Fruit Set in Solanaceous Vegetable Crops as Affected by Floral and Environmental Factors

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ABSTRACT

The fruit set, yield and quality of the Solanaceous vegetable crops, tomato (*Lycopersicon esculentum* Mill.), peppers (*Capsicum annuum* L.) and eggplants (*Solanum melongena* L.), especially when cultivated out of season, are profoundly influenced by the climatic conditions prevailing during the stages of reproductive development. Although the effects of unfavourable environmental conditions on the flower fertility, pollination and fertilization of these species have formed the basis for numerous studies, there has been no overall review of the literature relating to this issue for over twenty years. However, in view of the increasing concern about the effects of environmental stress on crop production, a significant amount of experimental work relating to the physiology of fruit set has been published since then, including information on the effects of stress on the reproductive physiology of tomato and pepper, and to a lesser extent eggplant. This work is reviewed here with particular reference to male and female gametophyte development, pollination and fertilization.

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INTRODUCTION

The Solanaceous species, tomato (*Lycopersicon esculentum* Mill.), pepper (*Capsicum annuum* L.) and eggplant (*Sola-num melongena* L.), are sub-tropical crops that in the temperate zones are cultivated in the field and under cover for the production of fruit for the fresh market and for processing. Because the total yield of these crops is determined by

Invited Review

both the number and the weight of fruit, it is essential that the plants set a high number of fruit and that these develop to the desired size. In other words, high yields are initially dependent on the profusion of flowering and the success of pollination and fertilization.

As in many other crops, the potential of tomato, pepper and eggplant to set fruit is greatly influenced by environmental, cultural and biotic factors. The climatic conditions are of particular importance, since these crops (especially tomato) are cultivated throughout the year, and it is well known that one of the limiting factors for out of season production is poor fruit-set under unfavourable climatic conditions.

During winter and early spring it is not uncommon for apparently normal tomato flowers to fail to set fruits (Calvert 1964). This phenomenon is observed for crops that are sown in heated greenhouses in Northern Europe in October or early November in order to achieve reasonable yields in early spring when the prices are high. During midwinter, flower induction is adversely affected by low light intensity and short day length (Picken 1984). On the other hand, although the Mediterranean climate is more favourable in terms of light and temperature for the cultivation of Solanaceous crops (e.g. 60,000 ha of greenhouses along the coastal belt of the Mediterranean basin are cultivated with tomatoes), during winter and early spring temperature stress may occur due to low temperatures or diurnal temperature fluctuations (Romano and Leonardi 1994), resulting in poor fruit set and quality (Rylski *et al.* 1994). Additionally, in these greenhouses, high temperatures during late spring and summer reduce fruit set of tomato (Peet *et al.* 1997), eggplant (Passam and Khah 1992) and bell pepper (Erickson and Markhart 2001, 2002).

Sexual reproduction in many cultivated plants (e.g. tomato, pepper, rice, soybean, wheat) is more sensitive to high temperatures than the vegetative processes, and therefore the plant's reproductive organs are more vulnerable to changes in temperature prior to and during the early stage of flowering (Sato *et al.* 2002; Raja Reddy and Kakani 2007). This problem is likely to become a major issue in the near future because of the predicted increase in the Earth's surface temperature by between 1.5 and 11.8°C by 2100 (Stainforth *et al.* 2005) and to the more frequent occurrence of short periods of extreme temperatures due to the greenhouse effect (Mearns *et al.* 2001; Meehl and Tebaldi 2004).

Double fertilization of the angiosperms requires the release of pollen from the anthers, the adhesion of pollen grains to a receptive stigma (pollination), their hydration and germination, pollen tube growth through the style, the mitotic division of the generative cell (in bi-cellular pollen grains), the entrance of the pollen tube into the embryo-sac and the release of the male gametes. The failure of even one of these processes, results in a lack of fertilization (Heslop-Harrison 1987).

In this review the effect of environmental factors on the fruit set of Solanaceous vegetables will be discussed, with particular reference to the processes involved in fruit set from the initiation and development of flowers and thereafter. Although Picken (1984) extensively reviewed pollination and fruit set in tomato, in this review more recent information on these two processes, as well as the physiology of flower fertility of tomato and corresponding information on eggplant and pepper is presented. It is hoped that this literature survey will assist in clarifying the increasingly important issue of fruit set, yield and quality of Solanaceous vegetables under conditions of stress.

FLOWER MORPHOLOGY OF SOLANACEOUS VEGETABLES

Tomato (*Lycopersicon esculentum* Mill.)

In the present review, we use the 'established' nomenclature in which tomato is grouped under the genus *Lycopersicon*. In more recent nomenclature based on molecular data, it has been proposed that tomato should be placed as a clade within the genus *Solanum* as *Solanum lycopersicon* L. (Spooner *et al.* 1993).
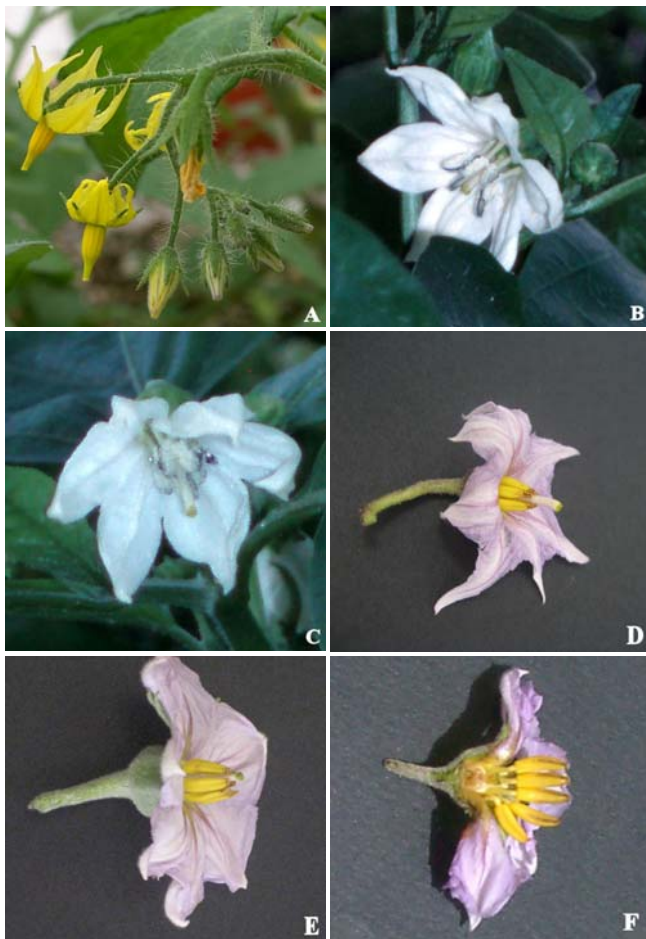
Flowering - inflorescence

The tomato plant is day-neutral and flowers under either short or long days; thus it sets fruit at most latitudes (Benton-Jones 2008). Flowers are borne in monochasial racemose cyme inflorescences, which are initiated by the apical meristem and consist of a main axis bearing lateral flowers without bracts (**Fig. 1A**). The plants follow a sympodial developmental pattern in which, after the production of seven to eight true leaves, the apical meristem gives rise to a lateral monochasial inflorescence (Sawhney and Greyson 1972; Hareven *et al.* 1994; Lozano *et al.* 1998). The number of flowers within an inflorescence depends mainly on the cultivar and environmental conditions. Increased irradiance or decreased plant density and lower temperatures positively influence the number of flowers formed in an inflorescence (Heuvelink 2005). Branching of the inflorescences is promoted when plants experience low temperatures at night (e.g. 10°C) during inflorescence initiation (Calvert 1957, 1959; Aung 1976). However, it is the mean diurnal temperature, rather than day or night temperature alone, that controls branching and flower number (Hurd and Cooper 1967). According to Phatak *et al.* (1966) cooling of the root system rather than the shoot was more effective in increasing flower number in tomato. Sometimes, depending on the cultivar, environmental conditions (e.g. temperatures <10°C during inflorescence initiation) or the position of the inflorescence on the plant, branched inflorescences having two or more main axes are produced, with a higher number of flowers per inflorescence or truss (Kinet and Peet 1997). The tomato plant is made up of a superposed series of sympodium units, showing similar pattern of development throughout growth, formed with an axillary bud, a certain number of leaves (2-4) and their respective internodes (Vegetti and Pilatti 1998). Therefore, the inflorescences appear at intervals of 2-4 (usually 3) leaves throughout the reproductive life of the plant and usually bear eight to sixteen flowers (Picken 1984; Vegetti and Pilatti 1998), but compound inflorescences with as many as 300 flowers have been recorded (Atherton and Harris 1986). It is not uncommon for the last-formed flower of an inflorescence to abort while the bud is still very small, less than 2 mm in diameter. Within a single inflorescence, stages of reproductive development may include at any one time small fruit, open flowers and unopened flower buds (Atherton and Harris 1986).

Flower morphology

Tomato flowers are pendent, hermaphroditic, yellow and typically six-merous. Although primitive tomatoes have the Solanaceous trait of five flower parts, modern tomato varieties often have more than five petals and sepals (Benton-Jones 2008). The calyx tube is very short and bears six leafy linear to lanceolate green sepals. The rotate corolla consists of a short supporting tube and six broad lobes. In the fully expanded flower the lobes are much reflexed and brilliant yellow in colour. The flower is hypogynous, the ovary is multilocular and consists of 2-7 green carpels, depending on the cultivar, which are fused together and each carpel contains many ovules. The androecium consists of six bi-lobed, yellow anthers, united by interlocking hairs to form a hollow cone which encloses the pistil. The neck of the cone consists of sterile extensions of the anthers which closely surround the stigma.

Determinate and indeterminate tomato cultivars

Tomato cultivars are classified as determinate or indeterminate depending on the capacity of the shoot system for continued sympodial development. Indeterminate cultivars pro-

Fig. 1 Flower types of solanaceous vegetables. (**A**) Tomato inflorescence. (**B**) Normal pepper flower. (**C**) Long-styled pepper flower. (**D**) Long-styled eggplant flower. (**E**) Medium-styled eggplant flower. (**F**) Short-styled eggplant flower.

duce branching systems that grow indefinitely and have a growth habit that is prostrate or scandent. After the primary shoot of an indeterminate cultivar has formed a terminal inflorescence, extension of the shoot axis continues through the growth of a series of lateral shoots that together constitute the primary sympodium. Each shoot in the series normally produces three, or more rarely four, leaves and a terminal inflorescence. Extension of the primary sympodium is through the growth of a bud in the axil of the last-formed leaf of the preceding shoot. These plants are favoured in greenhouses as they produce high yields over an extended period (Atherton and Harris 1986; Heuvelink 2005).

Determinate cultivars produce branching systems of limited growth and develop in the form of a bush. In these plants, the growing point in the axil of the last-formed leaf of the primary shoot may be transformed into an inflorescence without the initiation of further leaves. Since no new leaves or axillary buds are initiated, extension of the shoot axis is halted with the formation of the second inflorescence. Strong axillary buds develop at the base of the stem, producing a bushy habit, which is ideal for unsupported growth in the field. In these plants synchronization of fruiting permits once-over mechanical harvesting, so it is important that flowering of both the primary and lateral shoots should be concentrated into as short a time as possible (Atherton and Harris 1986; Heuvelink 2005). According to Heuvelink (2005), tomato cultivars are incorrectly termed 'indeterminate' and 'determinate'. Botanically, both types are determinate, since each inflorescence terminates the main axis.

