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Solanaceous Fruits

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CONTENTS

AU: Abbreviations that appear only once have been removed from the list with the spelled out version used in the text.

AU: This abbreviation is used for gibberellic acid and gibberellins in the text. Can one be used for consistency?

List of Abbreviations

ABA	Abscisic acid
BER	Blossom-end rot
CI	Chilling injury
GA	Gibberellic acid
GLK	Golden-like transcription factor
PAs	Polyamines
PPO	Polyphenoloxidase

32.1 Introduction

Many of the myriad of ovaries from the *Solanaceous* species fertilized every year will produce physiologically damaged fruit, out of a predefined and accepted range of normality. Although the quality and marketable yield losses caused by physiological disorders are variable and highly dependent on the interaction between the genotype and the environment, in severe cases they could be dramatic. Some physiological disorders occurring in fruit belonging to the *Solanaceae* family have been extensively studied. This has resulted in a relatively clear identification of their cause/s and mechanism/s and has contributed to establishing the most appropriate prevention and control strategies. In contrast, the biological mechanisms underlying some metabolic dysfunctions are still under investigation. The expression of physiological disorders is, in some cases, complex; different problems could lead to similar manifestations and any given disorder could induce variable symptoms depending on its severity. While some of these alterations are caused by a single factor, they are most often the result of the converging action of several predisposing agents. Some disorders such as blotchy ripening have been difficult to induce experimentally, and their study under controlled conditions is still challenging. Based on their symptoms, *Solanaceous* fruit physiological disorders can be classified as: (i) those disrupting normal growth and altering shape such as catface, zippering, and puffiness; (ii) those causing mechanical failure and compromising integrity such as cracking; (iii) those resulting in tissue collapse, pitting, browning, and necrosis (blossom-end rot [BER], sunscald, and chilling injury [CI]); and (iv) those affecting ripening or seed development (green shoulders, yellow shoulders, blotchy ripening, other surface discolorations, CI, excessive seed number, or hardening and bitterness).

32.2 Catface, Zippering, and Puffiness

Catface is expressed as malformation and the cracking of fruit at the blossom end. Tomatoes showing this disorder usually present deep clefts that may cover the pericarp to varying degrees (Figure 32.1a). Puckered or swollen areas result from different rates of cell growth. Damaged regions usually have corky or necrotic tissues (Peet, 2009). Catface may be caused by any disturbance to flower parts during blossoming and fruit set. It has been frequently associated with unfavorable environmental conditions, such as low temperatures (<15°C for several days) (Gruda, 2005).

Zippering refers to fruit presenting thin vertical superficial scars, providing the appearance of a zipper (Figure 32.1b). It has been related to setting under high relative humidity. Zippering may result from the attachment of the anthers to the ovary in newly formed fruit (Maboko and Du Plooy, 2013). However, other localized damages to the ovaries could induce similar symptoms. Although it can appear in fruit grown under most weather conditions, it tends to be higher early in the season when lower temperatures occur. It may be more prevalent in fruits produced in improperly ventilated greenhouses.

Puffiness is used to refer to fruit usually showing flat or angular sides. Internally, tomato locules may be partially full of gel or even empty and the fruit may be hollow to different degrees depending on the severity of the disorder (Figure 32.1c). Stresses or environmental conditions impairing pollen viability, pollination, fertilization, or seed formation can lead to puffy fruit.

The strategies to reduce catface, zippering, and puffiness include the use of cultivars that are less susceptible. Catface is more prevalent on large-fruited cultivars, such as beefsteaks or heirloom varieties (Frasca et al., 2014). Genotypes with a determinate growth habit have been suggested to be less prone to catface. Growth disorders could be limited by avoiding whenever possible pollination at extreme temperatures (Kawasaki, 2015). Cultural practices that have been associated with zippering, catface, and puffiness include excessive pruning and nitrogen fertilization (Peet, 2009). Their relationship with the disorders has not been fully established, but they are thought to change in whole plant sink to source balance, and likely auxin levels and gradients.

