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Greenhouse Tomato Fruit Cuticle Cracking

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I. INTRODUCTION

Research has been directed toward improving the internal and external quality of tomato fruit produced in greenhouses (Dorais et al. 2001a). One of the major problems encountered by greenhouse tomato growers is fruit cuticle cracking (CC), also called russeting, hair cracking, swell cracking, shrink cracking, rain check, crazing, and cuticle blotch. In contrast to concentric and radial fruit cracking where large (one or more cm long by a few mm wide) and deep (a few mm) cracks occur in circles around the stem scar (Fig. 5.1) or radiating from the stem scar (Fig. 5.2), CC are very fine hair-like cracks (0.1 to 2 mm in length) limited to the cuticle and first layers of cells of the epidermis that develop in concentric circles around the stem scar (Fig. 5.3A) or are oriented in all directions on the sides and bottom of the tomato, giving a net-like appearance to the surface of the fruit (Fig. 5.3B). Cuticle cracking downgrades the quality of tomato because it causes poor appearance (roughened skin and

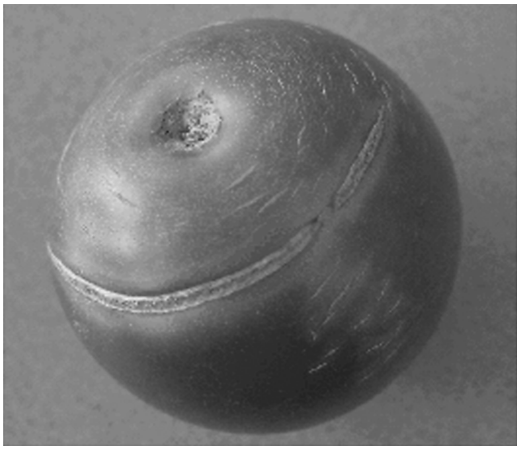

Fig. 5.1. Circular cracking of greenhouse tomato fruit.

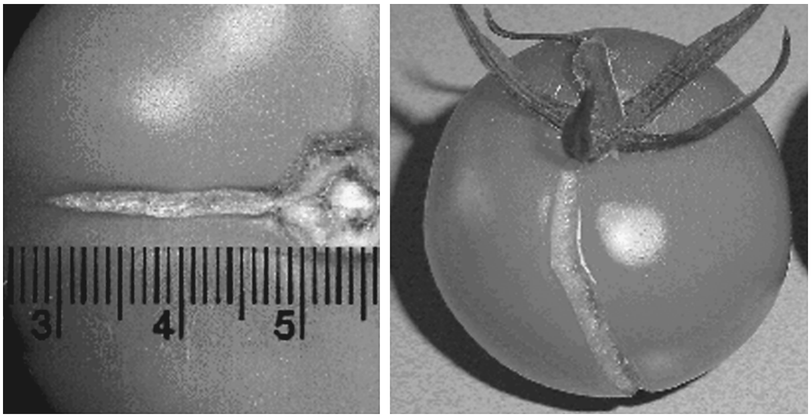

Fig. 5.2. Radial cracking of greenhouse tomato fruit.

cork tissue) and reduces shelf life (Hayman 1987), while concentric and radial fruit cracking immediately renders the fruit unmarketable for fresh consumption. Since the information on CC of greenhouse tomato fruit is limited, we occasionally refer to literature on concentric and radial cracking in field-grown tomato (fruit cracking), and CC in greenhouse sweet pepper.

The appearance of tomato CC occurs in the last phase of fruit growth, 42–49 days after anthesis (DAA) (Bakker 1988; Ehret et al. 1993). In field-grown tomato, initiation of CC was noted on 2% of the affected fruit at

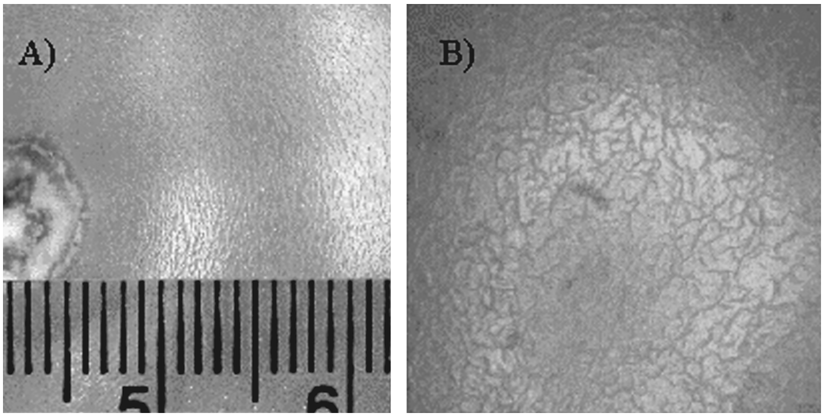

Fig. 5.3. Concentric cuticle cracking (CC) on the shoulder (A), and multidirectional CC (net-like appearance) on the side (B) of a greenhouse tomato fruit.

