Chapter 7
Fruit Set and Temperature Stress

Yasushi Kawasaki

Abstract In fruit vegetables, inhibition of fruit set by both high and low temperatures decreases the yield. Because one of the main reasons for fruit abortion is a decrease in pollen viability, which is usually caused by suboptimal mean daily temperature, periodic checking of pollen viability may help to detect and prevent fruit abortion. Although observation of pollen grain germination or pollen tube elongation at the base of the style is a reliable way to evaluate pollen viability, staining with acetocarmine is recommended as a fast method in the production field. To improve fruit set under temperature stress, temperature management, heat- and chilling-tolerant cultivars, and parthenocarpy can be used. In greenhouse production, temperature management is the most popular method to improve fruit set. However, heating or cooling incurs high energy costs. Local temperature management offers a low-cost alternative. Fruit set was improved by heating flower trusses of tomato and basal stems of eggplant. Breeding of heat- and chilling-tolerant cultivars is being attempted. To develop chilling-tolerant tomato cultivars, breeders are exploring wild relatives. Parthenocarpy can be achieved by spraying plants with growth regulators, but this involves high labor costs. Therefore, parthenocarpic cultivars are being developed.

Keywords Fertilization • Greenhouse production • Parthenocarpy • Pollen viability • Pollination • Temperature management • Tomato

7.1 Introduction

For production of fruit vegetables influenced strongly by fruit set, maintaining fruit set is essential. Two main factors—assimilate deficiency and suboptimal (higher or lower than optimum) temperatures—inhibit fruit set in cultivated plants.

Fruit abortion caused by assimilate deficiency occurs under high fruit load (Aloni et al. 1996; Bertin 1995) or prolonged low-light conditions (Rylski and Spigelman 1986). Insufficient assimilate translocation to the flowers suppresses fruit set and

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development. Irregular fruit set, known as ‘flushing,’ is a serious problem in sweet pepper production that causes strong fluctuations in market supply and labor demand (Heuvelink and Körner 2001; Marcelis and Baan Hofman-Eijer 1997).

Fruit abortion caused by temperature stress occurs when temperatures are considerably higher or lower than the optimum. Some crops grown in greenhouse (e.g., tomatoes, sweet peppers, cucumbers) are often exposed to suboptimal temperatures because they are grown in various regions and temperature conditions. For example, crops can be exposed to low temperatures in winter in Europe and North America (Osborne and Went 1953; Picken 1984), whereas high temperatures can cause problems in summer in Asia (Abdul-Baki and Stommel 1995; Dane et al. 1991; Nkansah and Ito 1995; Sasaki et al. 2005). If fruit set could be maintained under such temperature stresses, significant fruit yield increases and cost reductions could be expected. Therefore, many studies are now in progress to improve fruit set under suboptimal temperatures.

In this chapter, I overview fruit abortion in vegetable crops affected by temperature stress in the production field, especially in greenhouse production of tomato. I also discuss some approaches to improve fruit set.

7.2 Suboptimal Temperature Stress Affects Fruit Set

Inhibition of fruit set by temperature stress occurs when temperature exceeds the optimal range for a particular crop. Fruit set is affected more by mean daily temperature than by temperature during the day or during the night, or by the day–night temperature differential (Peet et al. 1997). The mean daily temperature range for stable fruit set differs for different crops: 13–25 °C for tomato (Charles and Harris 1972; Osborne and Went 1953; Sato et al. 2000), 16–25 °C for eggplant (Kikuchi et al. 2008; Nothmann and Koller 1975; Passam and Khah 1992; Sun et al. 1990), 18–25 °C for sweet pepper (Cochran 1936; Rylski and Spigelman 1982; Shaked et al. 2004), and 20–30 °C for cucumber and melon (Maestro and Alvarez 1988; Hikosaka et al. 2008). However, these ranges can change with light intensity and cultivar.

