Physiological Disorders in Tomato Fruit Development

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Abstract

Physiological disorders are abnormalities in fruit color or appearance that are abiotic in origin. These abnormalities are often confused with damage from pathogens or insects (biotic damage). Physiological disorders are distinguished from deficiencies of a single nutrient, and physical, chemical or herbicide injury. Causes of physiological disorders include genetic susceptibility, environmental factors, watering practices, nutrition, and cultural practices such as pruning and training. For most physiological disorders, a number of factors are involved, and there is almost always a genetic component. This complex interplay of factors is poorly understood for most disorders, and in some cases contradictory results have been reported. There are also a number of different names for many disorders. Although there are many interactions, for the purposes of this discussion, physiological disorders are divided into groups: nutrient imbalances, especially between potassium and nitrogen or magnesium (blotchy ripening, greywall); calcium amount or movement into the fruit (gold fleck or speck, blossom-end rot); temperature extremes (catfacing, boat fruit, rough fruit, puffiness, sunscald); genetic predisposition (green or yellow shoulder) and watering (cracking, russeting, rain check, shoulder check). Secondary effect of pathogens or insects (ghost spot from Botrytis, dimpling from thrips, uneven ripening from silverleaf whiteflies, patterning as a result of tomato spotted wilt or pepino mosaic virus) can also be considered physiological disorders, but are not reviewed here since the cause is biotic.

INTRODUCTION

The disorders discussed below have both genetic and environmental components, and in many cases the exact cause of the disorder is not well understood or involves a complex of factors. Thus, although the discussion is divided into separate categories in almost all cases more than one factor or category is involved. Physiological disorders covered in this review have a characteristic set of symptoms whose origin cannot be attributed solely to a biological agent or to a single environmental or cultural factor. The following discussion does not include descriptions of nutrient deficiencies, air pollution damage, herbicide injury or chilling injury. Secondary effects of pathogens or insects (ghost spot from Botrytis, dimpling from thrips, uneven ripening from silverleaf whiteflies, patterning as a result of tomato spotted wilt or other virus) can also be considered physiological disorders, but are not reviewed here since the cause is biotic.

For many physiological disorders, little in-depth research has been done and the cause is poorly understood both in terms of why cultivars differ in susceptibility and why certain environments or cultural practices predispose plants to the disorder. Physiological disorders have been reviewed by Kinet and Peet (1997), Dorais and Papadopoulos (2001), Dorais (2001), Gruda (2005), Peet (2005), and Savaas et al. (2008).

NUTRIENT IMBALANCES

Blotchy Ripening Complex

Of all the physiological disorders of tomato, the ripening disorders (blotchy ripening, greywall and internal browning) are the least understood. There is disagreement over whether ripening disorders are physiological, biotic or genetic in origin and whether symptoms represent distinct disorders or different manifestations of the same disorder. Similar fruit symptoms appear on plants infected with certain viruses, but in this case leaves will normally also show symptoms (Savvas et al., 2008). Dorais et al. (2001) reported an increase in uneven fruit coloring/blotchy ripening under low light. Fruit deficient in potassium are more susceptible to blotchy ripening, grey wall, and may lack good fruit coloration. Plants growing under optimal conditions and carrying high fruit loads can take up to 140-230 mg potassium per day from the nutrient solution. In contrast, only 80-110 mg of nitrogen and 22-35 mg phosphorus per plant per day are taken up (Morgan, 2006). Thus maintaining high potassium in the fruit is particularly challenging (Morgan, 2006). All that can be said to generalize about ripening disorders is: 1) cultivars differ in susceptibility; 2) the incidence increases when potassium is low and decreases when potassium is raised; 3) affected areas of the fruit eventually show signs of tissue necrosis, usually involving the vascular system; and 4) affected areas are usually lower in soluble solids and titratable acidity, decreasing fruit quality. Usually fruit with ripening disorders are unmarketable.