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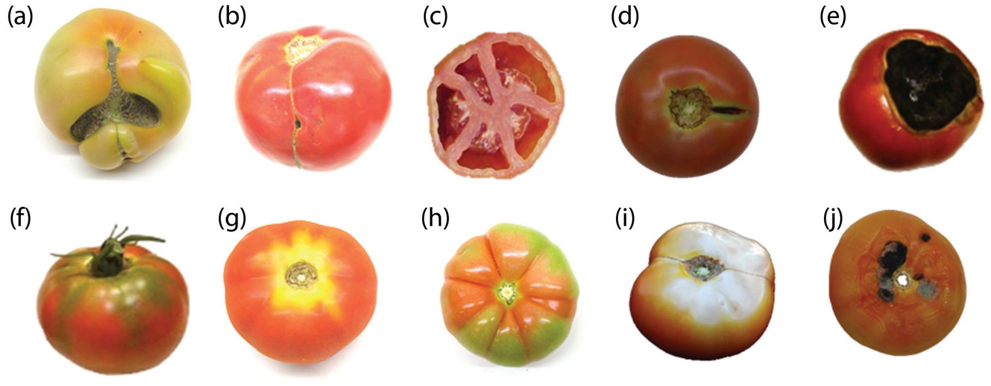

FIGURE 32.1 Physiological disorders in tomato fruit: a. Catface, b. Zippering, c. Puffiness, d. Cracking, e. Blossom-end rot, f. Green shoulders, g. Yellow shoulders, h. Blotchy ripening, i. Sunscald, and j. Chilling injury.

32.3 Cracking

Cracking is the splitting of the fruit epicarp caused by mechanical tissue failure. Internal cell layers could also be affected once the fruit cuticle and epidermis collapse. The disorder has been frequently associated with oscillations in fruit growth rate (Olle and Williams, 2016; Peet, 2009). Cracking usually increases under high temperatures and after rainy periods, when water becomes readily available (Domínguez et al., 2012; Paran and Fallik, 2011). Radial cracking is more common; it starts from the stem scar and progresses toward the blossom end (Figure 32.1D). Instead, concentric cracking develops in circles as a ring or a series of rings around the stem scar (Peet, 2009). Cuticular cracking is characterized by concentric cracks starting on the fruit shoulders (Huang and Snapp, 2004; Lara et al., 2014; Lichter et al., 2002). Cracking may occur at all stages of fruit growth, but the fruits become more susceptible as ripening proceeds, in association with cell wall disassembly and firmness loss.

Varieties differ greatly in their susceptibility to cracking, so selecting tolerant genotypes is one of the most effective practices to reduce the problem (Abdel-Razzak et al., 2016). Avoiding soil moisture fluctuations and plant disequilibrium due to excessive pruning or high nitrogen fertilization would also prevent cracking (Abdel-Razzak et al., 2016). Sun-exposed fruit are more prone to show cracking, so maintaining good foliage cover is also recommended. Treatments with calcium chloride, reinforcing the cell walls, may reduce fruit cracking (Huang and Snapp, 2004; Lichter et al., 2002).

32.4 Blossom-End Rot (BER)

BER symptoms appear first as a water-soaked area at the blossom-end of the fruit. The damaged tissue can expand and evolve into a sunken, black, and dry rot (Figure 32.1e) (Casado-Vela et al., 2005; Savvas et al., 2008) that, in severe cases, may spread and cover extensive areas of the pericarp (Grant, 2016). At the cellular level, disruption of the plasma membrane and tonoplast is observed; the cell wall may acquire a wavy shape and plastids and intercellular compartments may have a swollen appearance (Hocking et al., 2016).

Although the relationship between calcium deficiency and BER has not always been obvious (Saure, 2014), a large number of evidences have shown that this is the main cause. Calcium deficiency would affect cytoskeleton and membrane function, interfere with normal cell signaling, and impede the formation supramolecular association of unesterified pectins within the cell wall (Ho and White, 2005; Madani and Forney, 2015; Ronen, 2013). BER has been frequently reported in tomato and pepper. In eggplants, it can occur as well at the blossom-end of the fruit (Figure 32.2a), though calcium deficiency has also been shown to manifest as an internal fruit rot (Draper and Burrows, 2002).

