses generally block most of the UV radiation and may reduce or/and modify the spectral quality received by plants, affecting tomato health-components (see section on light).

Protected cultivation and greenhouse technology which are largely spread around the world (greater than 450 000 ha, around 13% of the total tomato production, Dorais et al. 2001a) are the best alternative for using land and other resources more efficiently. Moreover, greenhouses provide a controlled environment that offers a great opportunity to improve the concentration of phytonutrients in tomato. From 40 tomato varieties, greenhouse-grown cluster and round tomato types contained more lycopene (30.3 mg kg^{-1}) than field-grown tomato (25.2 mg kg^{-1}), whereas cherry types had a higher content in field-grown (91.9 mg kg^{-1}) than in greenhouse-grown (56.1 mg kg^{-1}) (Kuti and Konuru 2005). The ascorbic acid content of surface-irrigated tomato grown in a greenhouse was found to be 66% higher than in those grown with surface irrigation outdoors (Mahajan and Singh 2006).

Plant growth promoters

Phytohormones such as auxins, gibberellins, cytokinins and abscisic acid have been implicated in anthocyanin biosynthesis and accumulation in several plant species (Sheoran et al. 2006). Although growth regulator application may not be allowed in some countries, some reports mention that they can improve the health quality of tomato. For example, foliar application at the three-leaf stage of $30 \mu\text{M}$ DCPTA (2-(3,4-Dichlorophenoxy)triethylamine) increased the fruit lycopene content by 28% (Hsu and Yokohama 1991). Similarly, pre-germination seed treatment with up to $30 \mu\text{M}$ of DCPTA for 6-h increased the content of lycopene from 58 to $118 \mu\text{g per g fw}$ and of β -carotene from 2.2 to $5.7 \mu\text{g per g fw}$ in greenhouse-grown tomato (Keithly et al. 1990). Gibberellic acid and cycocel also increased fruit β -carotene. In field-grown tomato, a 25% increase in the ascorbic acid content of the fruit was noted after applying alar solution (1,500 and 3,000 mg/kg). Gibberellic acid, cycocel and phosphon also increased the ascorbic acid content of the fruit (Dumas et al. 2003).

Maturity at harvest

The stage of fruit development at harvest is one of the major factors determining the health quality of fruit because there is an important change in the profile of antioxidants during ripening. Fruit ripened on the plant generally has higher phytonutrient content than table-ripened fruit. Tomato fruit harvested green or at the breaker stage and ripened to table-ripeness contained less ascorbic acid than fruit ripened on the vine (Betancourt et al. 1977; Kader et al. 1977). However, Dumas et al. (2003) reported that ascorbic acid was or was not affected by the ripening stage at harvest, depending of the cultivar studied. Tomato fruit harvested at full ripeness has higher levels of carotenoids and antioxidant activity in the water-insoluble fraction, whereas the main phenolic content and the antioxidant activity of the water-soluble fraction decrease at later stages of ripeness. For example, the lycopene content of four tomato cultivars increased from less than 0.10 μg per g fw in green fruit to about 50 μg as fruit matured to the red-ripe stage and to 70 μg when the fruit became overripe, softened, and began to decay (Thompson et al. 2000). In cherry tomato, lycopene increased during ripening by 20-fold and β -carotene by 3-fold. It has been observed that β -carotene synthesis stopped after the colour of the tomato had changed from orange to red (Koskitalo and Ormrod 1972). Conflicting data concerning the accumulation rate of β -carotene during ripening have been attributed to different growing conditions and cultivars. Phytoene and phytofluene content is linearly correlated with the ripening index and formed 6.8% of the total carotenoids at the red stage. Although fruit of full ripeness exhibited the highest level of α -, β -tocopherol, chlorogenic acid (a main phenol compound) declined during ripening. On the other hand, proteins (1.0–1.3 g/100 g), fats (0.1–0.2 g/100 g), fibre (1.4–1.7 g/100 g), and ash (0.6–0.7 g/100 g) did not vary during tomato ripening (Raffo et al. 2002).

