



Effect of Temperature on the Growth and Development of Tomato Fruits

S. R. ADAMS*, K. E. COCKSHULL and C. R. J. CAVE

Horticulture Research International, Wellesbourne, Warwick CV35 9EF, UK

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Tomato fruits ripened 95, 65, 46 and 42 d after flower opening when plants were grown under controlled environmental conditions at 14, 18, 22 and 26 °C, respectively. A similar response to temperature was observed when the temperature of individual trusses was modified while the plants were grown at 20 °C. These data were used to develop a thermal time model for fruit maturation. However, when buds/fruits were heated at different stages in their development, the thermal time model proved to be a poor predictor of the time of ripening. Fruits were more sensitive to elevated temperature in their later stages of maturation. Temperature also affected the rates of fruit growth in volume; these could be adequately described using a Gompertz function. Low temperatures reduced absolute volume growth rates and delayed the time at which the absolute growth rate became maximal. However, the response of fruit growth to temperature differed when only the temperature of the fruits was modified. There was a tendency towards small parthenocarpic fruits at both high (26 °C) and low (14 °C) temperature regimes which, combined with low flower numbers and poor fruit set at 26 °C, resulted in low fruit yields. Temperature also affected the shoot dry matter content and partitioning.

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Key words: Tomato, *Lycopersicon esculentum*, fruit, growth, ripening, temperature, temperature stress, parthenocarpic.

INTRODUCTION

There is interest among tomato growers in systems to predict yields, due to an increasing need to be able to schedule their crops with precision to meet stringent retail demands for continuity of high quality product. However, while relationships between the photo-thermal environment and cumulative crop yields are reasonably well understood (e.g. Cockshull *et al.*, 1992), the effects on the weekly pattern of crop yield are harder to predict. Consequently, a better understanding is required of the factors that affect the growth and development of tomato fruits.

Tomato plants have, within certain limits, the ability to integrate temperature. Plants exposed to a fluctuating temperature regime often suffer no overall loss of yield when compared with those grown in a constant regime having the same mean temperature (Hurd and Graves, 1984; Khayat *et al.*, 1985; de Koning, 1988, 1990). Furthermore, dry matter partitioning is not greatly affected by temperature (Heuvelink, 1995a). However, fluctuations in temperature may affect the pattern of crop yield as the rate of developmental events such as fruit maturation is determined largely by temperature (Hurd and Graves, 1985). Indeed, commercial crop yields fluctuate greatly from week to week; this probably reflects changes in the time taken for fruits to ripen (Adams *et al.*, 2001).

Hurd and Graves (1984, 1985) found that the time taken for fruits to mature decreased throughout the early part of the season, probably in response to higher mean air temperatures. Fruits took 66 d to ripen in a 15 °C night

temperature regime, compared with 74 d at a nominal 11 °C night (Hurd and Graves, 1985). Verkerk (1955) found that fruits took 90 d to mature at 13 °C, 53 d at 19 °C and 40 d at 25 °C; this can be expressed as a thermal time requirement of 840 °C d with a base temperature of 3.5 °C (Aikman, 1996). However, a thermal time model of this type may not be appropriate, as de Koning (1994) indicated that the sensitivity of fruits to temperature interacted with their stage of development, with fruits being less sensitive to temperature in the middle stages of their development. Furthermore, temperature extremes can inhibit the ripening process (Lurie *et al.*, 1996).

Temperature affects not only the time of fruit ripening but also the rate of fruit growth. Pearce *et al.* (1993a) found that in the short term (records taken at 20 min intervals over several days) the expansion of tomato fruits was closely related to temperature and did not appear to be limited by assimilate supply. The growth rates of fruit were found to be positively related to fruit temperature between 10 and 30 °C, with an increase in fruit diameter of 5 µm h⁻¹ °C⁻¹. However, fruit expansion rates recorded in the glasshouse crop were often below those expected from the prevailing temperatures due to the water status of the plants (Pearce *et al.*, 1993b). Over the course of its development the growth of an individual fruit tends to follow an asymmetric sigmoidal curve (Monselise *et al.*, 1978), where the growth rate is maximal when less than half the time taken to achieve the final weight has elapsed (Heuvelink and Marcelis, 1989). This can be modelled satisfactorily using either a Gompertz function (Grange and Andrews, 1993; Bertin, 1995; Aikman, 1996) or a Richards function (Heuvelink and Marcelis, 1989). Elevating the

* For correspondence. Fax +44 (0) 1789 470552, e-mail steven.adams@hri.ac.uk

temperature often increases the fruit growth rate, but it has a greater effect in hastening maturity and, as a result, the final mean weight of tomato fruits is reduced (Hurd and Graves, 1985; Sawhney and Polowick, 1985). However, Marcelis and Baan Hofman-Eijer (1993) showed that the effect of temperature on the growth of cucumber was dependent on assimilate availability. This study aims to investigate in more detail the response of tomato fruits when grown under both constant and changing temperature regimes under controlled environmental conditions.