7.2.1 High-Temperature Stress

A number of studies investigated the effects of high-temperature stresses on plant productivity. Many focused on the effects of acute, transient, high-temperature treatments (e.g., 40–50 °C for 2–4 h), known as heat shock (Banzet et al. 1998; Neta-Sharir et al. 2005; Nover et al. 1983). Although such studies are important, heat-shock conditions are rarely encountered in the production field, where fruit set is affected by prolonged, moderately high mean daily temperatures (e.g., 25–35 °C for several weeks). Sato et al. (2000) showed that fruit set percentage in tomato was decreased under such moderate heat stress, and suggested that this decrease was related to a reduction in pollen grain release. They also determined that 8 to 13 days before anthesis is the period of the highest sensitivity to heat stress (Fig. 7.1) (Sato et al. 2002). A decrease in pollen grain viability and different composition in carbohydrate content in the androecium were shown (Sato et al. 2006).

Reduction in pollen viability is considered as the main factor preventing fruit set at high temperatures. In *Phaseolus vulgaris* L., this reduction was explained in relationship to the development of anther tissues (Suzuki et al. 2001). At the pollen tetrads stage, heat stress affects the structure and function of the tapetum, playing a crucial role in supplying nutrients to pollen mother cells and regulating release of pollen grain. Tapetum malfunction causes pollen sterility. In tomato, high temperature at the pollen tetrads stage leads to the enlargement of tapetal cells, resulting in pollen sterility (Iwahori 1965). In the field, tomato pollen viability drops drastically when mean daily temperature exceeds 27 °C (Kawasaki et al. 2009).

Fruit set can be suppressed by ovule sterility even if pollen is highly viable (Charles and Harris 1972; El Ahmadi and Stevens 1979). Ovule viability is also reduced by high-temperature stress. It was suggested that ovary development is more tolerant to high-temperature stress than pollen and ovule development, because parthenocarpic fruits induced by plant growth regulators develop under high temperature when normal fruit set is inhibited (Sasaki et al. 2005).

7.2.2 Low-Temperature Stress

Similar to high temperature, low temperature reduces fruit set because of a reduction in pollen viability. In tomato, normal pollen development, pollen germination, and pollen tube growth are suppressed under low-temperature conditions (Charles and Harris 1972; Dempsey 1970). Although no information about structural abnormalities in vegetable crops under low temperature could be found, reduction of pollen viability at low temperature was explained by a structural abnormality of the tapetum in rice (Gothandam et al. 2007). Ovule viability is less affected by low temperature (Charles and Harris 1972). In greenhouse production, low-temperature stress is not considered as great a problem as high-temperature stress, because it can be easily alleviated by heating.

7.2.3 Evaluation of Fruit Set and Pollen Viability

Monitoring pollen viability enables earlier evaluation of fruit set than visual observation (Fernández-Muñoz et al. 1994; Heslop-Harrison et al. 1984). If fruit abortion is predicted early, measures to improve pollen viability can be taken. Assessing pollen viability is also used in breeding for pollen tolerance to suboptimal temperatures (Fernández-Muñoz et al. 1995; Domínguez et al. 2005). Among the methods for testing pollen viability, counting pollen tubes at the base of the style

