The European Journal of Plant Science and Biotechnology ©2007 *Global Science Books*

A Review of Recent Research on Tomato Nutrition, Breeding and Post-Harvest Technology with Reference to Fruit Quality

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ABSTRACT

The continued importance of tomato (*Lycopersicon esculentum* Mill.) as a vegetable and salad commodity is reflected by the large volume of research on virtually all aspects of the crop. Since 2000, over a thousand scientific papers per year relating to tomato research have been published, not including those in the less widely read literature, conference and workshop proceedings. In the present paper, we survey recent findings in the areas of tomato nutrition, the influence of salinity on nutrition and growth, tomato breeding and genetic resources, and the post-harvest physiology, storage and ripening of fruit. Research findings are considered particularly with respect to fruit quality, as reflected in the quality standards of the European Union.

Keywords: antioxidants, ethylene, genetics, heavy metals, markers, nutrients, ripening, salinity, storage, transgenic

Abbreviations: ACC, 1-aminocyclopropane-1-carboxylate; **AVG**, aminoethoxyvinylglycine; **BER**, blossom-end rot; **Fe-EDDHA**, iron ethylenediaminedihydroxyphenylacetic acid; **GA_3**, gibberellic acid; **IAA**, indole-3-acetic acid; **IPP**, isopentenyl diphosphate; **LDPE**, low-density polyethylene; **1-MCP**, 1-methylcyclopropene; **NFT**, nutrient film technique; **QTLs**, quantitative trait loci, **RH**, relative humidity; **ROS**, reactive oxygen species; **SA**, salicylic acid

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Received: 28 February, 2007. Accepted: 20 April, 2007.

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INTRODUCTION

A significant impact of globalization on horticulture has been an increasing demand for quality improvement and the wider adoption of quality standards for fruit, vegetable and salad commodities. Tomato (*Lycopersicon esculentum* Mill.) is a major horticultural crop with an estimated global production of over 120 million metric tons (F.A.O. 2007). Salad tomatoes must have a flavour, colour and texture that satisfy the consumer's preference. At the same time they must be suitable for post-harvest handling and marketing, even over large distances. In addition, processing tomatoes must have the rheological characteristics required by the relevant food processing industry.

In the European Union (E.U.), the application of quality standards to fresh tomatoes has increased the uniformity in size, maturity and presentation of produce. However, the most significant quality characteristic of a product (i.e. its flavour and aroma) are not affected by such standards, but by the genetic characteristics of the species or cultivar, the cultivation procedures employed (especially the nutrient status of the plant; **Fig. 1**), the stage of harvest and the post-harvest technology employed.

In the present paper, we survey recent research on tomato mineral nutrition, breeding and post-harvest technology, particularly where relating to the quality of the fresh fruit.

MINERAL NUTRITION OF TOMATO

Nutrition is a complex process involving 16 essential nutrients, as well as many other chemical elements that are either beneficial or harmful to plant metabolism. Furthermore, the response of a crop, such as tomato, to a particular nutrient status may vary with cultivar and exogenous factors, such as cultural practices, substrate and environmental conditions. The provision of nutrients to the plant in quantities that are optimal for their subsequent utilization is a primary aim of crop fertilizer programmes and, since both yield and quality are adversely affected by any deviation from this optimum, it is essential at all times to avoid an excess or lack of nutrients. In recent years, an appreciable volume of horticultural research has been devoted to the subject of tomato nutrition and standard concentration levels for nutrient supply to tomatoes have been proposed (e.g. for crops in peat-based media, by Bryson and Barker 2002).

Responses to specific nutrients and nutrient ratios

Nitrogen

Nitrogen is the only nutrient that can be supplied to plants in both anionic (NO_3^-) and cationic (NH_4^+) form (Forde and Clarkson 1999). Hence, the fraction of ammonium to the total nitrogen supply may considerably influence the total cation to anion uptake ratio (Imas *et al.* 1997; Savvas *et al.* 2006). However, changes in this ratio are electrochemically compensated for by commensurate alterations in the influx or efflux of protons (H^+) or basic anions in the root zone, thereby significantly influencing the rhizosphere pH (Barber 1984; Lea-Cox *et al.* 1996; Imas *et al.* 1997). In turn, the pH of the external medium may influence the uptake of P and micronutrients, thereby inducing serious nutritional disturbances (Islam *et al.* 1980; Imas *et al.* 1997; Adams 2002). Furthermore, the form of nitrogen supplied to the plants may influence the uptake of other macronutrients due to ion antagonism (Marschner 1995). Last but not least, the N form also influences plant metabolism, due to differences in the intracellular assimilation pathways (Raab and Terry 1994; Gerendás *et al.* 1997). In view of this background, many investigations have recently been concerned with the responses of tomato to the N form supplied to the plants via fertilization.

Earlier studies concerned with the effects of nitrogen source on tomato and its interactions with other nutritional and environmental factors indicated that tomato is susceptible to the supply of ammonium as a sole or dominating nitrogen form (e.g. Kirkby and Knight 1977; Ganmore-Neumann and Kafkafi 1980; Pill and Lambeth 1980; Magalhães and Wilcox 1983; Errebhi and Wilcox 1990; Imas *et al.* 1997). More recent studies have confirmed this consideration. Thus, according to Claussen (2002), the use of ammonium as sole or dominating N source in a solution culture of tomato resulted in impaired growth and yield restrictions. Siddiqi *et al.* (2002) and Akl *et al.* (2003) observed a restriction of both the vegetative growth and the fruit yield of tomato when NH_4-N/total-N in the nutrient solution was higher than 0.1. However, Claussen (2002) and Dong *et al.* (2004) observed an increase in both total and fruit dry weight when the ammonium fraction was 0.25. According to Akl *et al.* (2003), the impaired growth of tomato when the ammonium fraction was in the range 0.15-0.25 of the total-N supply was associated with low pH levels (<5) in the root zone. In contrast to Siddiqi *et al.* (2002) and Akl *et al.* (2003), Claussen (2002) maintained the rhizosphere pH above 6 by adding $CaCO_3$ to the growth medium. Thus, it seems that the lowest level of NH_4-N/total-N, that impairs the growth and yield of tomato, is mainly dictated by its impact on the rhizosphere pH, which is influenced not only by the nitrogen form but also by environmental factors (Chaignon *et al.* 2002).

With respect to fruit quality, a NH_4^+-N-dominated nitrogen supply may markedly increase the incidence of fruits with blossom-end rot (BER) (**Fig. 1B**), an effect which is ascribed to a depression of Ca uptake by the enhanced external NH_4^+ levels (Kirkby and Mengel 1967; Siddiqi *et al.* 2002; Akl *et al.* 2003; Heeb *et al.* 2005b). Siddiqi *et al.* (2002) and Heeb *et al.* (2005a) state that the supply of 0.1 of total-N in the form of NH_4^+ (10% of total N) is capable of enhancing the flavour of the fruits, presumably by elevating glutamine and glutamate levels.

The interactions between salinity and nitrogen form were recently studied by Ben-Oliel *et al.* (2004), who found that the addition of 1 mM ammonium to 7 mM nitrate in the nutrient solution had an ameliorating effect on tomato fruit yield under salinity.

Tan *et al.* (2000b) used ^{15}N- labelled compounds in a hydroponic culture of tomato and found that the absorption, translocation, and assimilation of urea is poor at the seedling stage, but increases to almost similar levels with that of NO_3-N at the reproductive growth stage. Based on

Fig. 1 Nutrient disorders of tomato. (**A**) Nitrogen deficiency. (**B**) Calcium deficiency (blossom-end rot). (**C**) Phosphorus deficiency. (**D**) Potassium deficiency.

the above results, Tan *et al.* (2000b) suggest that urea may be used as an N-source in soilless grown tomato crops, provided the plants are at the reproductive growth stage.

Phosphorus

Modern tomato cultivars and hybrids exhibit high relative growth rates and therefore rely on an adequate supply of phosphorus for optimal development and high yields. Indeed, as reported by de Groot *et al.* (2002), the relative growth rate of tomato increases sharply with increasing plant P concentration when the latter is below the critical level of adequacy. Results from recent research have indicated that foliar application of phosphorus in greenhouse tomato enhances the concentrations of chlorophyll, K, P, Mg and Fe in the leaves, accelerates fruit maturity and increases marketable yield and quality (Chapagain and Wiesman 2004). According to de Groot *et al.* (2001), at mild P limitation the assimilate supply is not the limiting factor for reduced growth rates, but at severe P limitation the rate of photosynthesis is depressed, as indicated by the decrease in starch accumulation. Under conditions of severe P deficiency, the leaf N concentration is also suppressed, due to a decrease in leaf cytokinin levels (de Groot *et al.* 2002).

In addition to its effect on growth, the level of P may also influence the reproductive efficiency by improving pollen performance (**Fig. 2B**). Thus, according to Poulton *et al.* (2001), mycorrhizal infection and high soil P levels are capable of increasing pollen quality (*in vitro* and *in vivo* pollen performance) as well as pollen quantity, thereby enhancing fitness through the male function. Furthermore, a high P supply may ameliorate the adverse effects of excessive Co concentrations (0.5 mM or more) (Chatterjee and Chatterjee 2002) as well as Zn toxicity (Kaya and Higgs 2002) on tomato. An excessive supply of P rarely imposes toxicity symptoms in soil grown tomato crops due to the low solubility of this nutrient element in the soil solution. However, in soilless culture, the occurrence of phosphorus toxicity is likely, since excess P is not immobilized in insoluble forms. Jones (1998) suggests a P concentration of 1% in the dry weight as the critical level between sufficiency and toxicity for tomato plants. Toxic levels of P in the leaves of tomato may also be imposed by Zn deficiency (Kaya and Higgs 2001).

Potassium

The K requirements of tomato are extraordinarily high due to the rapid growth of the plant in combination with the heavy fruit load (Chapagain and Wiesman 2004). To cope with high K requirements, tomato has evolved efficient mechanisms to acquire potassium under conditions of low K levels in the root zone (Chen and Gabelman 2000; Rubio *et al.* 2006). These mechanisms are governed by genes expressed only under conditions of too low K levels in the root zone, and which are induced either by a root-localized signal or because of root sensing of the mineral in the surrounding environment (Wang *et al.* 2002); it seems that these genes are not associated with K nutrition under conditions of normal K supply.

As reported by Mulholland *et al.* (2001), high levels of air humidity may considerably restrict the K concentration in young expanding leaflets near the shoot apex compared with standard air humidity; under such conditions, leaf expansion, yield, and the proportion of Class 1 fruits may be drastically reduced. When tomato is grown under conditions of limited K supply, sodium may partially substitute for potassium. Indeed, according to Walker *et al.* (2000), the growth of tomato plants cultivated in a K-deficient nutrient solution (0.5 mM K^+) was severely depressed in comparison with K-replete plants (4.5 mM K), while the supply of 1 or 5 mM NaCl virtually restored growth to the level of K-replete plants.

Calcium

Recent research has revealed that a low calcium level in the root zone is rarely a limiting factor for the vegetative growth of tomato (del Amor and Marcelis 2006). Nevertheless, the calcium nutrition of tomato demands special attention because this nutrient is intimately involved in the occurrence of the physiological disorder BER, which may considerably reduce fruit quality and market acceptability (Ho *et al.* 1993; Grattan and Grieve 1999). BER is caused by a local deficiency of Ca in the distal part of the fruit, which results in a disruption of tissue structure in that area (Adams 2002). Various factors, including the cultivar, the external concentrations of Ca, NH_4-N, K, and Mg, salt or water stress, oxygen availability in the root zone, air relative humidity, and air temperature, may aggravate or ameliorate the occurrence of this physiological disorder (Saure 2001; Navarro *et al.* 2005). As a result of the involvement of so many factors in the occurrence of BER, no absolute, critical fruit Ca concentration associated with the appearance of this disorder has been identified (Ho and White 2005). According to Hao and Papadopoulos (2004), the incidence of BER at an external Ca concentration of 3.75 mM increased linearly with increasing Mg levels in the root zone, while it was not affected by Mg concentration at 7.5 mM Ca. Nevertheless, as suggested by Ho and White (2005), the manipulation of the nutrient levels in the root zone or the growth environment are not adequately effective measures in reducing BER because they affect apoplastic Ca concentration in fruit tissue indirectly. Therefore, these authors suggest spraying Ca directly on to young fruits in order to prevent BER.

Higher transpiration and temperature levels enhance water uptake, thereby increasing the transport of Ca to the leaves via the xylem (Taylor *et al.* 2004). However, under such conditions, the transport of water to fruits is reduced due to competition with the leaves, and thus translocation of Ca to fruits is also restricted, thereby increasing the percentage of fruits with BER (Adams 2002). On the other

Fig. 2 Tomato cultivation, artificial pollination and fruit quality. (**A**) Hydroponic cultivation of cherry tomato. (**B**) Pollen collection. (**C**) Controlled pollination. (**D**) Tomato grading. (**E**) Large-grade tomatoes packed in a single layer. (**F**) Pre-packed plastic boxes of cherry tomatoes.

hand, too high levels of air humidity in greenhouses originating from energy saving measures may reduce transpiration to levels imposing Ca deficiency in the leaves of tomato, with subsequent loss of yield and quality (Hamer 2003).

Another aspect related to the application of Ca in tomato cultivation that has recently been studied is its effect on the occurrence of some fungal diseases. Thus, as reported by Ehret *et al.* (2002), spraying of tomato leaves with various combinations of Ca salts was as effective as elemental S in reducing powdery mildew (*Erysiphe orontii*) colony counts on leaves. The suppression of powdery mildew development in tomato by foliar Ca application was ascribed to both osmotic (concentration) and ion-specific effects. Furthermore, an enhanced supply of calcium significantly increases the resistance of tomato to bacterial wilt caused by *Ralstonia solanacearum*, while highly resistant cultivars are characterized by a high Ca uptake (Yamazaki *et al.* 2000).

Magnesium

High levels of Mg in the root zone seem to be beneficial for tomato. As reported by Adams (2002), a Mg concentration of approximately 4 mM in the root zone of tomatoes grown in NFT resulted in deficiency symptoms in the leaves, while increasing the Mg level to 6 mM maintained the plants free of deficiency symptoms throughout the season. Similar results were reported by Hao and Papadopoulos (2003, 2004) for tomato grown on rockwool.

Iron

Iron deficiency is the most frequent nutritional problem faced by most cultivated plants when the pH level in the root zone is too high. However, tomato does not seem to be susceptible to iron deficiency under conditions of moderately high pH (6-7) in the root zone (Islam *et al.* 1980; Akl *et al.* 2003). Nevertheless, the application of part of nitrogen in the form of ammonium may reduce chlorosis symptoms in tomato, especially in soilless grown crops (Sonneveld 2002). The use of iron chelates either via irrigation or by foliage spraying is another effective means of preventing or even curing an iron deficiency (Fernández and Ebert 2005; He *et al.* 2005). According to Sánchez *et al.* (2005), the combination of Fe-EDDHA with organic compounds such as commercial humic substances or mixes of amino acids may further improve Fe uptake.

Iron deficiency in tomato is characterised by a drastic reduction of the leaf chlorophyll content (Dasgan *et al.* 2003). According to Mills and Jones (1996), a Fe concentration of 60 mg kg^{-1} in the leaf petioles opposite or below the top flower cluster is the lowest critical level for the occurrence of iron deficiency in tomato. However, it seems that the activities of Fe-containing enzymes, specifically ascorbate peroxidase, catalase, and guaiacol peroxidase, are more reliable criteria for the characterization of the Fe nutritional status of tomato than the tissue Fe level (Ruiz *et al.* 2000; Dasgan *et al.* 2003).

Besides the rhizosphere pH, many other factors, such as the genotype, the levels of soluble Fe, phosphorus, bicarbonates, organic matter and moisture content in the root zone, may influence the uptake of Fe by tomato (Ruiz *et al.* 2000; Dasgan *et al.* 2004). Thus, recent research (Rivero *et al.* 2003) has indicated that the uptake of Fe by tomato, as well as the activities of enzymes related to the metabolism of this micronutrient within the plant, specifically Fe-chelate reductase, aconitase, guaiacol peroxidase, catalase, and Fe-superoxide dismutase, are diminished by heat stress (T=35°C). Furthermore, the ability of the root system of tomato to acquire Fe is greatly influenced by genotypic variations among cultivars (Dasgan *et al.* 2002, 2004), and this variation may be even wider in the case of grafting tomato on to iron efficient rootstocks (Rivero *et al.* 2004). According to Wang *et al.* (2002), several genes are involved in Fe uptake under Fe-limiting conditions in the root zone and the expression of these genes is induced within one hour after withholding Fe from the roots of intact plants. Li *et al.* (2004) isolated the ferric-chelate reductase gene *LeFRO1* from tomato, the transcription of which was induced in roots under conditions of iron deficiency. *FER* is another gene isolated from tomato that seems to play a central regulatory role in controlling the whole iron deficiency responses and iron uptake by tomato roots (Ling *et al.* 2002; Yuan *et al.* 2005).

Manganese

Manganese deficiency is a frequently occurring nutritional disorder in tomato crops. Recent research has indicated that the growth of tomato may be severely restricted by either a too high or a too low Mn concentration in the root zone (Shenker *et al.* 2004). Reuter and Robinson (1986) suggest a concentration range of 50-500 mg kg^{-1} in mature leaves as adequate for tomato. However, Shenker *et al.* (2004) found that the growth and the chlorophyll content of plants with a leaf Mn concentration of 16.8 mg kg^{-1} were not significantly lower that those of plants with leaf Mn levels falling within the above range of adequacy, while a leaf Mn concentration of 207.4 mg kg^{-1} was associated with toxicity symptoms. According to Mills and Jones (1996), a Mn concentration of 250 mg kg^{-1} in the leaf petioles is the maximum safe level for tomato. Nevertheless, the critical level for the appearance of Mn toxicity may be influenced by various other factors, such as the magnesium to manganese ratio (Horst 1988; Le Bot *et al.* 1990).

Normally, a too high Mn concentration in the root zone is expected to reduce Fe uptake due to competition in uptake mediated by common metal transporters, which are located in the plasma membrane (Marschner 1995; Korshunova *et al.* 1999). Nevertheless, in some cases an increase in the external Mn concentration may also enhance the shoot Fe concentration in tomato (Gunes *et al.* 1998; Shenker *et al.* 2004).

Zinc

An optimal zinc supply in tomato is indicated by Zn concentrations ranging from 20 to 250 mg kg^{-1} in the leaf petioles opposite or below the top flower cluster (Mills and Jones 1996). Zinc deficiency is visually manifested by thinner and shorter internodes, upward twisting leaf borders, and unevenly distributed chlorotic flecks on the old leaves (Bergmann 1988). As reported by Kaya and Higgs (2001), zinc deficiency in tomato was alleviated by foliar application of Zn at 23 mg L^{-1}. Zinc toxicity in tomato may be ameliorated by foliar spraying with P- and Fe-containing fertilizers (Kaya and Higgs 2002).

Copper

Tomato is rather susceptible to low rhizosphere pH (Akl *et al.* 2003) and this response seems to be at least partly due to the occurrence of Cu toxicity (Chaignon *et al.* 2002). Overall, tomato seems to be subsceptible to excessive Cu concentrations in the root zone. Indeed, as reported by Liao *et al.* (2000), Cu concentrations higher than 5 mg L^{-1} in the recirculating nutrient solution depressed biomass production in shoots and roots of tomato grown in a NFT system. Copper retention by roots limits Cu translocation to shoots via the xylem (Liao *et al.* 2000). As a result, with increased Cu availability in the root zone the increase in root Cu concentration is much greater than that in the shoots, which means that the leaf Cu level is not a reliable indicator for Cu toxicity in tomato. In most cases, Cu toxicity considerably reduces the uptake of Fe by tomato, thereby imposing visible symptoms similar to those of Fe deficiency (Bergmann 1988).

Boron

Boron deficiency in fresh-market tomatoes is a widespread problem that reduces yield and fruit quality (Davis *et al.* 2003). As reported by Smit and Combrink (2004), at too low B levels in the root zone, the leaves of tomato are brittle and appear pale-green, a considerable fraction of flowers abscises and the fruits lack firmness, a problem that is worsened during storage. According to Smit and Combrink (2004), the above symptoms appeared at a B concentration level of 0.02 mg L^{-1} in the nutrient solution supplied to a crop grown on quarz-sand, but a B concentration of 0.16 mg L^{-1} seemed to be optimal for tomato and levels of up to 64 mg L^{-1} did not cause any toxicity symptoms. Furthermore, a suboptimal boron supply may considerably reduce fruit set, especially if no other means for pollination (e.g. vibration) are applied (Smit and Combrink 2005). In another study, it was shown that an enhanced boron supply (B foliar spray at 300 mg L^{-1}) was associated with a less frequent incidence of the physiological disorder shoulder check crack (Huang and Snapp 2004a), the visible symptoms of which are described under 'nutrition and fruit quality'. Davis *et al.* (2003) reported that the delivery of B either through the nutrient solution (1 mg L^{-1}), or by foliar spraying (1.87 mg L^{-1}) of boron chelated with mannitol, to tomato grown in river sand, was associated with increased plant growth and tissue K, Ca and B concentrations. In the above study, foliar spraying with boron significantly enhanced fruit B and K concentrations in comparison with no boron supply, which indicates firstly that B is translocated from the leaves to the fruit and secondly that B is also involved in K translocation within the plant. Enhanced uptake of Ca, Mg, Na, Zn and B with higher B levels in the root zone has been reported by Smit and Combrink (2004).