MATERIALS AND METHODS

General plant culture

Seeds of tomato (*Lycopersicon esculentum* Mill. 'Liberto') were sown into seed trays containing a peat-based seed and modular compost and were germinated in a glasshouse compartment set to provide a minimum temperature of 22 °C. After 9 or 10 d, when cotyledons were horizontal, seedlings were pricked out into 1 l pots containing a peat-based potting compost. Plants raised in the glasshouse were selected for uniformity and then moved to growth rooms (Weiss Technik Ltd, Colleshill, UK) in which experimental treatments were applied.

At first flowering, plants were potted up into 9.7 l pots containing a peat-based potting compost and were irrigated with a complete nutrient solution, initially by hand and subsequently through an automatic drip irrigation system. Initially plants were supported by canes; they were later strung from wire supports. In the first experiment plants were 'layered' so as to produce a canopy structure similar to that produced in a commercial tomato crop. This involved the regular removal of side shoots, weekly layering of the crop and removal of leaves once they were below the truss that was being picked. However, for expts 2 and 3, plants were stopped above the seventh or eighth truss, respectively. In all experiments fruits were picked at the yellow/orange stage on three occasions per week.

In experiment 1, 20 plants were grown in each growth room (3 × 3 × 3 m), but this number was reduced to 15 plants in expts 2 and 3 to provide space for the chambers that enclosed particular trusses (see below). Metal halide lamps provided approx. 315 μmol m⁻² s⁻¹ PAR at a height of 1.7 m for 12 h d⁻¹ (equivalent to 13.6 mol m⁻² d⁻¹). The CO₂ concentration was enriched to 1000 ppm during the light period and the vapour pressure deficit was controlled at 0.6 kPa both day and night.

Experiment 1. Four constant temperature regimes

Four growth rooms were set to provide constant temperature regimes of 14, 18, 22 and 26 °C. Seeds were sown on 14 Sep. 1998 and young plants were transferred to the rooms after 21 d. Data on flower opening and fruit picking dates, and weights and diameters of the first and fifth proximal fruits of each truss, along with the first ten fruits on the third truss, were collected from 16 of the 20 plants within each room. The number of buds, flowers, set fruits and mature fruits was recorded for each truss on these

plants, as was the yield. The diameters (mean of two equatorial measurements) of 16 fruits per treatment from the third truss (whenever possible one fruit per plant) were recorded at regular intervals from fruit set until picking.

For each temperature regime, five randomly selected plants were chosen for growth analysis. Throughout the experiment all of the leaf material removed from these plants was oven-dried and weighed, as were samples of ripe fruits to determine their dry matter content. After 27 weeks from sowing, the remaining leaves, stems and truss stalks were separated, dried and weighed. Unripe fruits were also weighed and samples dried to determine their dry matter content. The experiment was terminated at this time, with the exception of the 14 °C treatment which, due to the greatly reduced growth rate, was allowed to continue for a further 9 weeks. In this room the remaining plants were repositioned to maintain the same spacing between plants.

Experiment 2. The effect of heating and cooling individual trusses

In experiments where whole plants are exposed to different temperatures the degree to which temperature has a direct effect on fruit growth and development cannot be distinguished from indirect effects via other plant processes. To overcome this limitation, chambers were constructed in which the temperature of an individual truss could be controlled independently of that of the surrounding air. Trusses were enclosed in transparent chambers (145 mm in diameter and 305 mm long) constructed from Kuvex and Perspex. Preliminary tests indicated that fruit development was unaffected by enclosing them in these chambers. Conditioned air was blown into the base of the chambers and vented via a hole at the top. The temperature of the air passing over the truss was measured continuously and was manipulated by heating elements or heat exchangers connected to a glycol chilling unit situated outside the room to maintain the air temperature within approximately ±0.5 °C of the desired air temperature. In some of the chambers the desired air temperature was the same as that within the room and so the temperature of the air blown into these chambers was not manipulated.

Seeds were sown on 9 Feb. 1998 and plants were transferred to growth rooms after 43 d. The room air temperature was set at 20 °C and on each occasion the third truss was enclosed in a chamber in which the air was cooled to 15 °C, maintained at 20 °C, or elevated to 25 °C. There were five replicate plants per treatment. The trusses were placed within the chambers after the proximal flowers had set fruit (9 d after the most proximal flowers had opened), by which time the distal buds were flowering. Treatments were positioned according to an extended Latin square design (plants comprised a 3 × 5 array). Flower opening and picking dates, and weights and diameters of the ten most proximal fruits were recorded for each treated truss. Furthermore, the diameter (two equatorial measurements) of two fruits per treated truss (normally fruits 3 and 4 from the proximal end) was recorded weekly or twice weekly for fruits under 30 mm diameter. The chambers were removed briefly to allow measurements of fruit diameter and picking.