Any practice affecting the demand of calcium either by the fruits or by other competing organs would impact BER. In tomato, early cultivars as well as genotypes with higher loads or larger fruit will be more susceptible to BER (Olle and Williams, 2016). BER may occur at any time during the growing season, but would be more likely in plants showing active vegetative growth due to excessive nitrogen fertilization or pruning (Draper and Burrows, 2002; Madani and Forney, 2015). The first fruit produced when the plants have been expanding rapidly are usually the most affected (Grant, 2016).

The availability of calcium in the soil can impact on BER incidence and severity. Plants growing in carbonate-rich soils or with a high pH (>7.5) will have lower soluble calcium availability in the rootzone, possibly increasing plant susceptibility to BER. However, studies have also shown that total fruit tissue calcium content is not the main factor determining fruit susceptibility to BER, but calcium distribution at the cellular level. Accordingly, tomato plants overexpressing a high active tonoplast antiporter H^+ / Ca^{2+} that transports calcium into the vacuole were more susceptible to BER than wild-type plants (Tonetto de Freitas et al., 2011). In this study, calcium deficiency in the apoplast was suggested to increase membrane permeability, leading to higher fruit susceptibility to BER. Regardless of that, BER has been in many cases related to the inability of the plant to uptake and/or allocate the

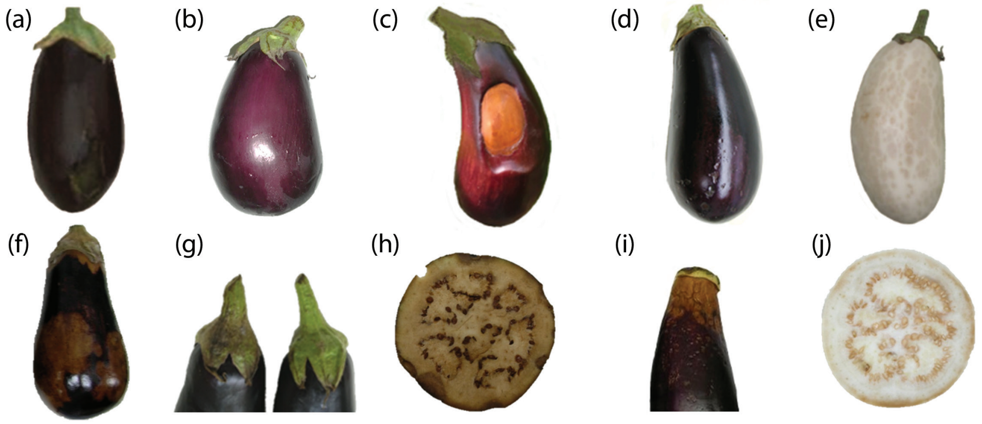

FIGURE 32.2 Physiological disorders in eggplant fruit: a. Blossom-end rot, b. Peel discoloration, c. Sunscald, d. Surface pitting, e. Surface browning, f. Surface scalds, g. Calyx bronzing, h. Pulp and seed browning, i. Pericarp peel under the calyx browning, and j. Excessive seed number and hardening.

required calcium in the fruit or even within the cell rather than to its deficiency in the growing medium. All environmental and cultural factors modulating these two processes would impact BER (Olle and Williams, 2016; Tonetto de Freitas and Mitcham, 2012). Excessive nitrogen fertilization with NH_4^+ salts may reduce Ca^{2+} absorption. Application of growth promoting substances such as gibberellins (GAs) can induce BER. Tonetto de Freitas and Mitcham (2012) reported that weekly treatments with GAs reduced the apoplastic water-soluble calcium and increased membrane permeability and BER incidence in tomato. In line with this, treatments with the GAs biosynthesis inhibitor prohexadione prevented BER even though the plants were growing at very low calcium levels. In order to better understand the hormonal regulation of Ca^{2+} partitioning and allocation in tomato plants, the same authors subjected tomato plants to weekly sprays with abscisic acid (ABA) and evaluated changes in calcium homeostasis (Tonetto de Freitas et al., 2014). The treatments increased Ca^{2+} accumulation in the fruit blossom-end zone, and controlled BER.