Another recently investigated aspect related to boron nutrition in tomato is the interaction between boron and salinity or water stress. According to Ben-Gal and Shani (2002, 2003), under conditions of simultaneous boron deficiency and salt or water stress, the extent of growth suppression is determined by the factor imposing the most severe stress and not by an addition of the effects of both restrictive factors. Hence, a dominant-stress-factor model following the Liebig-Sprengel law of the minimum may be used to describe the responses of tomato to simultaneous exposure to boron and salinity or boron and water shortage. Furthermore, Ben-Gal and Shani (2002) found that the yield response of tomato to boron nutrition correlates better with B concentration in the irrigation water and soil solution than with the levels of boron in the plant tissue. According to Alpaslan and Gunes (2001), soil boron concentrations of 5 mg kg^{-1} or higher are expected to impose boron toxicity symptoms.

Molybdenum

In a recent experiment with tomato, it was shown that sulphate and molybdate compete for the same carrier and transport sites during uptake, and that sulphate deficiency leads to excess Mo uptake (Alhendawi *et al.* 2005). Nevertheless, the impact of these findings on tomato nutrition is limited, due to the high tolerance of this plant species to excessive molybdenum concentrations in the plant tissue.

Salinity

A comprehensive review of research carried out up to 1999 on the responses of tomato to salinity has been presented by Cuartero and Muñoz (1999). As indicated in previous investigations, the tomato plant is moderately sensitive to salinity (Maas and Hoffman 1977), although considerable differences between cultivars may be observed (Alian *et al.* 2000). In soilless culture, where the salinity in the root zone can be better manipulated by means of nutrient solution composition and irrigation frequency, tomato can tolerate total salt concentrations of up to 2.5-2.9 dS m^{-1} in the root zone without yield losses (Shannon *et al.* 1987; Sonneveld and Welles 1988; Sonneveld and van der Burg 1991). The exact level may vary depending on cultivar sensitivity (Caro *et al.* 1991) and environmental conditions (Sonneveld and Welles 1988; Li *et al.* 2001; Karlberg *et al.* 2006). Increasing the salt concentration in the root environment to levels higher than the above range affects yield, due mainly to a restriction of the individual fruit size (Adams and Ho 1989; Adams 1991; Willumsen *et al.* 1996; Cuartero and Muñoz 1999; Li *et al.* 2001; Navarro *et al.* 2005). However, at very high salinity levels, the number of fruits per plant is also affected by salinity (Cuartero and Muñoz 1999). According to Adams and Ho (1989), van Ieperen *et al.* (1996) and Olympios *et al.* (2003), the number of fruits per plant was restricted when the level of salinity in the root zone was 8 dS m^{-1} or higher. The suppressive effect of moderate salinity on tomato fruit size seems to originate from a restriction of water transport into the fruit, which results in enhanced rates of dry matter accumulation (Johnson *et al.* 1992; Plaut *et al.* 2004). Mavrogianopoulos *et al.* (2002) stated that the reduced transport of water into tomato fruit under saline conditions is a result of whole-plant osmotic adjustment. Moreover, most experiments concerned with the response of tomato to moderate salt stress revealed a higher sensitivity of fresh fruit yield to salinity compared to that of the vegetative growth (Shalhevet and Yaron 1973; Katerji *et al.* 1998). Tomato seems to be salt sensitive during early development (Kütük *et al.* 2004). For example, according to Olympios *et al.* (2003) tomato is more susceptible to high salinity (8.7 dS m^{-1}) at an early stage of development than in the later growing stages. According to Stanghellini *et al.* (2002), the effects of salinity on tomato were reversible and the leaching of the salts from the root environment resulted in full recovery of growth in the plant parts that had not reached the rapid growth phase when the plants were exposed to salinity (EC 9 dS m^{-1}).

Comparisons of tomato responses to different salinity sources have led to the conclusion that the exposure of tomato to low and moderate salinity affects fruit growth mainly through osmotic effects rather than ion specific toxicity, provided that the basic nutrient supply is balanced and adequate (Adams and Ho 1989; Adams 1991; Sonneveld and van der Burg 1991). The primary mechanism in the tolerance of sodium by tomato under conditions of NaCl-salinity is active exclusion, combined with retention of Na by the xylem parenchyma of the roots, stems and petioles of older leaves, which enables the maintenance of low Na levels in the younger, photosynthetically active leaves (Shannon *et al.* 1987). In agreement with this, An *et al.* (2005) found that the increased salt tolerance of some tomato cultivars was related to a higher root-to-shoot ratio and to an enhanced ability to exclude Na from the shoot. Nevertheless, it seems that the responses of tomato to salt stress conditions are also determined by the concentration of endogenous ABA, which acts as a signal for the activation of stress adaptation mechanisms (Chen *et al.* 2003; Mulholland *et al.* 2003).

The deleterious effects of salinity on tomato biomass production can be ameliorated by an enhanced supply of calcium (Grattan and Grieve 1999). According to Flores *et al.* (2001) and Ben-Oliel *et al.* (2004), the supply of part of the nitrogen in the form of NH_4-N in salt-stressed tomato seems to increase the rate of N assimilation, as well as the levels of Fe and chlorophyll in the plant tissues, thereby mitigating salt injury. Furthermore, better root aeration, which enhances the oxygen supply to the root cells, may considerably enhance the salinity tolerance of tomato (Bhattarai *et al.* 2006). Recent strategies in breeding salt tolerant tomato cultivars focus not only on the selection of reliable nutritional and biochemical indicators (Juan *et al.* 2005) but also on the use of molecular markers and genetic transformation (Cuartero *et al.* 2006; Xu and Shi 2006). Borsani *et al.* (2001) used mutagenesis to identify plant genes required for salt tolerance in tomato. Nevertheless, despite some promising results, the development of salt-tolerant cultivars by means of transgenesis has not yet been achieved (Foolad 2004).

Other strategies that might be applied to improve the growth and yield performance of tomato include the increase of air humidity during hot weather, especially in Mediterranean countries (Cuartero and Muñoz 1999; An *et al.* 2005) and the grafting of tomato on to salt tolerant rootstocks (Chen *et al.* 2003; Estañ *et al.* 2005). Enhanced salt tolerance of tomato grafted on to some rootstocks seems to be associated with a higher ability of the root system of the latter to exclude Na^+ and Cl^- from the shoot (Fernández-García *et al.* 2002; Santa-Cruz 2003; Estañ *et al.* 2005). Recently, Stevens *et al.* (2006) tested the application of 0.1 mM salicylic acid (SA) via root drenching as a means of improving the salt tolerance of tomato and found that SA-treated plants exposed to salinity exhibited higher survival and relative shoot growth rates compared to untreated plants. Nevertheless, further research is needed on this topic to confirm these results and the cost of using salicylic acid on a commercial scale has to be estimated.

Unlike the growth and yield of tomato, fruit quality is favoured by moderate salinity levels. This aspect will be discussed in more detail in the Section under the heading "Nutrition and fruit quality".

Responses to beneficial elements and heavy metals

Under the intensive growing conditions prevailing in the modern greenhouse industry, the occurrence of non-nutrient chemical elements at concentrations much higher or much lower than those corresponding to the natural adaptation of tomato is not a rare exception. Therefore, in recent years, many investigators have been concerned with the responses of tomato to toxic concentrations of heavy metals or to the beneficial effects of non-nutrient elements, such as silicon, nickel, etc.

Nickel

One of the non-nutrient chemical elements that can be classified as "beneficial" for plant growth is nickel. The occurrence of Ni at low concentrations in the root zone may be of value to the nitrogen assimilation and growth of tomato, while an increased supply of Ni may be deleterious for the plants (Tan *et al.* 2000a). Nickel is an essential component of the enzyme urease, which catalyses the assimilation of urea within the plant tissues (Marschner 1995). Therefore, the beneficial effects of Ni on plant growth are observed in plants fed with urea. According to Tan *et al.* (2000a), Ni is beneficial for urea-fed tomato plants when supplied at a concentration of 0.1 mg L^{-1} via the nutrient solution. In contrast, a concentration of 1 mg L^{-1} in the root zone may be harmful for tomato plant growth (Tan *et al.* 2000a).

Silicon

Another chemical element with stimulatory effects on tomato growth is silicon. The favourable effects of Si on plant growth seem to originate from reinforcement of the cell walls due to the deposition of Si in the form of amorphous silica ($SiO_2 \cdot nH_2O$) and opal phytoliths (Inanaga and Okasaka 1995; Epstein 1999). According to Miyake and Takahashi (1978), silicon should be considered an essential nutrient for tomato. Nevertheless, tomato belongs to the plants classified as Si excluders, and, therefore, the silicon concentration is higher in the roots than in the shoots (Dannon and Wydra 2004; Heine *et al.* 2005).

According to Dannon and Wydra (2004), addition of silicon to the nutrient solution may significantly reduce the incidence of bacterial wilt caused by *Ralstonia solanacearum* in tomato grown in hydroponic culture. Recently, it was shown that silicon alleviates the deleterious effects of NaCl-salinity on tomato plant growth (Stamatakis *et al.* 2003; Al-Aghabary *et al.* 2004; Romero-Aranda *et al.* 2006). The stimulatory effect of Si on the growth of tomato plants exposed to NaCl-salinity was ascribed to a restriction of Na and Cl uptake (Stamatakis *et al.* 2003), improvement of the plant water status (Romero-Aranda *et al.* 2006) and enhancement of the activities of superoxide dismutase and catalalase, which protect the plant tissues from oxidative damage induced by salt (Al-Aghabary *et al.* 2004). Furthermore, Si was found to increase net photosynthesis in tomato plants exposed to NaCl-salinity (Romero-Aranda *et al.* 2006), a response that may be associated with an enhancement of the leaf chlorophyll content, and the photochemical efficiency of photosystem II (Al-Aghabary *et al.* 2004).

In soil-grown tomato crops, an inadequate supply of Si is rather unusual, due to the abundance of Si in the earth's crust. However, in commercial hydroponics (**Fig. 2A**), plants are grown on inert substrates and, therefore, the supply of Si depends mainly on the silicon concentration of the irrigation water used to prepare the nutrient solution. Thus, if the silicon concentration in the irrigation water is low, tomato may benefit from the extra addition of Si (1-2 mM) to the nutrient solution. According to Stamatakis *et al.* (2003), the addition of 2.25 mM Si to the nutrient solution in soilless culture may also reduce the occurrence of BER in tomato fruit, provided that the plants are not exposed to salinity.

Selenium

Selenium is long known to be an essential element for human and livestock nutrition (Marschner 1995). Although selenium is not considered an essential nutrient element for plants, its concentration in edible tissues of cultivated plants has recently attracted some interest due to its positive effects on human health, including protection against various forms of cancer (Anderson and Scarf 1983; Ip 1998). Selenium is translocated from the shoot to the fruit of tomato, but the rate of translocation is reduced with increasing sulphate supply to the plants (Pezzarossa *et al.* 1999). Recent research has indicated that inorganic selenium supplementation (e.g. 1.5 mg Se per kg of soil) in tomato crops may enhance the Se content of the tomato fruit, thereby serving as a natural means to increase the daily Se intake by humans (Carvalho *et al.* 2003). Furthermore, when grown in soils rich in Se (40 mg kg^{-1}), tomato was capable of taking up considerable amounts of Se and translocating them to non-edible plant parts, particularly leaves, stems, and roots (Carvalho *et al.* 2003). Hence, tomato can also serve as a selenium scavenger to remediate Se-contaminated soils.

Aluminium

The aluminum concentration in the root zone of most agricultural crops is usually very low, but it can increase to toxic levels when the pH of the soil or the nutrient solution retained in the root zone of soilless grown crops falls below 5.5 (Marschner 1995). Increased tolerance to Al toxicity may originate from the exudation of citric acid by the roots, which can contribute to detoxification of Al and increased phosphate availability, but tomato seems to be rather susceptible to high Al concentrations in the root zone (Luo *et al.* 1999). According to Cramer and Titus (2001), an elevated concentration of dissolved inorganic carbon (CO_2 + HCO_3^-) may ameliorate Al toxicity in tomato crops by providing supplementary carbon for organic acid synthesis.

Cobalt

Cobalt is a constituent of cobalamin (vitamin B_{12}), which is an essential coenzyme of three enzyme systems; methionine synthase, ribonucleotide reductase, and methylmalonyl-coenzyme A mutase. These enzymes are required by *Rhizobium* in the process of inorganic nitrogen fixation (Dilworth *et al.* 1979). Consequently, Co is considered a beneficial mineral element for legumes. Furthermore, since cobalamin is essential for livestock and humans, care should be taken to ensure an adequate supply of Co to forage plants. With respect to tomato, there is no report indicating any requirement of cobalt by this crop. However, excessive Co concentrations in the root zone may pose a problem for tomato in some cases, particularly when the plant is grown in serpentine soils or in soils enriched with sewage sludge (Perez-Espinosa *et al.* 2002). The toxic effects of Co on tomato were studied in a crop grown in refined sand and the results indicated that plants respond to 0.05 mM Co in the nutrient solution by growth suppression (Gopal *et al.* 2003). At higher Co concentrations (0.1-0.5 mM), plant biomass was more severely suppressed and visible toxicity symptoms occurred, the intensity of which increased with rising external Co levels (Gopal *et al.* 2003). In tomato plants suffering from Co toxicity, the concentrations of Fe, chlorophyll a and b, and the activity of catalase are depressed, while that of peroxidase, acid phosphatase, and ribonuclease tends to increase (Chatterjee and Chatterjee 2002). Increased supply of Fe (Chatterjee and Chatterjee 2002) and P (Chatterjee and Chatterjee 2003) may partially ameliorate the toxic effects of Co on tomato.

Cadmium

Cadmium is a heavy metal which is highly toxic for plants and animal organisms. Due to its relatively high mobility in both soil and plant tissue, Cd constitutes a serious threat for human health and, therefore, many recent investigations have been concerned with its impact on various agricultural crops. When tomato is exposed to relatively high Cd concentrations, the leaf structure is disorganized in a manner characterised by a smaller mesophyll cell size, reduced intercellular spaces, as well as severe alterations in chloroplast fine structure, which exhibits atypical shape and dilation of the thylakoid membranes (Djebali *et al.* 2005). These biochemical and ultrastructural changes are manifested in premature senescence of the leaves. Cadmium remains predominantly located in the roots of tomato, which seem to play the role of Cd-trapping (Chiraz *et al.* 2003). A concentration of 0.05 mM Cd in the soil or nutrient solution is high enough to induce toxicity symptoms in tomato (Ouariti *et al.* 1997).

Mercury

The exposure of tomato to high levels of mercury, originating from anthropogenic soil contamination, impairs growth and may lead to plant death. In a recent investigation, it was shown that Hg concentrations as high as 10 μM in the root zone are toxic to tomato and the phytotoxic effects are brought about by an enhanced production of active oxygen species (mainly H_2O_2) and subsequent lipid peroxidation (Cho and Park 2000). In the above study, it was found that Hg accumulates predominantly in roots rather than in the shoot of tomato.

Nutrition and fruit quality

Product quality is a complex characteristic that depends on several factors and includes both objective, measurable quality traits as well as subjective, sensory characteristics (Auerswald *et al.* 1999; Schnitzler and Gruda 2002). In the last decades, quality concerns have become increasingly important worldwide and, therefore, many investigations have addressed the impact of plant nutrition on the quality of tomato fruit.

It is well known, that an adequate supply of potassium enhances the titratable acidity of tomato fruit (Davies and Winsor 1967; Adams *et al.* 1978; Davies and Hobson 1981), thereby considerably improving the sensory quality of tomato. Low levels of potassium supply in soilless cultivated tomato plants are associated with ripening disorders (Adams 2002). As reported by Hartz *et al.* (2005), enhanced fertilization with potassium improves fruit colour, while at the same time reducing the incidence of yellow shoulder and other fruit colour disorders. In contrast to K, an increase of the nitrogen supply to tomato above a threshold level considered as optimal for greenhouse production may reduce fruit quality by decreasing the sugar content (Davies and Winsor 1967). As reported by Parisi *et al.* (2006), a high nitrogen supply (250 kg ha^{-1}) impaired some important quality characteristics of the tomato fruit, such as pH, soluble solids, glucose and fructose content, as well as the ratio of reducing sugars to total solids. The inclusion of part of nitrogen in the form of NH_4-N may improve fruit quality by increasing the content of sugars and organic acids when compared with solely nitrate nutrition (Flores *et al.* 2003). As suggested by Heeb *et al.* (2005b), the supply of reduced nitrogen forms, such as ammonium or organic nitrogen, to tomato results in an improved fruit flavour. With respect to phosphorus, it appears that the variation of P supply in soil grown tomato crops does not significantly influence the total soluble solids, pH, acidity of the tomato juice, or the fruit colour characteristics (Oke *et al.* 2005). Nevertheless, the available information regarding the impact of P on tomato fruit quality is currently rather limited.

Calcium plays a key role in the quality of tomato fruit, due mainly to its impact on the occurrence of the physiological disorder BER (**Fig. 1B**) (for more details on this topic see section “Responses to specific nutrients and nutrient ratios”). Furthermore, an enhanced supply of calcium may reduce the incidence of shoulder check crack, another physiological disorder that leads to a deterioration in fruit quality (Lichter *et al.* 2002). This defect appears as a surface roughness that develops primarily on the shoulder area of the fruit, which spoils the appearance and severely restricts the storability of the fruits (Huang and Snapp 2004a). Microscopic inspection of the damaged fruits by the above authors revealed that the surface roughness consisted of many microscopic cracks that occurred in parallel lines. As reported by Huang and Snapp (2004b), weekly sprays of tomato fruit in the field with a solution containing 50 mM $CaCl_2$ consistently reduced the incidence of fruit-cracking to a moderate degree. Magnesium is not directly involved in the fruit quality of tomato, although under conditions of severe Mg deficiency the size and overall appearance of the fruit may be reduced. However, an increase of the Mg supply above the standard recommended levels, though not toxic for the plants, may considerably increase the incidence of BER, unless accompanied by a commensurate increase in calcium supply (Hao and Papadopoulos 2004).

With respect to trace elements, the fruit quality of tomato is affected predominantly by boron, while the other micronutrients may deteriorate the fruit quality of tomato only when the plants exhibit severe deficiency symptoms, which result in an overall imbalance of plant metabolism. According to Huang and Snapp (2004a), an inadequate supply of boron results in an increased incidence of the disorder shoulder check crack, while spraying the tomato foliage with B consistently reduces the percentage of fruits affected with this disorder. Furthermore, a low boron supply reduces the firmness of tomato fruits and this problem is exacerbated during storage (Smit and Combrink 2004). As reported by these authors, fruit set, development, and colour, as well as total soluble solids, firmness and shelf life, seemed to be close to optimum when tomato was supplied with a balanced nutrient solution containing 0.16 mg L^{-1} B.

In addition to the individual nutrients, the total salt concentration in the root zone is a crucial factor for fruit quality. There is a general consensus that a moderate increase of salinity in the root environment improves the fruit quality of tomato (Auerswald *et al.* 1999; Savvas 2001; Kraus *et al.* 2006). The favourable effects of salinity on the quality of tomato are mainly an increasing dry matter content, and higher sugar and titratable acid concentrations in the fruit juice (Ehret and Ho 1986a; Adams and Ho 1989; Gough and Hobson 1990; Sonneveld and van der Burg 1991; Serio *et al.* 2004; Tabatabaei *et al.* 2004; Krauss *et al.* 2006). Nevertheless, although high salinity increases the total soluble solids and titratable acids in fresh tomato fruits, these differences seem to disappear after storage for two weeks at 15°C (Cramer *et al.* 2001). According to Gough and Hobson (1990), taste panels respond more to sweetness than to acidity, when testing the sensory quality of tomato fruits.