Experiment 3. Investigating the stages of sensitivity of fruits to temperature

To assess whether fruits are equally sensitive to temperature throughout their development, trusses were placed in the chambers described in expt 2, with an elevated air temperature (25 °C) at different stages of fruit development. Due to the size and position of trusses, treatments prior to flower opening were applied by enclosing the trusses in re-sealable polyethylene bags. As with the chambers, the bags were vented at the top and had air of a controlled temperature blown into the bottom.

Seeds were sown on 7 Sep. 1999 and were moved to the growth rooms after 27 d. Thirty plants, split between two growth rooms, were grown at a temperature of 18 °C. Six temperature treatments were applied to the third truss of the plants using an incomplete Latin square design (plants comprised a 6 × 5 array across the two growth rooms), with five replicate plants for each treatment. The timings of treatments are expressed in relation to the time of flower opening of the fourth flower on the third truss. Treatments included 25 °C for 8 d prior to flower opening, for the first 3 weeks after flower opening, for weeks 4, 5 and 6 after flower opening, and from the beginning of week 7 until fruit ripening. Constant temperature regimes of 18 °C and 25 °C were also included. These treatments commenced at the same time, 12 d prior to flower opening at 18 °C and 8 d prior to flower opening at 25 °C, and continued until fruit ripening. The dates of flower opening and of picking fruits, together with the weights and diameters of the ten most proximal fruits, were recorded for each treated truss.

RESULTS

Experiment 1. Four constant temperature regimes

Plants grown at 26 °C had a poor appearance and by the end of the experiment approx. 40% of the terminal meristems were blind. Trusses tended to be abnormal; some aborted while others had reduced bud numbers. There was poor fruit set and fruits tended to be either parthenocarpic (seedless) or have low seed numbers. Plants grown at 22 °C and 18 °C produced normal fruits and had a normal canopy structure, whereas growth was greatly reduced at 14 °C and trusses had many flowers and were prone to splitting. Furthermore, at this temperature fruits were parthenocarpic, small, hard and of no marketable value. The effect of temperature on the pattern of yield and mean fruit size can be seen in Fig. 1A and B.

Temperature significantly ($P < 0.001$) affected the dry matter content: at 14 °C shoots (the mean value for stems, leaves, truss stalks and fruits) had a dry matter content of 12.5% compared with 7.7, 7.1 and 10.2% at 18, 22 and 26 °C, respectively. After 27 weeks there were also significant differences ($P < 0.001$) in the partitioning of dry matter within the plant (Fig. 2A and B). The dry matter partitioned to fruits was reduced in the highest and lowest temperature regimes. When all fruits were considered (both ripe and green), 47.8, 72.0, 75.1 and 44.6% (s.e.d. = 4.77) of fresh weight and 44.4, 61.2, 61.8 and 29.1% (s.e.d. = 4.13) of the dry matter was partitioned to fruits at

14, 18, 22 and 26 °C, respectively. Temperature also affected the rate of plant development and the number of fruits set per truss (Table 1). Although temperature affected the homogeneity of variance for some data sets, analysis of variance has been used to present a standard error of difference as the coefficient of variation was small in all instances.

The mean fruit development times, based upon data collected for the first and fifth fruits of each truss, are shown in Table 1. A linear response was found between the rate of progress to maturity (the reciprocal of the time to ripen) and temperature ($r^2 = 0.98$, 2 d.f.). As well as the effect of temperature, there was also a significant effect of truss position ($P < 0.001$) within the 14 °C treatment. At this temperature the fifth fruits of each truss ripened on average 8.6 d earlier (s.e.d. = 0.63) than the most proximal fruit. Furthermore, data from the third truss showed delayed maturity ($P < 0.001$) at both the proximal and distal ends of the truss in all but the highest temperature regime.

The increase in fruit volume over time was calculated for fruits on the third truss, assuming that fruits were spherical (Fig. 3A). A three-parameter Gompertz function was fitted to each data set, from which the absolute growth rates of fruits (first derivative of the Gompertz functions) were determined (Fig. 3B). Increasing the temperature from 14 °C to 22 °C increased the maximum absolute growth