CALCIUM-RELATED DISORDERS

Blossom-End Rot (BER)

1. Description. At the anatomical level, the earliest symptoms are areas of white or brown locular tissue. Symptoms next appear in the fruit placenta in the case of internal blossom-end rot or in the blossom-end pericarp in the case of external blossom-end rot (Adams and Ho, 1992). Externally, the disorder begins as a small, water-soaked spot at or near the blossom scar of green tomatoes. As the spot enlarges, the affected tissue dries out and turns light to dark brown, gradually developing into a well-defined, sunken, leathery spot. Internal BER, consisting of black necrotic tissues in the parenchyma around the young seeds and the distal placental tissues (Adams and Ho, 1992) often develops in the same fruit.

2. Causes. Interactions between daily irradiance, air temperature, water availability, salinity, nutrient ratios in the rhizosphere, root temperature air humidity and xylem tissue development in the fruit all contribute to BER incidence (Dorais and Papadopoulos, 2001). Although BER shows up in distal fruit tissue, and a gradient in fruit calcium concentration has been shown (Adams and Ho, 1992), Dorais and Papadopoulos (2001) cited evidence that calcium content and cation distribution within the fruit is not directly related to BER.

Ho et al. (1993) reported a positive relationship between BER incidence and the product of the average daily solar radiation integral and temperature during the period of rapid fruit growth. They separated high light and high temperature effects from each other in a series of greenhouse experiments in which the effects of raising temperatures by 2°C were compared to those of shading to reduce light. Added heating was found to increase BER incidence to a much greater extent than added sunlight, presumably because high temperatures increase the rate of fruit expansion more than does extra light. A rapid rate of fruit enlargement (Ho et al., 1993) would increase the demand for calcium in plasmalemma synthesis because of the higher rate of cellular enlargement. This may explain the observation of DeKock et al. (1982a) that thinning tomatoes to 1 or 2 fruit per truss increases the size of the fruit at first but subsequent trusses were severely affected by blossom-end rot. Dorais and Papadopoulos (2001) summarize the work of Ho and co-workers by concluding that lack of coordination between accelerated cell enlargement, due to high import of assimilates, is generally linked to fruit susceptibility to BER when

at the same time poor development of xylem within the fruit reduces the supply of calcium.

The incidence of BER also increases in saline conditions. Salinity decreased both total calcium uptake and the calcium content of the fruit (Adams and Ho, 1993). Salinity reduced calcium uptake mainly by restricting water uptake. Raising the salinity by adding major nutrients such as Mg and K rather than NaCl, increased BER even more (Adams and Ho, 1993), presumably because of competition of these cations with calcium. Similarly, providing nitrogen in the ammonium, as opposed to the nitrate form has been associated with higher BER levels (DeKock et al., 1982b). Xylem development inside the fruit was also restricted by salinity (Belda and Ho, 1993), decreasing the fruit's ability to transport calcium to the distal end. Since high salinity increases such fruit quality parameters as fruit dry matter content, sugar content, acidity and shelf life, it is sometimes increased in soilless culture, despite lower fruit production and the risk of BER. Nederhoff (1999) found that increasing EC (8 mS cm^{-1}) at night but normal levels (2 mS cm^{-1}) during the day showed some potential for improving tomato fruit quality with minimum loss of production. However, BER was not reduced in this treatment, although Van Ieperen (1996) had previous noted a reduction of BER when EC was low during the day and high at night.

Recent work summarized by Dorais and Papadopoulos (2001) has suggested that fruit quality can be increased but BER avoided by careful control of ratios of the various cations. High leaf, but not mature fruit, K:Ca ratios are correlated with high BER. High fruit concentrations of organic acids increase BER susceptibility, as does ion activity ratios (mol L^{-1}) of K and the total of calcium and magnesium, and between magnesium and calcium in the root zone. Maintaining ion activity ratios of 0.1 and 0.2-0.4, respectively for these two ratios should allow the use of high salinity without BER development. When the ratio of calcium is low relative to either potassium or magnesium, plants are susceptible to BER because of the increased concentration of organic acids in the fruit. These high concentrations reduce uptake and availability of calcium.

