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Crop Cycle Influences the Effectiveness of Pollination Techniques in Greenhouse Tomato

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Summary

Fruit set limits the productivity of the tomato crop in the greenhouse. In North Mediterranean conditions two tomato crop cycles can be carried out in the same year. Environmental constraints limiting pollination in the cycles may impose the use of different pollination techniques, both from the productive and from the economical point of view. The aim of this study is to analyze whether flower vibration, bumblebee pollination, or auxin spraying, improve fruit production of early and late tomato greenhouse crops.

Treatments were more effective in the early crop, carried out in spring, than in the late one in summer-autumn. For both crop cycles, the highest production was for the bumblebee pollinated plants. The mechanical flower vibration technique and the auxin treatment significantly increased production in the early crop, but they were ineffective in the late cycle crop. However, treating the early crop with auxins may result in nipple-shape fruits. Earliness was not affected by the treatments. Fruit set was improved by all treatments tested and in both crop cycles. In both seasons, the use of bumblebees was the most successful treatment, and the maximum effectiveness was observed during the periods of low night temperatures in the early cycle, when fruit set was limited due to impaired production of viable pollen and/or poor pollen release. Auxin and vibration enhancement of fruit set was higher for the early than for the late crop cycle. The environmental conditions were determinant for the effectiveness of the treatments. Moreover, the bumblebee efficiency was demonstrated not only when the climatic factors were limiting for tomato fruit set, but also when fruit-set was not limited by natural climatic conditions.

Key words. auxins – bumblebees – *Lycopersicon esculentum* – mechanical vibrator

Introduction

The tomato production and quality decreases when plants are cultivated out of the main season, either in the field or in unheated greenhouses. One of the major causes for this poor crop performance is the incomplete fruit set. The typical commercial flower morphology determines that self pollination is the main pollen transfer system, while the level of cross pollination in the field is very low (Groenewegen et al. 1994). As tomato flowers do not produce nectar, they are not frequently visited by insects.

Flower or plant shaking helps releasing the pollen grains from the anthers and transferring them to the stigma, therefore, assuming that viable pollen is produced, high self-pollination and fruit set rates are obtained (Rylski 1979; Geisenberg and Steward 1986). In the open field the wind is usually responsible for this activity; in the greenhouse, without wind and with few insects, the flower pollination and the corresponding fruit set is inadequate (Shelby et al. 1978). A plant protection technique, now in use in Mediterranean greenhouses, is the covering of the greenhouse openings with insect proof screens, thereby reducing the natural greenhouse ventilation (Muñoz et al. 1999) and the permeability of the greenhouse to the outside natural pollinators. As a result, pollination is restricted to a greater degree.

Low temperatures in winter and early spring (Picken 1984; Baytorun et al. 1999), and high temperatures in summer (Peet and Bartholomew 1996), have also negative effects on pollination and fruit set. These environmental constraints, among others, alter the pollen grain development, transfer, and germination, and also the fertilization of the ovary. If pollination and fertilization is not achieved, the flower will either abort (Ho and Hewitt 1986) or, under specific environmental conditions, produce parthenocarpic fruits (Rylski 1979). These seedless fruits are usually slow growing and will be smaller than the normal pollinated fruits (Abad and Guardiola 1986).

Different approaches for improving tomato pollination and fruit set are applied. In the Mediterranean greenhouse systems, three techniques in use are under discussion: a) establishing bumblebee (*Bombus terrestris*) hives in the greenhouse, b) mechanical pollination by vibration with an "electric bee", and c) spraying flower clusters with plant growth regulators, mainly auxins. Other pollination methods, such as the use of honeybees, air blowers, and manual or automatic shaking of the overhead wires, are seldom used. Any of these systems represent an economic cost. Velthuis and Doorn (2006) review on the efficiency of bumblebee pollination finds substantial gains in yield and fruit quality when compared with other fruit setting techniques such as mechanical vibration of

the inflorescence (Banda and Paxton 1991; Ravestijn and Sande 1991; Kevan et al. 1991; Abak et al. 1995; Dogterom et al. 1998; Pressman et al. 1999) or spraying with plant growth regulators (Orlowski and Grzeszczuk 2003; Dasgan et al. 2004). Analyses have been carried out only for single crop cycles, mostly in winter. Whenever the environmental conditions change, the efficiency of these treatments is to be re-evaluated.