the immature-green, 61% on mature-green, 27% on breaker, and 10% on red stages (Emmons and Scott 1997). Severity of CC is generally correlated to the length of time between crack initiation and fruit harvest (Bakker 1988; Ehret et al. 1993; Demers et al. 2001a). In fruit with severe CC (over 40% of fruit surface affected), cuticular cracks were initiated 6 to 7 days earlier than in fruit with light CC. Fruit most severely affected by CC (over 80% of fruit surface affected) had a longer total growth period and took more time to reach the harvest stage (pink stage) (Bakker 1988). Fruit left on the plant after the turning stage is more susceptible to CC (Peet 1992).

CC is common in greenhouse tomato production, where the percentage of harvested fruit affected can vary from 10% to 95% of total fruit (Bakker 1988; Demers et al. 2001a). Over the course of the year, incidence and severity of CC is highest during the summer months and usually low in spring and fall (Demers et al. 2000; Khosla et al. 2000). CC is a problem in many crops, including sweet pepper (Aloni et al. 1998; Aloni et al. 1999; Moreshet et al. 1999), apple (Faust and Shear 1972), pear (Borys and Bustamante-Oranegui 1990), grape (Considine 1982), and sweet cherry (Andersen and Richardson 1982; Belmans and Keulemans 1996).

The relationships between cultivars, greenhouse environment, cultural practices and CC are complex in tomato, and recent research has been focused on solving this problem (Chrétien et al. 2000; Demers et al. 2000; Demers et al. 2001a,b; Dorais et al. 2000, 2001c,e; Estergaard et al. 2001; Jobin-Lawler et al. 2002; Simard 2002). This paper presents fruit characteristics related to the development of CC, genetic aspects of fruit resistance to CC, and greenhouse climatic and cultural factors involved in its development. We conclude this review by identifying several prospects for future research.

II. FRUIT CHARACTERISTICS RELATED TO THE DEVELOPMENT OF CUTICLE CRACKING

Between species and cultivars, differences in susceptibility to fruit cracking and CC have been associated with fruit cuticle, epidermis and pericarp, fruit shape and size, fruit growth rate, fruit water status, and sugar content (Hankinson and Rao 1979; Koske et al. 1980; Bakker 1988; Den Outer and van Veenendaal 1987; Ehret et al. 1993; Wacquant 1995; Emmons and Scott 1997, 1998a; Demers et al. 2001a; Guichard et al. 2001).

A. Fruit Anatomy

Tomato fruit are composed of flesh (pericarp walls and skin) and pulp (placenta and locular tissue including seeds) (Ho and Hewitt 1986). The skin (epicarp or exocarp) is formed by the cuticle, which is highly integrated to the cell wall of the epidermis (Ho and Hewitt 1986; Emmons and Scott 1998a). CC in tomato fruit is initiated over the cell junctions, where the cuticle is formed of nonreticulate (amorphous) material. Above the epidermal cell wall, where the cuticle is formed of reticulate material deposited in layers, few cracks are initiated (Emmons and Scott 1998a). The cell junction region, because of its amorphous and noncontaining cellulose cuticle, might be less resistant to pressure as the fruit expands.

Genotypic differences in composition, skin anatomy, and cell morphology are related to tomato fruit cracking. Indeed, the proportion of trihydroxy C_{18} cutin monomers decreases during fruit development, which results in a slight reduction in the hydroxylation and intraesterification of the cutin matrix (Holloway and Baker 1970; Baker et al. 1982). The hydroxyl and ester links in the cutin matrix are important for the structural integrity of the cuticle. Other changes in the cuticle composition (increased triterpenols and flavonoids, decreased long chain hydrocarbons) occur during fruit development (Baker et al. 1982), and may also affect cuticle structural integrity, and consequently the CC susceptibility of tomato fruit. Sensitive cultivars had a deeper cutin penetration (3rd layer of epidermal cells) than less-resistant cultivars where cutin only penetrated to 2nd layer (Hankinson and Rao 1979), and had flatter epidermal cells or larger hypodermal cells (Cotner et al. 1969; Hankinson and Rao 1979). The crack resistance of the sticky peel (*pe*) mutant is associated with highly elastic skin (Ho and Hewitt 1986). Both high tensile strength and extensibility of the skin (elasticity), which vary during fruit development (they are very high during the immature stages of the tomato fruit and then decrease rapidly between mature-green to early pink stages), are important characteristics of tomato resistance to fruit cracking (Voisey et al. 1970; Kamimura et al. 1972; Hankinson and Rao 1979). Cuticle cracking-resistant genotypes such as ‘Fla. 7497’, ‘Freshmarket 9’, and ‘Campbell 28’ had combined thicker epidermal and cuticle layers (10.38–11.37 µm) than susceptible genotypes such as ‘Fla. 7181’ and ‘Suncoast’ (6.45–7.76 µm) (Emmons and Scott 1998a). Thicker cell walls, however, reduce the extensibility of the epidermis and increase fruit cracking and CC as reported by several authors (Den Outer and van Veenendaal 1987; Wacquant 1995; Guichard et al. 2001), and could explain why CC are initiated over the cell junctions. However, correlation between CC resistance and skin elasticity is not often made, although this physiological disorder occurs at the beginning of the last phase of fruit growth, which corresponds to the decrease of skin elasticity, increase of cell wall degrading enzyme activity (pectinases), and changes in the composition of the cuticle.