With respect to the impact of salinity on fruit firmness, contradictory results have been reported. Thus, Petersen *et al.* (1998), Botella *et al.* (2000) and Schwarz *et al.* (2001) observed enhanced firmness of tomato fruit with increasing salt levels in the root zone, while in the experiments of Krauss *et al.* (2006) fruit firmness was reduced by salinity. According to Cuartero and Muñoz (1999), the firmness of tomato fruit decreases only at high salinity levels (in excess of 10 dS m^{-1}) in the root zone. In other studies, the red fruit colour was enhanced and the shelf life of tomato was prolonged by nutrient solution salinity (Sonneveld and van der Burg 1991; Botella *et al.* 2000), whilst the incidence of the physiological disorders blotchy ripening (Sonneveld and Welles 1988; Mulholland *et al.* 2002), gold specks (Sonneveld and Voogt 1990; Mulholland *et al.* 2002), russeting (Sonneveld and van der Burg 1991) and fruit cracking (Chrétien *et al.* 2000) decreased. Gold specks are considered to be symptoms of Ca excess in tomato fruits (de Kreij *et al.* 1992). Thus, the favourable effect of salinity on gold specks is attributed to the decreased translocation of Ca into the fruits, which is observed when the plants are exposed to high external salt concentrations (Ehret and Ho 1986b). Furthermore, increasing the total salt concentration in the nutrient solution seems to enhance the concentrations of vitamin C, lycopene, and β-carotene in fresh tomato fruit (Petersen *et al.* 1998; Krauss *et al.* 2006), although this was not confirmed by the results of Fernández-Garcia *et al.* (2004). According to de Pascale *et al.* (2001) the total carotenoid and lycopene concentrations in tomato fruit are enhanced by moderate salinity but decrease as the level of salinity exceeds a threshold value. Recalculation of the data of Petersen *et al.* (1998) on a mg per fruit, or mg per 100 g dry fruit basis, revealed equal or even decreasing concentrations of these pigments with increasing salinity, in agreement with the previous results of Adams and Ho (1989). Only the sugar content of dry tomato fruit seems to increase slightly with increasing salinity (Petersen *et al.* 1998). Adams and Ho (1989) suggested that the increased concentrations of titratable acids and sugars in the fruit juice are merely due to the reduced water content (increased dry matter content) of the fruit imposed by increasing external salinity levels. The increase of the vitamin C and β-carotene concentrations in the fruit of salt stressed tomatoes may also be due to the restricted water content of the fruit. However, Sato *et al.* (2006) state that the increased concentration of soluble solids in the fruit of NaCl-treated plants was not the result of simple overall condensation due to the reduction of water transport. Nevertheless, in terms of consumer quality, the determining factors when assessing the response of tomato to nutrient solution salinity are the concentrations of the above constituents in the fruit juice. Indeed, Sato *et al.* (2006) found that the consumer grading of tomato fruit was determined by the concentrations of sugars, organic acids and amino acids in the fresh fruit. It can be therefore concluded, that moderate levels of salinity improve the fruit quality of tomato.

Based on the above data, one might expect the percentage of tomato fruits graded Class I to be enhanced by increasing salinity. Indeed, some researchers reported an increased proportion of fruits graded Class I when the salt concentration in the nutrient solution was increased above the standard recommended values (Adams and Ho 1989; Adams 1991). However, nutrient solution salinity restricts the mean weight of tomato fruit too (Chrétien *et al.* 2000; Krauss *et al.* 2006), while increasing the incidence of BER (Ehret and Ho 1986b; Sonneveld and van der Burg 1991; Adams and Ho 1992; Willumsen *et al.* 1996; van Ieperen 1996; Schwarz *et al.* 2001). As a result, in some cases, the favourable effects of salinity on the percentage of fruits graded as Class I may be counteracted by a higher percentage of small fruits and fruits with BER, as has been reported by Willumsen *et al.* (1996) and Chrétien *et al.* (2000).

Although the exposure of tomato to moderate salinity improves fruit quality it may reduce yield, but to a much smaller extent than that imposed on other vegetable fruits (Savvas 2001). Therefore, the recommended level of nutrient solution salinity for tomato cultivation in soilless culture has to be a compromise between these two contrasting effects. The current recommendation for tomato is a total salt concentration corresponding to an electrical conductivity (EC) of 2.6 dS m^{-1} in the nutrient solution supplied to the crop in order to maintain an EC level of 3.5-3.7 dS m^{-1} in the root zone solution (Sonneveld and Straver 1994; de Kreij *et al.* 1999). According to van Ieperen (1996) and Santamaria *et al.* (2004), nutrient solutions with a high EC during the night and a low EC during the day appear to improve fruit quality in soilless grown tomato without affecting fruit yield. Nevertheless, the application of such nutritional programmes, though potentially beneficial, may be not feasible in most commercial tomato crops, especially those grown in substrates.

TOMATO BREEDING

Like all known species of the genus *Lycopersicon*, tomato is a diploid; it has 2n=24 chromosomes, and a genome size of 2.0 pg/2c = 9.5×10^5 Kb/1c (950 Mbp), which is composed of 77% heterochromatin and 23% euchromatin (Peterson *et al.* 1996). Tomato chromosomes can easily be identified by pachytene analysis. With the development of trisomics, monosomics and translocations through chromosome engineering, tomato cytogenetic research has become one of the most advanced areas in the field of agriculture.

The genus *Lycopersicon* includes both self-incompatible and self-compatible species, with the latter varying in their degree of outcrossing. Tomato is self-pollinating, but can easily hybridize within the species or cross with wild relatives under appropriate conditions, thus permitting gene introgression from wild relatives. Moreover, tomato is considered a model research organism because it has a relatively short life-cycle, with a new cultivar "Microtom" being even shorter-lived (70-90 days from sowing to fruit ripening) (Dan *et al.* 2006).

Throughout the last century, tomato breeding has been based on various standard methods, including the pedigree method of hybridization followed by selection and backcrossing of desired traits from one parent into another, which has resulted in the generation of improved tomato varieties and hybrids with high quality and yield. Tomato improvement has increased by the exploitation of exotic resources and the introgression of new valuable genes into the tomato genepool. Classical breeding has not only developed cultivars with monogenic and dominant resistance for controlling certain plant pathogens, or by the combination of resistances in F_1 hybrids, but has also enabled the acquisition of good, value-added agronomic traits, such as high fertility and fruit setting, earliness, uniformity, adaptation, firmness and long shelf-life appropriate for shipping to distant markets. The replacement of inbred lines by hybrids has remarkably increased yield, while the genetic gain rate has been reduced due to low genetic diversity within cultivated tomatoes (Grandillo *et al.* 1999a). Initially, the exploitation of wild relatives for tomato breeding was limited to major genes controlling qualitative traits, such as resistance to pests and diseases, but omitting quantitative trait loci (QTL) alleles, which affect economically important agronomic traits. Since the 1980s, promising technologies have emerged to overcome the barriers of traditional techniques. These include molecular mapping, the identification of valuable QTLs and the limitation of genetic drag (Alpert *et al.* 1995; Grandillo and Tanksley 1996; Foolad and Chen 1999; Grandillo *et al.* 1999b). In the late 1980s, molecular markers were applied to tomato improvement programmes (Tanksley *et al.* 1989; Miller and Tanskley 1990; Rus-Kortekaas *et al.* 1994; Bredemeijer *et al.* 1998), and plants that had been genetically transformed for herbicide, virus and insect resistance were obtained (Fillatti *et al.* 1987; Nelson *et al.* 1988; Shah *et al.* 1988).

During the last five years the bulk of published work in tomato genetics and breeding refers to biotechnology and molecular techniques. The results of some of these studies in relation to tomato genetic resources and breeding achievements, are presented in the following section.

Tomato genetic resources

Genetic resources are the most valuable source of genetic material for any breeding process. They can be conserved *ex situ* in gene banks, *on farm* in cultivated material or *in situ* in wild species. Tomato genetic resources include old and new cultivars, primitive cultivars, breeding lines, landraces or heirloom tomatoes, and wild related species. To these genetic stocks can be added cloned genes (Frankel *et al.* 1995). Within cultivated tomato, genetic variation is very low; thus, there has long been an interest in searching for genes in exotic and primitive germplasm and closely related species. New breeding strategies now permit an in depth study and effective exploitation of the genetic diversity of wild relatives and landraces.

Tomato species

Tomato crosses with its wild relatives with varying degrees of difficulty; thus wild relatives can and have been used as sources of genes for crop improvement. Wild species are interesting resources of genetic variation for introgression breeding and comprise exclusive sources of many resistance genes for cultivated tomatoes (Rick 1995). The wild species *L. pennellii* (Corr.) D'Arcy, *L. peruvianum* Mill. and *L. pimpinellifolium* (Jusl.) Mill., represent a potential source of useful genes for salt tolerance during seed germination (Foolad 2004). The species *L. peruvianum*, *L. pimpinellifolium* and *L. hirsutum* Humb. & Bonpl. have been identified as potential sources for resistance to the pathogen *Clavibacter michiganensis* subsp. *michiganensis*, which causes bacterial canker of tomato (Kabelka *et al.* 2002). The species *L. peruvianum* is almost immune to *Oidium neolycopersici*, which causes powdery mildew on tomato, and provides resistant genes for tomato improvement (Bai *et al.* 2004). An *Mi* gene responsible for nematode resistance has been identified in *L. peruvianum* (Ammiraju *et al.* 2003), whereas resistance to whitefly (*Bemisia spp.*) has been found in wild populations of *L. esculentum* var. *cerasiforme* (Dun.) Afef. (Sanchez-Pena *et al.* 2006). The trichome characteristics from the wild species *L. cheesmanii f. minor* Riley and *L. pennellii* have been transferred to cultivated tomato and they affect the behaviour of *Myzus persicae* (Simmons *et al.* 2005). Phytochemical sesquiterpene carboxylic acid synthesis in *L. hirsutum f. typicum* Humb. & Bonpl. LA 1777, promotes host-resistance to insect pests, such as *Helicoverpa zea* and *Spodoptera exigua*, in cultivated tomato (Frelichowski and Juvic 2005). Attempts have been made to transfer the chilling tolerance found in *L. hirsutum* into cultivated tomatoes (Venema *et al.* 2000; Dolstra *et al.* 2002). Germplasm screening has revealed high levels of resistance to tomato fruitworm (*Helicoverpa armigera*) only in the wild *Lycopersicon* species, particularly *L. hirsutum* and *L. pennellii* (Takelar *et al.* 2006). *L. cheesmanii* has high sugar and β-carotene contents and is of great interest for quality improvement breeding (Nuez *et al.* 2004), while *L. peruvianum* has a distinctive aromatic fragrance that has been introduced into the cultivated tomato gene pool (Kamal *et al.* 2001). In virtually all instances of tomato genetic improvement, fruit quality is of paramount importance, which derives not only from the acquistition of desirable fruit traits, such as better aroma (Kamal *et al.* 2001) or colour (Nuez *et al.* 2004) and increased resistance to mechanical damage, but also from a reduction in the incidence of pests and diseases injurious to the fruit.

Landraces

Landraces (local populations, traditional cultivars or heirloom varieties) are heterogeneous, genetically dynamic populations that have evolved under low inputs of soil and agrochemicals and have been subjected to selection pressures for hardiness and local adaptability, rather than for productivity (Frankel *et al.* 1995). Tomato landraces are still cultivated for local use and consumption in many regions of the world. They frequently have distinctive organoleptic traits (flavour and aroma) and nutritional value. Within Europe, Italy, Spain, France and Greece possess a wealth of tomato landraces that provide the source for numerous, locally-named products. Examples include the cherry-like tomato named 'Corbarino', grown in the Campania region of Italy, the small-fruited tomato 'Santorini' grown on the island of Thera, Greece, and the tomato landrace types 'Muchamiel' and 'De la Pera' of the Valencia communities in Eastern Spain (Andreakis *et al.* 2004; Garcia-Martinez *et al.* 2006; Terzopoulos and Bebeli, unpublished).

The level of genetic variability differs among the various landraces and depends on the selection pressure that has been applied to each population. However, the wide diversity present within them offers landraces plasticity and homeostasis to adverse environments and provides them with the capacity to be cultivated in marginal areas. Their inter- and intra-population variability has been the subject of many studies in regions where such landraces are still cultivated, and the diversity in morphological and agronomic characters, fruit quality, soluble solids, micronutrient contents and volatile aroma compounds has been clearly established (Agong *et al.* 2001; Carbonell-Barachinna *et al.* 2006; Rao *et al.* 2006; Terzopoulos and Bebeli, unpublished). Moreover, tomato landraces have shown large and significant variation in flavour volatiles (Ruiz *et al.* 2005) and nutritional constituents (Andreakis *et al.* 2004). These distinctive quality characteristics have been exploited not only for fresh fruit improvement, but also in the development of high quality processed products, such as sweet and savoury tomato preserves.

Molecular breeding - Molecular markers

Irrespective of the tools adopted during the breeding process, the breeder has to take two major steps: first to find and/or create genetic variation and secondly to select the best genotypes. Even though the results of traditional breeding are undoubtedly clear and remarkable, it is nevertheless a very lengthy process. Recently, gene technology has made a significant impact on breeding through marker-assisted selection (MAS) and genetic engineering.

Numerous molecular marker systems have been used in tomato. These include restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLPs), simple sequence repeats (SSR) or microsatellites, intersequence simple repeats (ISSRs), cleaved amplified polymorphic sequences (CAPS), retrotransposon-based sequence specific amplification polymorphisms (SSAP), (Alvarez *et al.* 2001; Zhang and Stommel, 2001; Areshchenkova and Ganal 2002; Bonnema *et al.* 2002; Bredemeijer *et al.* 2002; Kochieva *et al.* 2002; Cooke *et al.* 2003; He *et al.* 2003; Tikunov *et al.* 2003; de Giovanni *et al.* 2004; Scott *et al.* 2004; Tam *et al.* 2005; Carelli *et al.* 2006; Rao *et al.* 2006; Sabatini *et al.* 2006).

Comparison between markers

Various studies have compared the efficiency of molecular markers used in tomato improvement. Reproducibility testing of RAPD and SSR (microsatellite) markers in tomato has shown that RAPDs are difficult to reproduce, while SSRs are characterized by robustness and repeatability (Rajput *et al.* 2006). SSAP was used to assess genetic diversity within tomato industrial lines and proved to be more informative than AFLP and SSR markers (Tam *et al.* 2005).

Applications of molecular markers

A description of diversity in genetic material is a prerequisite for its efficient use in plant breeding. DNA fingerprinting permits the analysis of the genetic distance between parents and predicts the performance of the progeny.

Molecular markers have been used in tomato in studies, such as germplasm characterization (Rao *et al.* 2006), the evaluation of genetic diversity and species relationships within the genus *Lycopersicon* (Alvarez *et al.* 2001; Kochieva *et al.* 2002; Tikunov *et al.* 2003), the genetic structure and diversity of wild *Lycopersicon* species populations (Nuez *et al.* 2004; Sifres *et al.* 2006), the determination of relationships between tomato cultivars and fingerprinting (He *et al.* 2003; Park *et al.* 2004; Rao *et al.* 2006), the purity control of cultivars and variety identification (Bredemeijer *et al.* 2002; Cooke *et al.* 2003), the identification of markers linked to important genes, map-based gene cloning, and genetic mapping (Saliba-Colombani *et al.* 2000; Areshchenkova and Ganal 2002).

Based on molecular markers, levels of intraspecific tomato polymorphism have been estimated to be very low. This is attributed to the self-pollination and self-fertilization of modern tomato cultivars, combined with their narrow genetic base (He *et al.* 2003; Tam *et al.* 2005; Sabatini *et al.* 2006). In contrast to the cultivated tomato, analysis carried out with RAPDs on the '*peruvianum* complex' revealed a large and variable degree of polymorphism which may be exploited in tomato breeding programmes (Egashira *et al.* 2000). The genetic distances within and between accessions of *Lycopersicon* species indicate that the self-incompatible species *L. peruvianum*, *L. pennellii* and *L. hirsutum* clearly have a higher genetic diversity than the self-compatible species (Kochieva *et al.* 2002). The molecular characterization of landraces has been carried out with many kinds of markers (Andreakis *et al.* 2004; Carelli *et al.* 2006; Garcia-Martinez *et al.* 2006; Rao *et al.* 2006). A combination of some SSR and AFLP markers revealed a unique fingerprint for even the most closely related traditional tomato cultivars in the south-east of Spain (Garcia-Martinez *et al.* 2006).

Marker-Assisted Selection (MAS)

Molecular markers can be used to help the breeder during the selection process. When the trait is controlled by a specific major gene of critical importance (e.g. the resistance to a disease that follows Mendelian inheritance), a molecular marker linked to this gene may be extremely useful for MAS in plant improvement. MAS can accelerate the exploitation of useful genes from wild species in breeding programmes, through introgression in the cultivated tomato followed by backcrossing. The steps required for the development of markers for use in MAS and the many advantages of MAS are reported in a review by Collard *et al.* (2005).

Markers of particular interest are the ones that link to disease resistance genes. A CAPS marker and two AFLP markers could be effectively used for MAS of the resistance gene *ol-2* to *Oidium lycopersicum*, which causes powdery mildew of tomato (de Giovanni *et al.* 2004). SSR markers linked to a late blight resistant gene in tomato have been identified and can be used in MAS (Zhu *et al.* 2006). A co-dominant CAPS marker derived from the *ovate* gene in tomato, which was mapped and cloned by Liu *et al.* (2002), could distinguish Italian ecotypes with a pear fruit shape. However, one of the lines did not perform according to CAPS assay, probably because the ovate mutation is not associated with a single phenotype (Tanksley 2004; Sabatini *et al.* 2006).

In tomato, most of the studies related to MAS are based on crosses carried out between cultivated tomato and related species. The level of genetic variation within the cultivated tomato, revealed by most of the common molecular markers, was very low, which is a burden for MAS with respect to a wide range of important agronomical traits.

Most traits of agricultural importance, such as yield and quality, are complex and they have polygenic control and quantitative inheritance. There are many regions within the genomes which contain genes that are associated with a polygenic trait and are called quantitative trait loci (QTLs). The identification of QTLs based only on conventional phenotypic evaluation is not possible. The efficiency of MAS backcrosses for the introgression of a quantitative trait locus (QTL) depends on the stability of QTL expression (Chaib *et al.* 2006).

Tomato maps

Saturated linkage maps are essential tools for genetic studies such as positional gene cloning, quantitative trait mapping and MAS (Collard *et al.* 2005). Linkage maps have been utilized for the identification of chromosomal regions that contain genes controlling simple traits (controlled by a single gene) and complex quantitative traits using QTL analysis, and tomato has one of the most saturated maps (Tanksley *et al.* 1992). Many single genes and QTLs that confer resistance to all major classes of plant pathogens have been mapped on the tomato molecular map (Grube *et al.* 2000).

Mapping QTLs as single Mendelian factors will have a strong impact on breeding programmes in using marker assisted selection.

QTLs for fruit traits

Tomato may be considered a model for fleshy fruit development. Domesticated tomatoes show a wide range of morphological diversity, whereas wild tomatoes produce small, round fruit. Most tomato fruit traits are quantitatively inherited. A large number of QTLs have been identified in tomato that are associated with fruit development, size, shape, colour, ripening, organoleptic quality and yield (Causee *et al.* 2001; van der Knaap and Tanksley 2001; Nesbitt and Tanksley 2001; Saliba-Colombani *et al.* 2001; Fulton *et al.* 2002; Liu *et al.* 2002; Causee *et al.* 2002; van der Knaap *et al.* 2002; Frary *et al.* 2003; van der Knaap and Tanksley 2003; Barrero and Tanksley 2004; Semel *et al.* 2006).

QTLs for plant traits

QTLs for leaflet and perianth size and shape characters, as well as stem morphology and stigma exertion, have been mapped (Coaker *et al.* 2002; Chen and Tanksley 2004; Frary *et al.* 2004). Genetic analysis of traits distinguishing outcrossing and self pollinating forms of currant tomato (*L. pimpinellifolium*) showed that the pollination mode is controlled by QTLs (Georgiady *et al.* 2002).

QTLs for biotic stresses

Even though many single genes controlling vertical resistance to various pathogens have been identified and transferred with crosses to elite pure lines and commercial hybrids, and continue to be of major importance to breeders, the polygenic durable resistance can be studied with QTL analysis. Powdery mildew, fusarium wilt and bacterial spot are among the diseases studied. Three QTLs for resistance to the fungus *Botrytis cinerea* were identified and can be introgressed into commercial cultivars (Foolad *et al.* 2002; Bai *et al.* 2003; Scott *et al.* 2004; Brouwer and St. Clair 2004; Finkers *et al.* 2007).