As could be inferred from what was previously mentioned, several practices should be considered to prevent and control BER:

- Determine if sufficient soluble calcium is present in the growing medium; if this is not the case, rely on external applications (Rubio et al., 2009).
- Maintain soil pH within the range 6.5–7.5 to minimize calcium immobilization especially as carbonates and phosphates.
- Avoid large fluctuations in soil water content by regular irrigation or mulching.
- Do not conduct strong pruning operations or excessive nitrogen fertilization, which would favor vegetative growth and increase calcium demand from strong sinks such as leaves.
- Modulate plant growth especially if environmental conditions are prone to promote rapid expansion. This can be done by managing nutrient and water availability and, whenever possible, by cooling down greenhouses.
- Growth regulators such as ABA could eventually be considered as well. Foliar applications of ABA could also be used to reduce the incidence of BER. However, it must be considered that once the symptoms are observed, it will be too late.
- The use of calcium sprays could be a useful strategy to prevent and control BER (Coolong et al., 2014). For best results, multiple applications starting early in development will facilitate diffusion into the pericarp. Calcium applications may, in some cases, improve firmness and reduce the incidence of postharvest diseases caused by opportunistic fungal pathogens (Madani and Forney, 2015; Manganaris et al., 2005).

32.5 Irregular Color

Uneven or nonsynchronic ripening in a gradient across the latitudinal axis is a common phenomenon in many fruits (Nguyen et al., 2014). While in many cases the whole fruit will complete the ripening process within a short time frame, sometimes discrete regions of the pericarp may remain unripe as others are ready to eat. Disorders related to failure to ripen usually have small effects on total yield but can reduce marketable yield substantially (Kader, 2002). Given that uniform ripening is an expected trait for most fresh fruit consumers and processors, if commercialized, the fruit would have reduced value. Green shoulders refers to fruit being unripe at the stem end (Figure 32.1f). It may be common in some tomato genotypes, especially when cultivated in highly fertile soils or with high nitrogen levels (Gent, 2007; Smillie et al., 1999). Several wild-type tomatoes display green shoulders due to the presence of a functional golden-like gene (GLK2) involved in chloroplast biogenesis. This transcription factor is expressed in the fruit in a latitudinal gradient, with higher expression in the stem end (Nguyen et al., 2014). Interestingly, in many cultivated genotypes, the GLK gene is mutated resulting in uniform ripening, a trait that was likely selected during tomato fruit domestication (Powell et al., 2012).

In some cases, tomato fruit can show white, yellow, and orange shoulders (Figure 32.1g). These disorders are caused by the subnormal accumulation of lycopene and other carotenoids (Darrigues et al., 2008). Depending on the maturity stage at which it occurs, this may be the result of delayed chloroplast to chromoplast transition, reduced carotenoid biosynthesis, or pigment bleaching. Direct sun exposure increasing fruit temperature and UV radiation interception may, at sub-lethal levels, be sufficient to redirect the transcription machinery to cope with stress, at the expense of normal ripening biosynthetic pathways (Lurie et al., 1996). In tomato, exposure to temperatures as low as 35°C inhibited central ripening enzymes such as 1-ammino cyclopropane 1-carboxylic acid synthase, polygalacturonase, and phytoene synthase, decreasing ethylene synthesis, softening, and lycopene accumulation (Yahía et al., 2007; Yoshida et al., 1984).

In eggplant, surface discoloration may result from reduced anthocyanin biosynthesis, especially if the fruits are growing under low irradiance (Kleinhenz et al., 2003; Landi et al., 2015) (Figure 32.2b). Lighter surface patches could also be observed in some cases of overripe fruit.

