THE EFFECT OF TEMPERATURE, FRUIT LOAD AND SALINITY ON DEVELOPMENT RATE OF TOMATO FRUIT

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1. Introduction

Time between flowering or fruit set of an individual fruit and harvest is important for planning and control of fruit load and yield of glasshouse tomatoes. Short term yield prediction, for instance, can be based on achieved fruit set and predicted fruit growth period. This paper describes the results of a number of experiments where fruit growth period is measured. The effect of temperature was modelled. This paper describes the main results of a study on growth and development of glasshouse tomato (de Koning, 1994)

2. Materials and methods

Several glasshouse experiments were conducted to quantify the effect of fruit load, salinity (EC) and temperature on fruit development. Investigated temperatures ranged from 17 to 23°C, except in one experiment which included 26°C 24-h mean temperature. Temperature experiments were conducted all with two replicates (compartments) per temperature. A distributed computer system was used for climate control and data acquisition (Bakker *et al.*, 1988). Temperature was measured every minute centrally in the compartments at 1.5 m above ground level. The tomato crops were trained according to a high wire system and were grown on rockwool slabs irrigated with a standard nutrient solution (Sonneveld and de Kreij, 1988) by means of a trickle irrigation system.

Flowering and harvestable trusses were recorded on two or three occasions each week for each plant and averaged per experimental plot. By interpolation in the averaged recordings of flowering and harvestable truss, the moment a particular truss started to flower and the time the first fruit of this truss could be harvested were estimated. Then, for each truss, the growth period and average temperature over this period were calculated. Since fruit growth period was not affected by truss number (de Koning, 1994), mean fruit growth period and average temperature were calculated per experimental plot. The effect of changing temperature on fruit development was investigated by moving plants for a fortnight to a higher or lower temperature at different stages of fruit development.

As in several applications it is preferred to use rates instead of durations, for constant temperature treatments fruit development rate (FDR) is calculated as the reciprocal of fruit growth period (FGP). The moment of anthesis and harvest ripe are defined as 0 and 1, respectively. In some cases the moment of harvest is regarded as 100% and then fruit development rate is expressed in percent per unit of time (*viz.* % d^{-1}).

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3. Results

In an experiment with two fruit load treatments at four temperatures, at 17 and 19°C the fruit growth period of fruits grown with only two fruits per truss was slightly longer than that of fruits grown on normally loaded plants (Table 1). Temperature had a very significant ($P<0.001$) effect and the response seemed to be slightly stronger at low fruit load as indicated by a significant ($P=0.013$) 'fruit load × temperature' interaction.

In another experiment three temperatures were combined with different levels of salinity and, at the highest temperature, two plant spacings. The electrical conductivity in the root medium did not affect fruit development rate (Table 2). Decreasing plant spacing tended to shorten the fruit growth period slightly. Temperature had a very significant ($P=0.002$) accelerating effect and there were no interactions with other factors. In a second experiment on salinity, applying 0.3, 0.6 and 0.9 S m^{-1}, the fruit growth period was not affected either (data not shown).

Data of five experiments on the effect of constant temperature on fruit development were analyzed together. In total 28 fruit growth period - temperature pairs were available. A quadratic relationship of temperature, with different intercepts for different experiments fitted the data adequately (Figure 1).

Fruit development rate (FDR=100/FGP) was well described by a linear function of the log-transformed temperature: $FDR = a + b \ln(T)$, (Figure 2). Parameter a varied from - 4.67 to - 4.45 % d^{-1} and differences coincided with the time of year the experiment was conducted, *viz*. expts 1, 2 and 5 in early spring versus expts 3 and 4 in late summer. Fruit development rate seems higher in summer. Expanding the model with different slopes (i.e. parameter b) in each experiment did not significantly decrease the residual variance. Hence, the response to temperature did not differ between experiments; $b = 2.131$. Generally, standard errors of predicted values for fruit growth development rate between 17 and 26°C were within 2% of the predicted value.

The interaction between temperature and fruit development stage on the duration of fruit development was investigated in two experiments. The obtained data suggested different response on temperature depending on fruit age. In order to analyze this effect the fruit growth period was divided into a certain number of sub-periods, and then the average temperature for every period was calculated for each individual fruit. These average temperatures were used as explanatory variables for the duration of the fruit growth period; $FGP=f(T_1, T_2 ... T_n)$. It was found by trial and error that dividing the total fruit growth period into five sub-periods gave a reasonable balance between accuracy and statistically significant parameters. As when describing fruit growth period for fruits grown at constant temperature, a relationship between the reciprocal of FGP, i.e. fruit development rate (FDR), with the natural logarithm of temperature was most successful.