Pepper (*Capsicum annuum* L.)

Flowering – inflorescence

The flowers of *Capsicum* form either singly or in small cymes within the leaf axils. Although in *C. annuum* flowers are usually solitary, whereas other species (*C. chinense* Jacq. and *C. frutescens* L.) have multiple flowers in the nodes, some accessions of *C. annuum* (e.g. the mirasol accession) have clusters of flowers at the node. Cluster type is associated with the fasciculated gene, which causes multiple flowers/fruits to form at a node (Bosland and Votava 2000). The species *C. annuum* is usually an annual and produces various types of fruits, including chilli peppers, red, green and yellow sweet peppers and paprika. By contrast, the species *C. frutescens* is a shrubby perennial producing small, red, very hot fruit, with several flowers and fruits per axil (Purseglove 1968). Pepper flower differentiation is more affected by temperature than day length (Bosland and Votava 2000).

Flower morphology

In most cases, *Capsicum* flowers are pentamerous, hermaphroditic, hypogynous with a diameter of 10-15 mm (**Fig. 1B**). The corolla is rotated and consists of 5-7 petals, 10-20 mm in length (Bosland and Votava 2000). The androecium consists of five short stamens with tubular-shaped anthers (1.2-2 mm in width and 2-4 mm in length) surrounding, but not touching, a single pistil. Under normal environmental conditions, the stigma is shorter than the anthers, and in most pepper cultivars the flowers are horizontal or pendent, so that the pollen can fall onto the stigma (Wien 1997). The shape and growth of the ovary determines the morphological characteristics of the fruits of each cultivar; for example, blocky and conical fruits are derived from round or elliptical ovaries, whereas oblong fruits develop from prismatic or conical ovaries.

Flower opening (anthesis)

Generally *Capsicum* flowers remain open for less than 24 h, but Aleemullah *et al.* (2000) found that during early spring and summer in a greenhouse, the flowers of the *Longum* group of chilli peppers remained open for 3–4 days. Although it has been observed that there is only one period of flower opening, initiated pre-dawn and completed within 5 h of sunrise, in the *Longum* chilli peppers anthesis occurred in 2 main peaks each day: a morning peak from pre-dawn to midday and a shorter afternoon peak between 2 and 4 pm. This pattern of two periods of anthesis within the same day is advantageous to the plants because the closure of flowers during the hottest period of the day (midday) reduces the drying of the stigma (Aleemullah *et al.* 2000). The stigma of the Solanaceae flowers secretes a stigmatic fluid which is essential for pollen adhesion, hydration and germination (Hoekstra and Bruinsma 1975). The stigma becomes receptive on the day of anthesis and remains so for a further two days. Pollen grains become fertile one day before anthesis, with maximum fertility on the day of anthesis (Rajput and Parulekar 1998), and are released from the anthers 1-4 hours after anthesis, depending on the cultivar (Kato 1989; Aleemullah *et al.* 2000).

Eggplant (*Solanum melongena* L.)

Flowering – inflorescence

Flowering in eggplant is extra-axillary (Shah and Patel 1970) and somewhat complex, as flowers are borne solitary, in clusters or mixed i.e., both solitary and cluster (Hazra *et al.* 2003a). The first (or 'basal') flower of the cyme (cluster), being often a solitary flower, is connected by its pedicel directly to the stem, while the other flowers of the same inflorescence ('additional') are located nearby but borne on

a separate axis (Nothmann *et al.* 1979). The 'basal' flower is well-developed, but the others are smaller, many of them being functionally sterile by having a style of reduced length (Prasad and Prakash 1968) and under developed or rudimentary ovary (Hazra *et al.* 2003a).

Flower morphology

Eggplant flowers are hermaphroditic, large, violet-coloured, and directed obliquely downwards. Typically, they are penta-merous, consisting of a calyx with five united and persistent sepals, and a corolla with five united, usually cup-shaped, petals. The androecium consists of five stamens, alternate with the corolla, and in the gynoecium the ovary is superior and the carpels are united (Rashid and Singh 2000). Solitary flowers and the basal flowers of the cyme are either long styled (**Fig. 1D**; style protrudes over anther tip) or medium styled (**Fig. 1E**; style just below the anther tip) and most of the additional flowers of the cyme are either pseudo-short styled (**Fig. 1F**; style length almost half of that of anther) or short styled (Hazra *et al.* 2003a). However, the number of anthers per flower varies from 6 to 20 or more, depending on the cultivar, and the anthers converge in such a way as to form a cone-like tube around the style, which is described as the "salt-cellar" anther cone tube (Glover *et al.* 2004).

Types of flower

Heterostyly in eggplant flowers (the difference in the position of the stigma in relation to the top of the anther cone) is a common phenomenon, which derives mainly from the occurrence of styles of different length, whereas stamen length does not vary (Murtazow *et al.* 1971). This phenolmenon is far more pronounced in eggplant than in tomato or pepper.

The position of the stigma relative to the anther cone is the main criterion for the classification of the different types of eggplant flowers. Initially, eggplant flowers were classified into two classes: (1) short-styled flowers, with the stigma lying below the anther pores, and (2) long-styled flowers, with the stigma protruding well above the anther pores, and furthermore short-styled flowers were grouped into true short-styled (having a style length of 0.25-0.57 cm) and pseudo short-styled (with style length of 0.58-0.79 cm, for cv. 'Muktakeshi'), whereas flowers with style lengths above 0.79 cm were characterized as long-styled (Smith 1931; Pal and Singh 1943). Subsequently, Krishnamurthi and Subramanian (1954) defined a fourth type of flower (classified as medium-styled), where the stigma rests at almost the same level as the anther pores. In accordance with this classification, four types of flowers, *viz.* true short, pseudo-short, medium- and long-styled, have been recognized in eggplant by Quagliotti (1962), Prasad and Prakash (1968), Chadha and Saimbhi (1977). The long and medium styled flowers with developed ovary are functionally fertile and the short and pseudo-short styled flowers are functionally sterile because of having either under developed or rudimentary ovary (Hazra *et al.* 2003a).

The frequency of occurrence of the different flower types in eggplant is a genotype-dependent characteristic (Prasad and Prakash 1968; Siddique and Husain 1974; Chadha and Saimbhi 1977; Baksh *et al.* 1979). According to Mohideen *et al.* (1977), depending on the cultivar, long-styled flowers range from 25-49%, medium-styled flowers from 6.1-31.7% and short-styled flowers from 19.3-58.7%. All types of style lengths are met on the same plant and even within the same cluster. In most of the cultivars, solitary flowers are either all medium-styled or all long-styled, while cluster flowers are mostly short-styled, or both medium and short-styled, or all medium-styled (Chadha and Saimbhi 1977).

Flower opening (anthesis)

In most of the flower buds, the petals start to separate be-

tween 7 and 8 am, and are completely open by 2 pm (Prasad and Prakash 1968). Rashid and Singh (2000) reported that anthesis starts from 7.30 am and continues up to 11 am, with a peak period of anthesis between 8.30 and 10.30 am. Hazra *et al.* (2003a) observed anthesis of eggplant flowers from 6.45 to 9.45 am. Flowers started closing from 2 pm, and were completely closed by night (Prasad and Prakash 1968). Repeated opening and closing of the flowers continues for up to five days, after which the corolla gradually turns brown and finally withers. Generally, the opening mode of eggplant flowers is influenced by flower age and the temperature and RH of the environment (Prasad and Prakash 1968).

POLLINATION AND FERTILIZATION

Anther morphology and pollination in the Solanaceae

Within the family Solanaceae, two genera which produce poricidal anthers are the genus *Solanum*, its sister genera *Lycianthes* and *Capsicum* (Bohs and Olmstead 1997). There are two main forms of anther cone present within these genera, described as 'pepper pot' and 'salt cellar' types (Glover *et al.* 2004). Species with a "salt cellar" anther cone have essentially free anthers held together in a loose cone. Pollen is released through a hole at the tip of the cone where the anthers do not quite meet, and is either shed into the centre of this cone or shaken from each individual anther directly onto visiting insects. This form of anther cone is widespread in the genus *Solanum*. Species, including tomato, with the more robust 'pepper pot' anther cone have a cone of fused anthers, and pollen is released from apical pores or slits at the tip of each anther. Anthers in 'pepper pot' cones have short, almost non-existent, filaments (Glover *et al.* 2004).

Pollination and fertilization in tomato

In tomato, pollen grains are released introrsely along longitudinal anther slits and fall onto the stigmatic surface (Picken 1984). The 'pepper pot' anther structure and the absence of insect pollinators usually ensure self-pollination in cultivated tomato. This is in contrast with the flowers of many wild *Lycopersicon* species, which have exserted stigmas (heterostyly, longistyly) and/or incompatibility mechanisms which favour outcrossing (Picken 1984; Kinet and Peet 1997; Benton-Jones 2008). Pollen transfer depends on the proximity of the stigma to the apex of the anther cone (Fernandez-Muñoz and Cuartero 1991). Tomato cultivars where the stigma is enclosed within the anther cone (inserted configuration) set fruits easily (Rick and Dempsey 1969), whereas in cultivars whose stigma protrudes beyond the anther cone (exserted configuration) both pollination and fruit-set are seriously deficient (Levy *et al.* 1978). Although the mature pollen is ready for transfer at the time of anthesis (i.e. flower opening), the stigma becomes receptive about 2 days previously and remains so for up to 4 days or more. Once pollen grains adhere to the stigma, pollen tubes start to grow within an hour and can reach the micropyle of the ovule within 12 h at 25°C (Dempsey 1970). Fertilization has been first observed after 18 h and most ovules are fertilized within 30 h at 20°C (Iwahori 1966). Thus, the extent of fertilization (i.e. the number of fertilized ovules per ovary) is dependent on the number of viable pollen grains reaching the stigma and the effect of environmental or physiological factors on the subsequent processes of pollen tube growth and fertilization (Ho and Hewitt 1986). The implication of these factors on tomato fruit-set will be discussed in details in the sections "effect of adverse temperatures on anther dehiscence, pollen release and pollination in relation to style length" and "effect of temperature and RH on stigma receptivity, *in vivo* pollen germination and pollen tube growth".

Pollination and fertilization in pepper

The flowers of pepper are generally self-pollinated, but to a lesser extent than tomato because of the 'salt cellar' type of anther cone in which the anthers and stigma are not normally in contact. Self-pollination is favoured by the fact that the stigma is usually sited below the level of the anthers, while the flowers are horizontal or pendent, so that pollen can fall onto the stigmatic surface. On the other hand, especially in the field, the open anther cone permits insects easy access to pollen (Wien 1997). Insects are further encouraged by nectar accumulated near the base of the petals (Vogel 1998), while in some flowers self-pollination may be reduced due to delayed anther dehiscence (Raw 2000). This explains the relatively high cross-pollination in pepper observed by Tanksley (1984), who found 41% outcrossing among tester lines inter-planted in fields of chilli peppers. Under excessively high temperatures (32-38°C) and low RH, style elongation occurs, thus inhibiting self-pollination (Wien 1997).