Blotchy ripening is characterized by the presence of regions of the fruit, not necessarily on the stem end, that fail to ripen (Figure 32.1h). These areas of the fruit have low concentrations of organic acids, dry matter, total solids, and sugars. Internally, the vasculature may show browning symptoms (Savvas et al., 2008). The symptoms associated with blotchy ripening can be confounded by disease or insect-feeding causes. Ripening inhibition with some similarities has also been reported in tomato fruit by silverleaf whitefly feeding (McCollum et al., 2004) or tobacco mosaic virus infection (Jenkins et al., 1965). The causes of blotchy ripening are not fully understood. Given that blotchy ripening is difficult to induce experimentally, our current understanding is still mainly empirical. Blotchy fruit are common when air temperatures oscillate too much, or are extreme (< 15°C or > 30°C), when light availability is low, and under inadequate potassium nutrition (Peet, 2009). Blotchy ripening is less prevalent in field-grown tomatoes than in greenhouse fruit.

The prevention of green shoulders can be achieved mainly by using cultivars that are mutated for GLK and avoiding heavy nitrogen fertilization. The prevalence of yellow shoulders may instead be reduced mainly by decreasing fruit sun exposure and ensuring proper potassium nutrition. The management of eggplant discoloration should rely on controlling exposure and avoiding the harvest of overripe fruit. No definitive control measures exist to control blotchy ripening. The main recommendations include: avoiding sudden changes in temperature and controlling factors that limit potassium supply (waterlogging, heavy soils, fertilization, high nitrogen applications, and dense canopies) (Savvas et al., 2008). Postharvest failure to ripen and to develop full color and flavor has also been reported as a CI symptom in tomato fruit (Van Der Ploeg and Heuvelink, 2005).

32.6 Sunscald

Sunscald results from the combined damage caused by high temperatures and radiation and consequently normally occurs on the sun-exposed sides of fruit (Conn, 2006). Although all plant organs may be damaged, fruits are particularly sensitive given their low transpiration rate compared to organs with higher surface areas such as leaves. Infrared radiation can rapidly increase fruit temperature and this will compromise normal ripening. The symptoms can start as localized bleached areas due to the degradation of pre-existing pigments or failure to ripen (Figure 32.1i) (Wien, 1997). As the severity increases, the affected area may be blistered. The damages may also evolve to blanched or brown, sunken zones as cell death takes place and tissues collapse, as occurs in eggplant fruit (Figure 32.2c). The fruit position in the canopy is the main factor determining the incidence and severity of sunscald (López-Marín et al., 2011). In general, the disorder is more frequent in fruit produced in open field crops than in greenhouses. Although sunscalds can appear at different developmental stages, ripe fruit seems to be more susceptible. Sun damage could even occur after harvest, if the fruit is not transported rapidly to packinghouse operations and cooled (Mohammed and Brecht, 2003).

Cultivars with a thick canopy usually show low sunscald incidence. Any practice reducing canopy density, such as thinning or pruning, should be carefully conducted to prevent fruit temperatures from reaching values over 35°C (Conn, 2006). Plants growing in poor and non-irrigated soils develop a low-density cover, and will then have highly exposed fruit (Dodds et al., 1997; Rabinowitch et al., 1983; Rosales et al., 2006). Proper fertilization and control of biotic adversities causing defoliation will protect fruit and thus reduce the incidence and severity of sunburns. On a smaller scale, shade cloths could provide some protection. However, for large-scale commercial production, the strategy may not be cost effective (López-Marín et al., 2011). Maximizing greenhouse ventilation may result in some evaporative cooling that would prevent sun damages. After harvest, the recollected fruits must be rapidly transported to the processing or packaging station, or maintained under shade nets to prevent direct solar radiation.