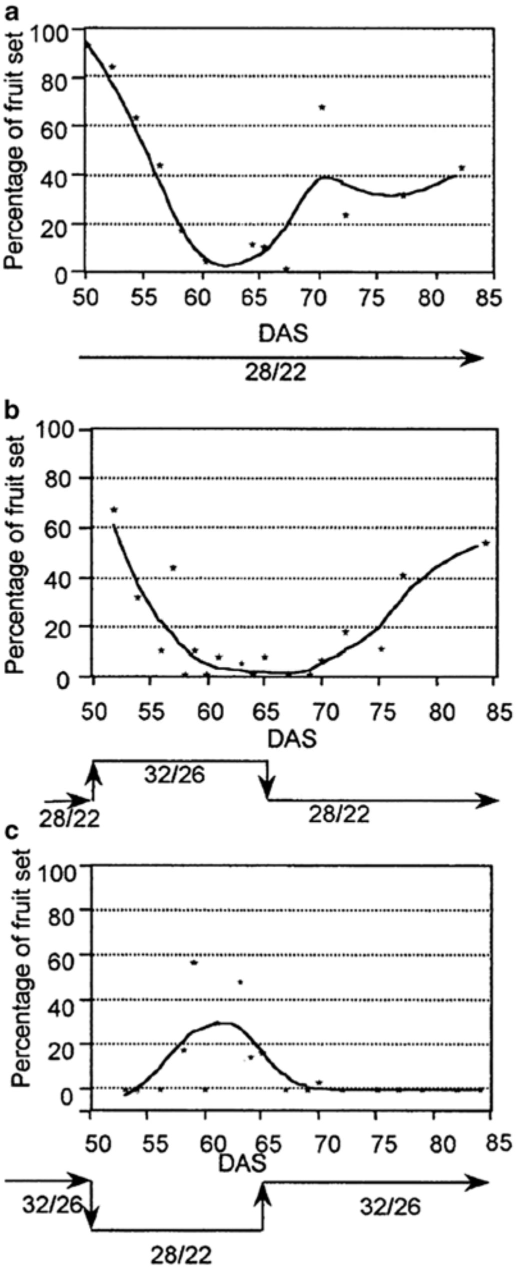

Fig. 7.1 Percentage of fruit set in control (day–night temperature, 28–22 °C) (**a**); 15 days at high temperature (32–26 °C) (**b**); 15 days high-temperature relief treatment (**c**). *DAS*, days after sowing. The decrease of percentage of fruit set in control is assumed to be caused by increasing fruit load. (From Sato et al. 2002, reprinted with permission from the publisher)

after artificial pollination are considered to be most reliable (Abdalla and Verkerk 1970; Charles and Harris 1972; Dempsey 1970). Because this method is laborious, many studies use a faster method: evaluation of pollen grain germination or pollen tube growth in vitro (Charles and Harris 1972; El Ahmadi and Stevens 1979; Sato et al. 2000, 2006). However, its potential ability to predict pollen performance depends heavily on optimization of the germination medium and temperature (Abdul-Baki 1992; Heslop-Harrison et al. 1984). Staining pollen with vital stains (Abdul-Baki 1992; Charles and Harris 1972; Domínguez et al. 2005) readily detects pollen viability and can be used in the production field because only stains and a simple microscope are needed. Fernández-Muñoz et al. (1994) noted that pollen staining, especially with acetocarmine, is the best method for large-scale applications to monitor field production or breeding, whereas counting pollen tubes at the base of the style is most reliable and is best for precise assessment of small samples.

Parthenocarpy is not affected by pollen and ovule viability at fruit set. Therefore, the ability of the ovary to develop has to be assessed to evaluate fruit set (Kikuchi et al. 2008; Sasaki et al. 2005). This procedure requires 2 to 3 weeks after anthesis to obtain results, and there is no alternative method available in the production field. A new method is required for earlier evaluation of parthenocarpic fruit set in the field.

7.2.4 Use of Insect Pollinators

In greenhouse production of fruit vegetables, insect pollinators are often used to reduce the labor of pollination or hormone treatment (Peet and Welles 2005). Honey bees and bumble bees are used as pollinators. The optimal temperature range is 15–30 °C for honey bees and 10–30 °C for bumblebees (Heinrich 1975; Kwon and Saeed 2003), and suboptimal temperatures can affect their activities; in particular, honey bees are sensitive to low temperatures in winter.

7.3 Techniques for Improvement of Fruit Set

In greenhouse production, temperature management by climate control is essential for improvement of fruit set and yield. Another approach is breeding for cultivars that are better adapted to suboptimal temperatures; the availability of such cultivars could considerably reduce costs of temperature management and CO_2 emission (Van der Ploeg and Heuvelink 2005). Parthenocarpy, which is not dependent on pollen viability, is also available as a technique to improve fruit set under unfavorable conditions.