In both pepper and tomato, anthers dehisce longitudenally about 1-2 h after flower opening, although in some cultivars a delay of up to 4 h has been observed (Kato 1989; Aleemullah *et al.* 2000). The period over which released pollen and the pistils retain their viability, seems to be affected by temperature. Kato (1989) reported that warm conditions during June-July promote pollen and pistil ageing. Thus, pistils that were pollinated artificially one day after anthesis produced 60-70% fewer seeds per fruit than those that were pollinated on the day of flowering. However, during winter the pistil and pollen retain fertility for two and three days after flowering, respectively (Kato 1989).

After pollen has been placed on the stigma, it remains inactive for a short time irrespective of the environmental conditions. The germination of pepper pollen, like that of tomato, is favoured by temperatures within the range of 21-30°C, accompanied by high RH. There is a considerable lag in seed-set, which occurs 42 h after pollination for plants grown at 27°/21°C, even though this time is less than that required for fertilization in tomato, owing to the shorter styles of pepper (Wien 1997). Peppers also have the capacity to set fruits parthenocarpically, especially under low night temperatures (12-15°C) (Rylski and Spigelman 1982; Polowick and Sawhney 1985).

Pollination and fertilization in eggplant

Because of the complex flowering pattern of eggplant, pollination and fruit-set are greatly affected by flower morphology. Eggplant anthers dehisce through apical pores, within 15-30 minutes of the first opening of the flower (Prasad and Prakash 1968). Pollen is released from the anthers at 9.30-10 am (Rashid and Singh 2000), but the duration of anther dehiscence is very irregular since it is affected by temperature and RH (Prasad and Prakash 1968). The eggplant stigma appears shiny and sticky when it is fully receptive, usually on the day of flower opening. Receptivity gradually decreases with age, and by the fifth day of flowering is negligible, and the stigma gradually turns brown (Prasad and Prakash 1968).

Heterostyly, fruit-set and fruit development in eggplant

Style length in eggplant is a particularly important factor with regard to pollination and fruit set. Although the combination of long-styled flowers (which are more frequent) and the obliquely downward orientation of the flowers favours self-pollination (Rashid and Singh 2000), pollen is often dispersed by wind, with the result that the stigma cannot receive a sufficient amount of pollen to satisfactorily set fruits. However, in long-styled flowers insects also assist pollination, albeit cross-pollination (Hawthorn and Pollard 1954). On the contrary, in short-styled flowers, where the stigma is located inside the downward-facing anther cone, pollen does not reach the stigma, and flowers abort (Nothmann *et al.* 1983; Kowalska 2006). In consequence, only long- and medium-styled flowers set fruit under normal field conditions.

Fruit set is more efficient in long-styled flowers, where it varies from 70-86.7% according to the cultivar (Quagliotti 1962; Prasad and Prakash 1968; Siddique and Husain 1974; Kowalska 2003, 2006). In medium-styled flowers, fruit set varies from 12.5-55.6% (Prasad and Prakash 1968; Kowalska 2006), whereas in pseudo-short-styled flowers only 5.0-16.7% fruit set occurs (Prasad and Prakash 1968). Passam and Bolmatis (1997) reported that short-styled (<0.5 cm) pistils totally failed to set fruit, and maximum fruit weight and seed formation were observed in flowers in which the stigmata at maturity were situated close to the anther pores. According to these researchers, the proximity of the stigma to the anther pores is of more importance for fruit set than style length alone.

Rylski *et al.* (1984) and Handique and Sarma (1995) reported that the androecium of short-styled flowers is fertile but the stigma is smaller in size, with under-developed papillae and a lower sugar content than the stigma of long-styled flowers. Because of the lack of well-formed papillae on the stigma, pollen grains fail to germinate, so even though the ovules and embryo sacs of short-styled eggplant flowers develop normally, fertilization is not possible. A similar case of pollen germination failure was reported to occur on the stigmata of short-styled flowers of *Solanum marginatum* L. (Dulberger *et al.* 1981). According to Hazra *et al.* (2003a), although pollens of the short and pseudo-short styled flowers with either under developed or rudimentary ovary are fully functional, even hand pollination failed to set fruits in these flowers suggesting that sterility in these flowers might be due to some problem related to development of ovary. Short-styled flowers are particularly common during the warm growing season, resulting in reduced fruit set and yield. Besides being a cultivar characteristic (Chadha and Saimbhi 1977), style length in eggplant is also influenced by external factors such as fruit load and plant age (Lenz 1970) and the cultivation environment (Wang *et al.* 1980; Nothmann *et al.* 1983). Due to the variability in flower morphology, eggplant is not an obligatory self-pollinated plant. Sambandam (1964) stated that 30-60% of the fruit set is attributed to pollination by contact, gravity, and air, and the rest to insects. This author reported 0.7-15%, outcrossing of plants in India. Hazra *et al.* (2003b) with the use of genotypes having simply inherited marker characters (pigmentation and prickliness) estimated 8.5% out crossing in eggplant.

Effect of cluster size and the position of the flower within the cluster on fruit set and fruit development

Both cluster size and the position of the flower within the cluster affect fruit-set and subsequent growth and quality of fruit. According to Nothmann *et al.* (1983), there is a decreasing gradient in weight from the basal long-styled to the additional short-styled flowers. In the cultivar 'Black Queen' the mean weight recorded for 'basal' flowers was 1.65 g, and for 'additional' flowers 0.64 g (Nothmann *et al.* 1979). The position of the flower in the inflorescence affects fruit quality during the cool season. During the warm season almost all the 'additional' flowers drop, but during the cool season some set fruit, which grow more slowly that those originating from the 'basal' flowers, resulting in undersized fruits of inferior colour (Nothmann *et al.* 1979). The percentage of flowers formed in clusters, rather than singly, in the cool season (55.7%) is much higher than in the warm season (10.2%). The fruits formed from flowers in clusters are smaller than those formed from single flowers and frequently do not attain marketable size (Nothmann *et al.* 1983).

According to Nothmann *et al.* (1983), there are three trends of fruit development in eggplant relating to cluster

size and the position of the flower in the cluster: (1) Basal fruit are always a stronger sink than the additional fruit; therefore the weight and color of the basal fruit are not influenced by the presence or absence of additional fruit. (2) Additional fruit represent a weaker sink, perhaps due to the smaller phloem area in their pedicels, or to the restriction in their growth caused by the stronger sink of basal fruit located in or near the same cluster. (3) Because colour development is related to growth vigor, the rate of color development is slower in additional fruit than in basal fruit (Nothmann *et al.* 1979).

Genotype-dependent fruit-set

The flowering and fruit-setting ability of eggplant is affected by temperature, soil-water potential and variations in climate (Nothmann *et al.* 1979; Tedeschi and Zerbi 1985; Sun *et al.* 1990). However, Passam and Khah (1992) found that genotype is also an important factor in the regulation of flowering and fruit-set, with concomitant implications for fruit and seed production. They found that although cv. 'Emi' flowered less profusely than cv. 'Long Negro', fruit set was higher because 'Emi' had the ability to set fruit with no or few seeds, whereas 'Long Negro' only set fruit following abundant fertilization. Therefore, although Mohideen *et al.* (1977) suggested that yield relates to the profusion of flowering, the fruit setting ability of the flowers also has to be taken into consideration.

Effect of fruit load on flower characteristics

Developing fruits reduce the growth of leaves, stems and roots in eggplant (Mochizuki 1959), as in other plant species (Leonard 1962), due to competition for assimilates and nutrients but also possibly as a result of growth inhibition caused by hormones produced in the fruits. This latter explanation is supported by Lenz (1970), who showed that developing fruits of eggplant reduce the pistil growth of flowers formed subsequently on the same plants, and this retardation lasts until the fruit have completed their development.

Fruit load has been found to negatively affect style length, flower and pistil mass (but not the growth of anthers and the length of anther cone), in both the basal and additional flowers even under climatic conditions that are favourable for fruit set, leading to a restriction of pollination and fruit set (Lou and Kato 1993; Passam *et al.* 2001; Khah *et al.* 2002). Following fruit maturation, however, the flower size and style length of newly formed flowers increased to their normal values (Passam *et al.* 2001; Khah *et al.* 2002). It is well known that, both stamen and pistil length are controlled by auxins, so auxins derived from developing fruits may inhibit pistil growth, suggesting that there is a control of sex expression in eggplants by developing fruits (Lenz 1970). Apart from the hormonal regulation of flowering, as Claussen (1986) suggests, fruits are strong sinks and might at least partly hamper vegetative growth and flower size by withdrawing leaf carbohydrates.

ENVIRONMENTAL FACTORS AFFECTING FRUIT SET

The effect of temperature on the fruit-set of Solanaceous vegetables

Temperature is a key factor for fruit-set in tomato (Rylski 1979), pepper (Wien 1997; Shaked *et al.* 2004) and eggplant (Sun *et al.* 1990). Night temperatures are the dominant factor for tomato fruit-set, with optimal values of 15-20°C. Peet *et al.* (1997) however, demonstrated that daily mean temperature is more critical than night-time temperature *per se* and at a daily mean temperature of 29°C, fruit number, fruit weight per plant and seed number per fruit decreased markedly compared with those at 25ºC. Hazra and Ansary (2008) supported this proposition because of huge reduction

in fruit set in 35 tomato genotypes in the spring-summer season under an average daily mean temperature of 26.8°C despite average night temperature of 19.2°C which remained just below the upper critical limit of 15 to 20°C. When temperatures fall below 10°C or rise above 23°C, at least one of the processes leading to successful fertilization is adversely affected (Picken 1984; Kinet and Peet 1997; Song *et al.* 2002; Pressman *et al.* 2007). Low temperatures mainly affect tomato microsporogenesis, resulting in poor pollen production or low pollen viability (Robinson *et al.* 1965; Charles and Harris 1972; Philouze and Maisonneuve 1978; Maisonneuve *et al.* 1982a), and may also cause heterostyly, limited anther dehiscence and incomplete pollen release, leading to poor pollination (Kinet and Peet 1997), low ovule viability, limited germination of pollen grains on the stigma and retarded growth of pollen tubes within the style (Dempsey 1970; Charles and Harris 1972).

Bell and chilli peppers are also very sensitive to cold and exhibit a high night temperature threshold of 18°C (Kato 1989; Ali and Kelly 1993) to 15°C (Rylski and Spigelman 1982; Polowick and Sawhney 1985) depending on the cultivar. Temperatures lower than these limits lead to the formation of larger flowers with swollen ovaries, shorter styles (Rylski 1973; Polowick and Sawhney 1985) and reduced pollen production and viability (Pressman *et al.* 1998a; Shaked *et al.* 2004), resulting in the production of either parthenocarpic fruits that tend to abscise (Usman *et al.* 1999), or small and flattened non-marketable fruits with few or no seeds (Rylski 1973; Pressman *et al.* 1998a). Therefore, in pepper low temperatures do not seem to impair fruit-set, but they reduce the number of seeded fruits and therefore fruit quality (Rylski *et al.* 1994).

The eggplant is the most thermophilic among the Solanaceous vegetables and temperatures of at least 15°C (night) and 23-25°C (day) are required for satisfactory vegetative growth and yield (Abak and Guler 1994). Eggplant does not tolerate low night temperatures and exhibits many abnormalities during the cool season, including low flower fertility, production of seedless fruits as a result of impaired pollen development and viability (Nothmann and Koller 1975) and abnormal fruit colour development (Nothmann *et al.* 1978). In heated plastic houses, Suzuki *et al.* (2005) reported lower marketable yield at a night temperature of 14°C compared to temperatures of 16 or 18°C.