B. Fruit Growth Rate

Growth of tomato fruit, from the fertilized ovary to a red ripe, takes from 49 to 70 days according to cultivar, fruit position on the cluster, climatic conditions, and cultural practices. Fruit growth can be divided into three phases. The first phase is characterized by a slow fruit growth (10% of the final weight) for 14–21 days, and very active cellular division. The second phase (for 21–35 days) is one of rapid growth due to cell enlargement, and most of the fruit weight is accumulated by the end of this mature-green stage. By 20–25 days after anthesis (DAA), the rate of growth per day increases to a maximum (0.35 g dw d^{-1}), and then declines. The third phase is characterized by slow growth and intense metabolic changes due to maturation. The cessation of assimilate import occurs about 10 days after the first change of color (Ho and Hewitt 1986). During the day, fruit growth rate increased from morning until midday, then decreased until the end of the day, and remained low through the night (Pearce et al. 1993a,b; Guichard et al. 2001).

Cuticular cracking initiation occurs after the time (20–25 DAA) when fruit absolute growth rates reach maximum values, and could not be related to an excessive stretching of the cuticle resulting from a high fruit growth rate. Indeed, the relative growth rates of tomato fruit with and without CC were similar at the time when cuticular cracks are initiated, supporting that fruit growth rate, at the moment cracks occur, is unrelated to the incidence of CC (Bakker 1988; Ehret et al. 1993). Moreover, no correlation between the severity of CC and the fruit relative growth rate at the time cracking was initiated (44 DAA) or at earlier dates (14 and 28 DAA) was found (Ehret et al. 1993). Variations of tomato fruit growth rate during the day (Pearce et al. 1993a,b; Guichard et al. 2001) resulting from changes in the plant water status (Section II.D) and air temperature (Section IV.B) may contribute significantly to CC.

C. Fruit Size and Shape

According to the theoretical model of Considine and Brown (1981) on the distribution of forces on the fruit surface, stress on the containing membrane increases as the radius of the spheroid increases. Hence, the skin of large fruit should be subjected to a greater stress than the skin of small fruit, and therefore should be more likely to crack. Indeed, the incidence and severity of tomato fruit CC were positively correlated to fruit size (Koske et al. 1980; Emmons and Scott 1998a); larger fruit was more frequently affected by CC than smaller fruit (Demers et al. 2001a). However, Ehret et al. (1993) found that decreasing the fruit load on the plant through fruit pruning increased both the size and amount of CC of the fruit, but suggested that the two factors changed independently. That is, increased size did not necessarily cause the increased CC (Ehret et al. 1993; Emmons and Scott 1998a; Demers et al. 2001a).

In a spheroid object, stress on the containing membrane also increases as the shape of the spheroid deviates from a perfect sphere toward an oblate or prolate spheroid (Considine and Brown 1981). Greenhouse tomato fruit generally have an oblate shape: 70–80% of fruit have a height (fruit diameter from the calyx to stylar end) to width (horizontal diameter) ratio between 0.75–0.85, resulting in a larger stress at the polar regions. The calyx itself also increases the stress force on the skin (Considine and Brown 1981). The presence of CC around the stem scar and on the side and bottom of spherical tomato fruit cultivars (Section I) supports this model. However, conflicting results are reported in the literature (few cultivars tested) and no clear relationship between tomato fruit shape and CC has been shown (Emmons and Scott 1998a). We also found no direct correlation between fruit shape and tomato CC (data not published).