7.3.1 Temperature Management

To alleviate high-temperature stress, ventilation, shading, and cooling are used in greenhouses. Although ventilation and shading are commonly used because of their low cost, they are sometimes insufficient for alleviation of heat stress during summer days in low-latitude regions because they cannot decrease the temperature below that outside, which can be high enough to inhibit fruit set. For cooling, evaporative systems, such as fogging and fan-and-pad, and heat pumps are available and are used by some advanced greenhouse farmers; these can decrease the temperature below that outside. On the other hand, fogging and fan-and-pad can, in principle, only decrease to wet-bulb temperature, and may be ineffective in humid climates (Peet and Welles 2005). Heat pumps are more effective in humid climates and demonstrated improvement of fruit set by night cooling (Willits and Peet 1998). However, both the setup and running costs of heat pumps are higher than those of other cooling systems.

In winter greenhouse production, thermal screens and heating are mainly used to prevent low-temperature stress. Peet and Welles (2005) wrote: ‘Pulling thermal curtains of porous polyester or an aluminum foil fabric over the plants at night reduces heat loss by as much as 20–30 % a year,’ and some lightweight retractable curtains are available not only as thermal curtains but also as shade. Heating systems that use fossil fuels and supply hot water or warm air are most popular among temperature management measures because they are easy to control, although they incur high energy costs. As Van der Ploeg and Heuvelink (2005) observed: ‘With increasing public concern about environmental problems, including CO_2 emissions from fossil fuels, the greenhouse sector will have to improve its energy efficiency.’

To reduce energy costs, a local temperature control technique is being developed (Kawasaki et al. 2010, 2011, 2013). As fruit abortion caused by temperature stress is affected only by the temperature of the flower, fruit set can be maintained so long as flowers are kept at the optimal temperature. In winter production of tomato, supplying warm air around flower trusses from suspended air ducts (Fig. 7.2) improves fruit set in comparison with the absence of general heating (Table 7.1) even though the lower plant parts are not warmed (Kawasaki et al. 2010). Furthermore, this technique reduces fuel consumption by 26 % in comparison with conventional temperature treatment without loss of fruit set and yield (Fig. 7.3) (Kawasaki et al. 2011). In eggplant, fruit set and yield can be maintained when basal stems are heated locally with a reduction of the temperature set-point by 2 °C (Moriyama et al. 2011).

7.3.2 *Breeding for Heat and Chilling Tolerance*

Wide genotypic variation among tomato cultivars in sensitivity of fruit set to high temperature (Firon et al. 2006; Levy et al. 1978; Rudich et al. 1977; Sato et al. 2004) makes breeding for heat-tolerant cultivars feasible. Tomato lines originating from tropical Asia are frequently used as breeding materials (Abdul-Baki and Stommel 1995; Dane et al. 1991; Nkansah and Ito 1995). These lines and cultivars show high photosynthetic performance (Nkansah and Ito 1995) and high sugar content in pollen grains under high-temperature conditions (Firon et al. 2006), which raises pollen viability, fruit set, and yield in comparison with non-heat-tolerant cultivars (Table 7.2). In addition, small-fruited genotypes with many flowers are less affected by heat stress than are larger-fruited cultivars (Dane et al. 1991).

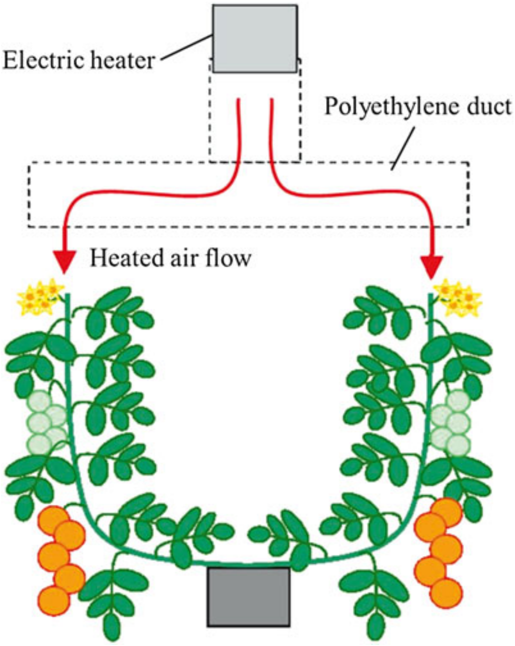

Fig. 7.2 Scheme of local heating that supplies heated air to flower trusses. (From Kawasaki et al. 2010, reprinted with permission from the publisher)