Although pollination, fertilization and the presence of seeds are required for normal fruit set and development, presence of mature seeds in eggplant reduces the quality of fruit for both fresh consumption and processing. The seeds render the fruit less palatable because the flesh becomes harder (Donzella *et al.* 2000), induce faster and more intense browning of the flesh upon cutting and increase the concentrations of saponin and solasonin compounds, which cause bitterness (Aubert *et al.* 1989). Therefore, in eggplant, although natural pollination and fruit-set is beneficial for high yield, parthenocarpic fruit formation is desirable for better quality. As a result, the experimental data concerning the implication of environmental factors on natural fruit-set of eggplant are scarce, whereas intense research activity is focused on breeding for parthenocarpic hybrids (Restaino *et al.* 1992; Hennart 1996).

According to Raja Reddy and Kakani (2007), the reproductive organs of the Solanaceous species (especially the male gametophyte) are more sensitive than the vegetative organs to high temperatures. So, in tomato, although the metabolic processes are favoured at relatively high temperatures (25-30°C), optimal fruit-set is observed at mean day temperatures of 21-24°C (Peet and Bartholemew 1996). In pepper, high temperatures during flowering impair pollen germination, pollen tube growth and fertilization, resulting in flower abscission and reduced fruit set (Usman *et al.* 1999; Aloni *et al.* 1991, 2001; Erickson and Markhart 2002). Floral bud abortion at day temperatures >34°C and night temperatures >21°C is a major problem in pepper crops (Rylski and Spigelman 1982), and in unheated greenhouses in the Mediterranean region a flux of anthesis, a high per-

centage of flower abortion and a progressive reduction in fruit weight and seed yield is observed under high daytime temperatures (Passam and Khah 1992). In eggplant too, high temperatures (30-35°C) impair flowering, depending on the cultivar (Mohideen *et al.* 1977).

Under warm Mediterranean conditions, the fruit-set of eggplant, decreases to as low as 10% (Passam and Khah 1992), mainly due to the combination of high temperatures and low humidity which negatively affect stigma receptivity and/or pollen germination (Passam and Bolmatis 1997). High temperatures (>30-35°C) also impair the fruit-set of tomato and pepper plants due to their detrimental effects on production and viability of pollen (Iwahori 1965; Sugiyama *et al.* 1966; Erickson and Markhart 2002), pollination and *in vivo* pollen tube growth (Shelby *et al.* 1978; Usman *et al.* 1999), and the induction of heterostyly (Charles and Harris 1972).

During the last decade, there has been increasing interest in the effect of the combination of moderately high day (32°C) and high night (26-28°C) temperatures on flower fertility and fruit-set of tomato and pepper. Although temperature stress limits fruit-set, its effect on the pollination physiology of these crops differs.

Effect of temperature on flower morphology and flower abortion

Lozano *et al.* (1998) observed that although low temperatures (17/7°C day/night) did not influence the vegetative growth of tomato, abnormalities in flower development occurred. These abnormalities could be grouped into three categories: (1) Changes in organ number (meristic changes), (2) Differences in the pattern of organ fusion, and (3) Changes in organ identity (homeotic changes). Many flowers formed under low temperatures show more than one type of abnormality.

Tomato plants grown under low temperatures during their reproductive development show a dramatic increase in the number of floral organs, mainly due to the initiation of a higher number of organ primordia in the floral meristems and the splitting of larger primordia to give rise to twin organs, such as twin flowers and/or stamens (Chandra-Sekhar and Sawhney 1984; Lozano *et al.* 1998). In pepper, night temperatures lower than 18°C result in the formation of larger flowers, with swollen ovaries and shorter styles than those of plants grown under higher temperatures (Polowick and Sawhney 1985). This has an indirect effect on the self-pollination of pepper flowers because the large ovaries push the anthers away from the stigmas (Kato 1989; Aloni *et al.* 1999), resulting in reduced pollination and parthenocarpy (Polowick and Sawhney 1985). Pepper flowers are particularly sensitive to temperature, since even at non-extreme conditions (18/15°C day/night) stamen deformation and abnormal, non-viable pollen was observed (Polowick and Sawhney 1985).

Aloni *et al.* (1999) provided evidence that the swelling of pepper ovaries induced by temperatures lower than 18°C results from increased assimilate translocation to the flower buds, since flower buds developing at night temperatures of 12°C contain more carbohydrates than those developing at 18°C. Temperature-induced flower deformations are also strongly correlated with changes in the concentrations of endogenous hormones (Atherton and Harris 1980; Polowick and Sawhney 1985). According to Pressman *et al.* (1998b), low temperatures increase auxin production or auxin response within the ovule, which is the main cause of ovary swelling.

Tomato and pepper flowers show striking differences in their response to the same low-temperature regime, indicating a non-generality of morphogenetic patterns in plant-environment response (Polowick and Sawhney 1985). Rylski (1979) and Sawhney (1983) reported that tomato cultivars with multilocular ovaries produce more carpels under cool conditions than under warm conditions. The increase in size of the floral meristem (due to a higher number of

cells) and the greater sensitivity of certain flower whorls to the increase in organ number resemble the phenotype caused by weak alleles at loci *CLV1* to *CLV3* of *Arabidopsis* (Lozano *et al.* 1998).

A lack of anther fusion, preventing the formation of the staminal cone, was observed in >60% of tomato flowers formed under low temperatures (17°C day, 7°C night), while carpel fusion was prevented at the level of the style in >30% of the same flowers. In addition, nearly 20% of the flowers formed at low temperature showed homeotic changes, resulting in chimeric organs, such as petaloid sepals and staminoid petals or, more frequently, petaloid or carpeloid stamens and stamen-like tissue associated with the carpels. These alterations are the consequence of late homeotic transformations in specific cells and cell lineages of the developing organs, whereas low temperatures did not affect the temporal and spatial patterns of organ initiation or the first stages of primordia development (Lozano *et al.* 1998). According to Lozano *et al.* (1998), the effects of low temperature on the expression of homeotic genes could be mediated through changes in hormone biosynthesis and/or sensitivity, since they found higher levels of GAs in flowers produced under low temperatures, whereas similar transformations were observed in tomato flower buds treated with GA (Sawhney 1983), and hormonal regulation of homeotic gene expression has been suggested in other cases (Estruch *et al.* 1993; Venglat and Sawhney 1996).

Although the effects of high temperatures on the flower morphology of the Solanaceae have been studied less than the effects of low temperatures, considerable research has been devoted to flower abscission under heat stress. High temperatures induce flower abscission in tomato, although according to Levy *et al.* (1978) this is an indirect effect of the failure of fruit-set, rather than a direct effect of temperature. However, Dinar and Rudich (1985a) showed that sucrose uptake by tomato flower buds is inhibited under heat stress conditions, implying that tomato flower abscission may be due to a restriction of the supply of assimilates to the developing flower buds.

The limited carbohydrate supply to developing flowers under heat may also be the reason for flower abscission in pepper under day temperatures >34°C or night temperatures >21°C, especially during the later stages of flower development (Rylski and Halevy 1974; Rylski and Spigelman 1982; Aloni *et al.* 1991, 1994). According to Aloni *et al.* (1991), high temperatures (35/25°C day/night) reduce acid invertase activity in the developing pepper flowers, but not in the young leaves, implying that heat stress has a specific effect on the capacity of the reproductive organs to take up assimilates. Apart from carbohydrate supply, there is evidence that flower abscission under heat stress is related to an increase of ethylene production by the flowers. However, the abscission rate depends more on the sensitivity of the cultivar to ethylene than ethylene production rate *per se* (Aloni *et al.* 1994). In addition, auxins have been found to retard flower abscission in tomato (Roberts *et al.* 1984) and pepper (Wien *et al.* 1989) by diffusing down the pedicel and preventing the separation of cells in the abscission layer (Wien *et al.* 1989).

Effect of temperature on microsporogenesis

As mentioned earlier, pollination and fruit-set of tomato, pepper and eggplant are impaired by high or low temperature stress, as well as by a combination of moderately high day and high night temperatures, which mainly affect the male gametophyte fertility. In order to reproduce, higher plants utilize a unique bi- or tri-cellular haploid male gametophyte, the pollen grain (Bedinger 1992). Pollen grains of tomato, pepper and eggplant are bi-cellular when released at anther dehiscence, meaning that the mitotic division of the generative cell takes place during pollen tube growth through the style (Nepi and Franchi 2000).

Extreme temperatures and microsporogenesis

Effect of low night temperatures: Several studies have demonstrated that poor fruit-set of tomato under low night temperatures (<10°C) is ascribed mainly to the negative effect of cold stress on microsporogenesis, since the effect on megagametogenesis and *in vivo* pollen germination and tube growth is relatively small (Robinson *et al.* 1965; Shannon *et al.* 1965; Charles and Harris 1972). Similarly, in pepper, low temperatures (10°C) during flower development seriously reduce the amount of pollen produced per flower and the viability of pollen grains (Pressman *et al.* 1998a; Shaked *et al.* 2004), which have thinner and less dense exine, and are smaller and elliptical in shape, as opposed to triangular in pollen produced under higher night temperatures (20°C) (Mercado *et al.* 1997). The severity of the effect increases with decreasing night temperatures over the range of 10-20°C during anthesis (Mercado *et al.* 1997; Pressman *et al.* 1998a) and is clearly due to pollen viability impairment by low night temperatures, since flowers formed under low temperature, but pollinated with pollen from plants grown under 'normal' temperatures, produce fruit with a significantly higher number of seeds than those set by pollen produced under low temperatures (Rylski 1973; Pressman *et al.* 1998a). However, unlike tomato, the receptivity of the stigma and the ability of the style to facilitate the growth of pollen tubes in pepper are also adversely affected by low temperatures (Pressman *et al.* 1998a).

Although eggplant produces seed-containing fruit in the warm season (late spring and summer), the number of seeds per fruit decreases as night temperatures fall in autumn (Nothmann and Koller 1975; Romano and Leonardi 1994; Uzun 2006). This is attributed to a progressive loss of pollen germinability, whereas female fertility is not similarly affected. However, temperature-induced male sterility in eggplant is transient, and full pollen fertility is regained as temperatures increase (Nothmann and Koller 1975). In Japanese varieties of eggplant, the minimum temperature for normal germination of pollen on the stigma is 20°C (Fujishita 1965). Abak and Guler (1994) showed that 30-35% pollen viability is sufficient for normal fruit-set of eggplant.

Cultivar differences in microsporogenesis under low temperatures: Genotype determines the temperature threshold for the negative effect of low temperatures on pollen production, viability and fruit-set in the Solanaceae. In tomato, Ercan and Vural (1994) noticed a 5°C difference in the low night temperature susceptibility threshold of two cultivars, and other genotypic differences have been reported relating to tomato fruit-setting ability under conditions of cold stress (Kemp 1965; Shannon *et al.* 1965; Charles and Harris 1972). In pepper, pollen production, pollen viability and the ability to set fruits under low night temperatures (10°C) also relates to the cultivar (Shaked *et al.* 2004). A minimal effect of low temperatures on fruit-set and fruit development of a cayenne-type cultivar was observed, whereas two bell-pepper cultivars showed higher susceptibility. In eggplant, Abak and Guler (1994) observed that when night temperatures were less than 10°C during mid-February, the viability of pollen (determined by tetrazolium staining) decreased to as low as zero in temperature-sensitive, open-pollinated genotypes, whereas the pollen viability of some F_1 cultivars was about 10%. However, when night temperatures rose slightly above 10°C, the pollen viability of the hybrids was much higher (47%), compared to the zero values of open-pollinated cultivars; but the difference was negligible when night temperatures increased to 15°C.