D. Fruit Water Status

In plants, water movement is controlled by a water potential gradient, that is, water moves from regions of high to low water potential. Fruit growth is closely linked to water movement to the fruit, which is positively correlated with changes in the stem water potential (Johnson et al. 1992; Pearce et al. 1993a,b; Leonardi et al. 2000; Guichard et al. 2001). In tomato fruit, 85% to 90% of water is imported via the phloem (Ho et al. 1987), together with assimilates (Bertin et al. 2000). Fruit shrinkage, which is associated with water flux out of the fruit, can occur after the night to day transition and is related to a temporary water stress associated with increased water demand as plant transpiration increases rapidly after illumination (Pearce et al. 1993a,b). Fruit shrinkage is also observed at midday under conditions that caused high plant transpiration—high solar radiation and low relative humidity (Leonardi et al. 2000), and could have a major impact on CC of tomato as variations in tension forces on the fruit skin is associated with changes in fruit turgor pressure (Ehret et al. 1993; Guichard et al. 2001). Consequently, early morning and the end of afternoon are the most likely moments of the day for initiation of CC (Wacquant 1995; Guichard et al. 2001). In sweet pepper, a daily cycle of fruit shrinkage and expansion resulted in severe CC (Aloni et al. 1999; Moreshet et al. 1999).

Water flux through the pedicel could also be involved in tomato fruit CC. The abscission zone in jointed pedicels prevented organic compounds (e.g., sugars) and water from entering the fruit (McCollum and Skok 1960). In fruit with a jointless pedicel (no abscission zone), water movement in and out of the fruit would not be restricted, thus possibly producing larger variations in the fruit water status, which could result in increased incidence of CC in the jointless pedicel fruit. Indeed, Emmons and Scott (1998a) observed for one segregating population that fruit with a jointless pedicel had a higher incidence of CC than fruit with jointed pedicel.

E. Assimilate Supply to Fruit

Several studies suggest that an increase in assimilate supply to tomato fruit is related to the development of CC. For instance, low fruit load on the plant resulted in an increase in tomato CC (Bakker 1988; Demers et al. 2001a) and percentage of fruit dry weight (Ehret et al. 1993). Under low fruit load or high light levels more assimilates are available for each individual fruit (Ehret et al. 1993; Demers et al. 2000; Khosla et al. 2000; Demers et al. 2001a). Increased assimilate supply to fruit may influence CC through its impact on water flux to the fruit (Guichard et al. 2001). Since water moves from regions of low to high concentration, higher sugar content in the fruit increases the movement of water from the stem and leaves into the fruit. The increased water intake by the fruit would result in a higher fruit turgor pressure, and thus increase the stress applied on the skin and increase the risk of CC. Indeed, when assimilate import to the fruit is eliminated but not the water movement through the xylem (girdled fruit), fruit cracking was eliminated (Peet and Willits 1995).

III. GENETIC ASPECTS OF FRUIT RESISTANCE TO CUTICLE CRACKING

Differences in susceptibility to CC or fruit cracking among various tomato cultivars have clearly been established in the past (Cotner et al. 1969; Voisey et al. 1970; Hankinson and Rao 1979; Davies and Hobson

1981; Cortés et al. 1983; Abbott et al. 1986; Ho and Hewitt 1986; Den Outer and van Veenendaal 1987; Wacquant 1995; Emmons and Scott 1998a). Many genes may be involved in the process of fruit cracking, and each type of cracking may be controlled by specific genes (Cuartero et al. 1981), making it difficult in selecting for resistant cultivars (Peet 1992). As a consequence, very few cultivars resistant to radial cracking (Peet and Willits 1995) and CC are currently available for greenhouse production. Less-susceptible cultivars currently available are of Dutch origin and were developed for growing conditions characterized by low light intensities such as those prevailing in northern Europe. Under conditions conducive to more rapid growth, these cultivars are very susceptible to CC and fruit cracking. Generally, 'Rapsodie', 'Trust', 'Quest', 'Clarion', 'Baronie', and 'Romance', which are frequently used by commercial growers, are susceptible to CC, while 'Rz 74/56' is slightly less sensitive to CC and 'Tradiro' is moderately resistant.

In studies on CC-resistant and sensitive genotypes of tomato, Emmons and Scott (1998a,b) observed that epicarp thickness was an important fruit characteristic that significantly affected genotype resistance to CC, while fruit shape and pedicel type (*jointed* vs. *jointless*) were of minor importance. Development of greenhouse tomato cultivars resistant to CC should also be done in accordance with other criteria such as resistance to diseases, yield, plant vigor, fruit type, fruit flavor, and fruit shelf life (Dorais et al. 2001a).

IV. CLIMATIC FACTORS RELATED TO THE DEVELOPMENT OF CUTICLE CRACKING

The incidence of tomato fruit CC varies through the growing season, suggesting the involvement of climatic factors (Ehret et al. 1993; Demers et al. 2000; Khosla et al. 2000; Demers et al. 2001a). Light, temperature, relative humidity, and CO_2 may affect CC development by their influence on fruit anatomy, growth, and turgor pressure.