In North Mediterranean conditions two 4 to 5 months long crop cycles per year are usually developed; one from late winter to early summer, and the other from middle or late summer to the beginning of the winter. This timing differs from the ones previously mentioned in other areas (Velthuis and Doorn 2006) and allows the crop escaping from the low winter temperatures and also from the higher summer temperatures, thus avoiding the associated expenses in heating and ventilation.

In horticultural production, the possibility of removing one cost factor has always to be considered. Therefore, detailed information and knowledge on the performance of the different pollination methods in the tomato in the different crop cycles of the Mediterranean greenhouse systems are required. The aim of this study is to analyze the performance of three methods for the improvement of pollination and fruit set in tomato, in the two most common greenhouse crop cycles under Mediterranean conditions.

Materials and Methods

Tomato plants (*Lycopersicon esculentum* Mill. cv. 'Bond') were grown in a soilless culture system on rockwool slaps, at a plant density of 2.8 plants m^{-2}. The plants were trained to a single stem, which was allowed to develop until the 5th truss, the usual practice for beefsteak tomatoes. The study was carried out in a commercial thermic-polyethylene greenhouse at the Mediterranean basin, in North-East Spain.

Bumblebee (*Bombus terrestris* L.) hives (Biobest Biological System) were established in an area inside the greenhouse previously isolated with an insect-proof net. In addition, inside this area another insect-proof net was used to isolate part of the plants from the pollinators, and three further treatments were carried out: a) self-pollination (control), b) auxin spraying (a mixture of NAA-amide and 4-CPA, Procarpil, Bayer), 3 ml L^{-1}, twice per week, and c) "electric bee vibration" of the inflorescences, 2 seconds three times per week. Twenty five plants were used per treatment, with a fully randomized distribution. Greenhouse temperature, relative humidity, and PAR radiation were monitored every 30 min with a Hobo® datalogger H8 (Onset Computer Corporation, Bourne MA, USA). The greenhouse was automatically heated when temperatures felt under 6 °C. From late May to early September, a shading screen was used to avoid extreme temperature increases commonly occurring inside greenhouses in the Mediterranean region.

The above four treatments were applied at two consecutive crop cycles. The plants at the early cycle were transplanted in early March and harvested until early July (121 d), while those of the late cycle, were transplanted in early August and harvested until late December (136 d).

The reproductive behaviour of the crop was analyzed by weekly recording the opened flowers, fruit set, and marketable fruits, in each plant truss. Earliness was expressed as number of days from transplanting to the first harvest per truss. The production of marketable and non marketable fruits was quantified. Marketable fruits were those over 50 mm in diameter, with regular shape and without external disorders, which was assessed visually. Too small or visually abnormal tomatoes were classified in five groups of non marketable fruits: a) small fruits, under 50 mm in diameter; b) nipple-shape fruits, visually distinguished by the elongation at the blossom end; c) fruits with both a) and b) disorders; d) fruits with catface anomalies, and e) fruits with other visual anomalies (blossom-end rot, cracking, misshapen fruits,...).

All data were analyzed through ANOVA. Percentages were previously transformed to arcsin values. Mean values were separated by Tukey at $P \leq 0.05$. For each pollination treatment, data differences between both crop cycles were analyzed by the corresponding t-tests.

Results and Discussion

Early Cycle

In the early cycle mean monthly temperature ranged from 17 to 24 °C, and relative humidity was quite stable around 64 %. At fruit set period of time, from April to May, the monthly minimum mean temperature was 11.1 °C, and the maximum 31.7 °C. During this period, temperatures only occasionally surpassed 36 °C (Fig. 1).