Effect of high day temperatures: High day temperatures (>32°C) have a detrimental effect on tomato flowering and fruit-set (Rudich *et al.* 1977), as well as on fruit size and quality (Levy *et al.* 1978; El Ahmadi and Stevens 1979).

Although high temperatures negatively affect megagametogenesis (Iwahori 1965; Sugiyama *et al.* 1966), and to a lesser degree pollination and pollen germination (Shelby *et al.* 1978), their negative effect on microsporogenesis is relatively higher (Iwahori 1966; Charles and Harris 1972). Therefore, extreme temperatures (low or high) reduce tomato fruit-set, mainly due to the limited production and viability of pollen (Peet *et al.* 1997, 1998).

This is also the case for pepper, where high temperatures (>32°C) during flowering may harm pollen germination, pollen tube growth, fertilization, flower abscission and fruit set (Usman *et al.* 1999; Aloni *et al.* 1991, 2001; Erickson and Markhart 2001, 2002), chiefly through their effect on stamen development, and to a lesser extent on pistil (Erickson and Markhart 2002; Karni and Aloni 2002). Temperatures >32°C induce pollen abnormalities in pepper, such as the formation of shrunk or empty pollen grains without noticeable exine (Erickson and Markhart 2002). Erickson and Markhart (2001) considered that the deleterious effect of high temperature (33°C) on pepper fruit-set is a direct temperature response, rather than temperature-induced water stress. They also suggested that limited fruit-set at high temperatures was due primarily to flower abscission and impaired pollen development, and not to reduced photosynthesis.

Apart from the effect of extreme temperatures on the male fertility of tomato and pepper, it has also been shown (Pressman *et al.* 2002, Sato *et al.* 2004, 2006, Firon *et al.* 2006) that a combination of moderately high day temperatures (32°C) and high night temperatures (26-28°C), impairs fruit-set, reduces the number of seeded fruits and induces flower abortion even though it permits normal vegetative growth. Although such combinations of temperatures are rather unusual in greenhouses even in summer, they may be encountered in field crops in sub-tropical regions. The restriction of fruit-set is caused by the detrimental effect of this form of stress on most of the processes leading to fertilization, including the release of pollen from the anthers and *in vivo* growth of the pollen tube (Pressman *et al.* 2002; Sato *et al.* 2004; Firon *et al.* 2006; Sato *et al.* 2006; Pressman *et al.* 2007); by contrast, the female reproductive organs are less affected (Peet *et al.* 1997, 1998). However, stress from an unfavourable combination of moderate-high night and day temperatures, unlike stress due to extreme temperatures, does not reduce the production of morphologically normal pollen (Sato *et al.* 2006), but decreases the viability of pollen, due to insufficient supply of carbohydrates to the pollen from the tapetum and other anther tissues (Sato *et al.* 2000).

Although eggplant is frequently cultivated in greenhouses during the warm season, there is apparently no published information on either the effect of high temperatures on pollen production and viability, or the upper temperature threshold for normal fruit-set. Studies concerning seasonal variations in the production of seeded fruits and on the quantity and viability of pollen produced (Nothmann and Koller 1975; Abak and Guler 1994; Romano and Leonardi 1994; Uzun 2006) report only that under warm conditions, following a cool growth period, the production of seeded fruits as a consequence of good pollen viability is restored.

Mechanisms of temperature-induced stress on microsporogenesis of the Solanaceae

Stages of microsporogenesis susceptible to temperature stress: Patterson *et al.* (1987) observed that during flower development there are two stages of acute sensitivity to low (7°C) night temperatures, about 11 days and 5-6 days before anthesis, each of which results in pollen that is devoid of chromatin. Although the presence and timing of both stages are supported by other studies (Maisonneuve 1982; Mutton *et al.* 1987), the occurrence of the second stage (5-6 days before anthesis) seems to be genotype-dependent, because Maisonneuve (1982) observed that a cultivar ('Coldset') that is susceptible to low temperatures exhibited in both the

stages, whereas a more tolerant cultivar ('Précoce') exhibited susceptibility only in the first stage. Tomato plants that formed flowers under 18°C day/7°C night produced viable pollen only 14 days after their transfer to higher temperatures, suggesting that night temperatures lower than 10°C negatively affect the male fertility of flowers that open about two weeks after their induction (Robinson *et al.* 1965; Mutton *et al.* 1987; Patterson *et al.* 1987).

This sensitive period coincides with the early stages of microsporogenesis, i.e. during the meiosis of pollen mother cells, the formation of tetrads and microspore release (Robinson *et al.* 1965; Shannon *et al.* 1965; Philouze and Maisonneuve 1978; Maisonneuve *et al.* 1982b; Picken 1984; Mutton *et al.* 1987). This is also the most sensitive stage of pepper microsporogenesis under low night temperatures (10°C) (Mercado *et al.* 1997). However, unlike tomato, pepper pollen fertility does not seem to be affected when low night temperatures are experienced during later phases of microspore development (Mercado *et al.* 1997). In eggplant there is apparently no published information on the stage of microsporogenesis, which is most sensitive to low temperatures.

Tomato microsporogenesis shows maximum sensitivity to extremely high temperatures (40°C) at the stage of pollen mother cell meiosis (8-9 days before anthesis in plants grown at 20°C, or 11-15 days under lower temperatures) (Iwahori 1965). The detrimental effects of high temperatures on pollen development were still severe five days before anthesis, but did not affect pollen maturation when applied 3 days before anthesis. These observations are in agreement with those for pepper, where Erickson and Markhart (2002) showed a decrease in fruit-set when flowers were exposed to moderately high temperatures (33°C) during early flower development (16–18 days before anthesis), corresponding to the stages of microspore mother cell meiosis, and from final tetrad formation to dissolution, whereas exposure to high temperatures just prior to anthesis had no effect on either the female or male organs (Erickson and Markhart 2002).

In general, early pollen development (meiosis of pollen mother cells, final tetrad formation, tetrad dissolution), seems to be the most susceptible stage of microsporogenesis to abiotic stress, not only in the Solanaceae but also in other species, such as cucumber (*Cucumis sativus* L.) (Whelan 1972), sugarbeet (*Beta vulgaris* L. ssp. *vulgaris*) (Majewska-Sawka *et al.* 1990) and *Arabidopsis* (Dawson *et al.* 1993). Moreover, it is likely that the susceptibility of tomato and pepper microsporogenesis to both high and low temperatures is governed by the same genetic system, since it occurs at more or less the same stage of pollen development. So, it may be expected that the genotypes which are tolerant to fruit-set under low temperatures, will also be able to produce fruit under high temperatures (Robinson *et al.* 1966).

Extreme temperatures also seem to impair tapetum functionality, since Iwahori (1965) observed inhibition of microsporogenesis due to a failure of tapetum degeneration when tomato plants were exposed for 3 hours to high temperature (40°C) on two consecutive days. Erickson and Markhart (2002) suggest that impaired pollen development under high temperatures is ascribed partly to tapetum malfunction, and Mercado *et al.* (1997) found that pepper pollen produced under low temperatures (10°C) had a thinner and less dense exine layer, indicating that the function of the tapetum was negatively affected because exine is mainly composed of sporopollenin derived from tapetal cells after microspore release.

Interaction of temperature stress with other environmental factors: The effect of temperature stress on microsporogenesis, pollen viability and therefore on fruit-set, is not specific even for a given genotype, since its interaction with other climatic factors, such as light intensity and RH is strong. However, because these interactions are still not clarified, there is a need for more experimental data, particularly concerning the relationship of assimilate availability to microsporogenesis.

The effect of low night temperature on tomato male fertility seems to depend on the climatic conditions that prevail during the light period of day. Favourable temperature and light levels during the day reduce the negative consequences of low night temperatures, and there appears to be a strong correlation between assimilate availability and the effect of low night temperatures on the production and viability of pollen (Karapanos 2007). Curme (1962) observed improved fruit-set at a night temperature of 7°C under higher light levels during the daytime, as did Rylski (1979) when low night temperatures (10°C) coincided with comparatively high day temperatures (22°C) under natural light. Maisonneuve (1982) reported that under adequate artificial lighting the day/night temperature regime of 20/8°C did not affect pollen viability. However, under natural lighting the same temperature regime (Philouze and Maisonneuve 1978; Maisonneuve *et al.* 1982a), as well as a combination of low day/night temperatures (6-7°C day/7-8°C night), resulted in low pollen viability (Maisonneuve 1982). These results imply a direct impact of light efficiency and assimilate availability on the severity of temperature stress on microsporogenesis.

In pepper, Pressman *et al.* (2006) reported that the exposure of plants to extremely high temperatures (36 ± 2°C), which were obtained by keeping the greenhouse closed during the day, alleviated the negative effects of low night temperature (10 ± 2°C) both on vegetative development and on the quantity and quality of pollen, resulting in better growth and male fertility than in plants grown under optimal temperatures (23 ± 2°C/18 ± 2°C day/night). These results may encourage the development of novel procedures for climate control in greenhouses of regions like the Mediterranean basin, where cold nights in winter are often followed by bright and sunny days (Pressman *et al.* 2006). According to Bakker (1989a), flowering and fruit-set in pepper are closely related to the 24-h mean temperature, over the range 16-24°C, although a positive effect of the amplitude of day and night temperatures on fruit-set has been observed. In tomato too, high day/night temperature amplitudes for a given 24-h mean temperature improve fruit-set and increase total yield, because of higher assimilation during the day and lower dissimilation and respiratory rates at moderately low night temperatures (Peet and Bartholomew 1996; Willits and Peet 1998).

Carbohydrate metabolism and male fertility under temperature stress: Acute environmental stress, such as extremely low or high temperatures, drought and boron deficiency, reduce the male fertility of several crops mainly through an effect on microspore meiosis and the disruption of pollen development at an early stage (Dorion *et al.* 1996; Saini 1997; Huang *et al.* 2000), decreasing pollen production and increasing the formation of misshapen, shrunken and infertile pollen grains. However, less intense environmental stress, such as moderately high day and night temperatures or moderately low night temperatures, also impair pollen fertility even if the quantity of pollen produced is not seriously affected (Aloni *et al.* 2001; Pressman *et al.* 2002; Shaked *et al.* 2004; Firon *et al.* 2006).

Pollen development and viability is directly related to the availability of carbohydrates because the developing pollen grains accumulate simple sugars (Pacini 1996). Tomato and pepper pollen have a similar pattern of carbohydrate metabolism during development. Sugars accumulate during the first stages of development, and starch is synthesized 3-4 days before anthesis, reaching a maximum level 2-3 days before anthesis, but thereafter is degraded so that mature pollen grains at anthesis contain no starch. On the other hand, sucrose accumulates from the 4th day before anthesis until anthesis. Starch biosynthesis and hydrolysis at the final stages of microsporogenesis is crucial for the germinability and viability of pollen grains (Polowick and Sawhney 1993; Pacini 1996; Aloni *et al.* 2001; Pressman *et*

al. 2002; Firon *et al.* 2006).