3. Control. BER is now relatively well understood, but control is still not always achievable in practice. The following general guidelines should be helpful however. As with all physiological disorders, cultivars differ in susceptibility, so alternative cultivars should be considered if problems arise. Second, the water supply must be conducive to uptake, i.e., not too saline, flooded, dry or otherwise restricted. Salinity should be reduced if it rises above 4-5 mS cm^{-1} in hot weather (Adams, 1999). Third, water must go to the fruit, as opposed to the leaves, which means avoiding daytime high temperatures and low humidity. Misting or fogging inside the greenhouse should reduce BER incidence. Finally, the rootzone calcium supply must be adequate and concentrations of competing cations should not be excessive. Potassium and magnesium in the nutrient solution at levels above about 400 and 80 mg L^{-1}, respectively, may reduce plant calcium uptake. Sodium concentrations above 500 mg L^{-1} will also decrease calcium uptake and increase BER (Adams, 1999). In their recent review, Dorais and Papadopoulos (2001) also suggest avoiding high (>26°C) root temperatures and low oxygen concentration, deleafing to avoid excessive canopy transpiration, shading, roof sprinkling, greenhouse fogging, keeping a proper fruit: leaf ratio, and spraying young expanding fruit with a 0.5-0.65% calcium chloride solution. Fruit are most susceptible to BER when there is a rapid visible size increase and particular care should be exercised during this period.

Goldspot, Goldspeck

1. Description. Gold specks or flecks are often observed around the calyx and shoulders of mature fruit, particularly in summer. In green fruit, the specks are white and less abundant. These specks decrease the attractiveness of the fruit and significantly shorten its shelf life (Janse, 1988). Cells with the characteristic gold appearance were identified by Den Outer and van Veenendaal (1988) as containing a granular mass of tiny calcium salt crystals, probably calcium oxalate.

2. Causes. These specks are considered to be symptoms of excess calcium in the fruit. De

Kreij et al. (1992) found that under conditions of high air humidity and high Ca/K ratios, more calcium was transported into the fruit and the incidence of gold speck increased. Increasing the P level increased also increased calcium uptake rate and increased speckling. As summarized in Ho et al. (1999), the level of goldspot was decreased by increasing NO_3 or reducing Cl, NH_4, K or EC in the feed, presumably because these reduced the uptake of calcium.

As temperatures increase during the growing season, the incidence of goldspot also increases, particularly when average temperatures were higher than usual. Since the amount of calcium in the fruit did not increase, high temperatures may increase the proportions of calcium deposited in the fruit as oxalate (Ho et al., 1999).

3. Control. The disorder can be reduced by avoiding susceptible cultivars (Ilker et al., 1977). Cultivars resistant to BER tend to be more susceptible to goldspot (Ho et al., 1999). Sonneveld and Voogt (1990) found that raising the electrical conductivity of the nutrient solution reduced gold speck incidence, as did increasing the K/Ca ratio and increasing Mg. Presumably in all 3 cases, the mechanism was prevention of excess Calcium uptake. Ho et al. (1999) recommended: lowering Ca in the hydroponic solution from 200 to 120 mg L^{-1}; lowering fruit temperature; applying low but sufficient N (180 mg L^{-1}); sufficient, but not too high K (400 mg L^{-1}); and avoiding P depletion (>5 mg L^{-1}). He reported that by following these guidelines, goldspot incidence was reduced while avoiding BER.