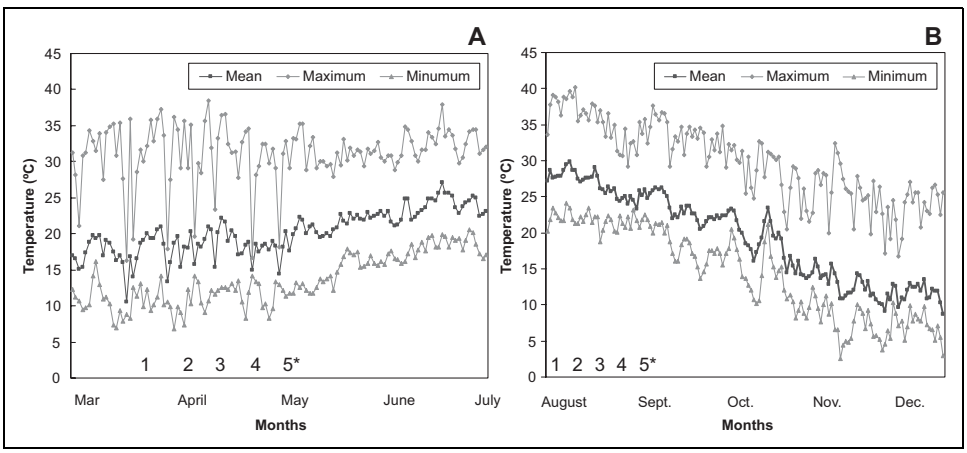


Fig. 1. Mean, maximum and minimum daily temperatures of the early (A) and late (B) crop cycles. * The numbers indicate the flowering inflorescence along the main stem at any given time.

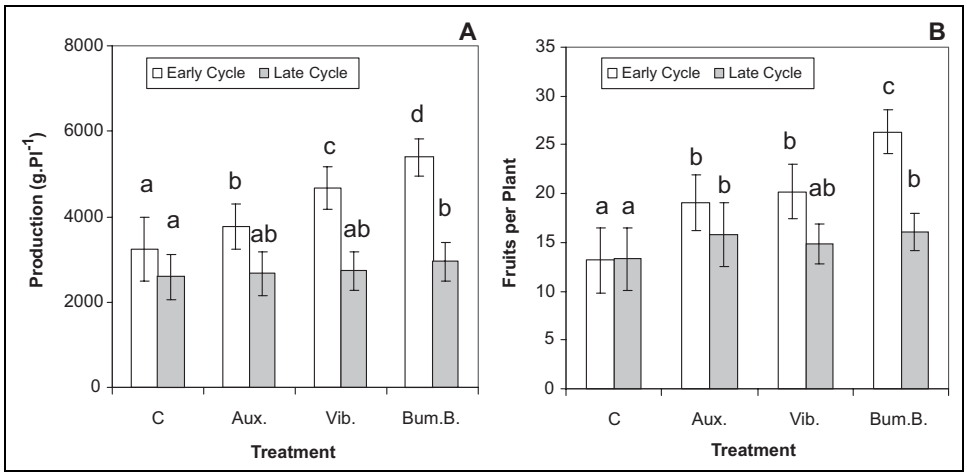


Fig. 2. Effect of treatments on total weight (A) and number of harvested fruits (B) per plant in the two crop cycles. Treatments: C = control, Aux. = auxin spraying, Vib.= electric vibrator, and Bum.B. = Bumblebees. Values are means ± SD. For each crop cycle, different letters among treatments indicate significant differences (P≤0.05).

Mean temperatures and relative humidity were near the optimum, while the maximum temperatures were not limiting for pollination and fertilization (Picken 1984). Suboptimal night temperatures under 10 °C prevailed during 16 d between late March and early April. Pollination requires night temperatures between 13 and 24 °C and day temperatures between 15.5 and 32 °C; at higher or lower temperatures fruit set decreases (Robinson et al. 1965; Charles and Harris 1972; Shelby et al. 1978; El-Ahmadi and Stevens 1979; Rylski 1979; Maisonneuve and Philouze 1982; Dane et al. 1991), thus detrimental effects of temperatures can be foreseen. Likewise, the night temperatures may have adversely affected pollen release (Charles and Harris 1972). No limitations in solar radiation should be expected since under Mediterranean conditions at the time of fruit set, radiation is already high.

In the early cycle, all treatments differed significantly in production. The highest production was measured in the treatment with bumblebee pollination (Fig. 2), and was 65, 43, and 15 % higher than in the control, auxin, and vibrator treatments, respectively. These results are consistent with those reported by Pressman et al. (1999) and by Dasgan et al. (2004) in winter tomato crops, who obtained a higher production with bumblebees than with auxin and vibrator treatments, but they did not analyze self-pollination. Earliness was not affected by the treatments, although in the auxin treated plants the first fruits were harvested a few days earlier.