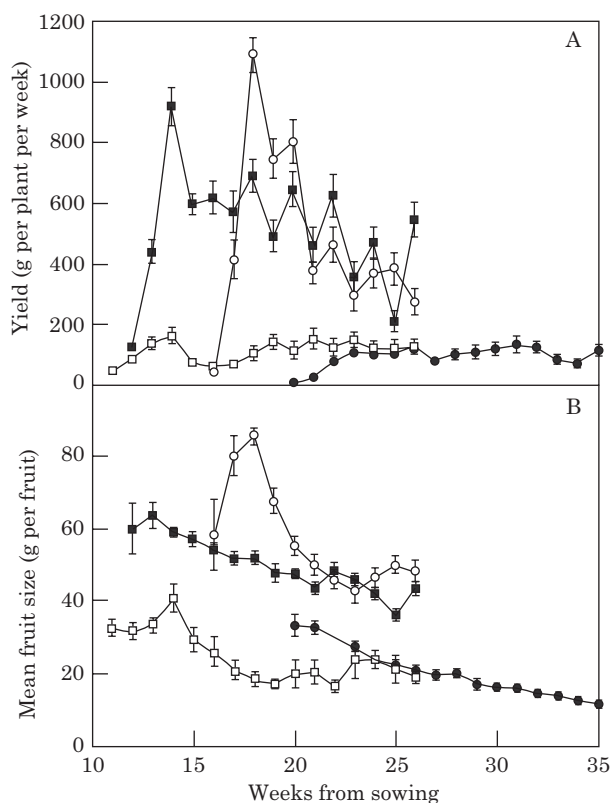


FIG. 1. The effect of temperature on the pattern of crop yield (A) and mean fruit size (B). Data represent the mean weekly values for 16 plants that were grown in controlled environment rooms set to provide constant temperatures of 14 (●), 18 (○), 22 (■) and 26 °C (□). Bars represent the s.e.m.

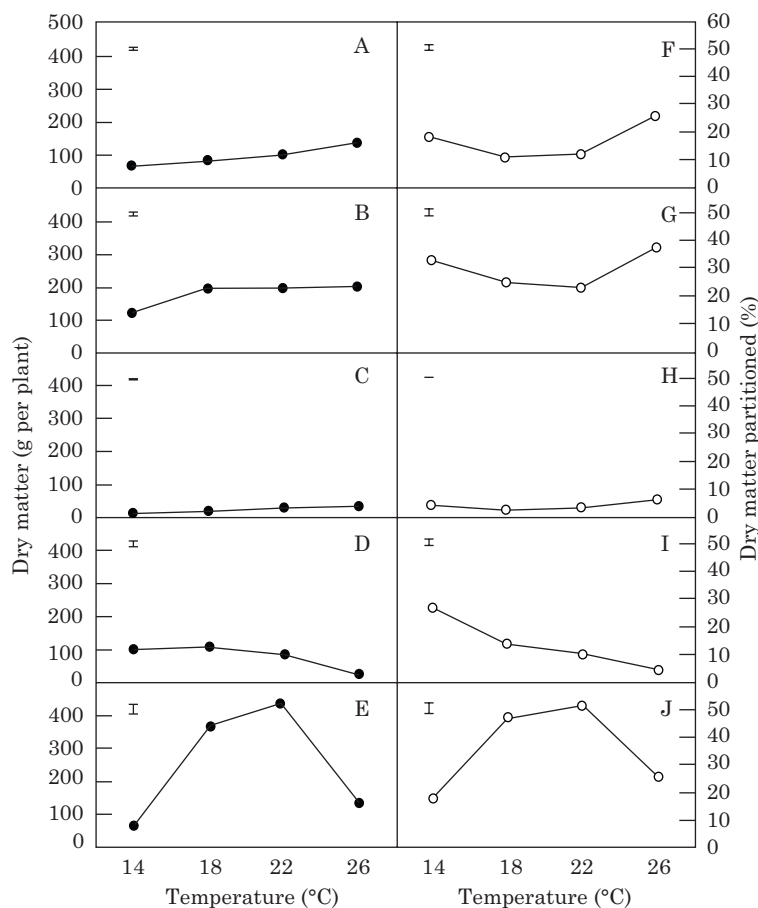


FIG. 2. Effect of temperature on the shoot dry matter partitioning of tomato plants expressed in terms of dry matter (A–E) and as a percentage of total shoot dry matter (F–J). Data are expressed in terms of the dry matter partitioned to stems (A, F), leaves (B, G), truss stalks (C, H), green fruits (D, I) and ripe fruits (E, J). Points represent mean values for five plants per temperature, recorded 27 weeks after sowing. Bars represent the standard errors of difference between the means.

TABLE 1. Effect of temperature on the growth and development of tomato 'Liberto'

	Temperature (°C)				s.e.d.
	14	18	22	26	
Rate of truss production (trussed d ⁻¹)	0.091	0.151	0.198	0.171	0.0048
Rate of flower opening (flowers d ⁻¹)	0.51	0.86	1.13	0.95	0.043
Fruit development time (d)	94.8	64.5	46.3	41.5	0.89
Number of flowers (flowers per truss)	16.3	13.1	15.0	9.1	0.73
No. set fruits (set fruits per truss)	12.4	8.4	9.6	4.4	0.59
Mean fruit size (g)	18.3	57.7	51.3	23.9	1.82

Data represent mean values calculated for the first 15 trusses and standard errors of difference between the means.

rate and hastened the period of most rapid growth and ripening. The maximum absolute volume growth rate was reduced at 26 °C.

