

Effect of Day and Night Temperature on Internode and Stem Length in Chrysanthemum: Is Everything Explained by DIF?

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In many plant species, including chrysanthemum, a strong positive correlation between internode length and DIF [difference between day (DT) and night (NT) temperature] has been observed. However, Langton and Cockshull (1997, *Scientia Horticulturae* 69: 229–237) reported no such relationship and showed that absolute DT and NT explained internode length rather than DIF. To investigate these conflicting results and to clarify the validity of the DIF concept, cut chrysanthemums (*Chrysanthemum* 'Reagan Improved') were grown in growth chambers at all 16 combinations of four DT and four NT (16, 20, 24 and 28 °C) with a 12 h daylength. Length of internode 10, number of internodes and stem length were measured on days 5, 10, 17, 22 and 27 after starting the temperature treatments. Internode length on day 10 showed a positive linear relationship with DIF ($R^2 = 0.64$). However, when internodes had reached their final length in all treatments (day 27), a much stronger positive linear relation was observed ($R^2 = 0.81$). A model to predict final internode length was developed based on the absolute DT and NT responses: both responses were optimum curves and no significant interaction between DT and NT occurred [final internode length (mm) = $-32.23 + 3.56DT + 1.08NT - 0.0687DT^2 - 0.0371NT^2$; $R^2 = 0.91$, where T_D is day temperature and T_N is night temperature]. It is shown that DIF can predict final internode length only within a temperature range where effects of DT and NT are equal in magnitude and opposite in sign (18–24 °C). Internode appearance rate, as well as stem length formed during the experiment, showed an optimum response to DT.

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Key words: Chrysanthemum, day temperature, DIF, elongation, internode length, modelling, night temperature, number of internodes, stem length, thermoperiodism.

INTRODUCTION

The control of stem length is particularly important in chrysanthemum cultivation since there are strict quality specifications for height (Karlsson and Heins, 1994). To achieve these quality requirements, chemical plant growth regulators are commonly used in both pot and cut chrysanthemums. However, their application is costly and environmentally unfriendly (Langton, 1998). The need to find effective environmentally friendly alternatives for regulating plant height is a priority (Erwin and Heins, 1995; Pearson *et al.*, 1995; Khattak and Pearson, 1997).

Final stem length is determined both by number of internodes and internode lengths (Pearson *et al.*, 1995). In species with a determinate growth pattern, such as chrysanthemum, new internodes are formed up to flower initiation. After this stage, the increase in stem length depends on internode elongation only. Thus, the stem elongation process is strongly correlated with both internode appearance rate (IAR, equal to leaf unfolding rate) and internode elongation rate.

Several growing conditions are known to affect chrysanthemum stem elongation, such as temperature, light intensity, light quality, photoperiod, relative humidity, CO₂ concentration and plant density (Carvalho and Heuvelink,

2001). Efforts have been concentrated on temperature manipulation to regulate stem length (Myster and Moe, 1995), and this is already widely practised, based on the DIF concept: the difference between day (DT) and night (NT) temperature (Langton and Cockshull, 1997b). The observation that stem length shows a different response to temperature during the photoperiod compared with the nyctoperiod was first investigated for tomato plants and termed 'thermoperiodicity' (Went, 1944). Since then, it has been reported for a wide range of plant species (e.g. Heuvelink, 1989; Erwin and Heins, 1995; Myster and Moe, 1995). Erwin *et al.* (1989) introduced the DIF concept when they found that plants of *Lilium longiflorum* Thunb. had the same final height when grown at the same DIF (using 25 combinations of DT and NT ranging from 14 to 30 °C), regardless of the mean temperature (MT). According to these authors, DT and NT influenced plant height in opposite ways. Increasing DT increased plant height, whereas increasing NT decreased plant height. Therefore, temperature combinations resulting in a negative DIF produced plants that were shorter than those grown under a positive DIF. Erwin *et al.* (1989) also reported a positive linear relationship between internode length and DIF. Thus, it was concluded that the absolute magnitude and sign of DIF were the critical factors determining internode and stem length (Erwin *et al.*, 1989). In fact, as later suggested by Langton and Cockshull (1997a), the temperature effect on

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stem length was exclusively a result of the influence of DIF on internode elongation since terminal flowers had already been initiated and, therefore, the final number of internodes had been determined before the start of the treatment.