QTLs for abiotic stresses

Sensitivity to injury at low temperatures (chilling injury) limits the application of refrigerated storage to tomato and is a serious quality constraint (see section on “post-harvest technology”). Therefore, many studies have been carried out on chilling tolerance using populations derived from crosses between *L. esculentum* and *L. hirsutum*, and many QTLs have been identified. Some have supported genetic control by multiple QTLs (Foolad and Lin 2001), while others found a single major and several minor QTLs (Truco *et al.* 2000; Goodstal *et al.* 2005).

Cloning of useful genes

If the DNA-based markers can also be placed on a map or genome sequence of a model organism, it becomes possible to clone the gene underlying the QTL. To date only a few genes have been cloned in this way (Liu *et al.* 2002). The cloning of a major QTL gene *fw2.2*, which is responsible for the major fruit difference between wild and cultivated forms, has contributed to the study of the molecular and physiological properties controlled by the gene (Frary *et al.* 2000; Nesbitt and Tanksley 2001).

Even genes for complex traits can be isolated through the use of molecular maps. Cloned genes provide new tools for plant breeders to improve the efficiency of plant breeding strategies via MAS and plant transformation.

Transgenic plants

Even though molecular marker techniques are frequently applied in plant breeding, the application of genetic engineering has been resisted within Europe. Currently, several cultivars of transgenic tomatoes are commercially available. Antisense RNA technology has been used to increase the shelf life and commercial sales of gene-spliced ‘Flavr Savr’ (i.e. delayed ripening tomatoes) and has been approved by the United States Food and Drug Administration (USDA). Virus-resistant tomato was the second transgenic crop to be commercialized (James 1997).

The aims of transformation are the development of plants that are resistant to specific pathogens, most desirably combining with the simultaneous transfer of genes controlling other significant plant and/or fruit characteristics. Herbicide resistance was one of the first targets of genetic engineering, since this can be exploited not only by the seed producer, but also by the herbicide manufacturer, which in effect means promoting a potential monopoly by the large multinationals active in both these fields.

Prerequisites for successful genetic transformation include an *in vitro* regeneration, DNA delivery system, functionally introduced DNA (integration of the introduced DNA into the chromosome for stable transformation), selection of transformed cells (promoters and markers) and their regeneration. For *in vitro* regeneration, tomato has been shown to be a particularly amenable plant (Bhatia *et al.* 2004).

Tomato transformation uses an *Agrobacterium*-mediated gene transfer method, where a disarmed non-pathogenic *Agrobacterium tumefaciens* naturally transfers part of its genome, which has been genetically modified, into the tomato cell nucleus. The genetically modified part of the genome, the transgene, contains the promotor (a regulatory sequence), the gene itself, the terminator sequence and in most cases selectable markers, which are sequences that control antibiotic or herbicide resistances and are used in order to select the regenerant plants carrying the transgene. The current protocols in tomato use leaf disc/cotyledon tissue, co-cultivated with disarmed *Agrobacterium tumefaciens* harbouring binary vectors. This protocol has been used to generate transgenic lines from several tomato cultivars expressing various genes of interest and selectable markers. Protocols for tomato transformation are given in a review by van Eck *et al.* (2006). The transformation efficiency, expressed as transformation rates and recovery of transgenic tomato plants, depends on the genotype, explants, growth regulators, bacterial concentration and *Agrobacterium* virulent gene inducers; but the appropriate manipulation of these parameters can lead to the increased production of transformed plants (Cortina and Culianez-Macia 2003; Ellul *et al.* 2003). One crucial point in the development of transformed plants is the selection marker that is used. It has been suggested that an alternative to antibiotic or herbicide resistance markers, such as a mannose selection marker gene, may lead to greater public acceptance of transformants (Sigareva *et al.* 2004).

Marker-free transgenic tomato plants harbouring a synthetic *Bacillus thurigiensis* endotoxin gene *cryIAc* have been obtained (Zhang *et al.* 2006). The resulting tomato fruits can be used for the production of oral vaccines and other immunotherapeutic proteins. The *cholera toxin B* subunit and the *ORF2* partial gene of hepatitis E virus have been expressed in transgenic tomato plants (Jani *et al.* 2002). Transgenic tomatoes enriched in flavones and flavonoids have been claimed to be beneficial against cardiovascular disease (Rein *et al.* 2006).

A root-specific *Tob* promoter was used to direct the expression of the *sarcotoxin IA* gene in tomato roots, so as to enhance host resistance against the parasitic weed *Orobanche aegyptiaca* (Radi *et al.* 2006). However, introgression of this resistance into the cultivated tomato in order to combine it with acceptable fruit qualities, has not been successful.

POST-HARVEST TECHNOLOGY

Tomatoes are harvested at various stages of ripeness and the storage conditions employed differ with each stage. In general, pre-cooling is required only if the fruit temperature is higher than 26-27°C and ripening is to be delayed. 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), fruit that are mature green or at the turning or breaking stage should not be subjected to temperatures lower than 12°C as chilling injury may occur, with adverse consequence for subsequent ripening and quality.

Post-harvest treatments prior to storage

Because tomatoes are sensitive to chilling injury, particularly during the early stages of ripening, the use of low temperatures for tomato storage is restricted. In consequence, a number of recent publications have examined pre-storage treatments aimed at retaining fruit quality during storage and reducing the susceptibility of fruit to chilling injury.

According to Saltveit (2001), the application of heat-shock to tomatoes prior to exposure to low temperatures increases their resistance to chilling injury. Using a method based on ion leakage from tissue discs for the assessment of chilling injury, it was found that a short heat treatment (45°C for 10 minutes) even after exposure of the fruit to low temperatures would reduce the subsequent development of chilling symptoms. Soto-Zamora *et al.* (2005a) exposed mature green tomatoes to heat treatments (34 or 38°C and 95% RH for 24 hours) prior to storage at 4 or 20°C for four weeks in an attempt to reduce chilling injury at 4°C. Although the higher temperature caused serious injury, treatment at 34°C was only slightly harmful (higher weight loss than the untreated control). When stored at 20°C, fruit that had been exposed to 34°C ripened similarly to those of the control, but at 4°C chilling injury occurred in both the control and the treated fruit, even though the synthesis of lycopene was higher in the latter. In parallel experiments (Soto-Zamora *et al.* 2005b), fruit were exposed to high temperature (38°C), but under a low O_2 concentration (5%) to inhibit the activity of oxidative enzymes implicated in the induction of thermal injury. Since neither the thermal injury induced at this treatment temperature nor chilling injury during storage was reduced, such heat treatments are clearly not appropriate for tomato storage. By contrast, Fallik *et al.* (2002), also in an attempt to delay ripening and reduce chilling injury, found that brief exposure of tomatoes at the pink stage of ripeness to high temperature (52°C by washing and brushing for 15 seconds or total immersion of fruit for 1 minute) prevented the appearance of chilling injury symptoms at 5°C for 15 days and in the case of washing transiently increased fruit resistance to *Botrytis*. For commercial exploitation of the technique, the authors recommend the shorter treatment time. According to Iwahashi and Hosoda (2000), the delay in ripening of mature green tomatoes following heat treatment (37°C for one day in their case) relates to a loss of existing protein in the pericarp and a synthesis of new proteins, including antioxidant enzymes and heat shock proteins. Heat treatment has also been proposed as a means of inhibiting microbial activity and fruit cracking under conditions of high humidity in modified atmosphere packaging (Suparlan and Itoh 2003), as well as for delaying colour change in cherry tomatoes (*L. esculentum* var. *cerasiforme*) (Ali *et al.* 2004).

Subjection of tomatoes at the light rose stage to anoxia for 24 hours also delayed the development of *Botrytis*, but only for up to four days after treatment when fruit were stored at 20°C. Although this treatment delayed the colour development of fruit, it did not affect their organoleptic characteristics (Fallik *et al.* 2003). However, when the treatment time was extended, fruit quality was adversely affected due to the accumulation of acetaldehyde and ethanol (Boukobza and Taylor 2002; Polenta *et al.* 2006).

Wang (2006) reported that methyl jasmonate and methyl salicylate reduced chilling injury in tomatoes and other fruits of tropical origin, while at the same time increasing the expression of genes responsible for the synthesis of heat shock proteins. Methyl jasmonate also increased the level of antioxidants and the activity of free radical scavenging enzymes, indicating that protection against chilling injury involved protection of tissues against free radical injury. Moreover, by increasing the levels of pathogenesis-related proteins, methyl jasmonate and methyl salicylate assist in the development of resistance to disease during low temperature storage (Ding *et al.* 2001, 2002).

Storage environment

The temperatures and RH recommended for the commercial storage of tomatoes at each stage of maturation have been well documented (Ryall and Lipton 1979), and therefore recent research has concentrated largely on physiological and biochemical changes during the ripening process.

Although fully ripe tomatoes may be stored for a short time at low temperatures, nevertheless adverse effects on fruit quality may occur. For example, ripe fruit that had been stored at 5°C for 4 days were deemed by sensory analysis to be significantly less aromatic, less sweet and more acidic than corresponding fruit stored for the same length of time at 20°C. The poorer aroma of fruit stored at 5°C was attributed to a loss of the principal volatile components, detected by gas chromatography (Maul *et al.* 2000).

Van Dijk *et al.* (2006a) developed models to forecast the loss of weight and firmness of tomatoes during storage at various temperatures, while de Ketelaere *et al.* (2004) adopted a non-destructive acoustic firmness sensor to group tomato cultivars according to firmness change during storage and in relation to harvest.

Van Dijk *et al.* (2006b) reported that the temperature (3-25°C) and stage of ripening (6 and 8 on the scale of the Dutch and Belgian Growers' Associations) influenced enzyme activity during 4 weeks of storage. The activity of polygalacturonase increased and pectin methyl esterase decreased over time, while that of β-galactosidase was at first induced and subsequently inactivated. A significant correlation between enzyme activity and near infra-red spectra of intact fruit was discerned only in the case of polygalacturonase, which is thus considered to be the major enzyme involved in fruit softening during storage. According to Mondal *et al.* (2003), lipoxygenase activity and the malondialdehyde and H_2O_2 content of tomatoes, harvested at the turning stage and stored for 14-15 days at 10, 25 or 35°C, increased with temperature. Moreover, the increase in these components was higher in a cultivar with a short storage life (5-7 days) than in that with a longer storage life (14-15 days). A temperature-related increase in ROS scavenging enzymes was also observed, indicating that fruit stored at high temperatures are susceptible to increased oxidative activity, leading to membrane damage and a loss of fruit integrity. Cultivar related differences in the activity of lypoxygenase, hydroperoxide lyase and alcohol dehydrogenase were reported by Yilmaz *et al.* (2002). Alcohol dehydrogenase activity in almost all cultivars was highest in fruit harvested at the red stage.

Enzyme changes during ripening also determine the changes in the flavour and aroma constituents of the fruit. Krumbein *et al.* (2004) stored three categories of tomato (long life, 'normal' life and cherry) harvested at the red, ripe stage at 20°C and 55% RH for 21 days (i.e. under shelf life conditions). Changes in flavour attributes and the majority of volatiles assessed followed a similar trend in each fruit category, with the strength of the characteristic 'tomato flavour', but also an undesirable 'mouldy flavour' (attributed to hexanal and 2-isobutylthiazole), increasing with time.

Controlled or modified atmospheres

Controlled or modified atmospheres have been shown to delay ripening during storage. Hatton *et al.* (1975) reported that atmospheres of 4-8% O_2 and 1-2% CO_2 prolonged storage life and delayed ripening at 12.8°C, but concentrations of O_2 lower than 4% or CO_2 higher than 4% resulted in uneven ripening. Dennis *et al.* (1979) found that fruits stored in 5% O_2 + 5% CO_2 had a better flavour than those stored in 3% O_2 + 5% CO_2. However, Batu (2003) observed that after 60 days storage of mature green or rose tomatoes at 13 or 15°C, those stored under controlled atmospheres of 5.5% O_2 + CO_2 (3.2, 6.4 or 9.1%) were less acceptable in terms of sweetness and aroma than those stored in air. Moreover, even short-term storage of red, almost fully ripe tomatoes under conditions of low or zero O_2 (e.g. in N_2 for 35 hours) adversely affects fruit aroma, due to a reduction in C-6 compounds and isobutylthiazole, and an increase in ethanol and acetaldehyde (Boukobza and Taylor 2002).

Modified atmospheres resulting from the enclosure of tomatoes in polyethylene or other forms of plastic packaging (**Fig. 2F**) may also delay fruit ripening and prolong storage life. Srinivasa *et al.* (2006) stored green, physiologically mature tomatoes in cartons covered with chitosan (biodegradable membrane) for 30 days at 27±1°C. Fruit showed better colour retention and firmness not only in relation to the control (fruit stored in air) but also in comparison with those enclosed in low-density polyethylene (LDPE) film. By contrast, Kantola and Helen (2001) found that the sensory quality of organically grown tomatoes stored for 3 weeks at 11±1°C and 75-85% RH in perforated LDPE, cellophane or biodegradable bags was not affected by the packaging material. However, these results apparently reflect the level of O_2 within the containers, since Muratore *et al.* (2005) showed that the quality characteristics (vitamin C, carotenoids) of plum tomato could be preserved satisfactorily in modified atmospheres produced by enclosure of fruit in biodegradable or polyolefin films only when the O_2 permeability of the film was sufficient to prevent anaerobic respiration. The inclusion of an ethylene adsorbent (granular activated carbon) within polypropylene bags in which tomatoes at the turning stage were stored at 8°C, reduced the level of ethylene within the storage atmosphere for 21 days. Colour change, softening and weight loss were reduced and quality on ripening was improved (Bailén *et al.* 2006).

Mondal *et al.* (2006) reported that when tomatoes are enclosed in polyethylene and stored at 25°C they are more resistant to oxidative stress than unenclosed fruit stored at the same temperature. This resistance derives from the increased activity of ROS scavenging enzymes such as superoxide dismutase, peroxidase, ascorbate peroxidase, catalase and glutathione reductase, which inactivate the ROS and thereby reduce the dangers of oxidative stress on membrane integrity. Low oxygen levels in modified or controlled atmospheres also inhibit polygalacturonase activity, thus reducing the rate of fruit softening (Kapotis *et al.* 2004). High concentrations of CO_2, on the other hand, are known to inhibit ethylene synthesis, apparently acting at a site prior to that of the conversion of ACC to ethylene (de Wild *et al.* 2005). Enrichment of the storage atmosphere with ozone, which may be of value in reducing the microbial activity of sliced tomatoes, causes a transient increase in respiration, resulting in increased fructose, glucose, ascorbate and fumarate levels, both in intact and sliced fruit (Aguayo *et al.* 2006). However, exposure of mature green fruit to atmospheres containing ethanol (from 2.5 to 25 ml per 2.5 kg fruit held in a total volume of 5 l) delayed ripening due to a reduction in ethylene synthesis and respiration, and a delay in the onset of the climacteric. A parallel delay in fruit softening was attributed to an inhibition of polygalacturonase and pectin methyl esterase, and the most effective treatment was that of 20 ml ethanol per 2.5 kg fruit (Thakur *et al.* 2000).

Lycopene, antioxidants, ascorbic acid and carotenoids

Colour is a major quality characteristic in virtually all fruits and vegetables and uniformity of colour within toma-toes is a principal requirement of the E.U. quality standards for this crop. All fruit within a box must be at the same stage of ripeness during marketing. Since the deposition of carotenoid pigments is responsible for the characteristic colour of ripe tomatoes (Fraser *et al.* 2001), an understanding of carotenoid synthesis in tomato is of immediate relevance to quality. During fruit ripening, maximum concentrations of α- and β-carotene occur at the turning to breaking stages (Meredith and Purcell 1966), after which lycopene accumulates (Davies and Hobson 1981). Although it was earlier considered that carotenoid biosynthesis occurred via the mevalonic acid pathway (Grierson and Kader 1986), recent research has suggested that carotenoids are in fact derived from isopentenyl diphosphate (IPP) and are produced in the plastids via the 1-deoxy-D-xylulose-5-phosphate, or Rohmer, pathway (Bramley 2002). This conclusion contrasts with that of Lois *et al.* (2000), who consider both pathways to be involved. Phytochrome has also been implicated in the induction of lycopene accumulation (Alba *et al.* 2000).

Apart from contributing nutritive elements, colour and flavour to the diet, tomatoes are also a valuable source of antioxidants, or chemo-protective compounds, and may thus be termed a "functional food" (Ranieri *et al.* 2004). The antioxidant potential of tomato is derived from a mixture of antioxidant biomolecules, including lycopene, ascorbic acid, phenolics, flavonoids and vitamin E, and is especially high in cherry tomatoes (Kaur *et al.* 2004).

The lycopene content and antioxidant activity of tomatoes varies between cultivars and is highest in cherry or small, cocktail fruit (Kaur *et al.* 2004; Molyneux *et al.* 2004). There is a correlation between fruit colour and total antioxidant concentration, with lycopene content increasing from the rose to red colour stages (Brandt *et al.* 2006; Helyes *et al.* 2006) and mature green tomatoes having a significantly lower total antioxidant content than red tomatoes (Wold *et al.* 2004). Red-fruiting cultivars also have a higher lycopene content than yellow, orange and black-fruiting cultivars (Cox *et al.* 2003). Lycopene synthesis during growth is inhibited at temperatures below 12°C and prohibited at >32°C. Unlike ascorbic acid synthesis, which is promoted by the exposure of fruit to full sunlight, lycopene synthesis is higher in fruit that are shaded by the foliage. The spectral quality of the light may also play a role; for example UV-irradiation has been found to affect the phenolic and carotenoid content of fruit to a degree that depends on the cultivar sensitivity (Giuntini *et al.* 2005; Luthria *et al.* 2006). In consequence, there is a seasonal effect on lycopene and antioxidant levels in fruit (Rosales *et al.* 2006; Toor *et al.* 2006), as well as an effect of irrigation and the nutritional status of the plant (see review by Dumas *et al.* 2003).

Because of their importance to human health (Madhavi and Salunkhe 1998), antioxidants may be considered a valuable quality attribute of tomatoes and it is important to minimize losses of these compounds during the post-harvest period. Fruit that are harvested at stages prior to full ripeness show an increase in lycopene content during post-harvest ripening. For example, Toor and Savage (2006) studied the changes in the antioxidant content of tomatoes harvested at the light red stage and stored for 10 days at 7, 15 and 25°C. The total antioxidant activity of fruit increased by 17-27% during storage. However, whereas phenolics and ascorbate increased only slightly and independently of temperature, the lycopene content of fruit after 10 days storage at 15 or 25°C was more than twice as much as that of fruit stored at 7°C. Although low temperatures during storage lower the lycopene content of fruit, even when harvested at a mature red stage, they do not necessarily reduce the total antioxidant capacity (Javanmardi and

Kubota 2006). Hence, the observation of Slimestad and Verheul (2005) that cherry tomatoes that are ripened on the plant have a similar carotenoid and ascorbate, but higher sugar, content than fruit harvested at the orange-yellow stage and ripened during storage, suggests that for maximum antioxidant content and sweetness, it is better to harvest ripe fruit and store at low temperature. Where possible, however, the length of storage should be limited, since the ascorbate content of fruit decreases even at low temperatures (Sablani *et al.* 2006). For the consumer, it is important to know that 52% of the total antioxidants (48% lycopene, 43% ascorbic acid, 53% phenolics) are located in the epidermis of the fruit, which in consequence should not be discarded during consumption (Toor and Savage 2005).

Ethylene in relation to storage, ripening and quality

Although the relationship of ethylene biosynthesis to the induction of the respiratory climacteric and the ripening processes of tomato and other fruits has been the subject of considerable research over the past 50 years (Goodenough 1986; Chaves and de Mello-Farias 2006), the mechanisms involved have still to be defined. Alexander and Grierson (2002) reviewed the role of specific isoforms of ACC synthase and ACC oxidase in regulating ethylene biosynthesis during ripening and discussed the role of ethylene receptors. Jakubowicz and Sadowski (2002) discussed the structure and catalytic activity of ACC synthase, as well as the organization, gene structure and transcriptional expression of ACC synthase genes, while two more reviews relating to ethylene receptors and the control of ethylene-mediated processes in tomatoes at the receptor level have also been published (Klee 2002; Klee and Tieman 2002).

Commercially, the promotion of ethylene biosynthesis is exploited for the induction or enhancement of fruit ripening (e.g. in banana and tomato), while inhibition of ethylene synthesis or removal of ethylene from the storage atmosphere is used to delay ripening and prolong storage.