TEMPERATURE EXTREMES AND LIGHT

Rough Fruit or Catfacing

Terminology is variable on these disorders. Fruit with a long scar at the blossom end are often described as ‘catfaced’ and may be called ‘boat-shaped’. Misshapen and unusually large fruits, which sometimes appear as many joined fruit growing together, and sometimes have open locules are described as ‘rough’. Both disorders develop under protracted low temperatures (Gruda, 2005). In the field, air temperatures of 17/10°C for a week are sufficient to induce abnormal flower development (Saito and Ito, 1971). Low temperature treatments during the sensitive period increase the number of locules in the fruit (Wien and Turner, 1994). Foliar sprays of GA_3 also induce the disorder and increase locule number (Wien and Zhang, 1991). The time of greatest sensitivity for an individual flower is well before anthesis. Barten et al. (1992) reported greatest sensitivity 19 to 26 days before anthesis for fruit grown at relatively high temperatures after cold treatment (32/18 or 29/18°C). When fruit were grown at lower temperatures after cold treatment, flowers were most sensitive earlier (26-35 days before anthesis) (Wien and Turner, 1994). In both cases, the target stage is probably the floral transition, the different timings resulting from the different temperatures prevailing after this transition. Dorais et al. (2001) reported that misshapen, swollen, and hollow fruit can occur at low light and non-optimal temperatures, especially in fruit between the 2^{nd} to 5^{th} cluster.

Sunscald, Sunburn or Sunscorch

1. Description. Green fruits exposed to direct sunlight ripen unevenly so that yellow patches appear on the side of the tomato fruit when it ripens. Symptoms are most likely to appear at the mature-green to breaker stages of development (Retig and Kedar, 1967). The texture of affected areas is leathery and firmer than the surrounding tissues. Yellow areas sometimes have a mottled appearance, and the surface is depressed (Hobson et al., 1977). Depending on the temperature and degree of injury, the area can become white and sunken. The tissue underneath the injured area is whitish and the cells partially collapsed, reducing the normal thickness of the locular walls (Hobson et al., 1977). This disorder can resemble green shoulder and high light is reported to increase the incidence of both sunscald and green shoulder. However, green shoulder is generally thought to have a stronger genetic component than sunscald.

2. Causes. Sunscald is caused by fruit pericarp temperatures exceeding 40°C

(Rabinowitch et al., 1974). In bright sunlight, surface temperatures may be more than 10°C higher than the air temperature (Venter, 1970). The increase in temperature is greatest in large, red fruit (Venter, 1970). The degree of injury to the fruit depends on irradiance, spectral quality, temperature and treatment duration (Adegoroye and Joliffe, 1983). If temperatures are over 30°C, but under 40°C, the area stays yellow (Grierson and Kader, 1986) because temperatures above 30°C prevent lycopene formation, while production of carotene continues up to 40°C (Tomes, 1963). High light first degrades the pigment, but then at high light intensities, cellular death and tissue collapse follows, turning the skin papery thin (Kays, 1999; Prohens et al., 2004).

Rabinowitch and Sklan (1980) correlated changes in superoxide dismutase levels in the fruit with sensitivity to sunscald. They suggested that the heightened sensitivity to sunscald of fruits which are suddenly exposed to high light and high temperature compared to fruits which develop under high temperature and light was associated with inadequate levels of superoxide dismutase. Conversely, fruit conditioned by high temperature treatment to resist sunscald damage had higher levels of this enzyme (Rabinowitch et al., 1982).

3. Control. Exposure of fruit pericarp to temperatures of 45°C over a 6-hour period, followed by a rest period at a lower temperature conditions fruit to high temperatures and offers some protection against sunscald (Kedar et al., 1975). The protective effect is only temporary, however. The best protection against sunscald is to utilize cultivars with enough foliage to cover the fruit and to provide enough water and pest protection to maintain the foliage. Crops planted at higher densities will also be less susceptible.

GENETIC PREDISPOSITION

Disorders with a genetic component were reviewed by Gruda (2005), Kinet and Peet (1997) and Grimbly (1986). These disorders include: fruit pox, zebra stripe, and zippering. Greenback, persistent green shoulder or yellow shoulder is considered a ripening disorder by Hobson et al. (1977), but primarily affects fruit from genotypes lacking the ‘uniform ripening’ gene (Picha, 1987). It is characterized as intense pigmentation of the pericarp shoulder near the stem (proximal). Like the ripening disorders, however, composition of affected tissue differs (Hobson et al., 1977; Picha, 1987) and environmental factors have been correlated with disorder incidence including high light, temperatures and high relative humidity. However, Smillie et al. (1999) reported that green shoulder increased with shading and suggested it was suppressed at very low and very high photosynthetic photon flux densities. The best control is undoubtedly choosing cultivars with the uniform-ripening gene but in excessive sunlight, some of these cultivars may also develop a proportion of white tissue in the locule walls (Hobson et al., 1977).