Many subsequent studies have shown similar results to those of Erwin *et al.* (1989) for several plant species, including pot chrysanthemum cultivars (e.g. Karlsson *et al.*, 1989; Jacobsen and Amsen, 1992; Bertram and Karlsen, 1994; Cockshull *et al.*, 1995). However, the effects of day and night temperature have not always been equal in magnitude and opposite in sign (LePage *et al.*, 1984; Karlsson *et al.*, 1989; Langton and Cockshull, 1997a), which is necessary for a clear DIF response. To clarify these responses, Langton and Cockshull (1997a) conducted a 10 d experiment in which they grew pot chrysanthemum cultivar 'Bright Golden Anne' under 24 combinations of DT and NT, ranging from 12 to 32 °C. A photoperiod of 12 h was applied to give day and night equal weight. No relationship was found between internode length and DIF. According to these authors, stem elongation in chrysanthemum responded to the absolute DT and NT rather than to DIF, and DT appeared to be the dominant factor controlling internode length. It was thus concluded that DIF is an artefact, lacking real biological significance, that can obscure the real importance of the absolute temperatures at which plants are grown (Langton, 1998). However, given the short duration of the experiment performed by Langton and Cockshull (only 10 d), the possibility exists that the measured internodes were not fully elongated, thereby invalidating their conclusions. Langton and Cockshull (1997a) were aware of this problem, but considered it unlikely that final internode lengths would have given a substantially better fit with DIF.

Despite numerous studies of the effects of temperature on extension growth of chrysanthemum (mainly pot chrysanthemum), this phenomenon is still not fully understood, leading to uncertainties over how to optimize the use of temperature (Langton, 1998). Furthermore, it is still not clear from the literature whether stem elongation in chrysanthemum is controlled by DIF. The aims of this paper are: (1) to test whether the conflicting results on DIF validity can be explained by differences in the stage at which internode length is measured; and (2) to identify the conditions where the use of DIF explains chrysanthemum internode length. To obtain more insight into the stem extension process, the time courses of internode length,

TABLE 1. DIF values (°C) resulting from the combination of four day temperatures and four night temperatures

Night temperature (°C)	Day temperature (°C)			
	16	20	24	28
16	0	+4	+8	+12
20	-4	0	+4	+8
24	-8	-4	0	+4
28	-12	-8	-4	0

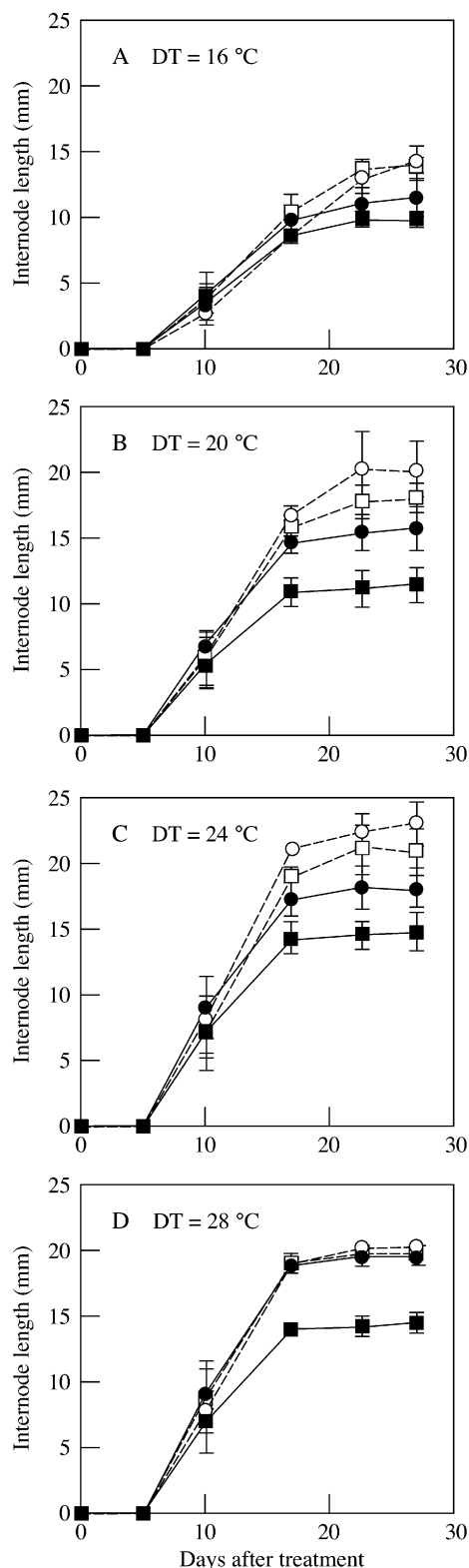


FIG. 1. Elongation patterns of internode 10 as a function of day temperature (DT) and night temperature [16 °C (open circles), 20 °C (closed circles), 24 °C (open squares), 28 °C (closed squares)] in chrysanthemum 'Reagan Improved'. Vertical bars indicate s.e.m. ($n = 2$) when larger than symbols.