Low temperatures adversely influence the carbohydrate content of tomato flowers, thus limiting the supply of carbohydrates to the developing pollen (Philouze and Maisonneuve 1978; Maisonneuve *et al.* 1982a; Maisonneuve 1982; Picken 1984). This effect is strongly correlated with the levels of solar radiation, which in turn determine the availability of assimilates. In tomato (Dinar and Rudich 1985a) and pepper (Aloni *et al.* 1991), heat stress causes a reduction in sucrose translocation from the photosynthesizing leaves to the flower, thus negatively affecting its development and fertility.

In pepper, low night temperatures (10 ± 2°C) resulted in a two-fold reduction of starch accumulation and a four-fold increase in the concentration of sucrose and reduced sugars (glucose and fructose) in developing pollen grains 3-4 days before anthesis, compared to pollen grains developing under optimal night temperatures. In contrast, the sugar content of the mature pollen grains at anthesis was significantly lower, thereby negatively affecting viability (Shaked *et al.* 2004; Pressman *et al.* 2006). In these pollen grains, there was >50% reduction in cell wall-bound and soluble acid invertase, suggesting an impairment of carbohydrate supply from the anther to the developing pollen under cold stress (Pressman *et al.* 2006).

The combination of moderately high day temperatures (32°C) and high night temperatures (26°C) also reduced the starch content of developing tomato pollen three days before anthesis, resulting in less soluble sugar in the mature pollen and therefore low pollen viability (Pressman *et al.* 2002; Firon *et al.* 2006). Under the same temperature regime, Aloni *et al.* (2001) observed reduced acid invertase activity and starch degradation during the late stages of pepper microsporogenesis, so that one day before anthesis the pollen grains contained more starch and sucrose and less hexose than pollen formed under normal conditions. These observations differ from previous ones on the effects of low night temperatures on the starch and sugar content of pepper pollen, indicating a different mode of carbohydrate metabolism disturbance by different forms of stress, or alternatively cultivar specificity (Shaked *et al.* 2004).

Unlike heat temperature stress, which negatively affects both photosynthesis and the translocation of assimilates to developing flowers in tomato (Dinar *et al.* 1983; Dinar and Rudich 1985a, 1985b), moderately high temperature stress did not influence the carbohydrate transfer from the leaves to the anthers, but limited the hydrolysis of sucrose through acid invertase to hexose within the anthers, thus resulting in a reduced supply of glucose from the anthers to the developing pollen. Glucose supply is essential during microsporogenesis, because it provides developing pollen grains with the *α*-1,4 bonds for starch synthesis (Sato *et al.* 2006). Stress in tomato due to exposure to moderate temperatures did not result in a lack of assimilates because the photosynthetic rate was not affected (Peet *et al.* 1997; Sato *et al.* 2006), but the consumption of carbohydrates during high night respiration (Sato *et al.* 2000) was higher. Therefore, it is likely that this form of stress negatively affects the supply of carbohydrates to developing pollen grains from the tapetum (Peet *et al.* 1998; Sato *et al.* 2000, 2001, 2002), but (unlike extremely high temperatures) does not alter the degeneration of tapetum (Sato *et al.* 2006). This phenomenon is genetically dependent, since Firon *et al.* (2006) found a positive cultivar-related correlation between male-fertility and pollen grain starch content three days before anthesis, as well as between fertility and the concentration of total soluble sugars in mature pollen.

Apart from carbohydrate metabolism, the combined application of moderately high day temperatures (32°C) and high night temperatures (26°C), negatively affects the supply of pollen grains with other essential elements, amino acids and, especially, proline, which is considered to be a key factor for pollen viability. Sato *et al.* (2006) reported lower proline concentrations in both microspores at the meiosis stage and mature pollen under moderately high temperature stress. It is likely that high night temperatures (26°C) cause this, because in *Vigna sinensis* pollen Mutters and Hall (1992) observed that proline transfer to the developing pollen takes place late at night and is reduced by high night temperatures (>24°C).

Effect of adverse temperatures on anther dehiscence, pollen release and pollination in relation to style length

Temperature stress impairs the processes leading to the transfer of pollen to the stigma. In general, tomato, pepper and eggplant are self-pollinated and self-compatible. So, adverse temperatures impair pollination mainly by altering style length relative to anther length, and in consequence the proximity of the stigma to the apex of the anther cone (Rylski 1973; Fernandez-Muñoz and Cuartero 1991; Nothmann *et al.* 1983; Kowalska 2006).

Low night temperatures (about 10°C) do not impair the release of tomato pollen from the anthers (Robinson *et al.* 1965), even though they induce a slight elongation of the stigma above the anther cone (Charles and Harris 1972). By contrast, high temperatures (>32°C) seriously affect tomato fruit-set, either by limiting pollen release from the anthers due to the failure of endothecium rupture (Iwahori 1965; Charles and Harris 1972; Shelby *et al.* 1978), the prevention of anther cone formation (Levy *et al.* 1978), the induction of heterostyly and/or a reduction in stigma receptivity (Charles and Harris 1972; El Ahmadi and Stevens 1979).

Under moderately high day temperatures (not more than 32°C) and night temperatures that do not exceed 22°C, insufficient pollination is evidently the main reason for reduced fruit-set, since pollen and ovule viability, pollen germination and the functionality of the gynoecium are not impaired (Shelby *et al.* 1978; Dane *et al.* 1991). At 32°C (day) and 26°C (night), impaired carbohydrate metabolism in the anthers restricts anther growth, resulting in short anthers and style exsertion (Sato *et al.* 2006), poor anther dehiscence and pollen release (Sato *et al.* 2000, 2002; Sato and Peet 2005). Therefore, under such conditions although fruit-set does not correlate well with the total production of pollen, it is closely related to the number of pollen grains released by anthers (Sato *et al.* 2000). According to Matsui *et al.* (2000), under normal conditions, the rapid swelling of pollen grains at maturation is the driving force for the final rupture of the septum and the splitting of the stomium and locule of the anther, thus leading to anther dehiscence and pollen release. However, under moderately high temperatures, the production of irregular-shaped and flattened pollen grains due to the impaired supply of carbohydrates, leads to the failure of anther dehiscence. This phenomenon is highly genotype-dependent and is also influenced by other climatic factors, such air movement (Sato and Peet 2005).

Style extension seems to be the dominant factor reducing tomato fruit-set under conditions of low light, short daylength and moderately high day temperatures (27°C) in plants sufficiently supplied with nitrogen (Charles and Harris 1972; Rudich *et al.* 1977; Levy *et al.* 1978; El Ahmadi and Stevens 1979), although Fernandez-Muñoz and Cuartero (1991) consider that temperature, not light intensity, is mainly responsible for stigma exsertion above the anther cone.

In pepper, low temperatures (8-10°C) during flowering induce style extension (Rylski 1973), whereas under moderately cold stress the formation of short styles and deformed stamens as well as flower swelling are common, impairing the proximity of the stigma to the anthers (Polowick and Sawhney 1985; Aloni *et al.* 1999).

Although the morphology of the eggplant flower, and in particular style length, determines fruit-set, experimental data on the effect of environmental conditions on flowering pattern and the occurrence of long-styled flowers are scarce. In general low temperatures reduce the occurrence of short-styled flowers, but their effect is genotype-dependent

(Nothmann *et al.* 1983).

Effect of temperature and RH on stigma receptivity, in vivo pollen germination and pollen tube growth

Although Calvert (1964) reported that in some tomato varieties night temperatures below 12.5°C adversely affect *in vivo* pollen germination, it has subsequently been shown that microsporogenesis is affected more than germination. Thus, pollen produced under favourable temperatures germinates satisfactorily *in vivo* at 10°C and pollen tubes reach the ovary (Shannon *et al.* 1965). Indeed, pollen germination on the stigma has been observed even at 5°C (Dempsey 1970). In pepper, Pressman *et al.* (1998a) suggested that low temperatures (<14°C) impair the functioning of the stigma, possibly by altering the chemical composition or decreasing the quantity of stigmatic fluid and thus reducing the availability of nutrients for pollen germination and pollen tube elongation..

Generally, temperatures above 30°C have a negative impact on pollen tube growth (Vasil 1987), although the pollen of 'Tabasco' peppers (*Capsicum frutescens* L.) germinates well *in vitro* at 35-40°C (Johri and Vasil 1961). At high temperatures the diameter and rigidity of the walls of the pollen tubes increase, resulting in swelling and even bursting of the pollen tube tip (Vasil 1987). Although the growth rate of tomato pollen tubes increases with temperature up to 35°C, pollen germination is inhibited at >37-38°C. So, the exposure of tomato flowers to 40°C, 18 hours after pollination, led to ovary abortion and endosperm degeneration due to the inhibition of pollen tube growth and a failure of fertilization (Iwahori 1966).

High temperatures are also detrimental for the *in vitro* germination of tomato pollen. Song *et al.* (2002) reported that pollen tube growth *in vitro* ceased quickly at temperatures >34°C, while the upper limit for *in vivo* pollen germination of tomato cultivated in open field is 38°C (Dempsey 1970). High temperatures negatively affect the activity of the enzyme S-adenosylmethionine decarboxylase (SAMDC) which regulates polyamine bioynthesis. Therefore, the application of the polyamines spermidine and spermine to open flowers before pollen release, as well as their incorporation in artificial germination media, alleviate the inhibition of *in vivo* and *in vitro* tomato pollen germination by high temperatures (Song *et al.* 2002).

In our laboratory, it was observed that high temperatures (>30°C) adversely affect *in vitro* germination and pollen tube growth of tomato (Karapanos *et al.* 2006), as well as the course of respiratory activity during 8 hours incubation (Karapanos 2007). During hydration at 30-35°C, the initial respiration rate of tomato pollen is high, but after 1-2 hours respiratory activity decreases, whereas at 15-20°C pollen respiration is linear over the 8 hour incubation period. The respiratory response is influenced by the season of pollen collection, since pollen formed under unfavourable climatic conditions showed a greater reduction in respiratory activity over time at high temperatures (Karapanos 2007).

During *in vivo* pollen tube growth, the pollen tube is supplied with carbohydrates derived from the hydrolysis of starch in the style tissues. Under moderately high temperatures, the availability of stylar carbohydrates is reduced, thus adversely affecting pollen tube growth. This phenomenon can be alleviated after a short period of relief at normal temperatures (Sato *et al.* 2002).

RH is an environmental factor that seriously affects the pollination and fruit-set of Solanaceous crops, in particular those grown in greenhouses. Since air movement in greenhouses is often low, RH crucially affects the ease of pollen grain release from the anthers. In addition, RH affects stigma receptivity by preventing or inducing drying. In tomato, high RH results in adhesion of pollen grains within the anthers and reduces the amount of pollen reaching the stigma. On the other hand, RH <70%, especially when combined with temperatures far from the range 17-24°C, reduces the ability of pollen grains to adhere to the stigmatic surface

(Picken 1984).