Logendra *et al.* (2004) applied Ethephon (2-chloroethylphosphonic acid) to tomatoes at the mature green or breaking stage whilst still on the plant. Application at the green stage reduced the number of fruit per truss, but also reduced the time to harvest without adversely affecting quality. Chomchalow *et al.* (2002) applied ethylene to fruit harvested at the mature green stage before and after exposure to low temperatures, and found that when ethylene was applied prior to exposure (but not afterwards) it offered a certain amount of protection against chilling injury. However, Kapotis *et al.* (2004) demonstrated that the exogenous application of ethylene to fruit stored in an atmosphere of 1% oxygen did not induce autocatalytic production of ethylene by the fruit. Treatment of tomatoes at the breaker stage with GA_3 or IAA (20 mM for 1 hour) caused an increase in ethylene biosynthesis (higher than that induced by exogenous ethylene application) as a result of the promotion of ACC synthase activity. The activity of α- and β-galactosidase and α-arabinofuranosidase was also stimulated, but fruit softening, chlorophyll breakdown and total carotenoid synthesis tended to be delayed. Moreover, GA_3- and IAA-treated fruit did not respond to the exogenous application of ethylene (100 ppm) with an increase of autocatalytic ethylene production (Sozzi *et al.* 2000). The effect of ethylene on the volatile components of tomato was reviewed by Zhu *et al.* (2005). The inhibition of ethylene biosynthesis by suppression of ACC synthase (Oeller *et al.* 1991) or ACC oxidase (Hamilton *et al.* 1990) caused a significant reduction in aroma volatiles, while non-ripening natural mutants that are affected for ethylene response lack the most potent odours (McGlasson *et al.* 1987).

The recent commercial availability of the ethylene inhibitor 1-MCP, has resulted in a number of studies of its application to tomato storage and ripening. Exposure of tomatoes to 1-MCP delays fruit ripening by a transient inhibition of both ethylene biosynthesis and the rate of respiration (Wills and Ku 2002; Ergun *et al.* 2006). The extent of inhibition depends on the duration of application and the stage of fruit ripening at treatment (Sisler *et al.* 1996; Hoeberichts *et al.* 2002; Wills and Ku 2002; Mir *et al.* 2004), while the effective concentration varies between cultivars (Watkins 2006). Although fruit recover the ability to ripen after 1-MCP treatment, inhibition can be reimposed by further applications (Hoeberichts *et al.* 2002; Mir *et al.* 2004). However, when 1-MCP was applied at the mature green or breaker stages, fruit showed a long delay in the development of colour, did not soften sufficiently, shrivelled and were susceptible to disease; by contrast, fruit treated at the rose or light red stages subsequently ripened satisfactorily (Hurr *et al.* 2005). According to Mostofi *et al.* (2003), the storage temperature after treatment significantly affects the colour development of tomatoes treated with 1-MCP at the mature green stage.

Apart from its effects on fruit ripening and colour development, 1-MCP may affect certain other quality traits. For example, Wills and Ku (2002) consider that 1-MCP improves fruit flavour by changing the ratio of total soluble solids to titratable acid, although this observation was not confirmed by Mir *et al.* (2004) who reported a slight change in the volatile components of fruit treated with 1-MCP at the mature green and breaker stages, but no change in sugars or titratable acid.

Watkins (2006) reviewed the effects of 1-MCP on fruit ripening with reference to its commercial application, while Feng *et al.* (2004) reported that analogues of 1-MCP, 1-ethylcyclopropene and 1-propylcyclopropene, also inhibit ethylene induced ripening of tomato and avocado, but to a lesser degree than 1-MCP. Another potentially useful application for 1-MCP is the prevention of fruit abscission. This may not only be of significance in crop production, but also in storage. Cherry tomatoes are frequently marketed as trusses of fruit, and treatment with 1-MCP can reduce fruit separation from the truss during storage and marketing (Beno-Moualem *et al.* 2004; Lichter *et al.* 2006). 1-MCP also delays the ripening of cherry tomato depending on the concentration and stage of ripening at application (Opiyo and Ying 2005).

Other methods of delaying ripening, either through the inhibition of ethylene biosynthesis or the removal of ethylene when formed, have also been investigated. TiO_2 mediates a photocatalytic breakdown of ethylene under UV-irradiation, thus delaying the ripening of mature green tomatoes both in air and in modified atmospheres (Maneerat *et al.* 2003). This reaction, the efficacy of which depends on the TiO_2 concentration and the intensity of UV-irradiation, also removes acetaldehyde and ethanol for up to eight days after treatment, thus inhibiting the formation of odours due to fermentation (Maneerat and Hayata 2006). Saltveit (2005) reported that the ability of AVG to inhibit ethylene synthesis in tomato pericarp discs correlated with an inhibition of protein synthesis. Elsewhere, Hong *et al.* (2004) reported that the vacuum infiltration of tomatoes at the early red stage with glucose solutions caused an inhibition of ethylene biosynthesis as a result of a reduction in the activity of ACC oxidase. However, interesting as these observations are, it is difficult to see how they can be exploited commercially.

CONCLUSIONS AND FUTURE PERSPECTIVES

Tomato is one of the most researched of all horticultural crops and considerable progress has been achieved in all the areas described within the present review. In particular, in the field of plant breeding, molecular techniques have opened new horizons for genetic improvement. New types of markers, such as the single nucleotide polymorphisms (SNPs) will influence future mapping and the utilization of MAS in tomato improvement. However, selection requires the screening of many plants and the cost of the markers is a limiting factor for their routine use in the breeding programmes of many counties. Even though there are many advanced studies in QTL mapping and MAS, their efficiency will be improved with the information obtained from gene expression studies. Functional genomics methods can be utilized to develop markers from genes themselves and the increase of information available in databases will allow data mining for the development of new markers. Transformation is a dynamic tool that surpasses the barriers of the gene pools and theoretically makes the transfer of every gene possible. Despite its rejection by many countries particularly within Europe, transgenic technology continues to advance and the most economically exploitable transformants are likely to be crop plants for use in pharmaceuticals or "nutraceuticals" (functional foods).

Future research in the area of tomato nutrition is likely to be increasingly concerned with the impact of nutrition on fruit quality, as well as on the molecular basis of the mechanisms implicated in the uptake and utilization of inorganic nutrients within the plants. Post-harvest, the major research input in the near future is still likely to revolve around the role of ethylene in fruit ripening and the physiological basis of ripening control. This and other post-harvest phenomena, such as chilling injury, attract attention within studies incorporating genetic modification. Although studies on the application of novel storage techniques are likely to continue, the degree to which currently available techniques may be further improved to provide a significant commercial impact is unclear, particularly within the technically advanced marketing system of the E.U.

REFERENCES

Adams P (1991) Effects of increasing the salinity of the nutrient solution with major nutrients or sodium chloride on the yield, quality and composition of tomatoes grown in rockwool. *Journal of Horticultural Science* **66**, 201-207

Adams P (2002) Nutritional control in hydroponics. In: Savvas D, Passam HC (Eds) *Hydroponic Production of Vegetables and Ornamentals*, Embryo Publications, Athens, Greece, pp 211-261

Adams P, Davies JN, Winsor GW (1978) Effects of nitrogen, potassium and magnesium on the quality and chemical composition of tomatoes grown in peat. *Journal of Horticultural Science* **53**, 115-122

Adams P, Ho LC (1989) Effects of constant and fluctuating salinity on the yield, quality and calcium status of tomatoes. *Journal of Horticultural Science* **64**, 725-732

Agong SG, Schittenhelm S, Friedt W (2001) Genotypic variation of Kenyan tomato (*Lycopersicon esculentum* Mill.) germplasm. *The Journal of Food Technology in Africa* **6**, 13-17

Aguayo E, Escalona VH, Artés F (2006) Effect of cyclic exposure to ozone gas on physicochemical, sensorial and microbial quality of whole and sliced tomatoes. *Postharvest Biology and Technology* **39**, 169-177

Akl IA, Savvas D, Papadantonakis N, Lydakis-Simantiris N, Kefalas P (2003) Influence of ammonium to total nitrogen supply ratio on growth, yield and fruit quality of tomato grown in a closed hydroponic system. *European Journal of Horticultural Science* **68**, 204-211

Al-Aghabary K, Zhu Z, Shi Q (2004) Influence of silicon supply on chlorophyll content, chlorophyll fluorescence, and antioxidative enzyme activities in tomato plants under salt stress. *Journal of Plant Nutrition* **27**, 2101-2115

Alba R, Cordonnier-Pratt MM, Pratt LH (2000) Fruit-localized phytochromes regulate lycopene accumulation independently of ethylene production in tomato. *Plant Physiology* **123**, 363-370

Alexander L, Grierson D (2002) Ethylene biosynthesis and action in tomato: A model for climacteric fruit ripening. *Journal of Experimental Botany* **53**, 2039-2055

Alhendawi RA, Kirkby EA, Pilbeam DJ (2005) Evidence that sulfur deficiency enhances molybdenum transport in xylem sap of tomato plants. *Journal of Plant Nutrition* **28**, 1347-1353

Ali MS, Nakano K, Maezawa S (2004) Combined effect of heat treatment and modified atmosphere packaging on the color development of cherry tomato. *Postharvest Biology and Technology* **34**, 113-116

Alian A, Altman A, Heuer B (2000) Genotypic difference in salinity and water stress tolerance of fresh market tomato cultivars. *Plant Science* **152**, 59-65

Alpaslan M, Gunes A (2001) Interactive effects of boron and salinity stress on the growth, membrane permeability and mineral composition of tomato and cucumber plants. *Plant and Soil* **236**, 123-128

Alpert K, Grandillo S, Tanksley SD (1995) *fw2.2*: a major QTL controlling fruit weight is common to both red- and green-fruited tomato species. *Theoretical and Applied Genetics* **91**, 994-1000

Alvarez AE, van de Wiel CCM, Smulders MJM, Vosman B (2001) Use of microsatellites to evaluate genetic diversity and species relationships in the genus *Lycopersicon*. *Theoretical and Applied Genetics* **103**, 1283-1292

Ammiraju JS, Veremis JC, Huang X, Roberts PA, Kaloshian I (2003) The heat-stable root-knot nematode resistance gene *Mi-9* from *Lycopersicon peruvianum* is localized on the short arm of chromosome 6. *Theoretical and Applied Genetics* **106**, 478-484

An P, Inanaga S, Xiang JL, Eneji AE, Nan WZ (2005) Interactive effects of salinity and air humidity on two tomato cultivars differing in salt tolerance. *Journal of Plant Nutrition* **28**, 459-473

Anderson JW, Scarf AR (1983) Selenium and plant metabolism. In: Robb DA, Pierpoint WS (Eds) *Metals and Micronutrients: Uptake and Utilization by Plants*, Academic Press, NY, pp 241-275

Andreakis N, Giordano I, Pentagelo A, Fogliano V, Graziani G, Monti LM, Rao R (2004) DNA fingerprinting and quality traits of Corbarino cherry-like tomato landraces. *Journal of Agriculture and Food Chemistry* **52**, 3366-3371

Areshchenkova T, Ganal MW (2002) Comparative analysis of polymorphism and chromosomal location of tomato microsatellite markers isolated from different sources. *Theoretical and Applied Genetics* **104**, 229-235

Auerswald H, Schwarz D, Kornelson C, Krumbein A, Brückner B (1999) Sensory analysis, sugar and acid content of tomato at different EC values of the nutrient solution. *Scientia Horticulturae* **82**, 227-242

Bai Y, Huang CC, van der Hulst R, Meijer-Dekens F, Bonnema G, Lindhout P (2003) QTLs for tomato powdery mildew resistance (*Oidium lycopersici*) in *Lycopersicon parviflorum* G1.1601 co-localize with two qualitative powdery mildew resistance genes. *Molecular Plant-Microbe Interactions* **16**, 169-176

Bai Y, van der Hulst R, Huang CC, Wei L, Stam P, Lindhout P (2004) Mapping *Ol-4*, a gene conferring resistance to *Oidium neolycopersici* and originnating from *Lycopersicon peruvianum* LA2172, requires multi-allelic, single-locus markers. *Theoretical and Applied Genetics* **109**, 1215-1223

Bailén G, Guillén F, Castillo S, Serrano M, Valero D, Martínez-Romero D (2006) Use of activated carbon inside modified atmosphere packages to maintain tomato fruit quality during cold storage. *Journal of Agricultural and Food Chemistry* **54**, 2229-2235

Barber SA (1984) Nitrogen. In: Barber SA (Ed) *Soil Nutrient Availability, a Mechanistic Approach*, Wiley-Interscience, NY, USA, pp 179-197

Barrero LS, Tanksley SD (2004) Evaluating the genetic basis of multiple-locule fruit in a broad cross section of tomato cultivars. *Theoretical and Applied Genetics* **109**, 669-679

Batu A (2003) Temperature effects on fruit quality of mature green tomatoes during controlled atmosphere storage. *International Journal of Food Sciences and Nutrition* **54**, 201-208

Ben-Gal A, Shani U (2002) Yield, transpiration and growth of tomatoes under combined excess boron and salinity stress. *Plant and Soil* **247**, 211-221

Ben-Gal A, Shani U (2003) Water use and yield of tomatoes under limited water and excess boron. *Plant and Soil* **256**, 179-186

Ben-Oliel G, Kant S, Naim M, Rabinowitch HD, Takeoka GR, Buttery RG, Kafkafi U (2004) Effects of ammonium to nitrate ratio and salinity on yield and fruit quality of large and small tomato fruit hybrids. *Journal of Plant Nutrition* **27**, 1795-1812

Beno-Moualem D, Gusev L, Dvir O, Pesis E, Meir S, Lichter A (2004) The effects of ethylene, methyl jasmonate and 1-MCP on abscission of cherry tomatoes from the bunch and expression of endo-1,4-β-glucanases. *Plant Science* **167**, 499-507

Bergmann W (1988) *Ernährungsstörungen bei Kulturpflanzen*, Gustav Fischer Verlag, Stuttgart, 380 pp

Bhatia P, Ashwath N, Senaratna T, Midmore D (2004) Tissue culture studies of tomato (*Lycopersicon esculentum*). *Plant Cell, Tissue and Organ Culture* **78**, 1-21

Bhattarai SP, Pendergast L, Midmore DJ (2006) Root aeration improves yield and water use efficiency of tomato in heavy clay and saline soils. *Scientia Horticulturae* **108**, 278-288

Bonnema G, van den Berg P, Lindhout P (2002) AFLPs mark different genomic regions compared with RFLPs: a case study in tomato. *Genome* **45**, 217-221

Borsani O, Cuartero J, Fernández JA, Valpuesta V, Botella MA (2001) Identification of two loci in tomato reveals distinct mechanisms for salt tolerance. *Plant Cell* **13**, 873-887

Botella MA, Del Amor F, Amorós A, Serrano M, Martínez V, Cerdá A (2000) Polyamine, ethylene and other physico-chemical parameters in tomato (*Lycopersicon esculentum*) fruits as affected by salinity. *Physiologia Plantarum* **109**, 428-434

Boukobza F, Taylor AJ (2002) Effect of postharvest treatment on flavour volatiles of tomatoes. *Postharvest Biology and Technology* **25**, 321-331

Bramley PM (2002) Regulation of carotenoid formation during tomato fruit ripening and development. *Journal of Experimental Botany* **53**, 2107-2113

Brandt S, Pék Z, Barna É, Lugasi A, Helyes L (2006) Lycopene content and colour of ripening tomatoes as affected by environmental conditions. *Journal of the Science of Food and Agriculture* **86**, 568-572

Bredemeijer GMM, Arens P, Wouters D (1998) The use of semi-automated fluorescent microsatellite analysis for tomato cultivar identification. *Theoretical and Applied Genetics* **97**, 584-590

**Bredemeijer GMM, Cooke PRJ, Ganal MW, Peeters R, Isaac P, Noordijk Y, Rendell S, Jackson J, Wendehake MSRK, Dijcks M, Amelaine M, Wick-

aert V, Bertrand L, Vosman B (2002) Construction and testing of a microsatellite database containing more than 500 tomato varieties. *Theoretical and Applied Genetics* **105**, 1019-1026

Brouwer DJ, St. Clair DA (2004) Fine mapping of three quantitative trait loci for late blight resistance in tomato using near isogenic lines (NILs) and sub-NILs. *Theoretical and Applied Genetics* **108**, 628-638

Bryson GM, Barker AV (2002) Determination of optimal fertilizer concentration range for tomatoes grown in peat-based medium. *Communications in Soil Science and Plant Analysis* **33**, 759-777

Carbonell-Barrachina AA, Agusti A, Ruiz JJ (2006) Analysis of flavor volatile compounds by dynamic headspace in traditional and hybrid culivars of Spanish tomatoes. *European Food Research Technology* **222**, 536-542

Carelli B, Gerald L, Grazziotin FSE (2006) Genetic diversity among Brazilian cultivars and landraces of tomato *Lycopersicon esculentum* Mill. revealed by RAPD markers. *Genetic Resources and Crop Evolution* **53**, 385-400

Caro M, Cruz V, Cuartero J, Estañ MT, Bolarin MC (1991) Salinity tolerance of normal-fruited and cherry tomato cultivars. *Plant and Soil* **136**, 249-255

Carvalho KM, Gallardo-Williams MT, Benson RF, Martin DF (2003) Effects of selenium supplementation on four agricultural crops. *Journal of Agricultural and Food Chemistry* **51**, 704-709

Causse M, Saliba-Colombani V, Lecomte L, Duffe P, Rousselle P, Buret M (2002) QTL analysis of fruit quality in fresh market tomato: a few chromosome regions control the variation of sensory and instrumental traits. *Journal of Experimental Botany* **53**, 2089-2098

Causse MV, Saliba-Colombani, Lesschaevel I, Buret M (2001) Genetic analysis of organoleptic quality in fresh market tomato. 2. Mapping QTLs for sensory attributes. *Theoretical and Applied Genetics* **102**, 273-283

Chaib J, Lecomte L, Buret M, Causse M (2006) Stability over genetic backgrounds, generations and years of quantitative trait locus (QTLs) for organoleptic quality in tomato. *Theoretical and Applied Genetics* **112**, 934-944

Chaignon V, Bedin F, Hinsinger P (2002) Copper bioavailability and rhizosphere pH changes as affected by nitrogen supply for tomato and oilseed rape cropped on an acidic and a calcareous soil. *Plant and Soil* **243**, 219-228

Chapagain BP, Wiesman Z (2004) Effect of potassium magnesium chloride in the fertigation solution as partial source of potassium on growth, yield and quality of greenhouse tomato. *Scientia Horticulturae* **99**, 279-288

Chatterjee J, Chatterjee C (2002) Amelioration of phytotoxicity of cobalt by high phosphorus and its withdrawal in tomato. *Journal of Plant Nutrition* **25**, 2731-2743

Chatterjee J, Chatterjee C (2003) Management of phytotoxicity of cobalt in tomato by chemical measures. *Plant Science* **164**, 793-801

Chaves ALS, de Mello-Farias PC (2006) Ethylene and fruit ripening. From illumination gas to the control of gene expression, more than a century of discoveries. *Genetics and Molecular Biology* **29**, 508-515

Chen G, Fu X, Herman Lips S, Sagi M (2003) Control of plant growth resides in the shoot, and not in the root, in reciprocal grafts of flacca and wild-type tomato (*Lysopersicon esculentum*), in the presence and absence of salinity stress. *Plant and Soil* **256**, 205-215

Chen J, Gabelman WH (2000) Morphological and physiological characteristics of tomato roots associated with potassium-acquisition efficiency. *Scientia Horticulturae* **83**, 213-225

Chen KY, Tanksley SD (2004) High-resolution mapping and functional analysis of se2.1: a major stigma exsertion quantitative trait locus associated with the evolution from allogamy to autogamy in the genus *Lycopersicon*. *Genetics* **168**, 1563-1573

Chiraz C, Houda G, Habib GM (2003) Nitrogen metabolism in tomato plants under cadmium stress. *Journal of Plant Nutrition* **26**, 1617-1634

Cho UH, Park JO (2000) Mercury-induced oxidative stress in tomato seedlings. *Plant Science* **156**, 1-9

Chomchalow S, El Assi NM, Sargent SA, Brecht JK (2002) Fruit maturity and timing of ethylene treatment affect storage performance of green tomatoes at chilling and nonchilling temperatures. *HortTechnology* **12**, 104-114

Chrétien S, Gosselin A, Dorais M (2000) High electrical conductivity and radiation-based water management improve fruit quality of greenhouse tomatoes grown in rockwool. *HortScience* **35**, 627-631

Claussen W (2002) Growth, water use efficiency, and proline content of hydroponically grown tomato plants as affected by nitrogen source and nutrient concentration. *Plant and Soil* **247**, 199-209

Coaker GL, Meulia T, Kabelka EA, Jones AK, Francis DM (2002) A QTL controlling stem morphology and vascular development in *Lycopersicon esculentum* × *Lycopersicon hirsutum* (Solanaceae) crosses is located on chromosome 2. *American Journal of Botany* **89**, 1859-1866