number of internodes and stem length were measured by a non-destructive method, and analysed separately for 16 day and night temperature combinations, ranging from 16 to 28 °C.

MATERIALS AND METHODS

Plant material and growing conditions

Block-rooted cuttings of *Chrysanthemum* 'Reagan Improved', obtained from a commercial propagator (Fides, De Lier, The Netherlands), were planted on 16 May 2001 (replication 1) and 13 Jun. 2001 (replication 2) in 14 cm pots containing a peat-based commercial potting compost (Lentse potgrond nr. 4; 85 % peat, 15 % clay). After 2 d in a common glasshouse environment (18 °C DT/16 °C NT and 18 h light), temperature treatments were imposed. Plants were selected for uniformity (8.0 ± 1.0 leaves per plant; 12.1 ± 2.0 cm stem length) and distributed over four artificially lit growth chambers (2.90 m \times 2.20 m \times 3.15 m).

Each growth chamber had a constant day and night temperature (16, 20, 24 or 28 °C). Since only four growth chambers were available, for each replication, plants were shifted at the start and end of each day according to their DT and NT treatment. Fluorescent tubes (Philips TL 58W, colour 84) were used continuously during the 12 h of daylight (between 0800 and 2000 h) providing $99 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic active radiation at plant level (LI-COR, model LI-191SA; Lincoln, USA). This light level resulted in a daily light integral ($4.3 \text{ mol m}^{-2} \text{ d}^{-1}$) that was similar to that received by plants growing in commercial glasshouses during the winter in The Netherlands (52°N). Plants were grown as individual plants under ambient CO₂ (growth chamber continuously ventilated) and at constant vapour pressure deficit (VPD = 0.57 kPa). Plants were watered by hand as required. The experiment ended when internode 10 had reached its final length in all temperature combinations

studied. This occurred 26 (replication 1) and 28 d (replication 2) after the start of the treatments, but was considered to have occurred on day 27 for both replicates in the analyses.

Temperature and relative humidity were automatically recorded at 5 min intervals using a commercial computer system (Hoogendoorn, Vlaardingen, The Netherlands). The 24 h mean temperatures of each growth chamber did not differ from the set points (16, 20, 24 or 28 °C). The corresponding mean VPD was slightly different from its set point and there were small differences between the replicates (0.51 ± 0.02 , 0.50 ± 0.03 , 0.57 ± 0.00 and 0.57 ± 0.00 kPa).

Treatments

Sixteen temperature treatments were applied resulting from all combinations of four DT and four NT (16, 20, 24 and 28 °C) (Table 1). All plants were moved each day according to their DT and NT combination; plants in constant DT and NT treatments were also moved out of, and back into, their growth chambers. To test the effect of this movement on stem length, four extra treatments (16, 20, 24 and 28 °C with constant DT and NT) were initiated in which plants were kept permanently inside the growth chamber.

Periodic non-destructive measurements were conducted on ten plants per experimental plot on days 0, 5, 10, 17, 21 and 26 (replication 1) and days 0, 5, 10, 17, 24 and 28 (replication 2) after the start of the treatments. Length of internode 10, number of leaves on the main stem (≥ 10 mm; equal to the number of internodes) and stem length were recorded. Internode 10 was chosen to guarantee that it developed under the treatment conditions, as it was not visible at the start of the treatments. A digital calliper was used to measure internode lengths.