Bakker (1989b) indicated the significance of air humidity for the production of greenhouse peppers, stating that when temperature is not a limiting factor, flowering, fruit-set, seed-set and fruit growth are determined by the RH inside the greenhouse. He found significantly increased fruit-set with high RH during the daytime, whereas night-time RH did not affect fruit-set. However, the number of fruits per plant was increased by low RH during the night, most likely because of higher flower production. Therefore, according to Bakker (1989b), for both increased fruit-set and total yield it is desirable to maintain the RH inside the greenhouse at high values (80-90%) during the day and low (60-70%) during the night-time. Because pepper pollen is released from the anthers 2-8 hours after sunrise, low RH during the night promotes pollination, whereas higher RH during the day promotes pollen germination on the stigma. The significance of air RH for pepper pollination and pollen germination was also shown by Baër and Smeets (1978), who found that artificial pollination obviated the effects of air RH on fruit-set and seed-set. In addition, high air RH over a 24 h day period enhances flower abscission during the early production period, while high RH at night decreases the number of open flowers (Bakker 1989a).

In long-styled flowers of eggplant, low RH coinciding with high daytime temperatures may result in stigma drying, thus reducing stigma receptivity and/or *in vivo* pollen germination (Passam and Bolmatis 1997). Additionally, Sun *et al.* (1990) found negative linear relationships between the fruit setting rate of eggplant cultivated during the summer and the average maximum temperature and precipitation. Fruit-set decreased by 0.83% and 5.89% when maximum temperature increased by 1°C over the range 28-34°C, and precipitation (up to 60 mm) by 1mm respectively, during the first five days of flowering, suggesting that the climatic conditions affected mainly the processes of pollination and fertilization. However, the effects of these two factors seemed to be separate and additive, since there was no interaction between them (Sun *et al.* 1990).

Adverse temperatures and ovule viability

Research on the effect of adverse environmental conditions on gynoecium functionality in general and on the viability of ovules in particular (female fertility) is limited to tomato, since to date only suggestions, and not experimental observations have been made for pepper and eggplant.

In tomato, low night temperatures are not detrimental for megagametogenesis (ovule development) and gynoecium functionality in general (Iwahori 1965, 1966). Plants exposed to night temperatures of 10°C were more fertile when used as female parents, and pollen was derived from plants grown under normal temperature conditions (Robinson *et al.* 1965; Shannon *et al.* 1965; Charles and Harris 1972). At even lower night temperatures (6°C, in combination with optimal day temperatures of 27°C) ovule viability was not impaired (Fernandez-Muñoz and Cuartero 1991). In pepper, it was suggested that low night temperatures limited the fruit and seed-set of artificially pollinated flowers of a susceptible variety, due to a negative effect on stigma and style functioning rather than on ovule viability, even though no experimental observations on these processes were made (Pressman *et al.* 1998a).

The combination of moderately high day temperatures (32°C) and high night temperatures (26-28°C) does not impair the development and fertility of tomato female reproductive organs (Peet *et al.* 1998). However, under day temperatures not exceeding 28°C, high night temperatures (>23°C) limit tomato fruit-set (Rylski 1979), mainly because of their detrimental effect on the functionality of the female reproductive organs (Peet and Bartholemew 1996; Willits and Peet 1998), possibly due to low carbohydrate content of flowers and hormonal imbalances (Willits and Peet 1998; Pressman *et al.* 2002).

Ovule development and fertility seem to deteriorate

when day temperatures are very high. At 40°C tomato megagametogenesis was impaired, whereas at 33°C no significant loss of embryo sac viability occurred (Iwahori 1965; Sugiyama *et al.* 1966). In a comparative study, the ovules of tomato were found to be more tolerant to high temperatures than pollen (Iwahori 1966; Charles and Harris 1972; Levy *et al.* 1978), although this effect appears to be genotype-dependent (El Ahmadi and Stevens 1979). Similarly, in pepper Han *et al.* (1996) and Peet *et al.* (1998), report that high temperatures limit fruit-set mainly via detrimental effects on pollen function and to a lesser extent on the maternal organs. It should be noted, however, that a lack of tomato fruit-set under extreme high temperatures (40°C) may also be caused by endosperm degeneration 24-96 hours after pollination, or even after successful fertilization (Iwahori 1966).

Light and the availability of assimilates affect pollination and fertilization of the Solanaceae

As with temperature, crops experience stress from both high and low irradiation. In northern Europe during winter, low light is a serious limiting factor for the Solanaceae grown under cover (thus supplemental lightning is often used), whereas in the Mediterranean basin during summer very high irradiance levels negatively affect the yield and quality of these crops in the greenhouse or in the field. For instance, irradiance of 0.7-1.54 MJ m^{-2} day^{-1} is typical for glasshouses of Holland during the winter (Bakker and Van Uffelen 1988), compared to 28 MJ m^{-2} day^{-1} in the field in Israel during summer (Rylski and Spigelman 1986a).

Marr and Hillyer (1968) observed abnormalities in tomato flowers formed under low light conditions (obtained by shading at 30, 45, 63%), such as splitting of the staminate cone, failure to develop a smooth cone, an increase in space between the anthers at their point of attachment to the flower, uneven rounding of the ovary and even elongated ovaries with fasciated stigmas and styles, resulting in oval shaped and 'cat-faced' fruit. The frequency of abnormal flowers and the severity of abnormalities were positively related to shading. According to Marr and Hillyer (1968), carbohydrate deficiency under low light may cause anther deformation, whereas abnormalities in the ovaries may arise from impaired N metabolism under shading. Moreover, it is well documented that low light (especially when combined with moderately high temperature) stimulates the exsertion of the style beyond the staminal cone of tomato flowers (Marr and Hillyer 1968; Charles and Harris 1972; Fernandez-Muñoz and Cuartero 1991).

Under conditions of low light, carbohydrate deficiency causes irregular meiosis of tomato pollen mother cells, whereas under less severe carbohydrate deficiency, pollen production and viability exhibit variability between flowers of the same cluster. In pepper, 80% shading for 6 days resulted in an increase in the abscission of flower buds and flowers, the seriousness of which varied with the cultivar. Abscission in pepper relates not only to carbohydrate levels (Aloni *et al.* 1996), but also to a significant increase in ethylene concentration in the buds of shaded plants (Wien *et al.* 1989). The differential response of pepper cultivars to flower retention and fruit-set under low light conditions may also be ascribed to the flower's capacity to accumulate sugars and starch during the day, as well as to assimilate partitioning in the flower buds (Turner and Wien 1994; Aloni *et al.* 1996).

Aloni *et al.* (1997) found the enzymes acid invertase and sucrose synthase to be responsible for the metabolism of imported sucrose and the accumulation of starch in the ovaries of pepper flowers. The activity of these sucrose-cleavage enzymes appeared to respond to light conditions. For example, increasing light intensity caused a slight decrease in acid invertase activity but enhanced sucrose synthase activity, thus increasing the concentration of sucrose, reducing sugars and starch. Also, exogenous feeding of flowers with sugars (sucrose, glucose and fructose) reduced

flower abortion, thus providing further evidence that sucrose entry into the flower sink is of great importance for flower set.

Heuvelink *et al.* (2004) observed an increase in pepper fruit set from 25 to 92% when the PAR irradiance was raised from 1.1 to 4.8 MJ m^{-2} day^{-1} in glasshouses in the Netherlands. On the contrary, shading (12, 26 and 47%) alleviated the stress by extreme irradiation during summer in a pepper field crop, and resulted in better vegetative development, increased seed-set, a higher number of seeds per fruit, higher mean fruit weight, size and pericarp thickness, and reduced the occurrence of sunscald. Yield and quality were better at 12 and 26% shading, whereas 47% shading reduced the number of fruits per plant, possibly because of lower fruit-set (Rylski and Spigelman 1986a). The abortion of pepper flowers due to low light or shading is occasionally desirable, since a heavy load of developing flowers and fruit at the lower pepper nodes results in serious fluctuations in yield (Heuvelink *et al.* 2004). Hence, the abortion of flower buds at the lower nodes caused by low light intensity or shading favours continuous plant growth, flowering, and fruit-set at the higher nodes, resulting in a longer fruiting period (Rylski and Spigelman 1986b).

Similarly, eggplants grown under high night temperatures or low light intensity in greenhouses exhibit retarded flower development, reduced flower size, small ovaries and short styles, which lead to heavy flower drop, (Saito and Ito 1973). Insufficient light, or shading, are reported to negatively affect vegetative growth, flowering and fruit-set of eggplant (Wang *et al.* 1980). Although research on the implications of light and assimilate availability for flowering and fruit-set of eggplant is scanty, it is clear that, as in tomato and pepper, limited light conditions are detrimental to flowering, fruit set and yield (Nothmann 1986; Passam and Khah 1992; Nkansah 2001; Khah *et al.* 2002).

Temperature stress, production of heat shock proteins and their implications for fruit-set in the Solanaceae

It has been observed that vegetative tissues exposed to extremely high temperatures produce heat shock proteins (hsps), which enhance the tolerance of these tissues to this form of thermal stress. In developing pollen, (especially the single-celled microspores) a subset of hsps is produced in response to heat stress, whereas the mature pollen of many plant species (e.g. *Zea mays* L., *Lilium longiflorum* Thunb., *Tradescantia paludosa* E.S. Anderson & Woodson) either does not produce hsps, or produces only a subset of hsps (e.g. *Sorghum* pollen when germinating *in vitro* at 42°C). So, the response of reproductive tissues to high temperatures in terms of hsps production is significantly less than that of the vegetative tissues (Frova *et al*. 1991; Mascarenhas and Crone 1996).

In immature pollen, even under favourable conditions of development, some genes encode hsps or heat shock cognate (hsc), suggesting that these genes are likely to encode further during pollen development (Mascarenhas and Crone 1996), even in the absence of thermal stress. This observation is consistent with that of Duck *et al.* (1989), who found intensive expression of hsc (*hsc70*) in immature anthers, developing microspores and other tissues of tomato plants, but not in germinating pollen even under thermal stress. According to Duck and Folk (1994) the proteins encoded by these hscs are possibly implicated in the transfer processes of tapetum elements to developing microspores, but not in thermal tolerance of mature tomato pollen. Despite the correlation of hsp synthesis in developing pollen with thermal tolerance, the inability of germinating pollen to synthesize hsps, is evidently responsible for the greater susceptibility of pollen to high temperatures once germination has been initiated. Moreover, although hscs are thought to act similarly to hsps under heat stress, and their presence in mature pollen is substantially higher than that of hsps, the accumulation of hscs is not adequate to provide thermal tolerance

(Mascarenhas and Crone 1996).

On the other hand, the 'compensation effect' of high temperatures in alleviating the detrimental effects of low night temperatures on pepper male fertility, could be attributed to a possible involvement of hsps produced under heat stress in protecting pollen development and function under low night temperatures (Pressman *et al.* 2006). The induction of hsps under heat stress and their involvement in protecting the developing pollen, as well as other organs, from the adverse effect of low night temperatures are currently under investigation (Pressman *et al.* 2006). However, it is likely that the mechanism of the 'compensation effect' involves more processes than just the production and involvement of hsps (Kaplan *et al.* 2004), for example signalling molecules and compatible solutes, or an interrelationship between hsps and osmolytes (Diamant *et al.* 2001).

Methods for increasing fruit-set under adverse climatic conditions

In the glasshouses of Northern Europe during winter, light is the limiting factor for fruit-set, since heating can overcome low temperatures. However, in most of the simple-structured greenhouses in the Mediterranean basin, during winter heating (when available) is applied only to protect the crop from frost, whereas in late-spring and summer crops may be subjected to extremely high temperatures and a lack of air movement due to poor climate control.