Table 3 comprises the results of the fittings of data-sets from both experiments separately and of a fitting of the combined data-set. In both experiments FGP is shortened by high temperature in the young development stage (first and second period), then the fruit becomes insensitive to temperature (third period) and close to the mature stage temperature has a very large impact, as represented by the values for b_{1-5}. Parameter a differed significantly ($P<0.001$) between both experiments.

On the basis of the values fitted for b_{1-5} of the 'five periods model' a third order polynomial of fruit development stage (FDS) seems a suitable function to describe the response of fruit development rate (FDR) to temperature during fruit development. As FDS can not be measured between anthesis and fruit colouring, FDR is defined to be constant at a reference temperature of 20°C. Consequently, at constant 20°C the fruit's development stage is proportional to its age. The fitted model is given by:

$FDS_0 = 0,$
$FDR_t = a+\ln(T_t/20)\times(b+c\times FDS_{t-1}+d\times FDS_{t-1}^2+e\times FDS_{t-1}^3),$
$FDS_t = FDS_{t-1}+FDR_t,$

where FDS_t is the fruit development stage at t days after anthesis (anthesis = day number 0), FDR_t is the fruit development rate (d^{-1}), T_t is the 24-h mean temperature (°C), a_{FDR} is a parameter representing FDR at constant 20°C and *b, c, d* and *e* are parameters of the temperature response curve.

The predicted fruit growth period is determined by the day number when FDS passes 1. In the fitting procedure (GENSTAT, Payne and Lane, 1987) the difference between estimated and measured FGP was minimized (least square difference). The initial value for parameter a_{FDR} was calculated from the equation based on constant temperature, while the initial values for *b, c, d* and *e* were obtained from fitting a third order polynomial to the values of parameters $b_{1\text{-}5}$ of the 'five periods model'.

The model gave a good fit to the data (Table 4). At a fruit development stage of about 0.3, the fruit development rate appears relatively insensitive to temperature, in contrast to young and near-mature fruits which are very temperature sensitive. This corroborates the results obtained by the 'five periods model'.

Temperature response of fruit development rate at 0.1, 0.3, 0.6 and 0.9 development stage is graphically presented in figure 3. The crossing of all response curves at 20°C in this figure is a consequence of the definition of the fruit development rate, which is then constant at this temperature.

4. Discussion

Of the variables investigated, temperature appears the principal factor determining the duration of the fruit growth period (FGP). In the present experiments FGP varied from about 73 days at 17°C to only 42 days at 26°C. Those data agree very well with observations by Rylski (1979). A reduction in the growth period of reproductive organs with increasing temperature has frequently been observed with several species, e.g. the fruit growth period of sweet pepper (Bakker, 1989), the grain filling period of wheat (Spiertz, 1977) and the boll maturation period of cotton (Mutsaerts, 1976). The fruit growth period can be well described by linearly relating its reciprocal (i.e. fruit development rate) to temperature. Using the same approach, good results were also obtained by Vos (1981), Auld *et al.* (1978) and Milford *et al.* (1985) when describing the duration of the grain filling period of wheat and the duration of leaf expansion for field bean and sugar beet, respectively. In the present study, little improvement was gained by relating fruit development rate (FDR) to the natural logarithm of temperature, which represents a slight decrease of the temperature effect at increasing temperature.

The accelerating effect of temperature is not equal during fruit development. The course of the temperature response reflects the sensitivity to temperature of successive physiological processes determining the fruit growth period. Just after anthesis, the affected processes may be cell division and seed growth, while near maturity the onset of processes involved in colouring will be accelerated by temperature.

For different experiments statistically significant differences were found for the parameter *a* in the model $FDR=a+b\times\ln(T)$. The differences in fruit development rate correspond to the season, i.e. early spring versus late summer. Fruit growth period in late summer is about 6 days less than in spring. At low irradiance, fruit temperature is equal to air temperature, but at high irradiance current temperature of exposed fruits may be up to 9°C higher (van Holsteijn, 1989). Therefore the observed season effect on FGP may be due to differences between (measured) air temperature and fruit temperature.