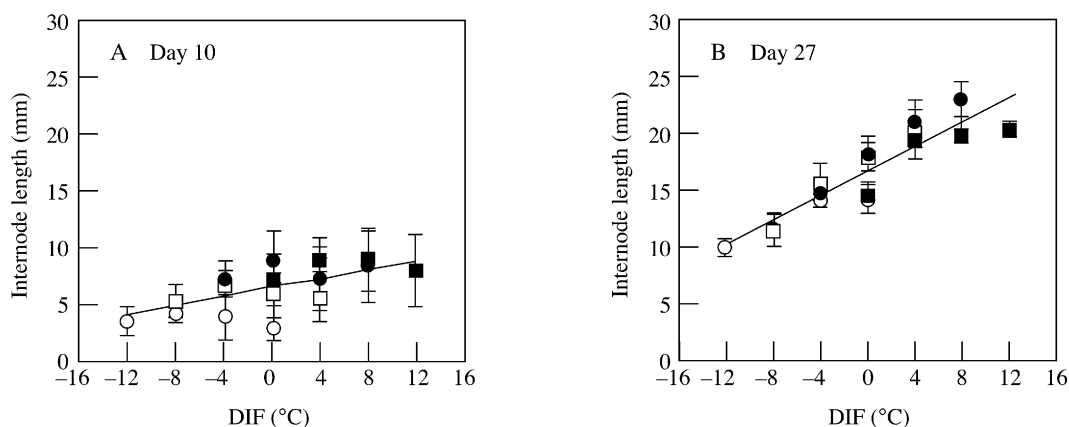


FIG. 2. Relationships between the length of internode 10 and DIF (°C) 10 d (A) and 27 d (B) after treatments started in chrysanthemum 'Reagan Improved'. Symbols represent 16 day and night temperature combinations, with a day temperature of 16 °C (open circles), 20 °C (open squares), 24 °C (closed circles) and 28 °C (closed squares). Regression lines: A, $y = 6.40 + 0.202x$, $R^2 = 0.64$; B, $y = 16.57 + 0.547x$, $R^2 = 0.81$. Vertical bars indicate s.e.m. ($n = 2$) when larger than symbols.

Statistical design and analysis

The experimental set-up was a complete randomized block design with the two replications in time as blocks. Each replication consisted of ten plants per plot (treatment) and plants from the same treatment were placed in two separate trays (five pots per tray). Linear regression analysis and ANOVA were conducted and treatment effects were tested at the 5 % probability level. The statistical software package Genstat 5 (IACR-Rothamsted, UK) was used.

TABLE 2. Regression models using one factor (DT, NT, MT and DIF) for final internode length, IAR and stem length formed during the experiment for chrysanthemum 'Reagan Improved'

Model	R^2_{adj}	s.e.*	F_{prob}^\dagger
Final internode length (mm)			
= 16.57 + 0.547 DIF	0.81	1.75	<0.001
= 28.75 - 0.554 NT	0.42	3.08	<0.001
= 4.69 + 0.540 DT	0.40	3.14	<0.001
= 16.87 - 0.014 MT	0.01	4.03	0.330
IAR (number of internodes d ⁻¹)			
= - 0.0022 DT ² + 0.113 DT - 0.75‡	0.88	0.03	<0.001
= - 0.0026 MT ² + 0.131 MT - 0.99‡	0.61	0.07	<0.001
= 0.281 + 0.0155 DT	0.72	0.05	<0.001
= 0.228 + 0.0179 MT	0.51	0.06	<0.001
= 0.622 + 0.0065 DIF	0.31	0.08	0.002
= 0.568 + 0.0024 NT	0.10	0.09	0.090
Stem length (cm)			
= - 0.146 DT ² + 7.82 DT - 72.9‡	0.88	2.58	<0.001
= - 5.18 + 1.40 DT	0.77	3.53	<0.001
= 25.65 + 0.88 DIF	0.60	4.63	<0.001
= 2.83 + 1.038 MT	0.18	6.63	0.021
= 33.66 - 0.364 NT	0.02	7.27	0.307

* Standard error of regression.

† F probability of regression.

‡ Significant quadratic model tested based on the graphical presentation of the data.