Several methods are employed to increase the fruit-set of the Solanaceae under unfavourable climatic conditions. In Mediterranean greenhouses, three techniques are mostly in use: (1) The introduction of bumblebee (*Bombus terrestris*) to the greenhouse, (2) Mechanical pollination by vibration, using an 'electric bee', and (3) The application of growth regulators, mainly auxins. In the glasshouses of Northern Europe, the most common aid to fruit-set is the use of bumblebees for improved pollination and CO_2 enrichment to counteract the deficiency of assimilates due to low light conditions.

Bumblebees can replace manual vibration for tomato pollination (van Ravestijn and van der Sande 1991) and are thought to be more effective than honey bees, especially in the Mediterranean region, because they forage at higher temperatures (Banda and Paxton 1991; Velthuis and van Doorn 2006). According to Velthuis and van Doorn (2006), 95% of all bumblebee sales worldwide are made to greenhouse tomato growers, which comprise a total of over 40,000 hectares. In pepper, other pollinating insects, such as honey bees, thrips, *Examalopsis* (Crane and Walker 1984) and *Bombus impatiens* (Shipp *et al.* 1994), improve fruit set and seed formation, but the use of *Bombus terrestris* is recommended for greenhouse pepper crops during winter and spring (Abak *et al.* 1997) since it not only enhances yield but also fruit quality (Roldán Serrano and Guerra-Sanz 2006).

The efficacy of bumblebees or the 'electric bee' depends on the production of viable pollen. In tomato, for example, if pollen production is adequate and the greenhouse is well ventilated, the contribution of these methods is marginal (Pressman *et al.* 1999). On the contrary, with medium pollen production, fruit-set can be improved significantly by bumblebees or frequent 'electric bee' vibrations. However, when pollen production is low, these two means can ensure only partial fruit set, and other methods (e.g. the application of growth regulators) should be considered (Pressman *et al.* 1999). Experimental data from our laboratory (Karapanos unpublished results) showed that under low night temperatures (<10°C), which induced male sterility in cherry tomato, only the application of NOA at 25 or 50 ppm led to the setting of normal sized, seedless fruits, whereas vibration with an 'electric bee' increased fruit-set, but resulted in small non-marketable fruits. However, climatic conditions that impair male fertility also limit bumblebee activity, because at temperatures <10°C or >32°C they stop foraging (Velthuis and van Doorn 2006).

Due to its flower structure, eggplant pollination requirements are different to those of tomato or pepper. Successful self-pollination in eggplant is strongly dependent on the proximity of the stigma to the anther pores and the transfer of pollen to stigma is hindered under greenhouse conditions of low air movement, lack of insects as pollinators and high humidity (Passam and Bolmatis 1997). Although many insect species visit eggplant flowers, the most efficient pollinators are honey bees and bumblebees (Amoako and Yeboah-Gyan 1991; Abak and Guler 1994; Abak *et al.* 1995, 2000; Miyamoto *et al.* 2006). Bumblebees are more efficient eggplant pollinators than the 'electric bee', giving about 25% higher yield in unheated plastic greenhouses in the Mediterranean region, and their efficiency during winter is increased if the greenhouses are heated to >12°C at night (Abak *et al.* 2000). Honeybees (*Apis mellifera*) visiting eggplant flowers, result in a high rate of pollen transfer, an increased number of seeds per fruit, and improved fruit-set, because they agitate the anthers tips repeatedly with their forelegs and mouthparts and they forage on 65-82% of the total pollen per flower (Miyamoto *et al.* 2006). Amoako and Yeboah-Gyan (1991) found that eggplant flowers pollinated by honey bees produced not only a significantly higher fruit yield but also more uniform fruit ripening. From these reports it may be concluded that honeybees are more efficient pollinators for eggplant than for tomato and pepper.

Plant growth regulators are also used as fruit-setting agents in tomato and eggplant, resulting in the production of seedless fruits, when natural pollination and fertilization is not functioning. In tomato the use of hormones is not encouraged because fruit quality decreases. Fruit size is often reduced in parthenocarpic fruits (Mapelli *et al.* 1978). Puffiness or hollowness (Rylski 1979), as well as malformations (oblate, fascinated, carpel protrudent and cat faced fruits) (Asahira *et al.* 1982), have been observed in seedless tomato fruits set by auxin. Although parthenocarpic fruits have been reported to have higher soluble solids (Falavigna *et al.* 1978), their acidity is lower, possibly because of the absence of locular tissue, a fact that could have an adverse effect on flavour, as a strong relationship between locular content of fruits and flavour has been shown (Stevens *et al.* 1977).

Moreover, in pepper although some substances induce parthenocarpy, they produce flattened, non-marketable fruits. For example, when NAA was applied to pepper stigmas, seedless fruit were set, but did not elongate, so that the mature fruit was flat and 30% lighter than that of seeded fruit (Heuvelink and Koner 2001). Similarly the application of STS, TIBA and AOA, resulted in flower and fruit malformation (Aloni *et al.* 1995; Pressman *et al.* 1998b). Foliar spraying with NAA or infusion of NAA or GA_3 and BA in pepper ovaries under low light stress, did not promote fruit-set, but led to flower abscission, possibly due to the induction of ethylene synthesis (Wien and Zhang 1991).

In tomato, different genotypes carrying genes for parthenocarpy have been discovered or selected, such as *pat*, *pat-2*, and *pat-3/pat-4* (Philouze 1983; Lukyanenko 1991). In these three genetic systems, the mechanism necessary for fruit set and development seems to be switched on before pollination and fertilization (Mazzucato *et al.* 1998). However, traditional plant breeding has so far exploited the parthenocarpic trait only in a few cultivars and none are grown commercially (Ho and Hewitt 1986; Ficcadenti *et al.* 1999). In pepper, although parthenocarpy occurs, subsequent fruit development is impaired and fruit quality is unacceptable (Rylski 1973; Pressman *et al.* 1998a).

On the other hand, natural parthenocarpy is a very useful, desirable and relatively common trait in eggplant. The occurrence of parthenocarpic eggplant fruit was mentioned as early as 1891, and several breeding programs have been conducted in order to introduce new parthenocarpic eggplant cultivars (Restaino *et al.* 1992; Hennart 1996). However, the parthenocarpic eggplant cultivars so far available still need plant hormone applications to produce fruits of marketable size (Leonardi and Romano 1997). Recently, a

parthenocarpic eggplant F_1 cultivar, 'Talina' was introduced and is now cultivated widely in Europe (Donzella *et al.* 2000; Acciarri *et al.* 2002), whereas in Japan the parthenocarpic trait of 'Talina' was introduced into the Japanese cultivars 'Nakate Shinkuro' and 'Nasu Chuukanbohon Nou 1' (Saito *et al.* 2005).

In the last decade transgenic parthenocarpic plants have been obtained for tomato (Ficcadenti *et al.* 1999; Carmi *et al.* 2003; Rotino *et al.* 2005) and eggplant (Donzella *et al.* 2000), using the chimeric gene *DefH9-iaaM* which drives parthenocarpic fruit development in several species belonging to different plant families, by promoting the synthesis of IAA, specifically in the placenta, ovules and tissues derived there from (Rotino *et al.* 1997; Ficcadenti *et al.* 1999). The performance of these tomato and eggplant transgenic parthenocarpic crops has been assessed in field and greenhouse trials. In tomato, under open field conditions, the transgenic plants showed a high capacity to produce parthenocarpic fruits, with quality characteristics comparable to non-seeded fruits. Total yield was not significantly different from that of non genetically-modified plants, although mean fruit weight was lower (Rotino *et al.* 2005). Similarly, in unheated greenhouses in the Mediterranean region during winter, genetically-modified parthenocarpic eggplants produced on average 33% more fruit than commercial, non-parthenocarpic and parthenocarpic cultivars treated with hormones, while cultivation costs were 10% less, due mainly to a reduction in labour for hormone application (Donzella *et al.* 2000). Similarly, Acciari *et al.* (2002) reported that transgenic *DefH9-iaaM* eggplants show at least 30-35% improved fruit productivity under both greenhouse and open field cultivation, irrespective of the cultivation season, and the seedless fruit have improved quality.

CONCLUSIONS – FUTURE PROSPECTS

Environmental conditions have a substantial impact on the yield and quality of tomato, pepper and eggplant grown under cover or in the field, not only because of their effect on assimilation, but also due to their influence on the reproductive processes leading to successful pollination, fertilization, fruit set and yield. In this review, an attempt has been made to assemble the information so far available, concerning the effect of climate on flower morphology and fertility in tomato, pepper and eggplant, in order to elucidate the mechanisms and physiology of impairment of floral functionality under stress conditions.

From the aforementioned, it is clear that adverse climatic conditions limit fruit-set in the Solaneceous fruit vegetable crops mainly by impairing male gametophyte fertility and secondly by hindering pollination and the functionality of the gynoecium. The production and viability of pollen grains are limited either by a possible malfunction of the tapetum, or by impaired carbohydrate metabolism and translocation, leading to a deficient supply of assimilates to the developing pollen. It should be noted that male fertility of the Solanaceous crops and other plant species is similarly affected by climatic as well as other environmental, abiotic stresses such as water deficit, drought stress, boron deficiency, etc., implying that the same mechanisms of reproductive physiology in plants are susceptible to environmental stresses.

The improvement of climatic control in modern greenhouses and the use of bumblebees as pollinators, natural gas for heating and additional lightning (particularly in Northern Europe) have helped restrict the negative consequences of extreme temperatures and low light on fruit-set. However, global warming and the more frequent occurrence of short episodes of extreme temperatures due to the greenhouse effect, emphasise the importance of continued research in this field.

Several cultural practices are employed to improve fruit-set under unfavourable climatic conditions, including the use of cultivars with good floral fertility under such conditions, parthenocarpic cultivars, hormones, 'electric

bee' vibrators or the introduction of bumblebees to the crop. Some methods are more effective or more costly than others, whereas their efficacy is still dependent on climatic factors. Cultural practices, such as the elevation of day temperature so as to alleviate the negative effects of low night temperatures on floral fertility (Pressman *et al.* 2006), may offer a novel way of increasing production and quality in greenhouses, while at the same time economising on energy. The importance of temperature stress, irradiance and RH to greenhouse production of tomato, pepper and eggplant indicates the need for more research on this subject.

Current breeding programmes focus on the production of cultivars capable of setting fruit under adverse climatic conditions and on the incorporation of genes leading to parthenocarpic fruit-set, mainly through genetic engineering. Although the wild relatives of the Solanaceous crops represent a pool of genes for tolerance to temperature stress, there are not enough experimental data on the physiological factors which are responsible for the ability of some tomato genotypes to produce viable pollen under adverse temperature. Apart from the selection of resistant genotypes, it is necessary to recognise and isolate genes that confer floral fertility under stress and to incorporate these into commercial cultivars. Introduction of genetically modified parthenocarpic tomatoes and eggplants with good agronomic characteristics shows that improvement of Solanaceous crops through genetic engineering is a promising approach, albeit one that may still pose a threat to the environment or even human health. Finally, the physiological causes underlying resistance to heat/cold stress in tolerant lines should be further investigated so as to include this characteristic in breeding programmes.

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