Collard BCY, Jahufer MZZ, Brouwer JB, Pang ECK (2005) An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: The basic concepts. *Euphytica* **142**, 169-196

Cooke RJ, Bredemeijer GMM, Ganal MW, Peeters R, Isaac, Rendell S, Jackson J, Roeder MS, Korzun V, Wendehake K, Areshchenkova T, Dijcks M, Laborie D, Bertrand L, Vosman B (2003) Assessment of the uniformity of wheat and tomato varieties at DNA microsatellite loci. *Euphytica* **132**, 331-341

Cortina C, Culianez-Macia FA (2004) Tomato transformation and transgenic plant production *Plant Cell, Tissue and Organ Culture* **76**, 269-275

Cox SE, Stushnoff C, Sampson DA (2003) Relationship of fruit color and light exposure to lycopene content and antioxidant properties of tomato. *Canadian Journal of Plant Science* **83**, 913-919

Cramer MD, Oberholzer JA, Combrink NJJ (2001) The effect of supplementation of root zone dissolved inorganic carbon on fruit yield and quality of tomatoes (cv 'Daniella') grown with salinity. *Scientia Horticulturae* **89**, 269-289

Cramer MD, Titus CHA (2001) Elevated root zone dissolved inorganic carbon can ameliorate aluminium toxicity in tomato seedlings. *New Phytologist* **152**, 29-39

Cuartero J, Bolarín MC, Asíns MJ, Moreno V (2006) Increasing salt tolerance in the tomato. *Journal of Experimental Botany* **57**, 1045-1058

Cuartero J, Muñoz RF (1999) Tomato and salinity. *Scientia Horticulturae* **78**, 83-125

Dan Y, Yan H, Munyikwa T, Dong J, Zhang Y, Armstrong CL (2006) MicroTom - a high-throughput model transformation system for functional genomics. *Plant Cell Reports* **25**, 432-441

Dannon EA, Wydra K (2004) Interaction between silicon amendment, bacterial wilt development and phenotype of *Ralstonia solanacearum* in tomato genotypes. *Physiological and Molecular Plant Pathology* **64**, 233-243

Dasgan HY, Abak K, Cakmak I, Römheld V, Sensoy S (2004) Inheritance of tolerance to leaf iron deficiency chlorosis in tomato. *Euphytica* **139**, 51-57

Dasgan HY, Aktas H, Abak K, Cakmak I (2002) Determination of screening techniques to salinity tolerance in tomatoes and investigation of genotype responses. *Plant Science* **163**, 695-703

Dasgan HY, Ozturk L, Abak K, Cakmak I (2003) Activities of iron-containing enzymes in leaves of two tomato genotypes differing in their resistance to Fe chlorosis. *Journal of Plant Nutrition* **26**, 1997-2007

Davies JN, Hobson GE (1981) The constituents of tomato fruit: the influence of environment, nutrition and genotype. *Critical Reviews in Food Science and Nutrition* **15**, 205-280

Davies JN, Winsor GW (1967) Effect of nitrogen, phosphorus, potassium, magnesium and liming on the composition of tomato fruit. *Journal of the Science of Food and Agriculture* **18**, 459-466

Davis JM, Sanders DC, Nelson PV, Lengnick L, Sperry WJ (2003) Boron improves growth, yield, quality, and nutrient content of tomato. *Journal of the American Society for Horticultural Science* **128**, 441-446

de Giovanni C, Dell'Orco P, Bruno A, Ciccarese F, Lotti C, Ricciardi L (2004) Identification of PCR-based markers (RAPD, AFLP) linked to a novel powdery mildew resistance gene (*ol-2*) in tomato. *Plant Science* **166**, 41-48

de Groot CC, Marcelis LFM, van den Boogaard R, Lambers H (2001) Growth and dry-mass partitioning in tomato as affected by phosphorus nutrition and light. *Plant, Cell and Environment* **24**, 1309-1317

de Groot CC, Marcelis LFM, van den Boogaard R, Lambers H (2002) Interactive effects of nitrogen and irradiance on growth and partitioning of dry mass and nitrogen in young tomato plants. *Functional Plant Biology* **29**, 1319-1328

de Ketelaere B, Lammertyn J, Molenberghs G, Desmet M, Nicolaï B, de Baerdemaeker J (2004) Tomato cultivar grouping based on firmness change, shelf life and variance during postharvest storage. *Postharvest Biology and Technology* **34**, 187-201

de Kreij C, Janse J, van Goor BJ, van Doesburg JDJ (1992) The incidence of calcium oxalate crystals in fruit walls of tomato (*Lycopersicon esculentum* Mill.) as affected by humidity, phosphate and calcium supply. *Journal of Horticultural Science* **67**, 45-50

de Kreij C, Voogt W, Baas R (1999) Nutrient solutions and water quality for soilless cultures. Brochure 196. Research Station for Floriculture and Glasshouse Vegetables (PBG), Naaldwijk, The Netherlands, 32 pp

de Pascale S, Maggio A, Fogliano V, Ambrosino P, Ritieni A (2001) Irrigation with saline water improves carotenoids content and antioxidant activity of tomato. *Journal of Horticultural Science and Biotechnology* **76**, 447-453

de Wild HPJ, Balk PA, Fernandes ECA, Peppelenbos HW (2005) The action site of carbon dioxide in relation to inhibition of ethylene production in tomato fruit. *Postharvest Biology and Technology* **36**, 273-280

Del Amor FM, Marcelis LFM (2006) Differential effect of transpiration and Ca supply on growth and Ca concentration of tomato plants. *Scientia Horticulturae* **111**, 17-23

Dennis C, Browne KM, Adamick F (1979) Controlled atmosphere storage of tomatoes. *Acta Horticulturae* **93**, 75-83

Dilworth MJ, Robson AD, Chatel DL (1979) Cobalt and nitrogen fixation in *Lupinus angustifolius* L. II. Nodule formation and functions. *New Phytologist* **83**, 63-79

Ding C-K, Wang CY, Gross KC, Smith DL (2001) Reduction of chilling injury and transcript accumulation of heat shock proteins in tomato fruit by methyl jasmonate and methyl salicylate. *Plant Science* **161**, 1153-1159

Ding C-K, Wang CY, Gross KC, Smith DL (2002) Jasmonate and salicylate induce the expression of pathogenesis-related-protein genes and increase resistance to chilling injury in tomato fruit. *Planta* **214**, 895-901

Djebali W, Zarrouk M, Brouquisse R, El Kahoui S, Limam F, Ghorbel MH, Chaibi W (2005) Ultrastructure and lipid alterations induced by cadmium in tomato (*Lycopersicon esculentum*) chloroplast membranes. *Plant Biology* **7**, 358-368

Dolstra O, Venema JH, Groot PJ, Hasselt PR (2002) Low-temperature-related growth and photosynthetic performance of alloplasmic tomato (*Lycopersicon esculentum* Mill.) with chloroplasts from *L. hirsutum* Humb. & Bonpl. *Euphytica* **124**, 407-421

Dong C-X, Shen Q-R, Wang G (2004) Tomato growth and organic acid changes in response to partial replacement of NO_3^--N by NH_4^+-N. *Pedosphere* **14**, 159-164

Dumas Y, Dadomo M, Di Lucca G, Grolier P (2003) Effects of environmental factors and agricultural techniques on antioxidant content of tomatoes. *Journal of the Science of Food and Agriculture* **83**, 369-382

Egashira H, Ishihara H, Takashina T, Imanishi S (2000) Genetic diversity of the "peruvianum complex" (*Lycopersicon peruvianum* (L.) Mill. and *L. chilense* Dun.) revealed by RAPD analysis. *Euphytica* **116**, 23-31

Ehret DL, Ho LC (1986a) The effects of salinity on dry matter partitioning and fruit growth in tomatoes grown in nutrient film culture. *Journal of Horticultural Science* **61**, 361-367

Ehret DL, Ho LC (1986b) Translocation of calcium in relation to tomato fruit growth. *Annals of Botany* **58**, 679-688

Ehret DL, Menzies JG, Bogdanoff C, Utkhede RS, Frey B (2002) Foliar applications of fertilizer salts inhibit powdery mildew on tomato. *Canadian Journal of Plant Pathology* **24**, 437-444

Ellul P, Garcia-Sogo B, Pineda B, Rios G, Roig LA, Moreno V (2003) The ploidy level of transgenic plants in *Agrobacterium*-mediated transformation of tomato cotyledons (*Lycopersicon esculentum* L. Mill.) is genotype and procedure dependent. *Theoretical and Applied Genetics* **106**, 231-238

Epstein E (1999) Silicon. *Annual Review of Plant Physiology and Plant Molecular Biology* **50**, 641-664

Ergun M, Sargent SA, Huber DJ (2006) Postharvest quality of grape tomatoes treated with 1-methylcyclopropene at advanced ripeness stages. *HortScience* **41**, 183-187

Errebhi M, Wilcox GE (1990) Tomato growth and nutrient uptake pattern as influenced by nitrogen form ratio. *Journal of Plant Nutrition* **13**, 1031-1034

Estañ MT, Martinez-Rodriguez MM, Perez-Alfocea F, Flowers TJ, Bolarin MC (2005) Grafting raises the salt tolerance of tomato through limiting the transport of sodium and chloride to the shoot. *Journal of Experimental Botany* **56**, 703-712

Fallik E, Ilic Z, Alkalai-Tuvia S, Copel A, Polevaya Y (2002) A short hot water rinsing and brushing reduces chilling injury and enhances resistance against *Botrytis cinerea* in fresh harvested tomato. *Advances in Horticultural Science* **16**, 3-6

Fallik E, Polevaya Y, Tuvia-Alkalai S, Shalom Y, Zuckermann H (2003) A 24-h anoxia treatment reduces decay development while maintaining tomato fruit quality. *Postharvest Biology and Technology* **29**, 233-236

FAO (Food and Agricultural Organization) (2007) FAOStat, core production 2005. Available online: http://faostat.fao.org/site/340/default.aspx

Feng X, Apelbaum A, Sisler EC, Goren R (2004) Control of ethylene activity in various plant systems by structural analogues of 1-methylcyclopropene. *Plant Growth Regulation* **42**, 29-38

Fernández V, Ebert G (2005) Foliar iron fertilization: A critical review. *Journal of Plant Nutrition* **28**, 2113-2124

Fernández-García N, Martínez V, Cerdá A, Carvajal M (2002) Water and nutrient uptake of grafted tomato plants grown under saline conditions. *Journal of Plant Physiology* **159**, 899-905

Fillati JJ, Kiser J, Ronald R, Comai L (1987) Efficient transfer of glyphosate tolerance gene into tomato using a binary *Agrobacterium tumefaciens* vector. *Biotechnology* **5**, 726-730

Finkers R, van den Berg P, van Berloo R, ten Have A, van Heusden AW, van Kan JAL, Lindhout P (2007) Three QTLs for *Botrytis cinerea* resistance in tomato. *Theoretical and Applied Genetics* **114**, 585-593

Flores P, Carvajal M, Cerdá A, Martínez V (2001) Salinity and ammonium/nitrate interactions on tomato plant development, nutrition, and metabolites. *Journal of Plant Nutrition* **24**, 1561-1573

Flores P, Navarro JM, Carvajal M, Cerdá A, Martínez V (2003) Tomato yield and quality as affected by nitrogen source and salinity. *Agronomie* **23**, 249-256

Foolad MR (2004) Recent advances in genetics of salt tolerance in tomato. *Plant Cell, Tissue and Organ Culture* **76**, 101-119

Foolad MR, Chen FQ (1999) RFLP mapping of QTLs conferring salt tolerance during vegetative stage in tomato. *Theoretical and Applied Genetics* **99**, 235-243

Foolad MR, Lin GY (2001) Genetic analysis of cold tolerance during vegetative growth in tomato, *Lycopersicon esculentum* Mill. *Euphytica* **122**, 105-111

Foolad MR, Zhang LP, Lin GY (2001) Identification and validation of QTLs for salt tolerance during vegetative growth in tomato by selective genotyping. *Genome* **44**, 444-454

Foolad R, Zhang P, Khan AA, Nino-Liu D, Lin Y (2002) Identification of QTLs for early blight (*Alternaria solani*) resistance in tomato using backcross populations of a *Lycopersicon esculentum* × *L. hirsutum* cross. *Theoretical and Applied Genetics* **104**, 945-958

Forde BG, Clarkson DT (1999) Nitrate and ammonium nutrition of plants: Physiological and molecular perspectives. *Advances in Botanical Research* **30**, 1-90

Frankel OH, Brown AHD, Burdon JJ (1995) *The Conservation of Plant Biodiversity*, Cambridge University Press, Cambridge, UK, 299 pp

Frary A, Doganlar S, Frampton A, Fulton T, Uhlig J, Yates H, Tanksley S (2003) Fine mapping of quantitative trait loci for improved fruit characterristics from *Lycopersicon chmielewskii* chromosome 1. *Genome* **46**, 235-243

Frary A, Fritz LA, Tanksley SD (2004) A comparative study of the genetic bases of natural variation in tomato leaf, sepal and petal morphology. *Theoretical and Applied Genetics* **109**, 523-533

Frary A, Nesbitt T, Grandillo S, van der Knaap E, Cong B, Liu J, Meller J, Elber R, Alpert K, Tanksley S (2000) fw2.2: a qualitative trait locus key to the evolution of tomato fruit size. *Science* **289**, 85-88

Fraser PD, Bramleya P, Seymour GB (2001) Effect of the Cnr mutation on carotenoid formation during tomato fruit ripening. *Phytochemistry* **58**, 75-79

Frelichowski Jr JE, Juvic JA (2005) Inheritance of sesquiterpene carboxylic acid synthesis in crosses of *Lycopersicon hirsutum* with incect-susceptible tomatoes. *Plant Breeding* **124**, 277-281

Fulton TM, Bucheli P, Voirol E, Lopez J, Petiard V, Tanksley SD (2002) Quantitative trait loci (QTL) affecting sugars, organic acids and other biochemical properties possibly contributing to flavor identified in four advanced backcross populations *Euphytica* **127**, 163-177

Ganmore-Neumann R, Kafkafi U (1980) Root temperature and percentage NO_3^-/NH_4^+ effect on tomato plant development. I. Morphology and growth. *Agronomy Journal* **72**, 758-761

Garcia-Martinez S, Andreani L, Garcia-Gusano M, Geuna F, Ruiz JJ (2006) Evaluation of amplified fragment length polymorphism and simple sequence repeats for tomato germplasm fingerprinting: utility for grouping closely related traditional cultivars. *Genome* **49**, 648-656

Georgiady MS, Whitkus RW, Lord EM (2002) Genetic analysis of traits distinguishing outcrossing and self-pollinating forms of currant tomato, *Lycopersicon pimpinellifolium* (Jusl.) Mill. *Genetics* **161**, 333-344

Gerendás J, Zhu Z, Bendixen R, Ratcliffe RG, Sattelmacher B (1997) Physiological and biochemical processes related to ammonium toxicity in higher plants. *Zeitschrift für Pflanzeneruährung und Bodenkunde* **160**, 239-251

Giuntini D, Graziani G, Lercari B, Fogliano V, Soldatini GF, Ranieri A (2005) Changes in carotenoid and ascorbic acid contents in fruits of different tomato genotypes related to the depletion of UV-B radiation. *Journal of Agricultural and Food Chemistry* **53**, 3174-3181

Goodenough PW (1986) A review of the role of ethylene in biochemical control of ripening in tomato fruit. *Plant Growth Regulation* **4**, 125-137

Goodstal FJ, Kohler GR, Randall, LB, Bloom AJ, St Clair D (2005) A major QTL introgressed from wild *Lycopersicon hirsutum* confers chilling tolerance to cultivated tomato (*Lycopersicon esculentum*). *Theoretical and Applied Genetics* **111**, 898-905

Gopal R, Dube BK, Sinha P, Chatterjee C (2003) Cobalt toxicity effects on growth and metabolism of tomato. *Communications in Soil Science and Plant Analysis* **34**, 619-628

Gough C, Hobson GE (1990) A comparison of the productivity, quality, shelf-life characteristics and consumer reaction to the crop from cherry tomato plants grown at different levels of salinity. *Journal of Horticultural Science* **65**, 431-439

Grandillo S, Tanksley SD (1996) QTL analysis of horticultural traits differentiating the cultivated tomato from closely related species *Lycopersicon pimpinellifolium*. *Theoretical and Applied Genetics* **92**, 935-951

Grandillo S, Zamir D, Tanksley SD (1999a) Genetic improvement of processing tomatoes: A 20 years perspective. *Euphytica* **110**, 85-97

Grandillo S, Ku HM, Tanksley SD (1999b) Identifying the loci responsible for natural selection in fruit size and shape of tomato. *Theoretical and Applied Genetics* **99**, 978-987

Grattan SR, Grieve CM (1999) Salinity-mineral relations in horticultural crops. *Scientia Horticulturae* **78**, 127-157

Grierson D, Kader AA (1986) Fruit ripening and quality. In: Atherton JG, Rudich J (Eds) *The Tomato Crop: A Scientific Basis for Improvement*, Chapman and Hall, London, UK, pp 241-280

Grube RC, Radwanski ER, Jahn M (2000) Comparative genetics of disease resistance within Solanaceae. *Genetics* **155**, 873-887

Gunes A, Alpaslan M, Inal A (1998) Critical nutrient concentrations and antagonistic and synergistic relationships among the nutrients of NFT-grown young tomato plants. *Journal of Plant Nutrition* **21**, 2035-2047

Hamer PJC (2003) Analysis of strategies for reducing calcium deficiencies in glasshouse grown tomatoes: Model functions and simulations. *Agricultural Systems* **76**, 181-205

Hamilton AJ, Lycett GW, Grierson D (1990) Antisense gene that inhibits synthesis of the hormone ethylene in the transgenic plant. *Nature* **246**, 284-287

Hao X, Papadopoulos AP (2003) Effects of calcium and magnesium on growth, fruit yield and quality in a fall greenhouse tomato crop grown on rockwool. *Canadian Journal of Plant Science* **83**, 903-912

Hao X, Papadopoulos AP (2004) Effects of calcium and magnesium on plant growth, biomass partitioning, and fruit yield of winter greenhouse tomato. *HortScience* **39**, 512-515

Hartz TK, Johnson PR, Francis DM, Miyao EM (2005) Processing tomato yield and fruit quality improved with potassium fertigation. *HortScience* **40**, 1862-1867

Hatton TT, Pantastico EB, Akamine EK (1975) Controlled atmosphere storage. 3. Individual commodity requirements. In: Pantastico EB (Ed) *Postharvest Physiology, Handling and Utilization of Tropical and Subtropical Fruits and Vegetables*, AVI, Westport, Connecticut, USA, pp 201-218

He C, Poysa V, Yu K (2003) Development and characterization of simple sequence repeat (SSR) markers and their use in determining relationships among *Lycopersicon esculentum* cultivars. *Theoretical and Applied Genetics* **106**, 363-373

He ZL, Yang XE, Stoffella PJ (2005) Trace elements in agroecosystems and impacts on the environment. *Journal of Trace Elements in Medicine and Biology* **19**, 125-140

Heeb A, Lundegårdh B, Ericsson T, Savage GP (2005a) Effects of nitrate-, ammonium-, and organic-nitrogen-based fertilizers on growth and yield of tomatoes. *Journal of Plant Nutrition and Soil Science* **168**, 123-129

Heeb A, Lundegårdh B, Ericsson T, Savage GP (2005b) Nitrogen form affects yield and taste of tomatoes. *Journal of the Science of Food and Agriculture* **85**, 1405-1414

Heine G, Tikum G, Horst WJ (2005) Silicon nutrition of tomato and bitter gourd with special emphasis on silicon distribution in root fractions. *Journal of Plant Nutrition and Soil Science* **168**, 600-606

Helyes L, Pék Z, Lugasi A (2006) Tomato fruit quality and content depend on stage of maturity. *HortScience* **41**, 1400-1401

Ho LC, Belda R, Brown M, Andrews J, Adams P (1993) Uptake and transport of calcium and the possible causes of blossom-end rot in tomato. *Journal of Experimental Botany* **44**, 509-518

Ho LC, White PJ (2005) A cellular hypothesis for the induction of blossom-end rot in tomato fruit. *Annals of Botany* **95**, 571-581

Hoeberichts FA, van der Plas LHW, Woltering EJ (2002) Ethylene perception is required for the expression of tomato ripening-related genes and associated physiological changes even at advanced stages of ripening. *Postharvest Biology and Technology* **26**, 125-133

Hong JH, Cowan AK, Koo Lee S (2004) Glucose inhibits ACC oxidase activity and ethylene biosynthesis in ripening tomato fruit. *Plant Growth Regulation* **43**, 81-87

Horst WJ (1988). The physiology of manganese toxicity. In: Graham RD, Hannam RJ, Uren NC (Eds) *Manganese in Soils and Plants.* Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 175-188