Experiment 2. The effect of heating and cooling individual trusses

When individual trusses were enclosed within chambers controlled at 15, 20 or 25 °C, temperature had a significant effect ($P < 0.001$) on the time taken for fruits to mature.

Fruits took 97.4, 56.6 and 42.3 d to mature at 15, 20 and 25 °C, respectively (s.e.d. = 1.37). There was also a significant effect of fruit position within a truss ($P < 0.001$) in the lowest temperature regime. At 15 °C there was an approximately linear delay in fruit maturation time down the truss from the proximal to the distal end, such that the eighth fruit took a mean of 11.2 d longer to ripen compared with the first fruit (s.e.d. = 2.25). There was no significant difference ($P > 0.05$) between temperature treatments with regards to the number of fruits on the third truss (mean of

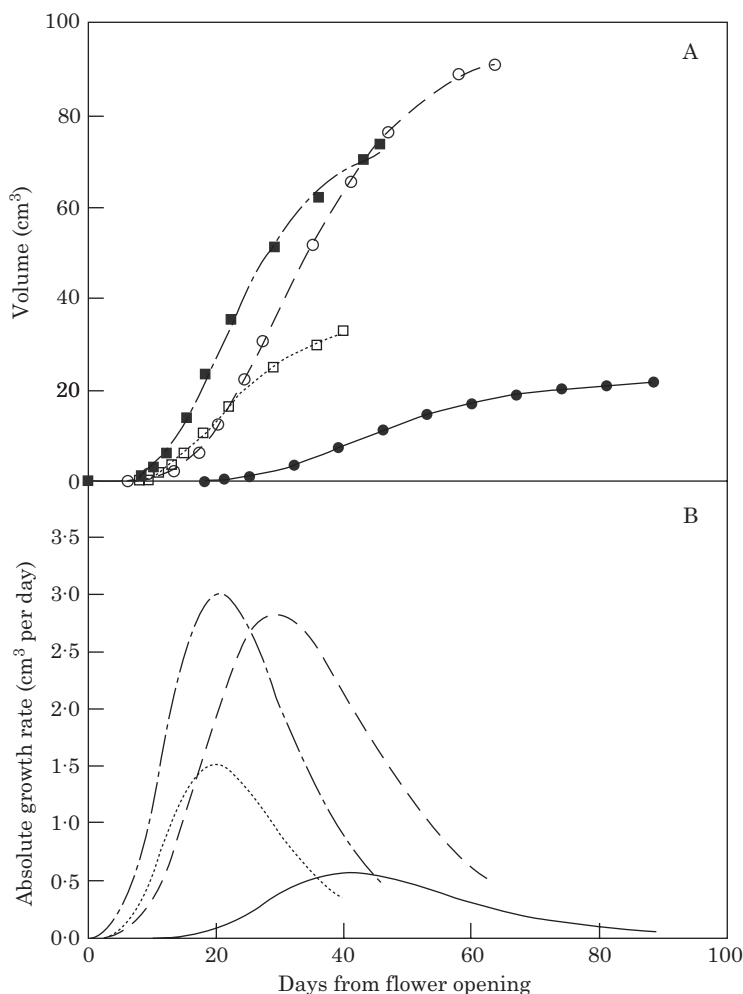


FIG. 3. Effect of temperature on growth (A) and absolute growth rates (B) of tomato fruit when plants were grown at 14(●,—), 18(○,— —), 22(■,— · —) and 26 °C (□, · · ·). Points represent the mean volume of 16 fruits calculated assuming fruits are spherical. Lines represent a Gompertz function fitted to each data set using Genstat 5 where $\text{volume} = a \exp(-\exp(b-ct))$, where a , b and c are constants and t represents time.

nine fruits per truss). The temperature treatments applied to the third truss had no effect on the other (untreated) trusses, with the exception of the fourth truss on the low-temperature treated plants which ripened 4 d after those in the other temperature treatments ($P < 0.001$).

As in expt 1, there appeared to be a linear relationship between the rate of progress to maturity and temperature (Fig. 4). When data for both experiments were combined in a single analysis, a linear relationship between temperature and the rate of progress to maturity meant that the effect of temperature could be expressed as a thermal time relationship, whereby fruit of 'Liberto' matured after 812 °C d ($1/0.00123$) above a base temperature of 5.7 °C ($0.007/0.00123$) ($r^2 = 0.98$, 5 d.f.).

Fruit diameters were used to estimate fruit volumes, and for each temperature regime a Gompertz function was fitted (Fig. 5A). As in the previous experiment, lowering the temperature resulted in lower absolute growth rates and a delay in the time at which the absolute growth rate became maximal (Fig. 5B). However, the maximum absolute growth rates were not reduced to the same extent, and in

contrast to the previous experiment, the net effect of reducing the maximum absolute growth rates was more than compensated for by the extended period of growth. Fruit weighed 75.8, 73.8 and 62.2 g at 15, 20 and 25 °C, respectively, although these differences were not significant ($P > 0.05$).