32.7 Chilling Injury

Tomato, pepper, and eggplant are susceptible to CI if stored below 7°C for 1–2 weeks. CI may arrest ripening in tomato. However, the disorder usually induces the formation of light-colored depressed areas. In eggplant, pitting (Figure 32.2d) pulp and seed browning, through the action of PPO family members, and surface scalds are the main symptoms associated with CI (Figure 32.2e) (Shetty et al., 2011). As damages proceed, CI could evolve in eggplant to large dark scalds (Figure 32.2f). Damaged fruit show increases in the production of polyamines (PAs) (Rodriguez et al., 2001) and ethylene (Concellón et al., 2005) and are highly susceptible to decay. Chilling-injured fruit are highly susceptible to *Alternaria* rot, as evidenced by the presence of a black dry mycelium covering the damaged areas (Figure 32.1j). In eggplant, CI can in some cases be accompanied by extensive browning in the calyx and pulp (Figure 32.2g and 32.2h) (Concellón et al., 2012; Zaro et al., 2015b). Seed browning has also been associated with CI in all three species (Figure 32.2h). Farneti et al. (2015) showed that chilling-injured tomatoes also have altered volatile profiles. Chilling damage is thought to result from a solid-to-gel transition of cell membranes that then reduces fluidity and functionality (Wang, 1989). Current views of CI acknowledge that low temperature stress results in widespread alterations of cellular metabolism superseding membrane disruption (Sevillano et al., 2009). As has been shown for other stresses, cell damage has been related to the overproduction of reactive oxygen species such as superoxide anions, hydroxyl radicals, and hydrogen peroxide, overcoming the fruit enzymatic and non-enzymatic antioxidative mechanisms (Aghdam and Bodbodak, 2014).

Different cultivars show variability in their susceptibility to CI. Japanese eggplant varieties are more prone to CI than American genotypes (Concellón, 2003). Interestingly, for the Japanese variety, even within the fruit the zone closer to the stem end is in general more susceptible to CI than the blossom-end (Concellón et al., 2007). The susceptibility to CI is also dependent on the ripening stage. Mature green tomato is more susceptible than red ripe fruit (Boonsiri et al., 2007; Lin et al., 1993). In contrast, Zaro et al. (2014) reported that small eggplants stored at 0°C showed less browning and CI symptoms than fruit at normal commercial maturity. CI is cumulative and may be initiated in the field prior to harvest (Cantwell and Suslow, 2002). Although CI manifestations will be observed under refrigeration, the symptoms develop more markedly once the fruit has been removed from the cold.

The most effective means of preventing CI is to avoid storage at damaging temperatures. Optimal temperatures for storage are 12–15°C for mature green fruit, 10–12°C for light-red fruit and 7–10°C for ripe tomatoes. Eggplant fruit are chilling-sensitive at temperatures below 10°C. As for other fruits, intermittent warming could reduce CI (Liu et al., 2015). However, its implementation under commercial conditions is not very practical (Biswas et al., 2016). Postharvest hot air treatments (35–45°C) and short UV-C exposure have been reported to alleviate CI, though they are not widely used (Andrade Cuvi et al., 2011; Wang et al., 2015). The cold acclimation induced by pre-storage exposure to other mild stresses is thought to be due to the accumulation of heat shock proteins with chaperonin functions (Lurie, 1998) and by the induction of antioxidative defenses (Andrade Cuvi et al., 2011). Some chemical treatments that have been experimentally effective in reducing CI include GAs (Ding et al., 2015), methyl jasmonate (Fan et al., 2016), salicylic acid (Ding et al., 2016), PAs (Serrano et al., 1996), and brassinosteroids (Aghdam and Mohammadkhani, 2014; Gao et al., 2015). 1-methylcyclopropene (1-MCP) delays senescence, maintains quality, and also reduces the browning of eggplant (Massolo et al., 2011). A recent study has tested with success the use of glycine betaine to reduce CI in sweet pepper (Wang et al., 2016).

32.8 Seed-Related Disorders

Excessive seed development is undesirable in fruits harvested at immature stages such as eggplant (Figure 32.2j). Fruits showing high seed number and size will have a lower visual appeal upon cutting and poorer texture during consumption, caused by seed hardening. Fruits showing profuse seed developments are also undesirable, since they show a high tendency to brown (Concellón et al., 2004). Fruit seed number and size are affected by the genotype (Daunay, 2008). In addition, for any given cultivar, they are determined by fruit maturity at harvest as well as by the prevailing environmental conditions during fruit set (Mahmood, 2012). As would be expected, delaying harvest would increase yields, but result in fruit having larger and lignified seeds. For fruit harvested at a similar maturity stage (based on size in eggplants), the number of seeds will differ depending on the period within the production cycle; fruit picked in spring or fall (early and late harvests) will show fewer seeds than eggplants harvested during the summer (Valerga personal communication). This may be caused by reduced fertilization, lower pollen viability, decreased pollinators activity, and/or lower ovule fertility under extreme environmental conditions (Nothmann and Koller, 1975). A smaller seed size is also found in fruit from early or late season harvests (Figure 32.3), which may be likely caused by seasonal variations in the relative fruit and seed growth rates (Valerga et al., 2016).