In contrast, the variation in low-temperature responses among current tomato cultivars is limited, which hampers breeding for enough levels of commercial yield at lower temperatures (Maisonneuve et al. 1986; Van der Ploeg and Heuvelink 2005). Therefore, breeders must look for alternative sources of variation in the low-temperature response of tomato. Two wild relatives of the cultivated tomato, *Solanum habrochaites* (*Lycopersicon hirsutum*) and *Solanum pennellii*, show high pollen viability and fruit set (Fernández-Muñoz et al. 1995; Zamir et al. 1981, 1982) and are considered as breeding materials for chilling tolerance.

7.3.3 Parthenocarpy

The defects of fruit set caused by temperature stresses can be mitigated to some extent if parthenocarpic fruits are available, because fruit set depends mostly on both the quality and quantity of pollen, which are not relevant to parthenocarpy. At very high temperatures, however, parthenocarpy is still inhibited (Kikuchi et al. 2008; Sasaki et al. 2005).

In commercial production, parthenocarpic fruits can be induced by plant growth regulators or can be a trait of parthenocarpic cultivars. Spraying flowers with auxins, gibberellic acid, or both can induce parthenocarpy. This technique is used in the commercial production of tomato and eggplant. In tomato, parthenocarpic fruits develop earlier than seeded fruits. In eggplant, parthenocarpic fruits have higher

Table 7.1 Effects of local heating around shoot apex and flower clusters on fruit set in two tomato cultivars

	Local heating (surface temperature of shoot apex)	No. of harvested trusses	No. of flowers	No. of fruits set	Fruit set (%)[a]	Flowering interval (day truss^{-1})[b]
Reiyo	High (13.0 °C)	9.3 A[c]	49.9 A	48.4 A	96.9 A	12.5 A
	Low (11.5 °C)	9.0 AB	48.7 A	46.5 A	95.5 A	13.2 AB
	None (9.6 °C)	8.7 B	53.6 A	47.9 A	89.3 B	13.6 B
Momotaro–Haruka	High (13.0 °C)	10.4 a	56.9 a	50.8 a	89.1 a	11.3 a
	Low (11.5 °C)	10.0 a	55.0 a	41.3 ab	75.1 b	11.7 b
	None (9.6 °C)	9.4 a	56.6 a	34.7 a	61.3 c	12.0 b
ANOVA[d]	Cultivar (C)	*	NS	*	**	**
	Local heating (H)	NS	NS	*	**	**
	C×H	NS	NS	*	**	NS

[a] Arcsine-transformed values were used for statistical analysis

[b] Mean interval between first flower anthesis on each truss

[c] Values within a column and cultivar followed by the same letter are not significantly different at $P < 0.05$ by Tukey's multiple comparison test ($n = 8$)

[d] * and ** indicate significant difference at $P < 0.05$ and 0.01, respectively; *NS* no significant difference at $P < 0.05$

Source: From Kawasaki et al. (2010); reprinted with permission from the publisher and translated from Japanese