IRRIGATION

Fruit Cracking

1. Description. Cracks may occur in circles around the stem scar (concentric cracking) or may radiate from the stem scar (radial cracking). Recently Huang and Snapp (2004a) have reported on ‘shoulder check’, described as a surface roughness concentrated on the fruit shoulder. They reported that the microscopic cracks were oriented parallel to each other, and the cracks penetrated into the epidermis as well as the cuticle.

2. Causes. Fruit cracking is a complicated disorder. In areas where rainfall is common during ripening, problems and losses can be very heavy. Cracked fruit is also susceptible to disease and insect contamination. Environmental and cultural factors associated with the disorder were summarized by Peet (1992) as follows: Fruit cracking occurs when there is a rapid net influx of solutes and especially water into the fruit at the same time ripening or other factors reduce the strength and elasticity of the tomato skin. Increases in fruit temperature raise gas and hydrostatic pressures of the pulp on the skin, resulting in immediate visible cracking in ripe fruit. In green fruit, cracking occurs later in the

ripening process when minute cracks created earlier expand to become visible. High light conditions, especially on unshaded fruit have also been associated with higher rates of fruit cracking. High light intensity raises fruit temperatures, especially on exposed fruit. Under high light conditions, fruit soluble solids and fruit growth rates are higher; both of these factors sometimes are associated with increased cracking.

Kamimura et al. (1972) proposed the following explanation for cracking of tomatoes after rain based on their studies of the effects of soil moisture levels on fruit skin. They showed that high soil moisture lowered the tensile strength of tomato fruit skin. Because of this low tensile strength, the fruit enlarged rapidly and developed many minute cracks. These minute cracks later developed into visible cracks. Under low soil moisture, Kamimura et al. (1972) found that the tensile strength of the skin was greater. As a result, plants grew more slowly and had fewer minute cracks. Changes in soil moisture during fruit growth also affected skin strength. Skin strength increased if soil moisture content decreased. Conversely, skin strength decreased if soil moisture content increased. In fact, changes from low to high soil moisture lowered skin strength compared to continued growth under any moisture regime. Such changes typically occur when drought is relieved by irrigation or rain. Cracking is particularly likely with continued wet weather or overhead irrigation because water enters the fruit through these minute cracks. In the greenhouse, excess watering has been shown to increase the incidence of radial cracking, and there are also a few reports in field tomato crops of increased cracking at higher levels of soil moisture (Peet and Willits, 1995). 'Shoulder check' is also associated with changes in soil moisture status, particularly an abrupt increase (Huang and Snapp, 2004a).

Anatomical characteristics of crack-susceptible cultivars are: 1) large fruit size, 2) low skin tensile strength and/or low skin extensibility at the turning to pink stage of ripeness, 3) thin skin, 4) thin pericarp, 5) shallow cutin penetration, 6) few fruits per plant, and 7) fruit not shaded by foliage (Peet, 1992). Although it has been difficult to breed for cracking resistance per se (Stevens and Rick, 1986) commercial cultivars bred for firm fruit and tough skin in order to decrease handling and shipping losses in field tomato production in North America are often quite resistant to fruit cracking. This is probably because these qualities are components of resistance to cracking. In addition, much of the crop is harvested at the green-mature stage, when it is less susceptible to cracking.

3. Control. Cultural practices which result in uniform and relatively slow fruit growth such as constant, preferably relatively low soil moisture, offer some protection against fruit cracking (Peet, 1992). In field crops, cracking is usually attributed to fluctuations in the water supply. The classic occurrence is when a long period of drought is followed by heavy rain. Cultural practices that reduce diurnal fruit temperature changes also may reduce cracking. In the field, these practices include maintaining vegetative cover. Greenhouse growers should maintain minimal day and night temperature differences and increase temperatures gradually from nighttime to daytime levels. For both field and greenhouse tomato growers, harvesting before the pink stage of ripeness and selection of crack-resistant cultivars probably offer the best protection against cracking. Huang and Snapp (2004b) reported control or at least a reduction in severity with calcium and boron sprays.

