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The effects of diurnal temperature regimes on growth and yield of glasshouse sweet pepper

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Abstract

The effects of temperature on growth and yield of October-sown sweet pepper (*Capsicum annuum* L.), cv. Delphin, were investigated in a glasshouse experiment. Twelve day/night temperature regimes (16/15, 16/21, 20/12, 20/15, 20/18, 20/21, 24/12, 24/15, 24/18, 24/21, 28/15 and 28/21 °C) were applied during the early post-planting period (early December to mid April). Fresh weight (g plant^{-1}) and leaf number were significantly related with (calculated) 24-h mean temperature, no significant effect of the day/night temperature amplitude was found. Plant height, leaf area and the leaf area/length ratio were significantly correlated to 24-h mean temperature as well as to the day/night temperature amplitude. The optimum 24-h mean temperature for vegetative growth was between 21 and 23 °C. Yields of total and class 1 fruit (kg m^{-2}) and number of class 1 fruit (m^{-2}) showed a maximum at a 24-h mean temperature of 21-21.5 °C. Raising the 24-h mean air temperature (within the range 16.3 to 23.8 °C) significantly reduced the mean fruit weight of class 1 fruits. The day/night temperature amplitude had a significant positive effect on these variables. The effect of the day/night temperature amplitude on vegetative growth as well as on yield was of minor importance compared to the effect of 24-h mean temperature.

Introduction

Temperature is one of the most important environmental factors influencing plant growth, development and yield. Recent results with glasshouse crops show a remarkably close relationship between the 24-h mean temperature and growth and yield (Slack & Hand, 1983, for cucumber; van den Berg, 1987, for roses; de Koning, 1988a, for tomatoes). There was apparently no effect of the day/night temperature amplitude with these crops. This opens the possibility for new temperature control procedures which yield maximum profit of energy saving measures (de

Koning, 1988b). However, for sweet pepper, the introduction of new temperature control procedures is hindered by the lack of information on the effects of 24-h mean temperature and the day/night temperature amplitude on growth, yield and fruit quality. The optimum temperature for photosynthesis of sweet pepper is high. According to Nilwik (1980) the maximum net photosynthesis is achieved between 24 and 29 °C. However, temperatures which optimize dry matter production do not necessarily result in highest yields. Effects of temperature on flowering (Rylski, 1972), fruit set (Rylski & Spigelman, 1982) and fruit shape (Rylski, 1973) account for variations in final yield.

In this study the effects of 24-h mean temperature and the day/night temperature amplitude were investigated with winter-grown sweet pepper. The aim was to find out whether the effect of temperature amplitude on vegetative growth and yield is marked, compared to the effect of 24-h mean temperature, and which parameters of vegetative growth and yield respond to day/night temperature amplitude.

Materials and methods

Sweet pepper (*Capsicum annuum* L.) plants, cv. 'Delphin' sown on 6 October 1986, were planted on 2 December 1986 (3.2 plants m^{-2}). The plants were grown on rockwool slabs in a gutter and irrigated with a nutrient solution with the aid of a trickle irrigation system, EC and pH 3.0 dS m^{-1} and 5.5, respectively. The composition of the nutrient solution was: NO_3^- 12.25, $H_2PO_4^-$ 1.25, SO_4^{2-} 1.25, NH_4^+ 0.25, K^+ 6.0, Ca^{2+} 3.75, Mg^{2+} 1.125 mmol.l^{-1}; and Fe 10, Mn 10, Zn 4, B, 25, Cu 0.5, Mo 0.5 μmol l^{-1}. Excess solution was recirculated. Root temperature was maintained at 20-21 °C. The plants were trained with two stems and flowers were removed from the first ten leaf nodes. No artificial pollination was applied.

The experiment was carried out in 24 compartments of the climate glasshouse at the GCRS (van de Vooren & Koppe, 1975). Temperature was measured at 1 m height with screened and aspirated PT-100 sensors, with a sample time of one minute. A computer system was used for environmental control and data storage (Bakker et al., 1988). The addition of pure CO_2 was controlled by Siemens conductometric devices (type Ultramat 21) to maintain a level of 700 ppm.