The number of fruits per plant was highest in the bumblebee treated plants, while the control plants carried 50 % less fruits (Fig. 2). The lower fruit number results obviously in lower competition for assimilates and was presumably responsible for the larger diameter and the higher weight of the control fruits (Table 1). Bigger fruits were expected for the fewer fruits produced on the auxin than on the bumblebee treated plants (Fig. 2). However, their weight was alike and their diameter was significantly lower, suggesting the involvement of other developmental factors, among them the inverse relationship between fruit size and parthenocarpy (Mapelli et al. 1978). In accordance with other previous reports (Ramin 2003),

Table 1. The effect of pollination techniques on mean fruit weight, fruit diameter, proportion of non marketable fruits, and number of opened flowers per plant.

	Treatment			
	Control	Auxin	Vibrator	Bumblebees
Early cycle				
Mean fruit weight (g)	249.0 ± 15.95 c*	198.5 ± 18.48 a	232.4 ± 13.60 b	204.7 ± 9.35 a
Fruit diameter (mm)	79.0 ± 1.36 d	72.7 ± 1.62 a	76.6 ± 1.15 c	73.8 ± 0.69 b
Non marketable fruits (%)	16.2 ± 1.76 b	13.3 ± 0.98 ab	13.1 ± 0.88 ab	8.8 ± 0.55 a
Number of opened flowers per plant	37.7 ± 4.93 b	33.2 ± 3.88 a	32.6 ± 3.54 a	34.6 ± 3.70 a
Late cycle				
Mean fruit weight (g)	196.2 ± 15.93 c	170.3 ± 15.06 a	183.8 ± 16.3 b	182.5 ± 12.13 b
Fruit diameter (mm)	76.2 ± 2.31 c	71.4 ± 2.06 a	73.9 ± 2.31 b	73.7 ± 1.81 b
Non marketable fruits (%)	9.4 ± 0.86 b	6.3 ± 0.53 ab	7.3 ± 0.72 ab	4.9 ± 0.37 a
Number of opened flowers per plant	28.7 ± 5.30 c	26.0 ± 3.40 bc	25.0 ± 3.51 b	21.6 ± 2.28 a

* Values are means ± SD. For each crop cycle, numbers followed by different letters indicate significant differences among treatments (P≤0.05).

Table 2. Non marketable fruits (%): small fruits (diameter ≤50 mm), nipple-shape fruits, fruits small and nipple-shape (S+N), fruits with catface anomalies, and fruits with other anomalies (Other A.) (blossom-end rot, cracking, misshapen fruits,...).

Treatment	Fruit disorder (%)									
	Early Cycle					Late Cycle				
	Small	Nipple	S+N	Catface	Other A.	Small	Nipple	S+N	Catface	Other A.
Control	67	0	0	26	7	35	0	0	8	57
Auxin	6	46	14	23	11	11	0	0	11	78
Vibrator	9	0	0	71	20	15	0	0	12	73
Bumblebees	17	0	0	62	21	20	0	0	0	80

and together with the well-known fact that auxin treatments are related to an increased production of parthenocarpic fruits with less seeds, it is suggested that the lower fruit weight of the auxin treated plants may be partially explained through a lower number of seeds (Gorguet et al. 2005). However, since the fruit seeds were not counted, direct evidence on the fruits nature cannot be acknowledged.

Bumblebee treatments produced the lowest percentage of non marketable production, which was significantly lower than the control (Table 1). Most non marketable fruits produced with the bumblebee or with the vibrator treatments were affected by catface disorders (Table 2), which is believed to have been triggered by abnormal development at flowering time (Jones 1999), partly due to cool temperatures under 12.8 °C (Charles and Harris 1972). During the fruit set period, in April and May, the greenhouse lower temperatures were frequently under this limit (Fig. 1). The increasing fruit setting in the control treatment as the trusses develop (Fig. 3) is indicative of the less limiting temperature conditions in late May. Nevertheless, the lower incidence of catface disorders in the control plants reveals that low temperatures are not the only reason for the incidence of this disorder in the bumblebee and vibrator treatments. These treatments could also have a mechanical effect on the flower: the contact between the vibrator and the flowers or the small fruits can scar the tissues; the bumblebees can also damage the flowers (Jones 1999; Velthuis and Doorn 2006) producing a catfacing-like effect to the fruits.