Huang J-S, Snapp SS (2004a) The effect of boron, calcium, and surface moisture on shoulder check, a quality defect in fresh-market tomato. *Journal of the American Society for Horticultural Science* **129**, 599-607

Huang J-S, Snapp SS (2004b) A bioassay investigation of calcium nutrition and tomato shoulder check cracking defect. *Communications in Soil Science and Plant Analysis* **35**, 2771-2787

Hurr BM, Huber DJ, Lee JH (2005) Differential responses in color changes and softening of 'Florida 47' tomato fruit treated at green and advanced ripening stages with the ethylene antagonist 1-methylcyclopropene. *HortTechnology* **15**, 617-622

Imas P, Bar-Yosef B, Kafkafi U, Ganmore-Neumann R (1997) Release of carboxylic anions and protons by tomato roots in response to ammonium nitrate ratio and pH in nutrient solution. *Plant and Soil* **191**, 27-34

Inanaga S, Okasaka A (1995) Calcium and silicon binding compounds in cell walls of rice shoots. *Soil Science and Plant Nutrition* **41**, 103-110

Ip C (1998) Lessons from basic research in selenium and cancer prevention. *Journal of Nutrition* **128**, 1845-1854

Islam AKMS, Edwards DG, Asher CJ (1980) pH optima for crop growth. Results of a flowing solution culture experiment with six species. *Plant and Soil* **54**, 339-357

Iwahashi Y, Hosoda H (2000) Effect of heat stress on tomato fruit protein expression. *Electrophoresis* **21**, 1766-1771

Jakubowicz M, Sadowski J (2002) 1-aminocyclopropane-1-carboxylate synthase – Genes and expression. *Acta Physiologiae Plantarum* **24**, 459-478

James C (1997) *Global status of transgenic crops in 1997*: ISAAA Brief No. 5, International Service for the Acquisition of Agriobiotech Applications, Ithaca, NY, USA, 31 pp

Jani D, Meena LS, Rizwan-ul-Haq QM, Singh Y, Sharma AK, Tyagi AK (2002) Expression of cholera toxin B subunit in transgenic tomato plants. *Transgenic Research* **11**, 447-454

Javanmardi J, Kubota C (2006) Variation of lycopene, antioxidant activity, total soluble solids and weight loss of tomato during postharvest storage. *Postharvest Biology and Technology* **41**, 151-155

Johnson RW, Dixon MA, Lee DR (1992) Water relations of the tomato fruit during growth. *Plant Cell and Environment* **15**, 947-953

Jones Jr JB (1998) Phosphorus toxicity in tomato plants: When and how does it occur? *Communications in Soil Science and Plant Analysis* **29**, 1779-1784

Juan M, Rivero RM, Romero L, Ruiz JM (2005) Evaluation of some nutriational and biochemical indicators in selecting salt-resistant tomato cultivars. *Environmental and Experimental Botany* **54**, 193-201

Kabelka E, Franchino B, Francis DM (2002) Two loci from *Lycopersicon hirsutum* LA 407 confer resistance to strains of *Clavibacter michiganensis* subsp. *michiganensis*. *Phytopathology* **92**, 504-510

Kamal AHM, Takashina T, Egashira H, Satoh H, Imanishi S (2001) Introduction of aromatic fragrance into cultivated tomato from the 'peruvianum complex'. *Plant Breeding* **120**, 179-181

Kantola M, Helén H (2001) Quality changes in organic tomatoes packaged in biodegradable plastic films. *Journal of Food Quality* **24**, 167-176

Kapotis G, Passam HC, Akoumianakis K, Olympios CM (2004) Storage of tomatoes in low oxygen atmospheres inhibits ethylene action and polygalacturonase activity. *Russian Journal of Plant Physiology* **51**, 112-115

Karlberg L, Ben-Gal A, Jansson P-E, Shani U (2006) Modelling transpiration and growth in salinity-stressed tomato under different climatic conditions. *Ecological Modelling* **190**, 15-40

Katerji N, Van Hoorn JW, Hamdy A, Mastrorilli M (1998) Response of tomatoes, a crop of indeterminate growth, to soil salinity. *Agricultural Water Management* **38**, 59-68

Kaur C, George B, Deepa N, Singh B, Kapoor HC (2004) Antioxidant status of fresh and processed tomato - A review. *Journal of Food Science and Technology* **41**, 479-486

Kaya C, Higgs D (2001) Inter-relationships between zinc nutrition, growth parameters, and nutrient physiology in a hydroponically grown tomato cultivar. *Journal of Plant Nutrition* **24**, 1491-1503

Kaya C, Higgs D (2002) Improvements in physiological and nutritional developments of tomato cultivars grown at high zinc by foliar application of phosphorus and iron. *Journal of Plant Nutrition* **25**, 1881-1894

Kirkby EA, Knight AH (1977) Influence of the level of nitrate nutrition on ion uptake and assimilation, organic acid accumulation, and cation-anion balance in whole tomato plants. *Plant Physiology* **60**, 349-353

Kirkby EA, Mengel K (1967) Ionic balance in different tissues of the tomato plant in relation to nitrate, urea, or ammonium nutrition. *Plant Physiology* **42**, 6-14

Klee H, Tieman D (2002) The tomato ethylene receptor gene family: Form and function. *Physiologia Plantarum* **115**, 336-341

Klee HJ (2002) Control of ethylene-mediated processes in tomato at the level of receptors. *Journal of Experimental Botany* **53**, 2057-2063

Kochieva EZ, Ryzhova NN, Khrapalova IA, Pukhalkyi VA (2002) Using RAPD for estimating genetic polymorphism in and phylogenetic relationships among species in the genus *Lycopersicon* (Tourn.) Mill. *Russian Journal of Genetics* **38**, 1104-1108

Korshunova YO, Eide D, Clark WG, Guerinot ML, Pakrasi HB (1999) The IRT1 protein from *Arabidopsis thaliana* is a metal transporter with a broad substrate range. *Plant Molecular Biology* **40**, 37-44

Krauss S, Schnitzler WH, Grassmann J, Woitke M (2006) The influence of different electrical conductivity values in a simplified recirculating soilless system on inner and outer fruit quality characteristics of tomato. *Journal of Agricultural and Food Chemistry* **54**, 441-448

Krumbein A, Peters P, Brückner B (2004) Flavour compounds and a quantitative descriptive analysis of tomatoes (*Lycopersicon esculentum* Mill.) of different cultivars in short-term storage. *Postharvest Biology and Technology* **32**, 15-28

Kütük C, Cayci G, Heng LK (2004) Effects of increasing salinity and 15N-labelled urea levels on growth, N uptake, and water use efficiency of young tomato plants. *Australian Journal of Soil Research* **42**, 345-351

Le Bot J, Goss MJ, Carvalho GPR, van Beusichem ML, Kirby EA (1990) The significance of magnesium to manganese ratio in plant tissues for growth and alleviation of manganese toxicity in tomato (*Lycopersicon esculentum*) and wheat (*Triticum sativum*) plants. *Plant and Soil* **124**, 205-210

Lea-Cox JD, Stutte GW, Berry WL, Wheeler RM (1996) Charge balance - a theoretical basis for modulating pH fluctuations in plant nutrient delivery systems. *Life Support and Biosphere Science* **3**, 53-59

Li YL, Marcelis LFM, Stanghellini C (2004) Plant water relations as affected by osmotic potential of the nutrient solution and potential transpiration in tomato (*Lycopersicon esculentum* Mill.). *Journal of Horticultural Science and Biotechnology* **79**, 211-218

Li YL, Stanghellini C, Challa H (2001) Effect of electrical conductivity and transpiration on production of greenhouse tomato (*Lycopersicon esculentum* L.). *Scientia Horticulturae* **88**, 11-29

Liao MT, Hedley MJ, Woolley DJ, Brooks RR, Nichols MA (2000) Copper uptake and translocation in chicory (*Cichorium intybus* L. cv. Grasslands Puna) and tomato (*Lycopersicon esculentum* Mill. cv. Rondy) plants grown in NFT system. I. Copper uptake and distribution in plants. *Plant and Soil* **221**, 135-142

Lichter A, Dvir O, Fallik E, Cohen S, Golan R, Shemer Z, Sagi M (2002) Cracking of cherry tomatoes in solution. *Postharvest Biology and Technology* **26**, 305-312

Lichter A, Guzev L, Dvir O, Farber I, Danshin A, Pressman E, Ganz S, Beno-Moualem D (2006) Seasonal changes in the abscission site in bunch tomatoes and differential response to 1-methylcyclopropene. *Postharvest Biology and Technology* **40**, 7-14

Ling HQ, Bauer P, Bereczky Z, Keller B, Ganal M (2002) The tomato FER gene encoding a bHLH protein controls iron-uptake responses in roots. *Proceedings of the National Academy of Sciences USA* **99**, 13938-13943

Liu J, Van Eck J, Cong B, Tanksley SD (2002) A new class of regulatory genes underlying the cause of pear-shaped tomato fruit. *Proceedings of the National Academy of Sciences USA* **99**, 13302-13306

Logendra LS, Mun JG, Gianfagna TJ, Janes HW (2004) Ethephon concentrates and advances harvest for limited cluster greenhouse tomato crops. *HortScience* **39**, 1650-1651

Lois LM, Rodríguez-Concepción M, Gallego F, Campos N, Boronat A

(2000) Carotenoid biosynthesis during tomato fruit development: Regulatory role of 1-deoxy-D-xylulose 5-phosphate synthase. *Plant Journal* **22**, 503-513

Luo HM, Watanabe T, Shinano T, Tadano T (1999) Comparison of aluminium tolerance and phosphate absorption between rape (*Brassica napus* L.) and tomato (*Lycopersicum esculentum* Mill.) in relation to organic acid exudation. *Soil Science and Plant Nutrition* **45**, 897-907

Luthria DL, Mukhopadhyay S, Krizek DT (2006) Content of total phenolics and phenolic acids in tomato (*Lycopersicon esculentum* Mill.) fruits as influenced by cultivar and solar UV radiation. *Journal of Food Composition and Analysis* **19**, 771-777

Maas EV, Hoffman GJ (1977) Crop salt tolerance – current assessment. *Journal of Irrigation and Drainage Division American Society of Civil Engineers* **103**, 115-134

Madhavi DL, Salunkhe DK (1998) Tomato. In: Sakunkhe DK, Kadam SS (Eds) *Handbook of Vegetable Science and Technology*: *Production, Composition, Storage and Processing*, Marcel Dekker Inc, New York, USA, pp 171-202

Magalhães JR, Wilcox GE (1983) Tomato growth and mineral composition as influenced by nitrogen form and light intensity. *Journal of Plant Nutrition* **6**, 847-862

Maneerat C, Hayata Y (2006) Efficiency of TiO2 photocatalytic reaction on delay of fruit ripening and removal of off-flavors from the fruit storage atmosphere. *Transactions of the American Society of Agricultural Engineers* **49**, 833-837

Maneerat C, Hayata Y, Egashira N, Sakamoto K, Hamai Z, Kuroyanagi M (2003) Photocatalytic reaction of TiO_2 to decompose ethylene in fruit and vegetable storage. *Transactions of the American Society of Agricultural Engineers* **46**, 725-730

Marschner H (1995) *Mineral Nutrition of Higher Plants* (2^{nd} Edn), Academic Press, London, UK, 889 pp

Maul F, Sargent SA, Sims CA, Baldwin EA, Balaban MO, Huber DJ (2000) Tomato flavor and aroma quality as affected by storage temperature. *Journal of Food Science* **65**, 1228-1237

Mavrogianopoulos G, Savvas D, Vogli V (2002) Influence of NaCl-salinity imposed on half of the root system of hydroponically grown tomato on growth, yield, and tissue mineral composition. *Journal of Horticultural Science and Biotechnology* **77**, 557-564

McGlasson WB, Last JH, Shaw KJ, Meldrum SK (1987) Influence of the nonripening mutants *rin* and *nor* on the aroma of tomato fruit. *HortScience* **22**, 632-634

Meredith FI, Purcell AE (1966) Changes in the concentration of carotenes of ripening Homestead tomatoes. *Proceedings of the American Society for Horticultural Science* **89**, 544

Miller JC, Tanksley SD (1990) RFLP analysis of phylogenetic relationships and genetic variation in the genus *Lycopersicon*. *Theoretical and Applied Genetics* **80**, 437-448

Mills HA, Jones Jr. J (1996) *Plant Analysis Handbook II*, MicroMacro Publishing Inc, Athens, GA, USA, 422 pp

Mir N, Canoles M, Beaudry R, Baldwin E, Mehla CP (2004) Inhibiting tomato ripening with 1-methylcyclopropene. *Journal of the American Society for Horticultural Science* **129**, 112-120

Miyake Y, Takahashi E (1978) Silicon deficiency of tomato plant. *Soil Science and Plant Nutrition* **24**, 175-189

Molyneux SL, Lister CE, Savage GP (2004) An investigation of the antioxidant properties and colour of glasshouse grown tomatoes. *International Journal of Food Sciences and Nutrition* **55**, 537-545

Mondal K, Sharma NS, Malhotra SP, Dhawan K, Singh R (2003) Oxidative stress and antioxidant systems in tomato fruits during storage. *Journal of Food Biochemistry* **27**, 515-527

Mondal K, Sharma NS, Malhotra SP, Dhawan K, Singh R (2006) Oxidative stress and antioxidant systems in tomato fruits stored under normal and hypoxic conditions. *Physiology and Molecular Biology of Plants* **12**, 145-150

Mostofi Y, Toivonen PMA, Lessani H, Babalar M, Lu C (2003) Effects of 1-methylcyclopropene on ripening of greenhouse tomatoes at three storage temperatures. *Postharvest Biology and Technology* **27**, 285-292

Mulholland BJ, Fussell M, Edmondson RN, Basham J, McKee JMT (2001) Effect of VPD, K nutrition and root-zone temperature on leaf area development, accumulation of Ca and K and yield in tomato. *Journal of Horticultural Science and Biotechnology* **76**, 641-647

Mulholland BJ, Fussell M, Edmondson RN, Taylor AJ, Basham J, McKee JMT, Parsons N (2002) The effect of split-root salinity stress on tomato leaf expansion, fruit yield and quality. *Journal of Horticultural Science and Biotechnology* **77**, 509-519

Mulholland BJ, Taylor IB, Jackson AC, Thompson AJ (2003) Can ABA mediate responses of salinity stressed tomato? *Environmental and Experimental Botany* **50**, 17-28

Muratore G, Del Nobile MA, Buonocore GG, Lanza CM, Asmundo CN (2005) The influence of using biodegradable packaging films on the quality decay kinetic of plum tomato (Pomodorino Datterino®). *Journal of Food Engineering* **67**, 393-399

Navarro JM, Flores P, Carvajal M, Martinez V (2005) Changes in quality and yield of tomato fruit with ammonium, bicarbonate and calcium fertilisation under saline conditions. *Journal of Horticultural Science and Biotechnology* **80**, 351-357

Nelson RS, McCormick SM, Delannay X, Dube P, Layton J, Anderson EJ, Kanieska M, Proksch RK, Horsch RB, Rogers SG, Fraley RT, Beachy RN (1988) Virus tolerance, plant growth and field performance of transgenic tomato plants expressing coat protein from tobacco mosaic virus. *Biotechnology* **6**, 403-409

Nesbitt TC, Tanksley SD (2001) *fw2.2* directly affects the size of developing tomato fruit, with secondary effects on fruit number and photosynthate distribution. *Plant Physiology* **127**, 575-583

Nuez F, Prohens J, Blanca JM (2004). Relationships, origin, and diversity of Galapagos tomatoes: implications for the conservation of natural populations. *American Journal of Botany* **91**, 86-99

Oeller PW, Min-Wong L, Taylor LP, Pike DA, Theologis A (1991) Reversible inhibition of tomato fruit senescence by antisense RNA. *Science* **254**, 437-439

Oke M, Ahn T, Schofield A, Paliyath G (2005) Effects of phosphorus fertilizer supplementation on processing quality and functional food ingredients in tomato. *Journal of Agricultural and Food Chemistry* **53**, 1531-1538

Olympios CM, Karapanos IC, Lionoudakis K, Apidianakis I (2003) The growth, yield and quality of greenhouse tomatoes in relation to salinity applied at different stages of plant growth. *Acta Horticulturae* **609**, 313-320

Opiyo AM, Ying T-J (2005) The effects of 1-methylcyclopropene treatment on the shelf life and quality of cherry tomato (*Lycopersicon esculentum* var. *cerasiforme*) fruit. *International Journal of Food Science and Technology* **40**, 665-673

Ouariti O, Gouia H, Ghorbal MH (1997) Responses of bean and tomato plants to cadmium: Growth, mineral nutrition, and nitrate reduction. *Plant Physiology and Biochemistry* **35**, 347-354

Parisi M, Giordano I, Pantangelo A, D'Onofrio B, Villari G (2006) Effects of different levels of nitrogen fertilization on yield and fruit quality in processing tomato. *Acta Horticulturae* **700**, 129-132

Park YH, West MAL, St Clair DA (2004) Evaluation of AFLPs for germplasm fingerprinting and assessment of genetic diversity in cultivars of tomato (*Lycopersicon esculentum* L.). *Genome* **47**, 510-518

Perez-Espinosa A, Moreno-Caselles J, Moral R, Perez-Murcia MD, Gomez I (2002) Effect of cobalt on chlorophyll and carotenoid contents in tomato plants. *Journal of Plant Nutrition* **25**, 1933-1940

Petersen KK, Willumsen J, Kaack K (1998) Composition and taste of tomatoes as affected by increased salinity and different salinity sources. *Journal of Horticultural Science* **73**, 205-215

Peterson DG, Price HJ, Johnston JS, Stack SM (1996) DNA content of heterochromatin and euchromatin in tomato (*Lycopersicon esculentum*) pachytene chromosomes. *Genome* **39**, 77-82

Pezzarossa B, Piccotino D, Shennan C, Malorgio F (1999) Uptake and distribution of selenium in tomato plants as affected by genotype and sulphate supply. *Journal of Plant Nutrition* **22**, 1613-1635

Pill WG, Lambeth VN (1980) Effects of soil water regime and nitrogen form on blossom-end rot, yield, water relations, and elemental composition of tomato. *Journal of the American Society for Horticultural Science* **105**, 730-734

Plaut Z, Grava A, Yehezkel C, Matan E (2004) How do salinity and water stress affect transport of water, assimilates and ions to tomato fruits? *Physiologia Plantarum* **122**, 429-442

Polenta G, Lucangeli C, Budde C, González CB, Murray R (2006) Heat and anaerobic treatments affected physiological and biochemical parameters in tomato fruits. *Food Science and Technology* **39**, 27-34

Poulton JL, Koide RT, Stephenson AG (2001) Effects of mycorrhizal infection and soil phosphorus availability on *in vitro* and *in vivo* pollen performance in *Lycopersicon esculentum* (Solanaceae). *American Journal of Botany* **88**, 1786-1793

Raab TK, Terry N (1994) Nitrogen-source regulation of growth and photosynthesis in *Beta vulgaris* L. *Plant Physiology* **105**, 1159-1166

Radi A, Dina P, Guy A (2006) Expression of *sarcotoxin IA* gene via root-specific tob promoter enhanced host resistance against parasitic weeds in tomato plants. *Plant Cell Reports* **25**, 297-303

Rajput SG, Wable KJ, Sharma KM, Kubde PD, Mulay SA (2006) Reproducibility testing of RAPD and SSR markers in tomato. *African Journal of Biotechnology* **5**, 108-112

Ranieri A, Giuntini D, Lercari B, Soldatini GF (2004) Light influence on antioxidant properties of tomato fruits. *Progress in Nutrition* **6**, 44-49

Rao R, Corrado G, Bianchi M, Di Mauro A (2006) $(GATA)_4$ DNA fingerprinting identifies morphologically characterized 'San Marzano' tomato plants. *Plant Breeding* **125**, 173-176

Rein D, Schijlen E, Kooistra T, Herbers K, Verschuren L, Hall R, Sonnewald U, Bovy A, Kleemann R (2006) Transgenic flavonoid tomato intake reduces C-reactive protein in human C-reactive protein transgenic mice more than wild-type tomato. *Journal of Nutrition* **136**, 2331-2337

Reuter DJ, Robinson JB (1986) *Plant Analysis, an Interpretation Manual*, Inkata Press, Melbourne, Australia, 218 pp

Rick CM (1995) Tomato (*Lycopersicon esculentum*) (Solanaceae). In: Smartt J, Simmonds NW (Eds) *Evolution of Crop Plants*, Longman, Essex, UK, pp 452-457