Twelve day/night temperature regimes were applied in duplicate, from planting (2 December 1986) until four weeks after the start of harvesting from the most advanced treatment (14 April 1987). The setpoints for heating, day/night, were 16/15, 16/21, 20/12, 20/15, 20/18, 20/21, 24/12, 24/15, 24/18, 24/21, 28/15 and 28/21 °C. Setpoints for ventilation, by day as well as at night, were 1 °C above the setpoints for heating. The setpoint modification from night to day and from day to night took three hours and started 2.5 h before sunrise and 1.5 h before sunset, respectively. It was not possible to continue the temperature regimes beyond 14 April because of increasing solar heat gain and rising outdoor ambient temperatures. For the rest of the growing season the same temperature regime was applied, i.e. 21 °C/15 °C for day/night, with ventilation at 22 °C/16 °C, respectively.

Daylength during the period in which the temperature regimes were applied increased from 8 h in early December to 14 h in April. Mean temperatures for day, night and the 24-h period were calculated over the periods 10.00-16.00 h, 22.00-04.00 h and 00.00-24.00 h, respectively, using the stored minute readings. The day/night temperature amplitude (*Ta*, °C) was calculated as the difference between day and night temperature.

On 17 February, when first fruit set occurred, plant height, number of leaves (width >2 cm), leaf area and fresh weight were recorded from four individual plants per treatment. Fruits were harvested red, once a week; their number (m^{-2}), weight (kg m^{-2}) and market grade were recorded. Malformed fruits and fruits with blossom end rot were graded in class 2. Vegetative growth parameters were related to mean temperatures from planting until 17 February, early and final yield was related to mean temperatures from planting until 14 April. The irradiance conditions (average daily total, 400-700 nm) in the glasshouses from planting until 17 February and 14 April were 0.70 MJ m^{-2} and 1.54 MJ m^{-2}, respectively. These values were calculated from outside measurements and corrected for transmission of glasshouses.

Although growth and yield of plants may be linearly related to the mean 24-h temperature (Slack & Hand, 1983), the response of plants to 24-h mean temperature may deviate from linearity when plants are grown under a differential day/night temperature regime (Warrington & Kanemasu, 1983). Therefore various second-order multiple regression functions, in which the mean 24-h temperature as well as the day/night amplitude were incorporated, were used for analysis of the data. Highest correlations were obtained with the following equation:

$$Y = a \times T + b \times T^2 + c \times Ta + d \qquad (1)$$

where: Y = variable, T = 24-h mean temperature in °C, Ta = temperature amplitude (difference between day and night temperature) in °C, a, b, c and d constants.

Results

Environment

Day, night and 24-h mean temperatures from 2 December 1986 until 17 February and 14 April, respectively, are listed in Table 1. Measured over the period in which the treatments were applied, deviations from the heating setpoints were generally less than 1 °C, except for the treatments including 16 °C day temperature and those including 12 °C night temperature (Table 1). Until 14 April, the mean day temperature varied from 18.2 to 27.9 °C, the mean night temperature from 13.1 to 20.8 °C and the mean 24-h temperature from 16.3 to 23.8 °C (Table 1). The day/night amplitude varied from −2.1 (regime 16/21 °C) to 12.5 (regime 28/15 °C).

Vegetative growth

The different treatments resulted in significant differences in vegetative growth (Table 2). The parameters given in Table 2 were analysed using Eq. 1 and temperatures until 17 February (Table 1). The values of the coefficients for the different relations are listed in Table 3. Fresh weight and leaf number were closely correlated

Table 1. Day, night and calculated 24-h mean temperature (°C) at different temperature regimes for two cropping periods of sweet pepper.