Experiment 3. Investigating the stages of sensitivity of fruits to temperature

When trusses were heated at different developmental stages some fruits were parthenocarpic and small, particularly if exposed to the elevated temperature regime following flower opening. As a result, mean fruit size was significantly reduced ($P < 0.001$) in treatments in which plants were heated continuously to 25 °C (42.5 g), and to 25 °C for the first 3 weeks (44.5 g). These weights can be compared with 71.8, 72.7, 65.4 and 74.3 g (s.e.d. = 7.9) attained in the treatments 18 °C continuously, 25 °C prior to flower opening, 25 °C for the second 3-week period and 25 °C from week 7, respectively.

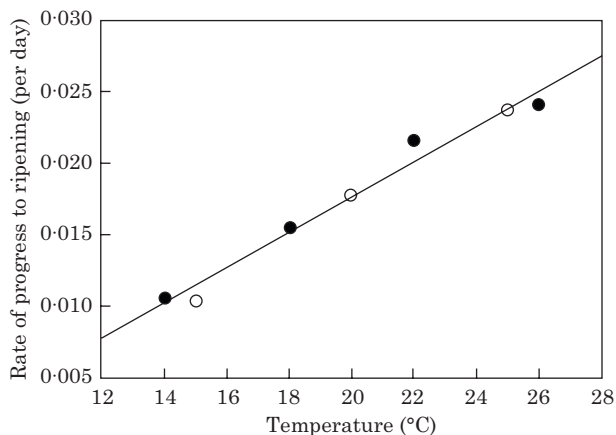


FIG. 4. Effect of temperature on the rate of progress to ripening (the reciprocal of the time from flower opening to maturity) for expt 1 (●) and expt 2 (○). The line was fitted by regression analysis; $1/r = -0.0070 (\pm 0.0018) + 0.00123 (\pm 0.000086) T$, $r^2 = 0.98$, 5 d.f., where r and T represent the days from flower opening to maturity and temperature, respectively.

As a few of the small parthenocarpic fruits exhibited very delayed ripening, fruits less than 30 g were excluded from the analysis of fruit development. Fruit ripened after 63.6 d (a rate of progress to ripening of 0.0157 d^{-1}) at 18°C compared with 39.2 d (0.0255 d^{-1}) at 25°C (s.e.d. = 2.21). While heating flower buds hastened flower opening, there was no significant effect of this treatment on the subsequent time fruits took to ripen ($P > 0.05$). Heating fruits for the first or second 3-week period, or from week 7 onwards, hastened maturity by 8.7, 9.8 and 11.2 d (s.e.d. = 2.21), respectively, compared with the constant 18°C regime. While these development times were not significantly different ($P > 0.05$), it is important to note that fruits heated from week 7 spent a mean of only 10 d in this elevated temperature regime before ripening.

By summing temperatures above 5.7°C , the thermal time model produced using data from expts 1 and 2 was used to predict the effect of heating at different times (Fig. 6). While fruits grown in a constant temperature regime matured 2–3 d earlier than predicted by the model, this was not the