A. Light

Cuticle cracking of greenhouse tomato fruit progressively increases as the natural light level increases in spring and summer (Demers et al. 2000; Khosla et al. 2000), and decreases with the decline in light level during the fall season (Ehret et al. 1993). However, no direct relationship between light level and CC of greenhouse tomato has been shown (Estergaard et al. 2001; Ehret et al. 2002; Simard 2002). In field tomato, a positive relationship between light level and CC was reported (Frazier and

Bowers 1947), but no direct relationship has been shown. Although decreased fruit cracking was measured when field tomato plants or fruits were shaded with muslin (Brown and Price 1934; Frazier and Bowers 1947), a decrease in the assimilate supply to the fruit could have explained this reduction. In contrast to sweet pepper (Moreshet et al. 1999) and apple (Faust and Shear 1972), the direct effect of light on tomato skin structure and CC has not been studied.

B. Temperature

Increasing CC with light level could be related to an increase in air and fruit temperature, as exposure of tomato fruit to direct sunlight increased fruit temperature (Cockshull et al. 1992). Corey and Tan (1990) suggested that with increasing fruit temperature, increasing gas pressure inside the fruit could cause the fruit to expand in volume, thus stretching the skin of the fruit. However, gas pressures inside the fruit are very low (Almeida and Huber 2001) and possible variations are unlikely to cause volume changes that can be related to fruit cracking and CC. Temperature is the most important climatic factor influencing sink strength and consequently photoassimilate partitioning between plant organs. Thus, an increase in fruit temperature could indirectly increase CC by an increase of assimilate supply to the fruit (Walker and Ho 1977) and an increase of the fruit growth rate (Pearce et al. 1993a,b). Recently, Simard (2002) observed under Quebec (Canada, 46–47° N, 71° W) conditions that CC was positively and linearly correlated with the averages of the day (optimal for minimizing CC at 20–21°C), night (optimal for minimizing CC at 18°C), and daily (24-hr) temperatures (optimal for minimizing CC at 19°C), as well as with the average of the day/night temperature differential (optimal for minimizing CC at <6°C). Similarly, it was shown that a daily temperature average between 19.25 to 20.25°C is optimal for minimizing CC of greenhouse tomato under British Columbia (Canada, 45°28 N, 73°45 W) conditions (Estergaard et al. 2001; Ehret et al. 2002). For lower daily temperature (average of 17°C), no difference in CC was noted when plants were grown under low day/high night, high day/low night or constant temperature regimes (Schilstra-van Veelen and Bakker 1985). Contrary to tomato, low night temperature resulted in increased CC in greenhouse sweet pepper due to a lower leaf transpiration rate and increased water flow to the fruit (Aloni et al. 1998; Moreshet et al. 1999).

C. Relative Humidity

Relative humidity (RH) indirectly affects the development of CC through its influence on plant transpiration, and consequently fruit water status.

High RH decreases leaf transpiration, which might result in increased fruit water supply and turgor pressure. Under such conditions, a greater stress would be applied to the fruit skin, which would increase the likelihood of the development of CC. This effect of high RH on CC would be more pronounced if the high RH occurred at night when leaf transpiration is already reduced. In a recent study of tomato CC in relation to many climatic and cultural conditions, Estergaard et al. (2001) found that CC was negatively correlated with vapor pressure deficit (VPD) during the night and positively correlated with VPD during the day, while Simard (2002) observed that tomato CC was negatively correlated with 24-hr average VPD. Similarly, tomato CC and fruit cracking were observed more frequently at low VPD (Bertin et al. 2000). For close RH intervals (low RH of 70%; high RH of 85%), however, occurrence and severity of tomato fruit CC was similar under high day/low night and low day/high night RH regimes (Demers et al. 2001a). Similarly, Schilstra-van Veelen and Bakker (1985) noted no significant difference in tomato fruit CC when plants were grown under either low day/high night (24-hr RH average of 81%), high day/low night (24-hr RH average of 82%), continuous low (78%) and continuous high (87%) RH regimes. Since the effect of RH on tomato CC is likely through its influence on the plant water status, it is possible that factors such as temperature, light and irrigation, which can also influence the plant water status, may affect the plant response to RH treatments and partly explained different results reported in the literature. On the other hand, clear interaction between RH and plant fruit load on fruit cracking has been observed by Bertin et al. (2000).

The use of misting for increasing RH during the summer increases the incidence of CC and fruit cracking (Bertin et al. 2000; Leonardi et al. 2000). This is due to a better plant water status, a lower plant transpiration, and an increase in the water and carbon fluxes entering the fruit (Guichard 1999).

D. CO_2 Enrichment

Enrichment of the atmosphere with CO_2 is common practice in greenhouse tomato production to increase photosynthesis, plant growth, fruit set, fruit size, and the number of fruit produced (Frydrych 1984; Yelle et al. 1987; Yelle et al. 1990). The lower leaf to fruit ratio resulting from higher number of fruit under high CO_2 concentration could explain the lower CC generally observed (Section V.A). Estergaard et al. (2001) suggested that, in British Columbia (Canada), the CO_2 level of the greenhouse atmosphere should be maintained between 785 and 950 μmol L^{-1} for minimizing CC of tomato. A similar finding was previously reported under 600–1500 μmol L^{-1} (Kretchman and Bauerle 1971).