Treatment day/night (°C)	2/12/86 - 17/2/87			2/12/86 - 14/4/87		
	day	night	24-h	day	night	24-h
16/15	17.4	14.9	15.7	18.2	14.9	16.3
16/21	17.8	20.9	19.3	18.5	20.6	19.2
20/12	20.3	13.3	16.1	20.9	13.1	16.6
20/15	20.3	15.3	17.2	21.2	15.4	17.9
20/18	20.6	17.9	18.8	21.1	17.8	19.1
20/21	20.6	20.9	20.6	21.1	20.6	20.7
24/12	24.4	14.6	18.7	24.7	14.0	18.9
24/15	24.2	14.9	18.8	24.5	15.0	19.3
24/18	24.1	17.9	20.5	24.5	17.9	20.8
24/21	24.3	20.9	22.2	24.7	20.7	22.3
28/15	27.8	15.4	20.6	27.9	15.4	21.1
28/21	27.8	20.8	23.7	27.9	20.8	23.8

Table 2. Vegetative growth parameters of sweet pepper grown at different temperature regimes on 17 February 1987 (all values expressed per plant).

Treatment day/night (°C)	Fresh weight (g)	Height (cm)	Leaf number	Leaf area (cm^2)	Area/length ratio (cm)
16/15	159.6	52.5	73.0	2829	53.9
16/21	231.7	68.5	96.0	3195	47.1
20/12	179.9	62.0	73.5	3523	56.6
20/15	187.2	66.0	85.5	3739	56.2
20/18	235.1	82.0	112.0	4645	56.6
20/21	226.4	83.5	128.0	4324	51.7
24/12	161.3	65.5	75.0	3714	56.1
24/15	239.7	84.5	111.5	5203	61.7
24/18	311.1	97.0	143.5	6293	64.7
24/21	259.7	95.5	139.0	5203	54.7
28/15	281.4	95.0	128.5	5827	61.5
28/21	204.2	87.0	108.0	4449	51.3
LSD ($P = 0.05$)	96.1	17.0	39.1	1373	12.2

Table 3. Coefficients a, b, c, d and the multiple correlation coefficient (r) for the relations between vegetative growth parameters (per plant) of sweet pepper and temperature (Eq. 1) on 17 February 1987.

Y-variable	a	b	c	d	r
Fresh weight (g)	157.6	- 3.76	n.s.	- 1397	0.618
Height (cm)	33.7	- 0.732	0.677	- 298	0.839
Leaf number	66.4	- 1.495	n.s.	- 611	0.740
Leaf area (cm^2)	2886.0	-67.4	102.7	-26388	0.757
Area/length (cm)	10.73	- 0.282	0.796	- 48.9	0.604

Presented coefficients (a, b, c and d) are significant at $P = 0.05$; n.s. = not significant. Multiple correlation coefficients (r) are significant at $P < 0.01$.

to 24-h average temperature, no significant effect of Ta on these parameters was found. Plant height, leaf area and the leaf area/length ratio were significantly related to 24-h mean temperature as well as to *Ta*. The day/night amplitude had a significant positive effect on these parameters (Table 3). From the coefficients in Table 3 can be calculated that raising the 24-h mean temperature from 16 °C to 20 °C (at $Ta = 0$), increases the leaf area per plant by 1800 cm^2. To obtain a comparable increase in leaf area at a given 24-h mean temperature, the day/night amplitude has to be increased from 0 °C to 18 °C. So the effect of the day/night amplitude on vegetative growth is relatively small compared to the effect of 24-h mean temperature in the range investigated. For all parameters observed, the maximum value is obtained at a 24-h mean temperature between 21-23 °C.

Fruit production

The early and final yield (kg m^{-2}) of class 1 fruit and of total fruit (class 1 + class 2), mean fruit weight (g $fruit^{-1}$) and the number of class 1 (m^{-2}) fruits are presented in Table 4. Yield of class 1 fruit was significantly lower at low temperatures, due to malformed fruits. Yield, number of fruits and mean fruit weight (class 1) were analysed using Eq. 1 and measured temperatures until 14 April. The coefficients for the different relations are presented in Table 5. In Fig. 1 the final total yield of class 1 fruit, as calculated with the coefficients from Table 5, is presented as a function of the 24-h mean temperature and *Ta*. From this figure it can be seen that the maximum yield (within the investigated temperature range) is obtained at a 24-h mean temperature of 21-21.5 °C. Also, early as well as final yield of total fruit and num-

Table 4. Total (class 1 + class 2) and class 1 fruit yield, mean fruit weight (MFW) of class 1 fruit, and number of class 1 fruit at different temperature treatments for two production periods.