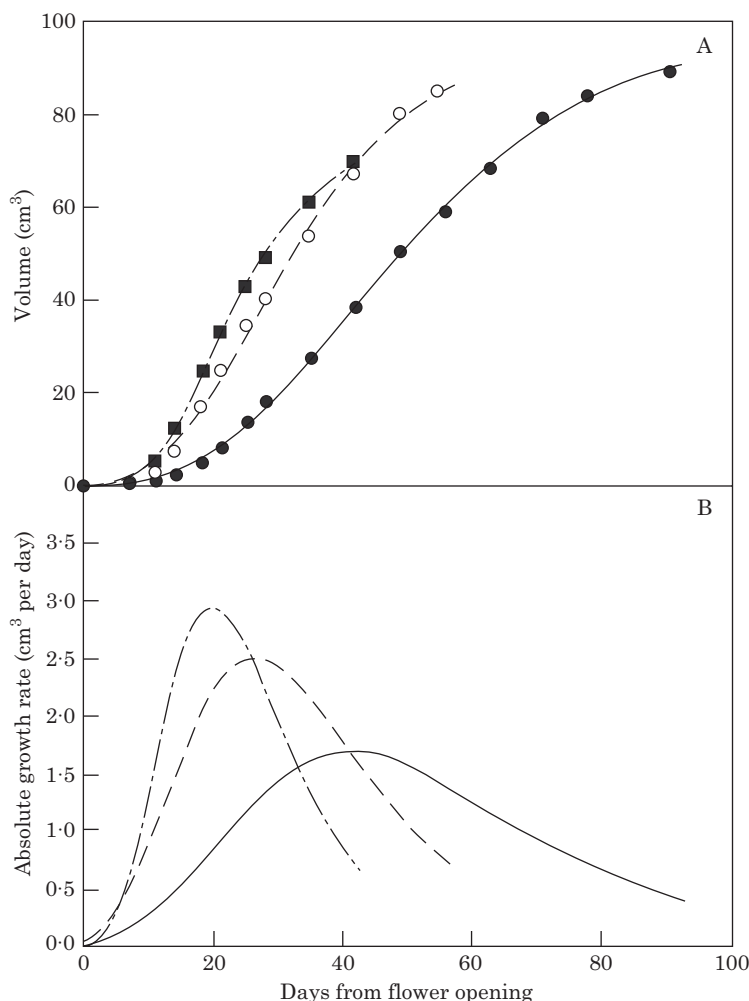


FIG. 5. The effect of heating or cooling individual trusses on growth (A) and absolute growth rates (B) of tomato fruit grown at 15°C (●, —), 20°C (○, - - -) and 25°C (■, - · - ·). Points represent the mean volume of ten fruits calculated assuming fruits are spherical. Lines represent a Gompertz function fitted to each data set using Genstat 5.

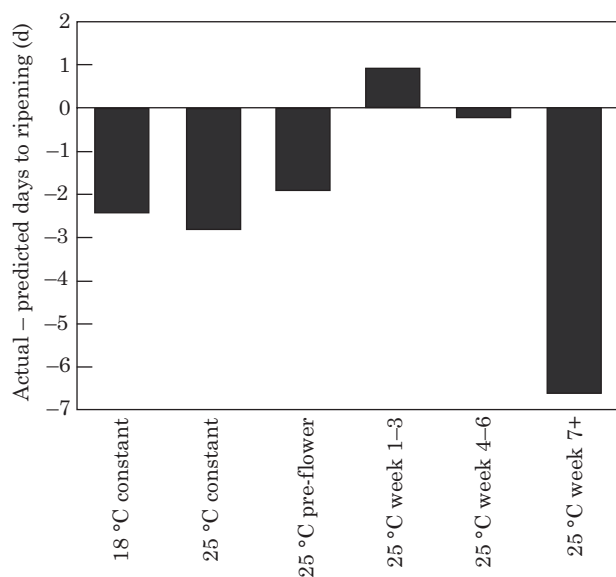


FIG. 6. The difference in the time taken for fruits to ripen when heated from 18 °C to 25 °C at different stages when compared to predictions made according to the thermal time model (Fig. 4). Five trusses were heated for each temperature treatment.

case when fruits were heated at an early developmental stage (before week 6), suggesting that they may be less sensitive to temperature at this time. However, fruits heated in their later stages of development (after week 7) ripened much quicker than the thermal time model predicted, suggesting that they were far more sensitive to temperature at that time.

DISCUSSION

In agreement with the findings of Verkerk (1955) and Hurd and Graves (1985), temperature had a considerable effect on the time of fruit maturation. The fact that the response to temperature was similar in the first two experiments suggested that the time of ripening was dependent on the temperature of the fruit, and that the temperature of other organs had little effect. The present work also showed that with respect to the time of ripening, the sensitivity of fruits to temperature increased in mature green fruits, in agreement with the findings of de Koning (1994). However, our findings do not support his other conclusion that high temperatures following flower opening, when cell division is taking place, dramatically hasten the time of ripening (de Koning, 1994). It may be that our temperature pulses of 3-weeks' duration were too long to see this effect, although the inconsistency certainly warrants further investigation.

The position of fruits on a truss was also shown to have some effect on the time of fruit ripening. Fruits ripened quicker at the proximal end of the truss in the 15 °C treatment of the second experiment, although this may reflect the fact that they were slightly older at the start of this treatment. However, positional effects were also observed in the first experiment where constant temperature regimes were used; ripening was delayed at both the proximal and distal ends of trusses. Cockshull *et al.*

(1992) found that under glasshouse conditions the fifth fruits of the first few trusses took longer to develop compared with the first fruits, although by the seventh truss there was little difference between them. While these fruits would have been surrounded by air of an identical temperature, the actual temperature of the fruits could have differed, which might, in part, account for these effects. In the work described here, some fruit temperatures were recorded by inserting thermistor probes into fruits (data not shown). Fruit temperatures were found to increase in the light period, particularly at the top of the canopy, even though the air temperature remained constant. The shoulder of fruits also tended to be warmer than the centre or underside, again highlighting the effect of incident radiation on fruit temperatures. Interestingly, Slack (1986) found that severe defoliation, which would have reduced the shading of fruits, also hastened fruit maturation, although unfortunately fruit temperatures were not recorded.