The observed absence of any effect of EC in the rooting medium on FGP as presented is convincing. However, several authors reported a few days decrease of FGP if salinity was raised (Mizrahi, 1982; Mizrahi *et al.*, 1982; Sharaf and Hobson, 1986).

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Tables

1. Duration of the fruit growth period (d) of normally loaded and extremely pruned (two fruits per truss) tomato plants (cv. 'Calypso', spring crop) at four temperatures (°C).

temperature	normal	pruned	LSD 5%
17	71.9	74.9	2.1
19	62.0	64.9	2.1
21	56.2	54.3	n.s.
23	48.6	46.8	n.s.

2. Duration of the fruit growth period (d) of tomato (cv. 'Liberto', spring crop) grown at three temperatures, two plant densities (only at 23°C) and three electrical conductivity levels in the root medium. Means were not statistically different (Student's *t*-test, P=0.05).

temperature (°C)	plant density (plants m^{-2})	fruit growth period EC (S m^{-1})			
		0.3	0.6	0.8	mean
19	2.1	58.2	57.6	57.3	
21	2.1	53.1	52.8	52.4	
23	2.1	49.3	49.5	49.8	49.5
23	1.6	47.1	48.4	48.7	48.1
mean		51.9	52.1	52.1	

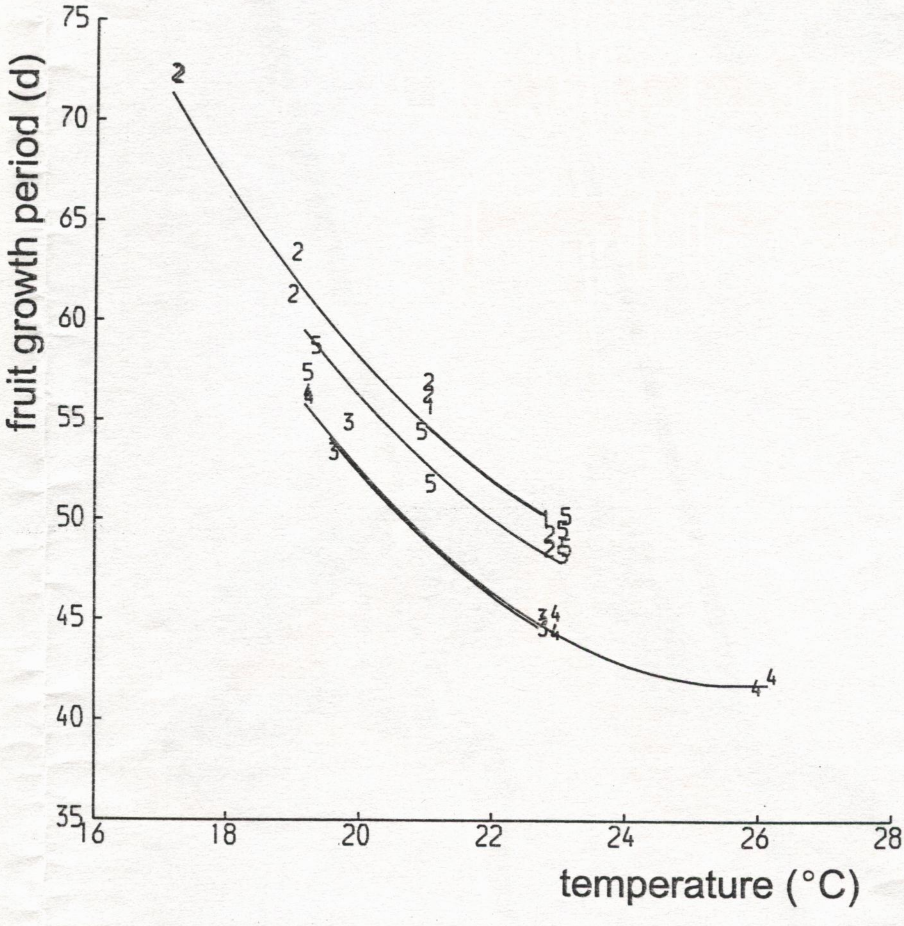
3. Parameters (standard errors within brackets) for the relationship: $FGP = 100/\{a_i+b_1\times\ln(T_1)+b_2\times\ln(T_2)+b_3\times\ln(T_3)+b_4\times\ln(T_4)+b_5\times\ln(T_5)\}$, where FGP is the fruit growth period (d), a_i is an experiment dependent parameter, $b_{1\text{-}5}$ are parameters and T_1, T_2, T_3, T_4 and T_5 are the average temperatures (°C) of five successive equal parts of the total fruit growth period. Experiment 1 was conducted in spring with cv. 'Calypso'. Experiment 2 was conducted in summer with cv. 'Calypso'.