Treatment day/night (°C)	Early yield (to 6/5/87)				Final yield (to 22/7/87)			
	total	class 1			total	class 1		
	kg m^{-2}	kg m^{-2}	MFW (g)	number (m^{-2})	kg m^{-2}	kg m^{-2}	MFW (g)	number (m^{-2})
16/15	0.00	0.00	*	0.0	7.44	2.17	216.9	10.0
16/21	2.34	2.08	134.1	15.1	9.53	8.45	143.5	60.0
20/12	0.82	0.00	*	0.0	9.54	5.56	157.2	35.3
20/15	1.88	1.50	148.6	10.7	10.51	8.44	158.3	53.3
20/18	2.55	2.40	155.9	15.3	9.69	8.75	164.3	53.5
20/21	3.38	3.23	144.4	22.3	10.39	9.58	154.5	62.3
24/12	3.82	3.63	175.1	20.8	11.58	10.31	177.3	58.2
24/15	3.75	3.66	185.6	19.8	11.81	11.21	185.8	60.2
24/18	3.25	3.16	155.2	20.5	10.62	9.70	159.2	61.1
24/21	3.42	3.33	138.6	24.1	10.54	9.89	156.1	63.4
28/15	3.83	3.72	159.8	23.3	10.82	10.21	156.1	57.7
28/21	3.51	3.38	129.0	26.2	10.02	8.87	141.1	63.0
LSD ($P = 0.05$)	0.96	0.73	28.3	5.6	1.28	1.07	15.4	6.3

Table 5. Coefficients *a*, *b*, *c*, *d* and the multiple correlation coefficient (*r*) for the relations (Eq. 1) between yield parameters of sweet pepper and temperature.

Y-variable	*a*	*b*	*c*	*d*	*r*
Early yield (to 6/5/87)					
Total yield (kg m^{-2})	4.933	−0.114	0.087	− 50.32	0.921
Class 1 yield (kg m^{-2})	5.191	−0.119	0.084	− 53.44	0.939
Number of class 1 (m^{-2})	26.06	−0.568	0.240	−275.2	0.950
Mean fruit weight (g)	19.3	−0.62	2.85	3	0.590
Final yield (to 22/7/87)					
Total yield (kg m^{-2})	5.01	−0.111	0.138	− 41.6	0.786
Class 1 yield (kg m^{-2})	12.08	−0.287	0.155	−117.4	0.925
Number of class 1 (m^{-2})	63.5	−1.470	0.097	−621	0.911
Mean fruit weight (g)	−16.8	0.292	1.678	372	0.584

Coefficients (*a*, *b*, *c*, *d*) significant at $P = 0.05$; correlation coefficients (*r*) significant at $P < 0.01$.

ber of class 1 fruit showed a maximum at a 24-h mean temperature of 21-21.5 °C, as can be calculated from the coefficients in Table 5. The mean fruit weight (class 1), however, was significantly reduced by raising the 24-h mean temperature (in the range from 16.3 °C to 23.8 °C).

The factor *Ta* had a significant positive effect on these variables. However, as with vegetative growth, this effect was small compared to the effect of 24-h mean temperature. As to the influence of temperature on yield of class 1 fruit, calculation using Eq. 1 shows that raising the 24-h mean temperature from 19 to 20 °C (at *Ta* = 0) has the same effect as increasing *Ta* with 6 °C.

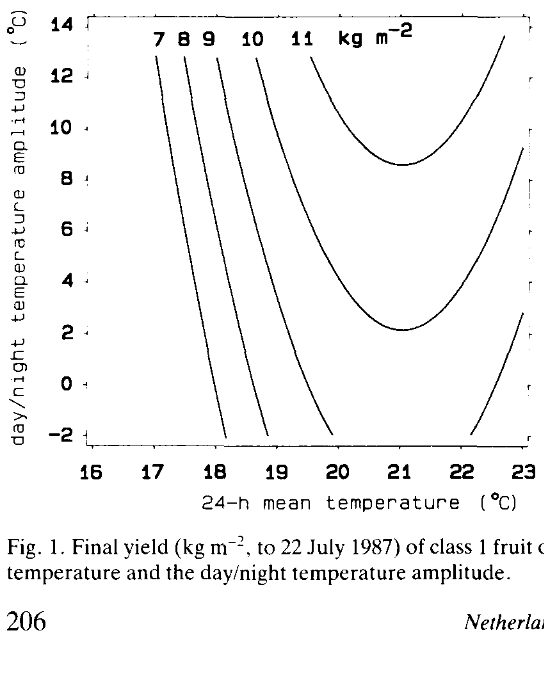

Fig. 1. Final yield (kg m^{-2}, to 22 July 1987) of class 1 fruit of sweet pepper as a function of the 24-h mean temperature and the day/night temperature amplitude.