V. CULTURAL FACTORS RELATED TO THE DEVELOPMENT OF CUTICLE CRACKING

A. Plant Balance

To insure long-term productivity, commercial greenhouse tomato growers adjust the balance between vegetative and reproductive growth by routinely pruning leaves and fruits to maintain plant vigor. While removal of older leaves had no significant effect on tomato CC (Ehret et al. 1993), a positive relationship between the number of leaves on the plant and tomato fruit CC has been found (Estergaard et al. 2001). For beefsteak tomato ‘Rhapsodie’, low leaf number (13–15 leaves, 42–46 cm long) should be kept on the plant to minimize CC (Estergaard et al. 2001). Increasing the leaf:fruit ratio by fruit pruning (Bakker 1988; Ehret et al. 1993; Bertin et al. 2000; Demers et al. 2001a) favors CC and tomato fruit cracking (Guichard et al. 2001), while decreasing the leaf:fruit ratio by deleafing decreases CC (Demers et al. 2001a). Fruit pruning had a much stronger effect on CC than leaf pruning (Demers et al. 2001a), and could be disastrous in terms of external appearance (CC) when used to promote individual fruit size under high VPD in summer (Bertin et al. 2000). Similarly, Ehret et al. (1993) observed increased CC in fruits from plants subjected to severe fruit pruning compared to deleafed and normally pruned plants. These results could be explained by changes in the source/sink balance of the plant leading to an increase in the supply of assimilates and water toward the fruit (Guichard et al. 2001). When comparing fruit of the same size but from the different leaf:fruit ratio treatments, both Ehret et al. (1993) and Demers et al. (2001a) noted that CC occurred more frequently and was more severe in treatments with high leaf:fruit ratio. Estergaard et al. (2001) found that higher average weekly yield (2.0–2.7 kg m^{-2} per week) related to lower levels of greenhouse tomato CC, and observed no significant differences in CC severities between truss positions. In order to minimize CC in beefsteak tomatoes in Canada, more fruits per truss are advised to be kept in summer than in spring and fall (Demers et al. 2001a). For example, under South Eastern Canadian growing conditions (42°02 N, 82°54 W), clusters of beefsteak tomato ‘Trust’ and ‘Rapsodie’ should be pruned to 4 fruit during spring (March until May) and fall (September until December), and to 5 fruit during the summer (June until August) to minimize CC (Demers et al. 2001a).

B. Irrigation

In modern greenhouse vegetable production, plants are grown in soil-less media. Fertilization is generally accomplished by adding soluble fertilizers in the irrigation water, and the resulting nutrient solution is distributed to plants using a drip irrigation system. The one exception is the nutrient film technique (NFT), in which roots grow in a continuously circulating shallow stream (film) of nutrient solution. The daily amount of nutrient solution and frequency of irrigation strongly influence CC and fruit cracking (Abbott et al. 1985; Abbott et al. 1986; Peet 1992; McAvoy 1995; Peet and Willits 1995; Chrétien et al. 2000). A larger supply of water (at constant number of irrigations) increases the average water potential in the root environment, which probably increased fruit turgor pressure and consequently caused CC and fruit cracking (Peet and Willits, 1995). Abbott et al. (1986) observed a reduction in the incidence of greenhouse tomato fruit cracking when the daily irrigation frequency was changed from 1 to 4 waterings per day, while total daily irrigation quantity remained the same. It has been shown that a sudden increase in media water content reduces the elasticity of the tomato cuticle (Kamimura et al. 1972). Infrequent irrigation probably results in alternation of episodes of low growth rate or even water efflux from the fruit and turgor loss (around midday) during periods of drought, and episodes of sudden high water flux entering the fruit immediately after irrigations. This may cause excessive turgor pressures resulting in CC as well as changes in epidermis and cuticle elasticity, causing changes in sensitivity for CC (Kamimura et al. 1972; Guichard et al. 2001). To reduce fruit cracking, Peet and Willits (1995) suggest that the amount of water provided to plants should be based on the amount of water the plants are using at the time. Results from a radiation-based water management study showed that the percentage of cracked fruit (CC and fruit cracking) did not increase when irrigation frequency (100 ml plant^{-1} per irrigation) was increased from 612 to 468 KJ. m^{-2} of solar radiation received (Chrétien et al. 2000). Drastic effects of inadequate watering (frequency and volume) on fruit cracking have been reported for field tomato (Brown and Price 1934; Frazier 1934; Frazier and Bowers 1947; Emmons and Scott 1997).