parameter	experiment 1		experiment 2		both experiments	
a_1	-5.775	(0.148)			-5.854	(0.129)
a_2			-6.096	(0.284)	-5.646	(0.139)
b_1	0.326	(0.053)	0.703	(0.109)	0.394	(0.047)
b_2	0.357	(0.060)	0.149	(0.108)	0.320	(0.052)
b_3	0.039	(0.057)	0.071	(0.092)	0.050	(0.048)
b_4	0.760	(0.058)	0.958	(0.103)	0.817	(0.050)
b_5	1.006	(0.056)	0.785	(0.083)	0.940	(0.046)
n	419		114		533	
R^2	0.863		0.902		0.934	

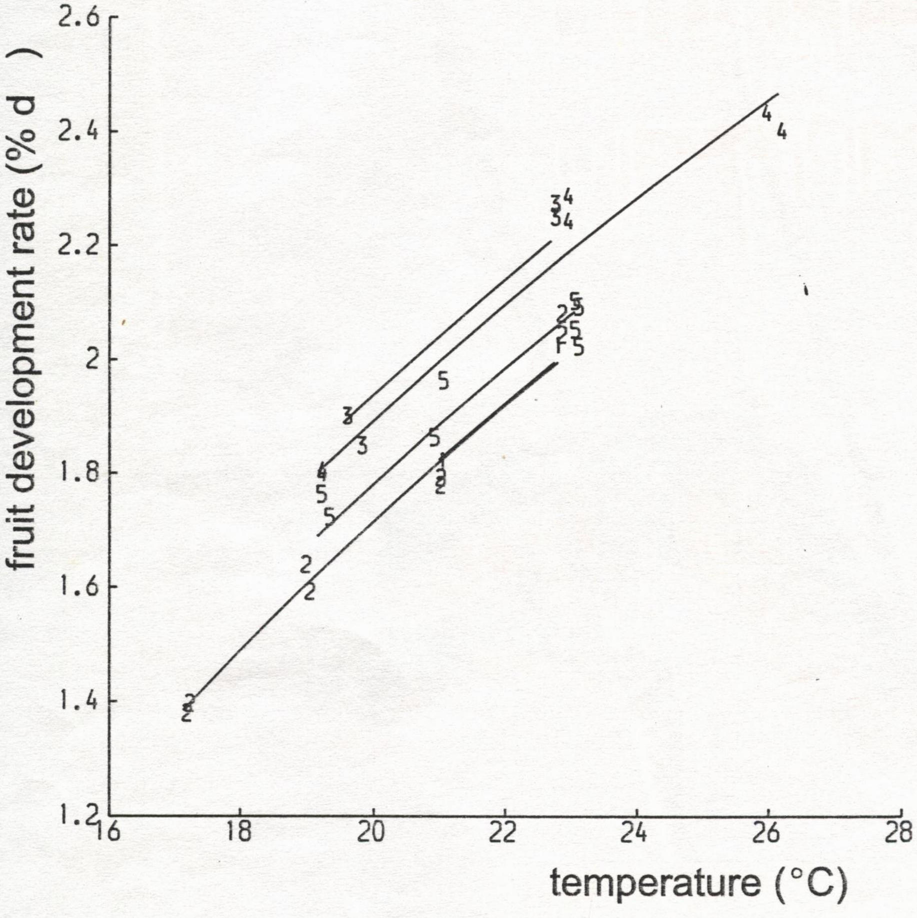
4. Parameters (standard errors within brackets) for the relationship: $FDR_t = a_i + \ln(T_t/20) \times (b+c\times FDS_{t-1}+d\times FDS_{t-1}^2+e\times FDS_{t-1}^3)$, where FDR_t is the fruit development rate (d^{-1}) at t days after anthesis, T_t is the 24-h mean temperature (°C), FDS_t is the fruit development stage, a is an experiment dependent parameter and b, c, d and e are parameters representing the temperature response. Experiment 1 was conducted in spring with cv. 'Calypso'. Experiment 2 was conducted in summer with cv. 'Calypso'.