Mechanical and pest injuries

In general, mechanical injuries such as bruising, surface abrasions, and cuts can result in accelerated loss of vitamin C (Lee and Kader 2000). Proper management and cultural practices to minimize

physical damage to the fruit is essential for preserving high quality. Many phenylpropanoid compounds are also induced in response to wounding (Dixon and Paiva 1995). On the other hand, pest pressures, by inducing defence reactions in the plant, may stimulate the production of antioxidant compounds, especially phenolics. Synthetic pesticides either stimulate or inhibit production of phytonutrients, but little is known about the effects on the composition of the edible part (Brandt and Molgaard 2001). It has been suggested that an increase in peroxidase activity observed after herbicide treatment may contribute to resistance to herbicides by playing a role in oxidative stress tolerance, in addition to detoxifying herbicides by catalysing their conjugation with glutathione. The effect of different herbicides on phenylalanine ammonia-lyase activity and therefore on phenolic biosynthesis has also been reported (Tomas-Barberan and Espin 2001). Moreover, applications of pesticides for pest control leads to fruit pesticide residues that may exceed the maximal level (Chavarri et al. 2004; Tsakiris et al. 2004); however, none of the farming choices (conventional, IPM, organic) available on the market are completely free of pesticide residues (Baker et al. 2002).

Future trends

Modelling

In recent years, modelling has become a significant research tool in horticulture. However, as noted in a survey of the literature (Gary et al. 1998), most modelling efforts (90%) have been in the area of plant growth and development with very little attention paid to other topics such as fruit and vegetable quality. An increased desire by consumers for healthy food has, in part, encouraged the recent development of models of fruit quality. Models of peach fruit quality have been developed for biochemicals which influence taste, such sugars, (Génard and Stouty 1996), citric acid (Lobit et al. 2003) and malic acid (Lobit et al. 2006). Fruit quality models have also been developed for post-harvest conditions in order to predict keeping quality of horticultural products (Schouten et al. 2002). Very few models exist for tomato quality. Verkerke and Kersten (2000) have proposed a predictive model of flavour based on

a few simple measurements of the fruit such as soluble solids content and percent extracted juice. In a recent review of factors which determine tomato fruit quality through effects on water and carbon fluxes to the fruit, Guichard et al. (2001) point out that little information is yet available to model aspects of fruit quality such as volatiles and pigments.

Some fruit quality modules have been developed for implementation within existing biomass production models. For example, a virtual fruit model has been developed for peach which simulates seasonal changes in several peach fruit quality traits by adapting and integrating three existing process-based models describing fruit dry mass growth, fruit fresh mass growth and sugar accumulation in the flesh into one system (Lescourret and Génard 2005; Génard et al. 2007). Their model was also shown to be sensitive to crop management and constitutes an important step towards quality trait modelling of fruits using different biological scales for explanation (Struik et al. 2005). Models of this nature may also be extended by including genotypic information (Quilot et al. 2005).

Overall, very little, if any, attention is paid to modelling nutritional quality of fruits, including tomatoes. One difficulty is that, in contrast with dry-mass-based traits, models on quality are species-specific. Furthermore, models that explain how phytonutrients are affected by environmental conditions and agricultural techniques are still not available because of the complexity of the system and the only partly-understood underlying mechanisms. A useful fruit quality model must take into account several quality traits, the underlying processes and their interactions (Lescourret and Génard 2005). However, by using new concepts and new experimental and modelling tools, models have been extended to cell metabolism and biochemical pathways (Giersch 2000; Struik et al. 2005). This is particularly important for the development of models which describe the behaviour of specific phytonutrients.

Since environmental pre-harvest conditions and cultural practices affect phytonutrients (see previous sections), holistic models integrating genotypic variation, light quality, mineral and water balance in the fruit, fruit carbohydrate content, growth regulators, and maturity at harvest are required. Recently, efforts have been made to integrate a systems biology

approach into crop growth models, creating opportunities for analysing complex phenotypical behaviour at the crop level (Minorsky 2003; Hammer et al. 2004).

Collectively, these recent efforts in modelling should provide the opportunity for the eventual development of predictive and mechanistic models of tomato fruit quality, including models of phytonutrient composition and concentration.

Genetic engineering

As consumers become more discriminating in their eating habits and as the demand for healthier foods increases, plant breeders and biotechnologists are beginning to realize that the development of genotypes with improved health benefits for consumers is just as important as the breeding of cultivars which primarily benefit the producer. Biotechnology offers opportunities to satisfy consumer demands for healthier foods.