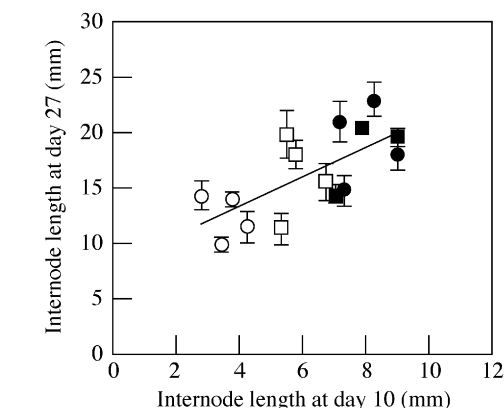
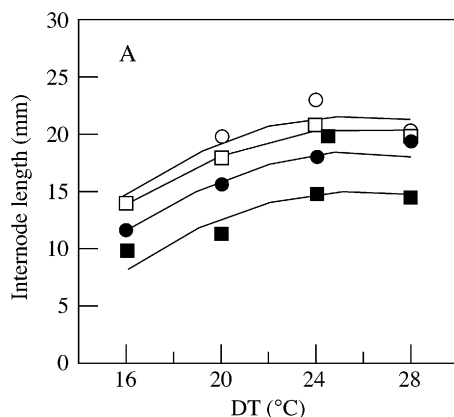


FIG. 3. Relationship between the length of internode 10 at 10 and 27 d after treatments started in chrysanthemum 'Reagan Improved'. Symbols represent 16 day and night temperature combinations, with a day temperature of 16 °C (open circles), 20 °C (open squares), 24 °C (closed circles) and 28 °C (closed squares). Regression line: $y = 7.89 + 1.36x$, $R^2 = 0.51$. Vertical bars indicate s.e.m. ($n = 2$) when larger than symbols.

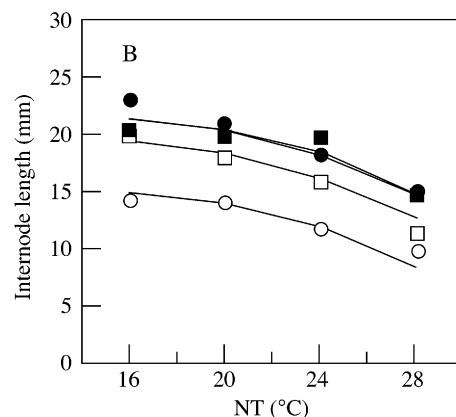


FIG. 4. Mean final length of internode 10 as a function of day temperature (DT) and night temperature (NT) in chrysanthemum 'Reagan Improved'. Symbols represent measured values from 16 day and night temperature combinations, with (A) NT of 16 °C (open circles), 20 °C (open squares), 24 °C (closed circles) and 28 °C (closed squares); (B) DT of 16 °C (open circles), 20 °C (open squares), 24 °C (closed circles) and 28 °C (closed squares). Solid lines represent regression model: final internode length (mm) = $-32.23 + 3.56 \text{ DT} + 1.08 \text{ NT} - 0.0687 \text{ DT}^2 - 0.0371 \text{ NT}^2$; $R^2 = 0.909$. $\text{LSD}_{15, 0.05} = 1.08 \text{ mm}$.

RESULTS

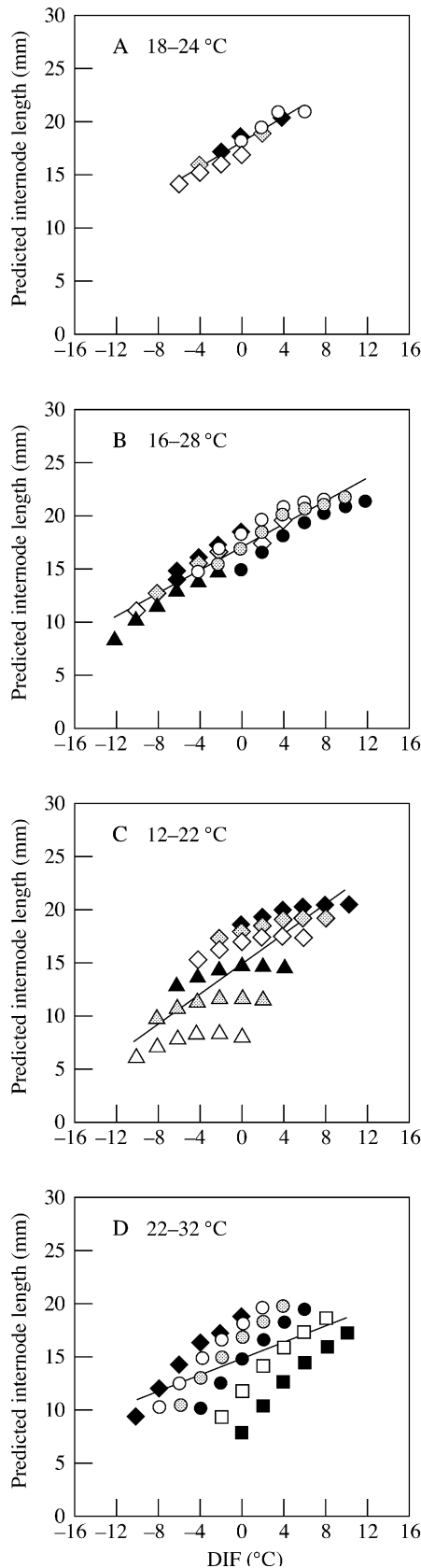
Effect of temperature on internode length