C. Mineral Nutrition

Since the development of tomato CC is related to variations in tension forces on the fruit surface caused by various climatic and cultural factors during the period when the epidermis loses its elasticity, mineral nutrients associated with the stability, elasticity, and flexibility of the cell wall are important in the prevention of tomato CC and fruit cracking (Wilson 1957; Gill and Nandpuri 1970; Simon 1978; Jobin-Lawler et al. 2002). Inside the cell, calcium linked to pectic acids of the middle lamellae is responsible for maintaining cell wall and tissue rigidity (Marschner 1995). Calcium pectate is also involved in cell wall plasticity and elongation (Yamauchi et al. 1986). In periods of rapid plant growth (for example, under high irradiance), an accelerated cellular enlargement and fruit development require an additional supply of nutrients such as calcium. Due to the immobility of Ca in the phloem, Ca in the leaves will not be remobilized to the fruit and Ca supply to the fruit is restricted to the xylem water that accounts for less than 15% of total water import by a fruit (Ho et al. 1987). Therefore, Ca distribution to fruit is less than 2% of total calcium content (Ehret and Ho 1986b; Ho 1999). In addition, Yamauchi et al. (1986) showed that boron plays an important role in calcium metabolism of the cell wall. A boron deficiency in tomato plants can decrease the calcium concentration associated with pectic compounds. Consequently, boron has a stabilizing effect on calcium complexes of the middle lamella and is thus essential to the maintenance of the structure of the cell wall (Clarkson and Hanson 1980). Early works showed that boron and calcium sprayed individually or in combination had a highly significant effect in reducing tomato fruit cracking (Wilson 1957; Gill and Nandpuri 1970). Recently, it has been shown that weekly or bi-monthly cluster calcium and boron spraying (6.6 g L^{-1} $CaCl_2$ + 3g L^{-1} borax) on 40- to 60-day-old fruit reduced significantly the proportion (11%–15%) and the severity (47%–66%) of fruits with CC and increased the proportion of fruits of Class 1 (Dorais et al. 2000; Dorais et al. 2001c,e; Jobin-Lawler et al. 2002). Boron concentration in those fruits was two times higher than control fruits (water spraying), which is beneficial for human health (Hunt and Stoecker 1996). They also observed that the commercial spray ramp spraying at low concentration (0.38 g L^{-1} Borax + 6.66 g L^{-1} $CaCl_2$ on fruit and leaves) reduced the occurrence and severity of CC by 25% and 50%, respectively, compared to the water control treatment, without visual boron phytotoxicity or yield and fruit size reduction. Under warmer growing conditions (higher radiation, temperature, and RH), however, Demers et al. (2001b) observed that similar calcium and boron concentration treatments produced slight necrosis spots (phytotoxicity) on the apex of the sepals.

Increasing the calcium level in the nutrient solution by 1.25- to 1.50-fold (238 to 371 ppm Ca) of the normal calcium concentration (144 to 238 ppm Ca) resulted in a decrease (5%, $P < 0.10$) of the incidence of CC of greenhouse tomato fruit (Demers et al. 2001b), while Schilstra-van Veelen and Bakker (1985) observed no significant decrease in tomato fruit CC when the calcium concentration of the nutrient solution fed to the plants was increased by 1.6-fold. Increasing the calcium level in the nutrient solution is a practice that should be used carefully, since its effect on CC is little and may compete with other nutrients, such as potassium, and decrease other quality fruit attributes (Dorais et al.

2001a). Peet and Willits (1995) observed in their irrigation experiments that the number of fruits with blossom-end rot (BER), also caused by local Ca deficiency in the fruits, was inversely proportional to the number of cracked fruits. They attributed this to over-stimulation of water and concomitant Ca transport toward fruits, which reduces the incidence of BER, but increases the incidence of fruit cracking by an increase in turgor.

High N, P, and Cl levels in the nutrient solution can interact negatively (N) or positively (P and Cl) (De Kreij et al. 1992; De Kreij 1996) with Ca uptake in tomato (Van der Boon 1973; Bar-Tal and Pressman 1996) or have an effect on cell growth (Eggert and Mitchell 1967; Faust and Shear 1972). However, recently it was observed that N (100 to 309 ppm), P (minimum 20 to 72 ppm), and Cl (30 to 200 ppm) levels in the nutrient solution had no influence on the incidence and severity of tomato CC (Demers et al. 2001b).