There are a few examples of transgenic tomatoes with enhanced levels of specific health-beneficial compounds. Romer et al. (2000) developed a transgenic line containing a bacterial carotenoid gene which enhanced fruit β -carotene content, but at the expense of lycopene levels. Flavonoids, particularly rutin, in the skin of tomato fruit were increased 78-fold in transgenic tomato lines transformed with the petunia *chi-a* gene (Muir et al. 2001). Although flavonoids are not normally abundant in the flesh of tomato fruit, transgenic tomato lines over-expressing the maize transcription factors *LC* and *CI* showed high levels of flavonoid glycosides, particularly kaempferol glycosides (Le Gall et al. 2003) in the fruit flesh. Tomato plants engineered to produce enhanced levels of the polyamines spermidine and spermine also exhibited increased lycopene levels in the fruit (Mehta et al. 2002). These sorts of studies will likely continue.

Another potentially exciting use for tomatoes is in the production of health-related biomolecules on a large agricultural scale. An example of this is in the delivery of edible vaccines. One key advantage of this approach is that antigens can be produced on a large scale in harvested tomato fruit which do not have to be refrigerated during transport or storage, as do conventional pharmaceutical antigens. Dalal et al.

(2006) have compiled a list of research projects using tomato plants as a source of antigens for hepatitis B and E, cholera, respiratory syncytial virus, and rabies virus. At least one example of transgenic tomato being used for the production of large amounts of an enzyme needed for human health also exists; Mor et al. (2001) have developed a transgenic tomato producing acetylcholinesterase which is needed to counteract organophosphate poisoning. Lastly, plants may be used to produce plantibodies, or plant-derived antibodies (Stoger et al. 2002; Dalal et al. 2006), and tomato may also be a candidate plant for that use.

As with any commercial cultivar, transgenic tomatoes showing traits for enhanced levels of health-beneficial phytochemicals will likely be influenced by the environment in terms of the actual amount of phytochemical produced, as described throughout this chapter. Hence, detailed studies of the behaviour of these plants and their response to the environment in which they are grown will be necessary.

Consumer acceptance of genetically modified (GM) plants for delivery of health-promoting phytochemicals and vaccines is uncertain. This alone may prevent further development of these bioengineered foods. In addition, regulatory agencies generally deal with scientific risk assessment and are ill-equipped to deal with the social impact of these technologies (Ma et al. 2005). For these reasons, proactive evaluation of the social considerations has been advocated in an effort to prevent premature rejection of promising new technologies (Castle and Dalglish 2005). Nevertheless, there are signs that the use of plants as vehicles for drug production and dissemination is viewed favourably. A recent survey taken in the United States found that of eight biotechnology applications using plants and animals, the use of plants to produce pharmaceutical drugs ranked the highest acceptance (Knight 2006). In another survey of Americans, the majority of respondents (68%) showed acceptance for use of plant-produced vaccines (Kirk and McIntosh 2005).

Conclusions

Although improved quality has long been a goal of breeding programs, the decline in some aspects of nutritional quality observed for tomatoes from 1950

to 1999 (Davis et al. 2004) suggests that not enough attention has been paid to nutrition. This is changing, and the goal is now to produce highly flavourful and nutritious tomatoes while maintaining the more grower-focused characteristics of high yield, disease resistance, and so on. However, the final quality is always a product of the interaction of genotype and environment. As documented in this review, many environmental factors can greatly impact the nutritional quality of tomatoes. Finding the best combinations of those factors to maximize nutritional quality, which in itself, is comprised of components which are often affected quite differently by a particular set of conditions, will be a challenge. The development of models of tomato nutritional quality may assist in defining the conditions required to maximize each (or all) of those specific health attributes. Although the ideal would be a single set of environmental (and genetic) conditions which promotes high nutritional quality in all tomatoes, this may not be logistically possible. Given the high degree of control over the environment that is possible in greenhouses, the quality of greenhouse-grown tomatoes, in particular, would stand to benefit the most from this information. However, the positive effects of some environmental conditions on nutritional quality are offset by negative effects on yield. This may mean that health-promoting tomatoes would be produced under unique growing conditions which do not necessarily garner the highest yields, and could then be marketed as a specific health-promoting food. In fact, much as tomatoes have for many years been bred and grown for specific purposes, the development and production of health-beneficial tomatoes is yet another niche for this versatile fruit to fill.

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