Nipple-shape fruits were produced only in the auxin treated plants (Table 2), which is attributed to the stylar apex elongation caused by auxins (Abad and Guardiola 1986). The incidence of this disorder decreases as temperature increases, which implies that the prevalence of this disorder depends on the environmental conditions at the time of auxin spraying. Excessive auxin spraying causes and enlarges fruit deformations previously induced by low temperatures (Geisenberg and Steward 1986). However, in the present experiment the product recommendations were carefully considered, and there were no negative effects of auxin dose.

The three pollination treatments, bumblebee, vibration, and auxins, where all effective in increasing fruit setting (Fig. 3), and small fruits, usually formed because of incomplete pollination (Picken 1984), were scarce (Table 2). Fruit setting was higher with bumblebees, intermediate with the vibrator and auxin treatments, and lowest in the control plants (Fig. 3). It is interesting to emphasize that all three treatments had a stable and similar fruit set effectiveness in all trusses, while there were big differences among trusses in the fruit set of control plants. Indeed, in the later the fruit set percentage amounted to 16 % in the first and 60 % in the fifth truss. This was ascribed to the above mentioned fruit set enhancement as the minimum temperatures increase. The application of the vibrator and the auxins to the last truss did not substantially improve fruit setting, bumblebee pollination being the only effective method for all trusses (Fig. 3). Bumblebees are better pollinators than mechan-

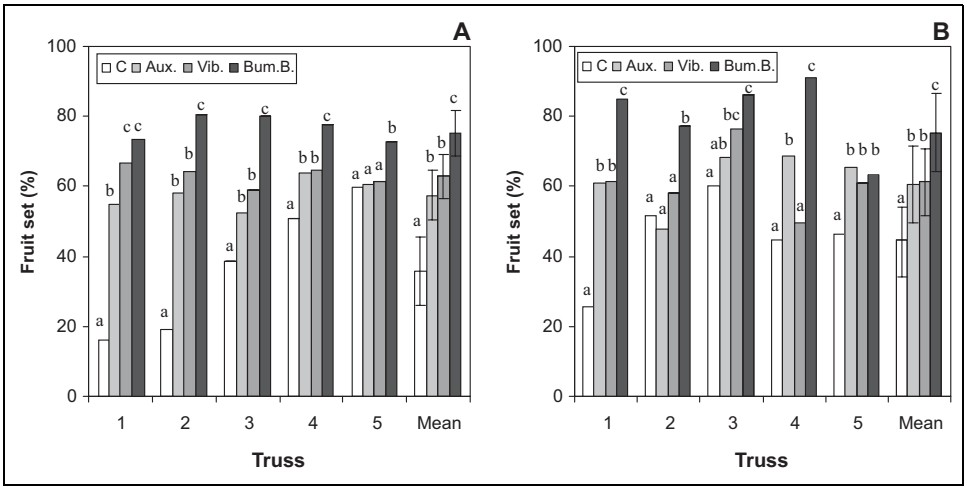


Fig. 3. Effect of treatments on fruit set of the first to the fifth truss, and average fruit set per plant (mean), in the early (A) and in the late (B) crop cycle. Treatments: C = control, Aux. = auxin spraying, Vib. = electric vibrator, and Bum.B. = Bumblebees. For the mean value bars indicate ± SD. For each crop cycle and truss different letters among treatments indicate significant differences (P≤0.05).

ical vibration because they forage every flower more than once per day, contrary to the mechanical vibration performed 2–3 times a week (Shipp et al. 1994; Pressman et al. 1999). Additionally, they can favour cross pollination, transferring viable pollen to male sterile flowers brought about by temperature. Vibration acts on the inflorescence and it hardly induces cross pollination.

There were significantly more flowers opened in the control plants (Table 1). The lower percentage of fruit setting in these plants (Fig. 3) may have favoured the opening of the late emerging flowers of the inflorescences. When fruit set is high, as in the bumblebee, vibrator and auxin treatments, the last flowers do not open because of the competition for assimilates with the already set fruits.