parameter	experiment 1		experiment 2		both experiments	
a_1	0.01702	(.000047)			0.01712	(.000004)
a_2			0.01905	(.000017)	0.01931	(.00002)
b	0.04471	(.00378)	0.05413	(.00039)	0.03923	(.00009)
c	-0.2675	(.0368)	-0.3139	(.0019)	-0.2127	(.0005)
d	0.5831	(.0907)	0.6249	(.0037)	0.4505	(.0008)
e	-0.3286	(.0633)	-0.3058	(.0028)	-0.2400	(.0009)
n	419		114		533	
R^2	0.856		0.882		0.913	

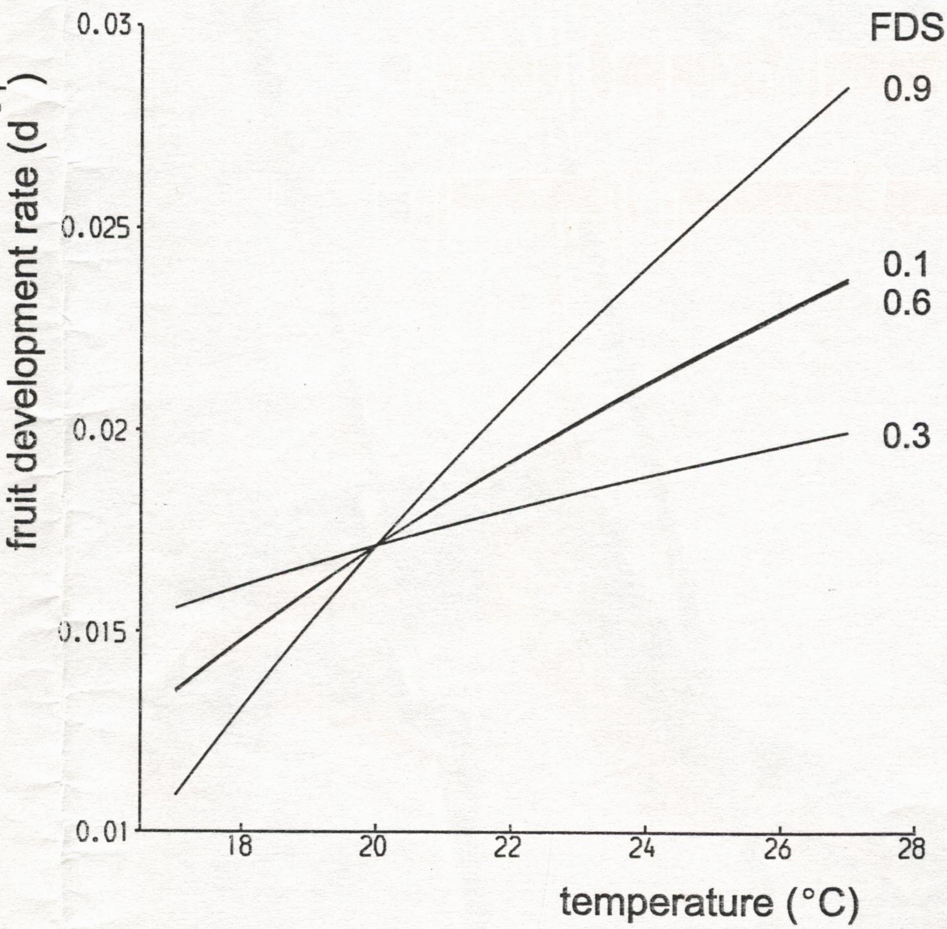
Figures



1. The effect of temperature on fruit growth period of tomato for five experiments. Expt 1, cv. 'Counter' in spring, Expt 2, cv. 'Calypso' in spring, Expt 3, cv. 'Calypso' in summer, Expt 4, cv. 'Calypso' in summer, Expt 5, cv. 'Liberto' in spring.



2. Relationship between fruit development rate of tomato for five experiments. Expt 1, cv. 'Counter' in spring, Expt 2, cv. 'Calypso' in spring, Expt 3, cv. 'Calypso' in summer, Expt 4, cv. 'Calypso' in summer, Expt 5, cv. 'Liberto' in spring.



3. Temperature sensitivity of fruit development rate of tomato (cv. 'Calypso') at 0.1, 0.3, 0.6 and 0.9 development stage (FDS).