Russeting (Cuticle Cracking)

1. Description. 'Russeting' is a disorder of the tomato skin in which minute, hairline cracks, invisible to the naked eye, cover up to 25% of the fruit surface (Bakker, 1988). It is also called rain check, crazing, swell cracking, shrink cracking, hair cracking, and cuticle blotch (Emmons and Scott, 1997). The fruit has a rough feel, and when examined closely the surface appears crazed rather than smooth. It is sometimes described as a poor skin 'finish' and significantly reduces the shelf life of harvested fruit (Hayman, 1987). Cracks appear as fruit approach maturation, six to seven weeks after fruit set and incidence of the disorder was highest early and late in the production season (Bakker,

1988). Cuticle cracking differs from 'shoulder check' in that cuticle cracking is characterized by microscopic cracks running in random directions that do not penetrate into the epidermis.

2. Causes. Conditions conducive to fruit cracking also appear to be conducive to russeting. Current research on the causes of fruit cracking have been summarized by Dorais et al. (2004) and Savvas et al. (2008). A low fruit load relative to leaf area tended to increase russeting, presumably by increasing the fruit growth rate. These conditions would be present at the beginning of harvest because relatively few fruit are present and late because the plants have been topped. Emmons and Scott (1997) did not find an increase in russeting in field-grown tomatoes in Florida by pruning either leaf or fruit, but did find the amount of russeting correlated with the amount of rain during the entire 2-week period before harvest. Fruit damage which resembles russeting can also be caused by insects such as mites and thrips and by sprays. Dorais et al. (2004) reviewed the causes of cuticle cracking. They concluded that tomato cracking increased with the averages of day, night, and 24-h temperatures, as well as the average of the day/night temperature differential. Reports differ on the effects of relative humidity (Savvas et al., 2008).

3. Control. To control russeting in soilless systems, the following practices are suggested: selecting a resistant cultivar; avoiding big fluctuations between day and night temperatures and relative humidities; avoiding large changes in electrical conductivity (EC) of the nutrient solution and maintaining a minimum EC of 3.0 in rockwool slabs; and minimal deleafing (Hayman, 1987). Procedures that stabilize the leaf area to fruit ratio and reduce fruit growth rate are sometimes also suggested. For example, not topping plants or permitting suckers to grow at the top of the canopy should reduce fruit growth rates at the end of the season and may also reduce fruit temperatures. In the field, Emmons and Scott (1997) suggest: staking plants; avoiding direct exposure of the fruit to the sun by protecting foliage from disease and damage during harvest; using resistant cultivars; and harvesting before rains, if possible. Control has also been reported by increasing calcium in the solution and by adjusting the leaf and fruit ratios (Savvas et al., 2008).

Edema (Oedema)

1. Description. This disorder is often mistaken for a bacterial or fungal disease. In its early stages the blister-like swellings on the leaf resemble an undifferentiated callus-type growth. The granulated appearance of the fresh blisters is caused by the splitting of the epidermis, presumably under pressure from within (Grimbly, 1986). This exposes the turgid parenchyma cells. These swollen parenchyma cells eventually erupt. Rupture of these cells over a period of time causes twisting and distortion of the leaves, and produces a necrotic area when the cells dry out.

2. Causes. This disorder is seen in a number of crops besides tomatoes, including cabbage and sweet potatoes. In all cases, it is caused by water provided to the leaves exceeding that used in transpiration for a period of several days. Sagi and Rylski (1978) showed that under high humidity and excess water, the symptoms increased as light intensity decreased, presumably representing the diminishing ability of the plant to transpire.

3. Control. In greenhouses or growth chambers, the disorder can be prevented or remedied. Decreasing watering and promoting transpiration by such measures as increased ventilation, higher temperatures and higher light should be effective. In the field, the disorder only appears when there are long periods of excess water and low transpiration. There is little that can be done in the field, assuming that irrigation has already been stopped, except for trying different cultivars.

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