Late Cycle

In the late cycle mean monthly temperature varied from 11.8 to 27.2 °C, and relative humidity was around 70 %. At fruit set time, August to September, the monthly minimum mean temperatures were 19–22 °C, and the maximum 31–36 °C. During this period, the temperature occasionally rose to 38–40 °C in early August and never dropped below 10 °C (Fig. 1). Minimum temperatures and relative humidity were in the appropriate range for pollination (Picken 1984); however, the maximum temperatures at fruit set time were over the scope, and harmful effects on pollination may be expected (Shelby et al. 1978; El-Ahmadi and Stevens 1979; Dane et al. 1991; Sato et al. 2000).

The highest production was obtained in the bumblebee pollinated plants (Fig. 2), which showed an increase of up to 14.3 % in comparison with the other three treatments. Significant differences in this cycle were detected only between bumblebee and control treatments. The vibrator and the auxin treatments were not significantly different from the control, neither from the bumblebee treatments, and earliness was not affected by any of the treatments. Consequently, at the assayed conditions, the use of auxin or vibration is questionable.

Although the late cycle lasted longer than the early one, its production was considerably lower (Fig. 2). This is likely related to the lower photosynthetic radiation available, 889 *versus* 2036 mol m^{-2}, respectively. In addition, the periods of high temperatures in summer and the low temperatures in late autumn (Fig. 1) stressed the crop at fruit growth time.

For all treatments, the percentage of non marketable fruits was lower than 10 %, and as for the early crop cycle, bumblebees significantly reduced it by ca. 50 % (Table 1). Neither the bumblebee treatment produced catfacing fruits, nor the auxin treatment produced nipple-shape fruits (Table 2). Temperatures at fruit setting were higher in the late cycle than in the early one (Fig. 1). The high percentage of non-marketable nipple-shape fruits in the auxin treated plants of the early crop, along with the absence of such fruits at the late cycle crop, is in accordance with the relevance of the environmental conditions at the auxin treatment time (Abad and Guardiola 1986), and suggests that only during the early cycle crop parthenocarpic fruits were produced.

Fewer flowers opened in the late than in the early cycle crop, regardless of the treatment (Table 1). The main reason was likely the high temperatures (Charles and Harris 1972; El-Ahmadi and Stevens 1979). Rylski (1979) found that in the second to fifth inflorescence flower abortion increased as day temperature rose from 17 to 27 °C, thus favouring the vegetative versus the reproductive growth, and increasing respiration. In these circumstances, in the early stage of the inflorescence growth, the availability of assimilates for flower development diminishes. Also, as in the early cycle, more flowers opened in the control plants (Table 1).

Fruit set was lowest in the control plants; the first truss had the minimum fruit set, but it was considerably higher than in the early cycle crop (Fig. 3), thereby suggesting that the high summer temperatures were less limiting than the low temperatures in the early cycle. Fruit set was similar for the vibration and the auxin treated plants, higher than in the controls, but significantly lower than in the plants grown with bumblebees. Again, it is remarkable that bumblebee treated plants had the highest fruit setting. The difference with the control plants was greater for the first trusses than for the last ones (Fig. 3), but as in the early cycle, the effectiveness of bumblebees on fruit setting remained high among trusses.

The tomatoes were somewhat smaller in the late than in the early cycle, which is attributed to the reduction in solar radiation available (Ho and Hewitt 1986). On the other hand, and as it was already found in the early cycle crop, control plants produced the heaviest and biggest fruits (Table 1), and as previously reported by Rylski (1979) under high day temperatures, auxin treated plants produced the smallest fruits.

Pollen germination is generally higher under mild temperatures than during the cold season (Karapanos et al. 2006); accordingly, differences between treated and control plants should be higher under cold conditions. In our study the main limiting fruit set factor of the early cycle was the low temperature; it might have restricted pollen formation and release, reduced germination, and slowed pollen tube growth (Robinson et al. 1965; Charles and Harris 1972; Rylski 1979; Maisonneuve and Philouze 1982), thus resulting in poor fertilization. In the late cycle, limitations in fruit set due to temperatures appeared only at the beginning of the culture: high temperatures may affect anther development, especially in tissues with important roles in pollen development and release (Sato et al. 2000; Sato and Peet 2005), and are deleterious to fruit development (Peet et al. 1998).