Discussion

At low temperatures, fruit set is much higher than at high temperatures (Rylski & Spigelman, 1982). Since the fruits are the main sink for assimilates, the vegetative growth of the plants is significantly reduced by the presence of fruits (Hall, 1977). The vegetative growth parameters (Table 2) were measured when first fruit set occurred, so the response of vegetative growth to temperature is considered to be unaffected by the presence of fruits. Although Nilwik (1981) investigated plants in a much earlier stage of growth, our results are comparable. From the results of the regression analysis (Table 3) it may be concluded that the effect of the day/night amplitude on plant height, leaf area and area/length ratio is small compared to the effect of the 24-h mean temperature. Fresh weight and leaf number were not significantly related to the day/night amplitude (Table 3). It may be concluded, therefore, that vegetative growth depends mainly on 24-h mean temperature. The optimum was found between 21 °C and 23 °C. The crop apparently integrates temperature over at least 24 h, and this reaction is comparable to other crops, e.g. cucumber (Slack & Hand, 1983), tomato (de Koning, 1988a), chrysanthemum (Cockshull et al., 1981) and roses (van den Berg, 1987). This creates also for sweet pepper the possibility of new temperature control procedures during the vegetative growth stage, like the one described by de Koning (1988b), to obtain maximum profit of energy saving measures.

Since it may be assumed that there are no interactions between light and temperature on vegetative growth in the range investigated (Horie et al., 1979) it seems reasonable to conclude that the optimum temperature for vegetative growth of sweet pepper does not deviate significantly from the optimum found in this experiment, at higher irradiance. This concurs with the results of Nilwik (1981), who found comparable optimum temperatures for vegetative growth at 4 to 5 times higher irradiance levels.

The highest production of total as well as class 1 fruit is obtained at a 24-h mean temperature of 21-21.5 °C (Fig. 1 and Table 5). This phenomenon should be considered in terms of differential effects of temperature during growth and development. Firstly, vegetative growth shows an optimum between 21 and 23 °C (Table 3), secondly flowering is enhanced by high temperature (Rylski, 1972). On the other hand, however, fruit set is significantly reduced by high temperatures (Rylski & Spigelman, 1982). Finally, low temperatures result in malformed fruits, partly due to absence of seeds and thickening of the style (Rylski & Spigelman, 1982). The overall result of these different effects is an optimum temperature for class 1 fruit production. Although the average fruit weight of class 1 fruit increased with decreasing temperature (Table 5), this increase cannot compensate for the reduction in number of fruits at low temperatures. The significant positive effect of the day/night amplitude on yield variables (Fig. 1 and Table 5) leads to the conclusion that at sub-optimal temperatures, it is more efficient to raise the day temperature than the night temperature. Friend & Helson (1976) concluded the same for dry weight responses of wheat. This reaction should be considered in terms of photosynthesis increase at higher day temperatures (Nilwik, 1980) and respiration, which is closely correlated to night temperature (Toki et al., 1978).

The main conclusion is that the temperature regime (day/night amplitude) is of minor importance compared to the effect of 24-h mean temperature, for vegetative growth as well as yield. Temperature research on growth and yield at various cultivation conditions should therefore concentrate on establishing the optimum 24-h mean temperature. Further improvements may then be made by applying different temperature regimes at the optimum 24-h mean temperature. Finally, from practical viewpoint, it can be concluded that the best blue-print control strategy for production of sweet pepper during the early winter months under North-West European light conditions, seems to maintain a 24-h mean temperature of 21-21.5 °C and a day/night amplitude of 7-9 °C.

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