D. Electrical Conductivity

Adjusting the electrical conductivity (EC) of the nutrient solution allows greenhouse growers to modify water availability to the plant (lower water potential), which will reduce the water flow into the fruit and therefore the rate of fruit expansion (Johnson et al. 1992). Under high ECs, tomato fruit generally have a smaller size (Ehret and Ho 1986a,b; Adams 1991; Pearce et al. 1993b; Hao et al. 1998; Dorais et al. 2001b), thicker and more resistant cuticle, a lower turgor pressure (Verkerke and Schols 1992), and a lower susceptibility to CC and fruit cracking (Sonneveld and Van der Burg 1991; Chrétien et al. 2000; Hao et al. 2000). However, fruit strength (sink activity) and the quantity of photoassimilates imported by the fruit are not affected by a moderate-high EC normally found in greenhouse hydroponic culture, and by a reduction in water absorption (Ehret and Ho 1986a; Ho 1996a,b). Increasing the EC by 1.3-fold of the control EC (2.6–4.6 compared to 2.0–3.5 mS cm^{-1}) for a greenhouse tomato spring crop reduced the incidence of fruit with CC and fruit cracking by 68% (Chrétien et al. 2000). Similarly, Hao et al. (2000) found that an EC of 3.82 mS cm^{-1} compared to 2.54 mS cm^{-1} decreased the incidence of tomato CC. For similar ECs (3.5 vs. 2.5 mS cm^{-1}), Schilstra-van Veelen and Bakker (1985) observed no significant effect, which could be explained by different growing conditions and cultivars (Cortés et al. 1983; Abbott et al. 1985, 1986). For greenhouse tomato plant grown in a split root system and irrigated with different EC values (0.75 to 5.0 mS cm^{-1}), high EC tended to decrease the CC index from 0.44 to 0.28 (0, unaffected, to 3, heavily affected fruit) (Sonneveld and Voogt 1990). Using a neural network model, Estergaard et al. (2001) found a significant effect of EC on CC of beefsteak-type tomato and recommend a range value of 3.90 and 4.35 mS cm^{-1} for minimizing greenhouse tomato fruit CC under their growing conditions. The relationship between EC levels and tomato CC could also be influenced by climatic factors such as CO_2 concentration. For example, a high supply of photoassimilate to the fruit under CO_2 enrichment associated with a high uptake of water under low EC increased the fruit susceptibility to fruit cracking.

Sudden dramatic changes to root zone EC during the day due to climatic variations can have a negative effect on plant water status and consequently on tomato fruit quality such as CC (Dorais et al. 2001b). However, studies on the influence of a diurnal-EC-variation strategy supplying a low EC feed solution during the active plant transpiration period and a high EC solution for the remaining part of the day on the occurrence of CC have not been conclusive (Adams and Ho 1989; Niedziela et al. 1993; Hao et al. 2000; Dorais et al. 2001d). Indeed, no difference in tomato fruit CC of plants fed with a nutrient solution with a varying EC (1.5 to 2.7 mS cm^{-1} during midday, 3.0 to 4.0 mS cm^{-1} for the remaining of the day) and plants fed with a solution with a constant daily EC (1.8 to 3.5 mS cm^{-1} according to the solar radiation) was found (Dorais et al. 2001d). For a similar daily EC average of 3.82 mS cm^{-1}, no difference was also observed in the incidence of fruit CC between tomato plants receiving a nutrient solution with a low EC in morning and noon and high EC in afternoon and night, and in plants fed with a constant EC nutrient solution (Hao et al. 2000). In comparable experiments with fluctuating EC levels, Van Ieperen (1996) observed a larger average fruit size and reduced incidence of blossom-end rot in fruits from plants grown at low EC during the day and high EC during the night compared to the constant average EC or opposite fluctuating EC treatment. He did not report effects on fruit cracking or CC.

VI. CONCLUSION

Synergistic and antagonistic effects of genetic, climatic, and cultural factors occur and influence greenhouse tomato CC. We conclude that a high fruit load should be kept on the plant according to an adequate plant vigor to minimize CC and insure long-term yield. Cuticle cracking may be considerably decreased by spraying a boron/calcium mix on the fruit or the crop, but this practice requires more labor. High temperatures, large day/night temperature differential, and high relative humidity are conditions propitious to the development of CC, and should therefore be avoided. Direct exposure of the fruit to solar radiation may also promote CC. Large variations in fruit water status should be avoided by coordinating the supply of water (frequency and volume, EC), nutrient, and photoassimilates with the stage of shoot and root development and fruit load.

Newly developed cultivars, satisfying the criteria of consumers and producers, should also be CC resistant. Future research should investigate the effects of relative humidity, temperature, mineral nutrition, and irrigation practices on the tomato fruit characteristics and fruit water status in relation with the development of CC. This knowledge is essential to the development of predictive models for tomato fruit CC. In addition, reducing CC can be achieved by developing appropriate and reliable irrigation management systems for different substrates based on the monitoring of moisture (TDR) and EC directly in the media and plant water and nutrient uptake (Dorais et al. 2001b). Better automated monitoring of greenhouse crops (Ehret et al. 2001) and water and nutrient supplies (Heinen 2001; Kläring 2001) would increase fruit quality by reducing fruit CC.

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