Vibration and Bumblebee increased fruit set by enhancing pollen release, especially in early spring, when it is sticky and aggregated (Maisonneuve and Philouze 1982; Picken 1984). Bumblebees were more efficient when day temperatures were mild than in the late cycle when the temperatures at fruit set were frequently above 32 °C and limited foraging. Auxins act in a different way; they substitute pollination and trigger fruit development (Gorguet et al. 2005). Under suboptimal temperatures parthenocarpic fruits can be spontaneously produced, but they do not reach commercial weight unless treated with auxins (Rylski 1979; Sato et al. 2001). Also, auxins may increase fruit set by improving fruit growth in poorly fertilized flowers (Rylski 1979).

The obtained results show that all treatments were effective in increasing fruit set, although bumblebees produced the best results in both crop cycles. In the early cycle, only bumblebees were capable of increasing fruit set after the fourth truss. The enhancement in fruit setting

increased the production, but not the fruit size, and earliness was not affected by any treatment in any of the two crop cycles. Nevertheless, the effectiveness of the three treatments in increasing final production was closely dependent on the cycle of the crop, and all three treatments were considerable less effective in the late than in the early crop cycle.

References

ABAD, M. and J.L. GUARDIOLA 1986: Influencia de las auxinas en la calidad del fruto de tomate cultivado en invernadero a baja temperatura. Investig. Agraria: Prod. y Protección Vegetal **1**, 9–23 (In Spanish).

ABAK, K., N. SARI, M. PAKSOY, O. KAFTANOGLU and H. YENINAR 1995: Efficiency of bumble bees on the yield and quality of eggplant and tomato grown in unheated glasshouse. Acta Hort. **412**, 268–274.

BANDA, H.J. and R.J. PAXTON 1991: Pollination of greenhouse tomatoes by bees. Acta Hort. **288**, 194–198.

BAYTORUN, A.N., S. TOPÇU, K. ABAK and Y. DASGAN 1999: Growth and production of tomatoes in greenhouses at different temperature levels. Gartenbauwissenschaft **64**, 33–39.

CHARLES, W.B. and R.E. HARRIS 1972: Tomato fruit-set at high and low temperatures. Can. J. Plant Sci. **52**, 497–506.

DANE, F., A.G. HUNTER and O.L. CHAMBLISS 1991: Fruit set, pollen fertility and combining ability of selected tomato genotypes under high-temperature field conditions. J. Am. Soc. Hort. Sci. **116**, 906–910.

DASGAN, H.Y., A.O. OZDOGAN, O. KAFTANOGLU and K. ABAK 2004: Effectiveness of bumblebee pollination in anti-frost heated tomato greenhouses in the Mediterranean basin. Turk. J. Agric. For. **28**, 73–82.

DOGTEROM, M.H., J.A. MANTTEON and R.C. PLOWRIGHT 1998: Pollination of greenhouse tomatoes by North American *Bombus vosnesenskii* (Hymenoptera: *Apidae*). J. Econ. Entomol. **91**, 71–75.

EL-AHMADI, A.B. and M.A. STEVENS 1979: Reproductive responses of heat-tolerant tomatoes to high temperatures. J. Am. Soc. Hort. Sci. **104**, 686–691.

GEISENBERG, C. and K. STEWARD 1986: Field Crop management. In: ATHERTON, J.G. and J. RUDICH (eds.): The tomato crop. Chapman and Hall, London, 511–557.

GORGUET, B., A.W. VAN HEUSTEN and P. LINDTHOUT 2005: Parthenocarpic fruit development in tomato. Plant Biol. **7**, 131–139.

GROENEWEGEN, C., G. KING and B.F. GEORGE 1994: Natural cross pollination in California commercial tomato fields. Hortscience **29**, 1088.

HO, L.C. and J.D. HEWITT 1986: Fruit development. In: ATHERTON, J.G. and J. RUDICH (eds.): The tomato crop. Chapman and Hall, London, 201–239.

JONES, J.B. 1999: Tomato plant culture. CRC Press, Boca Raton, USA, 11–50.