Fruit seed number content can be reduced by inducing parthenocarpy. This can be done with the use of auxins, GA, or a combination of both (Mahmood, 2012). The development of parthenocarpic cultivars is one of the main goals of eggplant breeding programs (Kikuchi et al., 2008). In addition, biotechnological changes leading to parthenocarpy have also been tested in eggplant (Acciarri et al., 2002; Du et al., 2016).

Bitterness is also a seed-related disorder of eggplant fruit (Cárdenas et al., 2015; Friedman, 2015). Already in the 17th century, reports mentioned it as a cause of eggplant rejection (Daunay and Janick, 2007). It is caused by the presence of the glycolakaloids α-solasonine and α-solamargine,

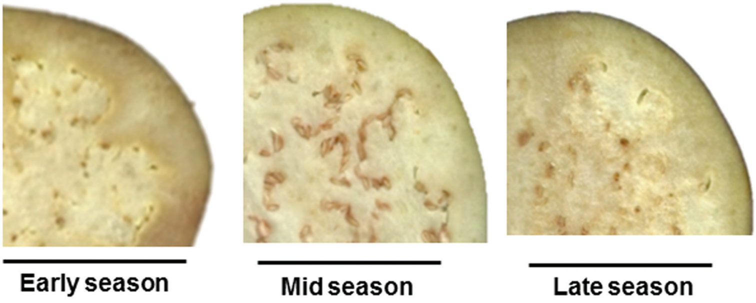

FIGURE 32.3 Seed abundance and size in eggplant fruit harvested at a similar developmental stage but at different moments in the production cycle.

secondary nitrogen-containing compounds with natural defensive roles. Different from potato tubers, these compounds in eggplants are preferentially accumulated in the inner tissues (Milner et al., 2011), particularly in the seeds, where they are present at several-fold higher levels than in the flesh (Aubert et al., 1989). If accumulated at sufficiently high concentrations, glyocalkaloids could be toxic (Friedman, 2015). In a study with 21 eggplant cultivars, Bajaj et al. (1979) reported a range normally below the limit of 200 mg kg^{-1} (62.5 to 205 mg kg^{-1}). Consequently, the main concern related to their presence is that they can impart a bitter taste to the fruit. However, primitive and wild genotypes are usually more bitter than modern genotypes (Wang et al., 2008). Mennella et al. (2010) and Sánchez-Mata et al. (2010), working with wild relative species (*Solanum integrifolium*, *Solanum aethiopicum* and *Solanum sodomaeum*; and *Solanum macrocarpon* L.), found that they could accumulate 5–10-fold higher levels of glycoalkaloids than common eggplant (*Solanum melongena* L.). Consequently, the incorporation of desirable traits by introgression of wild and allied species without increasing bitterness remains challenging (Mennella et al., 2012). An array of developmental, environmental, and processing factors can also affect the level of glycolakaloids in eggplant (Maga, 1994). Mennella et al. (2012) found that glycoalkaloids increase as the fruit develops. Solasonine and solamargine levels were higher in plants subjected to extreme stress conditions. In contrast, Gajewski et al. (2009) found that bitterness was unaffected by postharvest storage conditions. LoScalzo et al. (2016) found that glycoalkaloid levels remained practically unchanged after grilling or boiling.

The main strategies to prevent bitterness include cultivar selection and avoiding, when possible, stress conditions, as well as harvesting early during development. Putting eggplant slices in contact with salt for a few hours followed by a water rinse is a traditional method that has been used to favor glycoalkaloid leakage and reduce bitterness (Zaro et al., 2015a, b).

32.9 Acknowledgements

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