Rivero RM, Ruiz JM, Romero L (2004) Iron metabolism in tomato and watermelon plants: Influence of grafting. *Journal of Plant Nutrition* **27**, 2221-2234

Rivero RM, Sánchez E, Ruiz JM, Romero L (2003) Influence of temperature on biomass, iron metabolism and some related bioindicators in tomato and watermelon plants. *Journal of Plant Physiology* **160**, 1065-1071

Romero-Aranda MR, Jurado O, Cuartero J (2006) Silicon alleviates the deleterious salt effect on tomato plant growth by improving plant water status. *Journal of Plant Physiology* **163**, 847-855

Rosales MA, Ruiz JM, Hernández J, Soriano T, Castilla N, Romero L (2006) Antioxidant content and ascorbate metabolism in cherry tomato exocarp in relation to temperature and solar radiation. *Journal of the Science of Food and Agriculture* **86**, 1545-1551

Rubio L, Rosado A, Linares-Rueda A, Borsani O, García-Sánchez MJ, Valpuesta V, Fernández JA, Botella MA (2004) Regulation of K^+ transport in tomato roots by the TSS1 locus. Implications in salt tolerance. *Plant Physiology* **134**, 452-459

Ruiz JJ, Alonso A, Garcia-Martinez S, Valero M, Blasco P, Ruiz-Bevia F (2005) Quantitative analysis of flavour volatiles detects differences among closely related traditional cultivars of tomato. *Journal of the Science of Food and Agriculture* **85**, 54-60

Ruiz JM, Baghour M, Romero L (2000) Efficiency of the different genotypes of tomato in relation to foliar content of Fe and the response of some bioindicators. *Journal of Plant Nutrition* **23**, 1777-1786

Rus-Kortekaas W, Smulders MJM, Arens P, Vosman B (1994) Direct comparison of levels of genetic variation in tomato detected by a GACA – containing microsatellite probe and by random amplified DNA. *Genome* **37**, 375-381

Ryall AL, Lipton WJ (1979) *Handling, Transportation and Storage of Fruits and Vegetables (Vol 1) Vegetables and Melons* (2nd Edn), Avi Publishing Co, Westport, Connecticut, USA, 587 pp

Sabatini E, Rotino GL, Voltattorni S, Acciari N (2006) A novel CAPS marker derived from the *Ovate* gene in tomato (*L. esculentum* Mill.) is useful to distinguish two Italian ecotypes and to recover pear shape in marker assisted selection. *European Journal of Horticultural Science* **71**, 193-198

Sablani SS, Opara LU, Al-Balushi K (2006) Influence of bruising and storage temperature on vitamin C content of tomato fruit. *Journal of Food, Agriculture and Environment* **4**, 54-56

Saliba-Colombani V, Causse M, Gervais L, Philouze J (2000) Efficiency of RFLP, RAPD, and AFLP markers for the construction of an intraspecific map of the tomato genome. *Genome* **43**, 29-40

Saliba-Colombani V, Causse M, Langlois D, Philouze J, Buret M (2001) Genetic analysis of organoleptic quality in fresh market tomato. 1. Mapping QTLs physical and chemical traits. *Theoretical and Applied Genetics* **102**, 259-272

Saltveit ME (2001) Chilling injury is reduced in cucumber and rice seedlings and in tomato pericarp discs by heat-shocks applied after chilling. *Postharvest Biology and Technology* **21**, 169-177

Saltveit ME (2005) Aminoethoxyvinylglycine (AVG) reduces ethylene and protein biosynthesis in excised discs of mature-green tomato pericarp tissue. *Postharvest Biology and Technology* **35**, 183-190

Sánchez AS, Juárez M, Sánchez-Andreu J, Jordá J, Bermúdez D (2005) Use of humic substances and amino acids to enhance iron availability for tomato plants from applications of the chelate FeEDDHA. *Journal of Plant Nutrition* **28**, 1877-1886

Sanchez-Pena P, Oyama K, Nunez-Farfan J, Forfoni J, Hernandez-Vertugo S, Marquez-Guzman J, Garzon-Tiznado JA (2006) Sources of resistance to whitefly (*Bemisia* spp.) in wild populations of *Solanum lycopersicum* var. *cerasiforme* (Dunal) spooner G.J. Anderson et R.K. Jansen in Nortwestern Mexico. *Genetic Resources and Crop Evolution* **53**, 711-719

Santa-Cruz A, Martinez-Rodriguez MM, Perez-Alfocea F, Romero-Aranda R, Bolarin MC (2002) The rootstock effect on the tomato salinity response depends on the shoot genotype. *Plant Science* **162**, 825-831

Santamaria P, Cantore V, Conversa G, Serio F (2004) Effect of night salinity level on water use, physiological responses, yield and quality of tomato. *Journal of Horticultural Science and Biotechnology* **79**, 59-66

Sato S, Sakaguchi S, Furukawa H, Ikeda H (2006) Effects of NaCl application to hydroponic nutrient solution on fruit characteristics of tomato (*Lycopersicon esculentum* Mill.). *Scientia Horticulturae* **109**, 248-253

Saure MC (2001) Blossom-end rot of tomato (*Lycopersicon esculentum* Mill.) - a calcium- or a stress-related disorder? *Scientia Horticulturae* **90**, 193-208

Savvas D (2001) Nutritional Management of Vegetables and Ornamental Plants in Hydroponics. In: Dris R, Niskanen R, Jain SM (Eds) *Crop Management and Postharvest Handling of Horticultural Products. Volume I: Quality Management*, Science Publishers, Enfield, NH, USA, pp 37-87

Savvas D, Nasi E, Moustaka E, Mantzos N, Barouchas P, Passam HC, Olympios C (2006) Effects of ammonium nitrogen on lettuce grown on pumice in a closed hydroponic system. *HortScience* **41**, 1667-1673

Schnitzler WH, Gruda NS (2002) Hydroponics and Product Quality. In: Savvas D, Passam HC (Eds) *Hydroponic Production of Vegetables and Ornamentals*, Embryo Publications, Athens, Greece pp 373-411

Schwarz D, Kläring HP, Ingram KT, Hung YC (2001) Model-based control of nutrient solution concentration influences tomato growth and fruit quality. *Journal of the American Society for Horticultural Science* **126**, 778-784

Scott JW, Agrama HA, Jones JP (2004) RFLP-based analysis of recombination among resistance genes to fusarium wilt races 1, 2 and 3 in tomato. *Journal of the American Society for Horticultural Science* **129**, 394-400

Semel Y, Nissenbaum J, Menda N, Zinder M, Krieger U, Issman N, Pleban T, Lippman Z, Gur A, Zamir D (2006) Overdominant quantitative trait loci for yield and fitness in tomato. *Proceedings of the National Academy of Sciences USA* **103**, 12981-12986

Serio F, De Gara L, Caretto S, Leo L, Santamaria P (2004) Influence of an increased NaCl concentration on yield and quality of cherry tomato grown in posidonia (*Posidonia oceanica* (L) Delile). *Journal of the Science of Food and Agriculture* **84**, 1885-1890

Shah D, Horsch R, Klee H, Kishore G, Winter J, Turner N, Hironaka C, Sanders P, Gasser C, Aykent S, Siegel N, Rogers S, Fraley R (1986) Engineering herbicide tolerance in transgenic plants. *Science* **233**, 478-481

Shalhevet J, Yaron B (1973) Effect of soil and water salinity on tomato growth. *Plant and Soil* **39**, 285-292

Shannon MC, Gronwald JW, Tal M (1987) Effects of salinity on growth and accumulation of organic and inorganic ions in cultivated and wild tomato species. *Journal of the American Society for Horticultural Science* **112**, 416-423

Shenker M, Plessner OE, Tel-Or E (2004) Manganese nutrition effects on tomato growth, chlorophyll concentration, and superoxide dismutase activity. *Journal of Plant Physiology* **161**, 197-202

Siddiqi MY, Malhotra B, Min X, Glass ADM (2002) Effects of ammonium and inorganic carbon enrichment on growth and yield of a hydroponic tomato crop. *Journal of Plant Nutrition and Soil Science* **165**, 191-197

Sifres A, Pico B, Blanca JM, de Frutos R, Nuez F (2006) Genetic structure of *Lycopersicon pimpinellifolium* (Solanaceae) populations collected after the ENSO event of 1997-1998. *Genetic Resources and Crop Evolution* **54**, 359-377

Sigareva M, Spivey R, Willits MG, Kramer CM, Chang YF (2004) An efficient mannose selection protocol for tomato that has no adverse effect on the ploidy level of transgenic plants. *Plant Cell Reports* **23**, 236-245

Simmons AT, McGrath D, Gurr GM (2005) Trichome characteristics of F_1 *Lycopersicon esculentum* X *L. cheesmanii* f. *minor* and *L. esculentum* X *L. pennellii* and effects on *Myzus persicae*. *Euphytica* **144**, 313-320

Sisler EC, Serek M, Dupille E (1996) Comparison of cyclopropene, 1-methylcyclopropene, and 3,3-dimethylcyclopropene as ethylene antagonists in plants. *Plant Growth Regulation* **18**, 169-174

Slimestad R, Verheul MJ (2005) Content of chalconaringenin and chlorogenic acid in cherry tomatoes is strongly reduced during postharvest ripening. *Journal of Agricultural and Food Chemistry* **53**, 7251-7256

Smit JN, Combrink NJJ (2004) The effect of boron levels in nutrient solutions on fruit production and quality of greenhouse tomatoes. *South African Journal of Plant and Soil* **21**, 188-191

Smit JN, Combrink NJJ (2005) Pollination and yield of winter-grown greenhouse tomatoes as affected by boron nutrition, cluster vibration and relative humidity. *South African Journal of Plant and Soil* **22**, 110-115

Sonneveld C (2002) Composition of nutrient solution. In: Savvas D, Passam HC (Eds) *Hydroponic Production of Vegetables and Ornamentals*, Embryo Publications, Athens, Greece, pp 179-210

Sonneveld C, Straver N (1994) *Nutrient Solutions for Vegetables and Flowers Grown in Water or Substrates* (10th Edn) Serie: Voedingsoplossingen Glastuinbouw, No 8, PBG Naaldwijk – PBG Aalsmeer, The Netherlands, 45 pp

Sonneveld C, van der Burg AMM (1991) Sodium chloride salinity in fruit vegetable crops in soilless culture. *Netherlands Journal of Agricultural Science* **39**, 115-122

Sonneveld C, Voogt W (1990) Response of tomatoes (*Lycopersicon esculentum*) to an unequal distribution of nutrients in the root environment. *Plant and Soil* **124**, 251-256

Sonneveld C, Welles GWH (1988) Yield and quality of rockwool-grown tomatoes as affected by variations in EC-value and climatic conditions. *Plant and Soil* **111**, 37-42

Soto-Zamora G, Yahia EM, Brecht JK, Gardea A (2005a) Effects of postharvest hot air treatment on the quality of "Rhapsody" tomato fruit. *Journal of Food Quality* **28**, 492-504

Soto-Zamora G, Yahia EM, Brecht JK, Gardea A (2005b) Effects of postharvest hot air treatments on the quality and antioxidant levels in tomato fruit. *Food Science and Technology* **38**, 657-663

Sozzi GO, Trinchero GD, Fraschina AA (2000) Ethylene and glycosidase promotion in GA_3- and IAA-treated tomato fruit *(Lycopersicon esculentum* Mill.). *Journal of Plant Growth Regulation* **19**, 359-368

Srinivasa PC, Harish Prashanth KV, Susheelamma NS, Ravi R, Tharanathan RN (2006) Storage studies of tomato and bell pepper using eco-friendly films. *Journal of the Science of Food and Agriculture* **86**, 1216-1224

Stamatakis A, Savvas D, Papadantonakis N, Lydakis-Simantiris N, Kefalas P (2003) Effects of silicon and salinity on fruit yield and quality of tomato grown hydroponically. *Acta Horticulturae* **609**, 141-149

Stanghellini C, Challa H, Ya LL (2002) Response of tomato plants to a step-change in root-zone salinity under two different transpiration regimes. *Scientia Horticulturae* **93**, 267-279

Stevens J, Senaratna T, Sivasithamparam K (2006) Salicylic acid induces salinity tolerance in tomato (*Lycopersicon esculentum* cv. Roma): Associated changes in gas exchange, water relations and membrane stabilisation. *Plant Growth Regulation* **49**, 77-83

Suparlan, Itoh K (2003) Combined effects of hot water treatment (HWT) and modified atmosphere packaging (MAP) on quality of tomatoes. *Packaging Technology and Science* **16**, 171-178

Tabatabaei SJ, Gregory PJ, Hadley P (2004) Distribution of nutrients in the root zone affects yield, quality and blossom end rot of tomato fruits. *Journal of Horticultural Science and Biotechnology* **79**, 158-163

Talekar NS, Opena RT, Hanson P (2006) *Helicoverpa armigera* management: A review of AVRDC's research on host plant resistance in tomato. *Crop Protection* **25**, 461-467

Tam SM, Mhiri C, Vogelaar A, Kerkveld M, Pearce SR, Grandbastien MA (2005) Comparative analyses of genetic diversities within tomato and pepper collections detected by retrotransposon-based SSAP, AFLP and SSR. *Theoretical and Applied Genetics* **110**, 819-831

Tan XW, Ikeda H, Oda M (2000a) Effects of nickel concentration in the nutrient solution on the nitrogen assimilation and growth of tomato seedlings in hydroponic culture supplied with urea or nitrate as the sole nitrogen source. *Scientia Horticulturae* **84**, 265-273

Tan XW, Ikeda H, Oda M (2000b) The absorption, translocation, and assimilation of urea, nitrate or ammonium in tomato plants at different plant growth stages in hydroponic culture. *Scientia Horticulturae* **84**, 275-283

Tanksley SD (2004) The genetic developmental and molecular bases of fruit size and shape variation in tomato. *The Plant Cell* **16**, 181-189

Tanksley SD, Ganal MW, Prince JP, de Vicente MC, Bonierbale MW, Broun P, Fulton TM, Giovannoni JJ, Grandillo S, Martin GB, Messeguer R, Miller JC, Miller L, Paterson AH, Piñeda O, Roeder MS, Wing RA, Wu W, Young N (1992) High density molecular linkage maps of the tomato and potato genomes. *Genetics* **132**, 1141-1160

Tanksley SD, Young ND, Paterson AH, Bonierbale MW (1989) RFLP mapping in plant breeding: new tools for an old science. *BioTechnology* **7**, 257-264

Taylor MD, Locascio SJ, Alligood MR (2004) Blossom-end rot incidence of tomato as affected by irrigation quantity, calcium source, and reduced potassium. *HortScience* **39**, 1110-1115

Thakur AK, Singh A, Pandey M (2000) Inhibition of respiration, ethylene synthesis and cell wall softening enzyme activity in tomato fruit during ripening by ethanol. *Advances in Horticultural Science* **14**, 176-181

Tikunov YM, Khrustaleva LI, Karlov GI (2003) Application of ISSR markers in the genus *Lycopersicon*. *Euphytica* **131**, 71-80

Toor RK, Savage GP (2005) Antioxidant activity in different fractions of tomatoes. *Food Research International* **38**, 487-494

Toor RK, Savage GP (2006) Changes in major antioxidant components of tomatoes during post-harvest storage. *Food Chemistry* **99**, 724-727

Toor RK, Savage GP, Lister CE (2006) Seasonal variations in the antioxidant composition of greenhouse grown tomatoes. *Journal of Food Composition and Analysis* **19**, 1-10

Truco MJ, Randal LB, Bloom AJ, St. Clair DA (2000) Detection of QTLs associated with shoot wilting and root ammonium uptake under chilling temperatures in an interspecific backcross population from *Lycopersicon esculentum* X *L. hirsutum*. *Theoretical and Applied Genetics* **101**, 1082-1092

van der Knaap E, Lippman ZB, Tanksley S (2002) Extremely elongated tomato fruit controlled by four quantitative trait loci with epistatic interactions. *Theoretical and Applied Genetics* **104**, 241-247

van der Knaap E, Tanksley S (2001) Identification and characterization of a novel locus controlling early fruit development in tomato. *Theoretical and Applied Genetics* **103**, 353-358

van der Knaap E, Tanksley S (2003) The making of a bell pepper-shaped tomato fruit: identification of loci controlling fruit morphology in Yellow Stuffer tomato. *Theoretical and Applied Genetics* **107**, 139-147

van Dijk C, Boeriu C, Peter F, Stolle-Smits T, Tijskens LMM (2006a) The firmness of stored tomatoes (cv. Tradiro). 1. Kinetic and near infrared models to describe firmness and moisture loss. *Journal of Food Engineering* **77**, 575-584

van Dijk C, Boeriu C, Stolle-Smits T, Tijskens LMM (2006b) The firmness of stored tomatoes (cv. Tradiro). 2. Kinetic and Near Infrared models to describe pectin degrading enzymes and firmness loss. *Journal of Food Engineering* **77**, 585-593

van Eck J, Kirk DD, Walmsley AM (2006) Tomato (*Lycopersicum esculentum*). *Methods in Molecular Biology (Clifton NJ)* **343**, 459-473

van Ieperen W (1996) Effects of different day and night salinity levels on vegetative growth, yield and quality of tomato. *Journal of Horticultural Science* **71**, 99-111

Venema JH, Eekhof M, van Hasselt PR (2000) Analysis of low-temperature tolerance of a tomato (*Lycopersicon esculentum*) cybrid with chloroplasts from a more chilling-tolerant *L. hirsutum* accession. *Annals of Botany* **85**, 799-807

Walker DJ, Cerda A, Martinez V (2000) The effects of sodium chloride on ion transport in potassium-deficient tomato. *Journal of Plant Physiology* **157**, 195-200

Wang CY (2006) Reducing chilling injury and maintaining quality of horticultural crops with natural products and their derivatives. *Acta Horticulturae* **712 (I)**, 285-290

Wang YH, Garvin DF, Kochian LV (2002) Rapid induction of regulatory and transporter genes in response to phosphorus, potassium, and iron deficiencies in tomato roots. Evidence for cross talk and root/rhizosphere-mediated signals. *Plant Physiology* **130**, 1361-1370

Watkins CB (2006) The use of 1-methylcyclopropene (1-MCP) on fruits and vegetables. *Biotechnology Advances* **24**, 389-409

Wills RBH, Ku VVV (2002) Use of 1-MCP to extend the time to ripen of green tomatoes and postharvest life of ripe tomatoes. *Postharvest Biology and Technology* **26**, 85-90

Willumsen J, Petersen KK, Kaack K (1996) Yield and blossom-end rot of tomato as affected by salinity and cation activity ratios in the root zone. *Journal of Horticultural Science* **71**, 81-98

Wold A-B, Rosenfeld HJ, Baugerød H, Blomhoff R (2004) The effect of fertilization on antioxidant activity and chemical composition of tomato cultivars (*Lycopersicon esculentum* Mill.). *European Journal of Horticultural Science* **69**, 167-174

Xu WF, Shi WM (2006) Expression profiling of the 14-3-3 gene family in response to salt stress and potassium and iron deficiencies in young tomato (*Solanum lycopersicum*) roots: Analysis by real-time RT-PCR. *Annals of Botany* **98**, 965-974

Yamazaki H, Kikuchi S, Hoshina T, Kimura T (2000) Calcium uptake and resistance to bacterial wilt of mutually grafted tomato seedlings. *Soil Science and Plant Nutrition* **46**, 529-534

Yilmaz E, Scott JW, Shewfelt RL (2002) Effects of harvesting maturity and off-plant ripening on the activities of lipoxygenase, hydroperoxide lyase, and alcohol dehydrogenase enzymes in fresh tomato. *Journal of Food Biochemistry* **26**, 443-457

Yuan YX, Zhang J, Wang DW, Ling HQ (2005) AtbHLH29 of *Arabidopsis thaliana* is a functional ortholog of tomato FER involved in controlling iron acquisition in strategy I plants. *Cell Research* **15**, 613-621

Zhang Y, Li H, Ouyang B, Lu Y, Ye Z (2006) Chemical-induced autoexcision of selectable markers in elite tomato plants transformed with a gene conferring resistance to lepidopteran insects. *Biotechnoogy Letters* **28**, 1247-1253

Zhang Y, Stommel JR (2001) Development of SCAR and CAPS markers linked to the *Beta* gene in tomato. *Crop Science* **41**, 1602-1608

Zhu H, Wu T, Zhang Z (2006) Inheritance analysis and identification of SSR markers linked to late blight resistant gene in tomato. *Agricultural Sciences in China* **5**, 517-521

Zhu HL, Zhu BZ, Fu DQ, Xie YH, Hao YL, Luo YB (2005) Role of ethylene in the biosynthetic pathways of aroma volatiles in ripening fruit. *Russian Journal of Plant Physiology* **52**, 691-695