Fruit growth could be adequately described using a Gompertz function. Growth rates were maximal slightly before half the time taken for fruits to ripen had elapsed, and fruits were still growing slightly prior to harvesting. Grange and Andrews (1993) found that final fruit size was proportional to the maximum rate of increase in fresh weight, about 40 d after anthesis, and was also related to the maximum rate of increase in diameter which occurred between 15 and 20 d after anthesis. These different growth rates may have been related to cell numbers and hence potential fruit size. However, their work only considered the difference in size of fruits within a truss, as fruits were grown within the same temperature regime. It is clear from the data presented here that final fruit size was related both to fruit growth rates and the duration of growth. While elevated temperature regimes may increase growth rates (Pearce *et al.*, 1993a), they do not necessarily increase the final fruit size due to the effect of temperature on the duration of growth (Ho, 1996).

Heuvelink and Marcelis (1989) went further, and concluded that under non-limiting assimilate supply the maximum growth rate of tomato trusses was hardly influenced by temperature; the influence of temperature was mainly upon the time of maturation. However, this seems to contradict results of our second experiment in which temperature treatments were applied to individual trusses. Although this experiment was conducted under conditions where assimilate supply would have been limiting, it is hard to see why the actual growth rates responded to temperature in the way they did if the potential growth rate (sink strength) was unaffected by temperature.

Conventional long-season tomato crops are usually planted out in northern Europe at a time of year when light levels are low but then gradually increase, whereas the controlled environment rooms provided a constant daily light integral. As a result there tended to be a heavy fruit load on the first trusses at both 18 °C and 22 °C, and mean fruit size declined over the course of the experiment. There was some evidence to suggest that the rate of fruit development had a higher optimum temperature compared with either the rates of truss production or flower opening. The rates of truss production and flower opening were lower

at 26 °C than at 22 °C, whereas there was little evidence for an optimum temperature for fruit development time within the temperature range that was investigated. This resulted in a decreased number of fruiting trusses in the high temperature regime.

The constant 14 °C temperature regime produced fruits that were not only small and firm but also parthenocarpic. Over half the fruit sampled from the 26 °C temperature regime was also parthenocarpic and other fruit from this treatment had low seed numbers. Foster and Tatman (1937) noted that both high and low temperatures contributed to the appearance of parthenocarpic fruits, especially when large amounts of nitrogen were applied. However, Osborne and Went (1953) concluded that while very high or very low night-time temperatures or low carbohydrate content induced sterility in 'Essex Wonder', only low temperatures combined with ample carbohydrates induced parthenocarpic. Rylski (1979) indicated that parthenocarpic fruits were a result of low temperatures during flower development. While parthenocarpic fruits were small in our experiments, this may have been a direct effect of the treatment rather than an indirect effect of inducing parthenocarpic. Parthenocarpic is not always reported to reduce fruit size (Ho and Hewitt, 1986). There was also poor fruit set at 26 °C in the present experiments. Sato *et al.* (2000) suggested that poor fruit set at high temperatures was due to the effect of temperature on pollen grain release and germination. The number of pollen grains produced, photosynthesis and night respiration did not appear to limit fruit set (Sato *et al.*, 2000), although competition for assimilates could affect it (Bertin, 1995).

The partitioning of dry matter to fruits was lower than that recorded by Cockshull *et al.* (1992) for a long-season tomato crop where 69 % of dry matter was partitioned to fruits compared with 12.9 % to stems and 18.1 % to leaves. However, more dry matter was partitioned to fruits when compared with that recorded after 16 weeks by Ho (1996) for a number of different cultivars. However, it should be borne in mind that the fraction of dry matter partitioned to fruits increases over time as more trusses are produced (Heuvelink, 1995b, 1997), which probably accounts for some of these differences. Furthermore, temperature had a profound effect on developmental rates, which may explain why the dry matter partitioned to fruits appears especially low in the low temperature treatments. If plants had been sampled after a similar number of trusses had been produced, the effect of temperature on partitioning might have been different. In addition, partitioning to fruits is affected by fruit load, so reducing the number of fruits per plant diminishes the fraction of total biomass allocated to the fruits (Heuvelink and Buiskool, 1995; Heuvelink, 1997). Poor fruit set in the 26 °C treatment may have reduced dry matter partitioning to fruits grown at this temperature. Although temperature appeared to have affected the partitioning of dry matter within the shoot, Heuvelink (1995a) concluded that dry matter partitioning was not significantly affected by temperature. Developmental rates and fruit numbers were altered by temperature, which in turn affected partitioning; however, Heuvelink considered these to be 'indirect' effects.

Our results corroborate the finding of glasshouse experiments which suggest that fluctuations in weekly fruit yields may well result from fluctuations in temperature due to the increased sensitivity of mature green fruits to temperature (Adams *et al.*, 2001). However, for accurate yield predictions further work is needed to quantify the precise time and degree to which fruits become more sensitive to temperature, and to investigate the relationship between fruit and air temperatures under glasshouse conditions with high levels of solar radiation.

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