KARAPANOS, I.C., C. FASSEAS, C.M. OLYMPIOS and H.C. PASSAM 2006: Factors affecting the efficacy of agar-based substrates for the study of tomato pollen germination. J. Hort. Sci. Biotechnol. **81**, 631–638.

KEVAN, P.G., W.A. STARVER, M. OFFER and T.M. LAVERTY 1991: Pollination of greenhouse tomatoes by bumble bees in Ontario. Proc. Entomological Society of Ontario **122**, 15–19.

MAPELLI, S., C. FROVA, G. FORTI and G.P. SORESSI 1978: Relationship between set, development and activities of growth regulators in tomato fruit. Plant Cell Physiol. **19**, 1281–1288.

MAISONNEUVE, B. and J. PHILOUZE 1982: Action des basses températures nocturnes sur une collection variétale de tomate (*Lycopersicon esculentum* Mill.). I. Etude de la production de fruits et la valeur fécondante du pollen. Agronomie **2**, 441–452 (In French).

MUÑOZ, P., J.I. MONTERO and A. ANTON 1999: Effect of insect-proof screens and roof openings on greenhouse ventilation. J. Agric. Eng. Res. **73**, 171–178.

ORLOWSKI, M. and M. GRZESZCZUK 2003: Use of bumble bees for pollination of cherry tomato in unheated polyethylene tunnel. Vegetable Crop Research Bull. **59**, 75–82.

PEET, M.M. and M. BARTHOLOMEW 1996: Effect of night temperature on pollen characteristics, growth, and fruit set in tomato. J. Am. Soc. Hort. Sci. **121**, 514–519.

PEET, M.M., S. SATO and R.G. GARDNER 1998: Comparing heat stress effects on male-fertile and male-sterile tomatoes. Plant, Cell Environ. **21**, 225–231.

PICKEN, A.J.F. 1984: A review of pollination and fruit set in tomato. J. Horticult. Sci. **59**, 1–13.

PRESSMAN, E., R. SHAKED, K. ROSENFELD and A. HEFETZ 1999: A comparative study of the efficiency of bumble bees and electric bee in pollinating unheated greenhouse tomatoes. J. Hort. Sci. **74**, 101–104.

RAMIN, A.A. 2003: Effects of auxin application on fruit formation in tomato growing under stress temperature in the field. J. Hort. Sci. Biotechnol. **78**, 706–710.

RAVESTIJN, W. Van and J. VAN DER SANDE 1991: Use of bumblebees for the pollination of glasshouse tomatoes. Acta Hort. **288**, 204–212.

ROBINSON, R.W., S. SHANNON and W. MISHANEC 1965: Low temperature influences pollen production and fruit set of tomatoes. Farm Res. **31**, 13–15.

RYLSKI, I. 1979: Fruit set and development of seeded and seedless tomato fruit under diverse regimes of temperature and pollination. J. Am. Soc. Hort. Sci. **104**, 835–838.

SATO, S., M.M. PEET and J.F. THOMAS 2000: Physiological factors limit fruit set of tomato (*Lycopersicon esculentum* Mill.) under chronic mild heat stress. Plant Cell Environ. **23**, 719–726.

SATO, S., M.M. PEET and R.G. GARDNER 2001: Formation of parthenocarpic fruit, undeveloped flowers and aborted flowers in tomato under moderately elevated temperatures. Sci. Hort. **90**, 243–254.

SATO, S. and M.M. PEET 2005: Effects of moderately elevated temperature stress on the timing of pollen release and its germination in tomato (*Lycopersicon esculentum* Mill.). J. Hort. Sci. Biotechnol. **80**, 23–28.

SHELBY, R.A., W.H. GREENLEAF and C.M. PETERSON 1978: Comparative fertility in heat tolerant and heat sensitive tomatoes. J. Am. Soc. Hort. Sci. **103**, 778–780.

SHIPP, J.L., G.H. WHITFIELD and A.P. PAPADOPOULOS 1994: Effectiveness of the bumble bee, *Bombus impatiens* Cr. (Hymenoptera, *Apidae*), as a pollinator of greenhouse sweet pepper. Sci. Hort. **57**, 29–39.

VELTHUIS, H.W. and A. VAN DOORN 2006: A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. Apidologie **37**, 421–451.

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