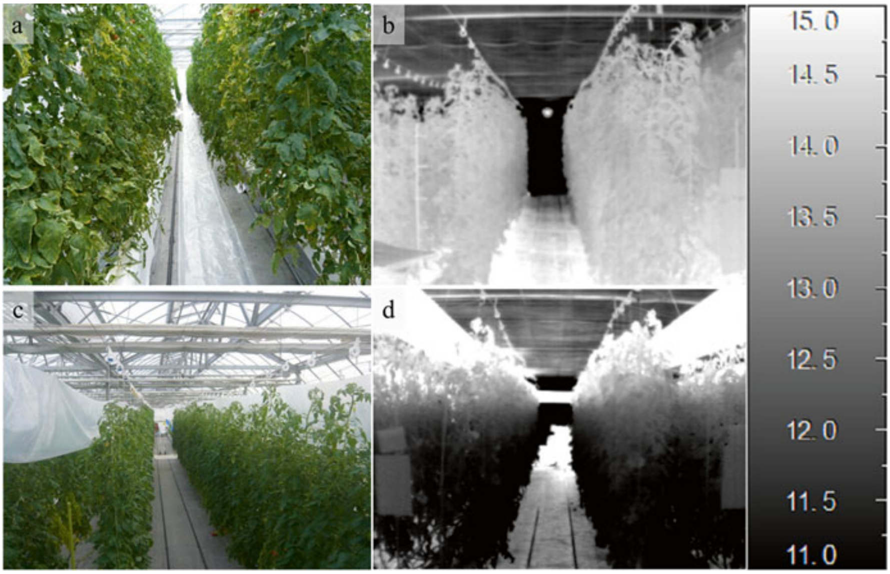

Fig. 7.3 Surface temperature of tomato plants under conventional heating (**a**, **b**) or local heating using air ducts arranged around flower trusses (**c**, **d**). The *gray-scale bar* indicates surface temperature measured with an infrared thermometer at midnight (Kawasaki et al. 2011)

value, because seedlessness prevents browning of fruit fresh upon cutting and lessens the content of saponin and solasonin compounds, which cause a bitter taste (Donzella et al. 2000). In parthenocarpic sweet pepper, yield fluctuation and blossom-end rot are reduced (Heuvelink and Körner 2001). However, spraying is as laborious as hand-pollinating and is difficult to implement in large-scale production.

Parthenocarpic cucumber cultivars are common. Some summer squash cultivars have the parthenocarpic trait (Robinson and Reiners 1999). Breeding for this trait is carried out in tomato (Takisawa et al. 2012; Philouze and Maisonneuve 1978) and eggplant (Kikuchi et al. 2008; Saito et al. 2007).

7.4 Conclusion

In greenhouse production of fruit vegetables, plants are often grown under suboptimal temperatures. High temperatures in summer and low temperatures in winter affect fruit set, especially in year-round production. To mitigate the fruit set defects, knowledge of optimal temperature ranges for particular crops and cultivars is important. Monitoring pollen viability allows fruit set to be predicted and necessary measures to be taken earlier than if fruit set is examined visually.

Maintaining optimum air temperature, which is most important for stable fruit set, is energy costly. Local temperature control can effectively reduce costs without

Table 7.2 Differences in fruit set between heat-tolerant and non-heat-tolerant tomato cultivars

Cultivar	Heat tolerance	Temperature (day/night, °C)	Fruit set[a] (%)	Reference
Duke	None	35/23	13 (54)	Abdul-Baki and Stommel (1995)
AVRDC-CL-1131	Tolerant		65 (71)	
Duke	None	29–36/17–24	6.6	Dane et al. (1991)
AVRDC-PT-3027	Tolerant		42.7	
Grace	None	31/25	26.7[b]	Firon et al. (2006)
FLA 7156	Tolerant		48.5[b]	
Hosen-Eilon	None	36.5–38.7/16.5–20.0	16.3	Levy et al. (1978)
Hotset	Tolerant		69.2	
F_4 (Hotset × Hosen-Eilon)	Tolerant × None		63.1	
Sataan	None	40/23[c]	44.6 (87.6)	Nkansah and Ito (1995)
Shuki	Tolerant		86.2 (70.0)	
Fresh Market 9	None	32/26	1.3 (56.1)	Sato et al. (2004)
FLA 7156	Tolerant		22.3 (46.8)	

[a] Values at optimal temperatures are in parentheses
[b] Pollinated with viable pollen of ‘Grace’
[c] Root-zone temperature was 25 °C constant

loss of fruit set and yield. Use of available heat- and chilling-tolerant varieties, and parthenocarpic cultivars, remarkably reduces energy costs of cultivation under unfavorable temperature conditions.

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