Time patterns and temperature responses. Internode length followed a sigmoid time course for all 16 day and night temperature combinations (Fig. 1). Five days after treatments had started, internode 10 was still not measurable under any conditions. In general, rapid internode elongation was observed between days 5 and 17, followed by a plateau. In some temperature treatments (e.g. all 28 °C NTs), internode 10 was already fully elongated by day 17 (Fig. 1), whereas in other treatments (e.g. 16 °C DT/16 °C NT) this was delayed by about 1 week (Fig. 1A). The experiment finished on day 27 when the final length of internode 10 had been achieved in all temperature treatments (Fig. 1).

Ten days after the treatments were imposed, internode length showed a significant ($P < 0.001$) positive linear

relationship with DT, which explained 84 % of its variance; no significant ($P = 0.97$) relationship was observed with NT.

At the same time, although internodes were not yet full-grown, a significant ($P < 0.001$) positive linear relationship ($R^2 = 0.64$) between internode length and DIF was found (Fig. 2A). However, this relationship was much closer ($R^2 = 0.81$) when internodes had reached their final length in all the treatments (day 27) (Fig. 2B). Thus, plants grown under temperature combinations that resulted in a negative DIF had shorter internodes compared with plants grown under a positive DIF. For example, the mean final length of internode 10 at 16 °C DT/28 °C NT (−12 °C DIF) was 48 % less than that at the reciprocal combination 28 °C DT/16 °C NT (+12 °C DIF). Similarly, plants grown at the same DIF (e.g. −4 °C DIF: 16 °C DT/20 °C NT or 24 °C DT/28 °C NT) had similar final internode lengths. Linear regression analysis showed that among the temperature variables studied (DT, NT, MT and DIF), DIF gave the best fit to the final internode length, accounting for 81 % of its variance (Table 2). Furthermore, only a poor relationship ($R^2 = 0.51$) between internode length at day 10 and final internode length (day 27) was found (Fig. 3).



Final internode length: modelling DT and NT responses. The individual effect of absolute DT and NT on final length of internode 10 is given in Fig. 4. An ANOVA of final internode length showed no significant interaction between DT and NT ($P = 0.091$). The quadratic terms were tested and found to be significant for both DT ($P < 0.001$) and NT ($P = 0.011$). This resulted in the following regression equation:

$$\text{final internode length (mm)} = -32.23 + 3.56DT + 1.08NT - 0.0687DT^2 - 0.0371NT^2 \quad (1)$$

where T_D is day temperature and T_N is night temperature.

Measured and predicted final internode length showed good agreement ($R^2 = 0.91$) (Fig. 4). Based on eqn (1), the optimum temperature for internode elongation was calculated, resulting in a much higher value for DT (25.9 °C) than for NT (14.6 °C). Thus, within the temperature range studied (16–28 °C), final internode length had an opposite response to DT and NT: a higher DT resulted in a quadratic increase in final internode length, whereas a higher NT resulted in a quadratic decrease in final internode length (Fig. 4).

Using eqn (1), final internode length was predicted for several ranges of DT and NT combinations, and was plotted against DIF (Fig. 5). Taking the first-order partial derivatives of eqn (1) with respect to DT and NT showed that, at

FIG. 5. Predicted final internode length in chrysanthemum 'Reagan Improved', based on eqn (1), as a function of DIF (°C) in four temperature intervals: (A) 18–24 °C; (B) 16–28 °C; (C) 12–22 °C; (D) 22–32 °C. Symbols represent day and night temperature combinations, with a day temperature of 12 °C (open triangle), 14 °C (grey triangle), 16 °C (black triangle), 18 °C (open diamond), 20 °C (grey diamond), 22 °C (black diamond), 24 °C (open circle), 26 °C (grey circle), 28 °C (black circle), 30 °C (open square), 32 °C (grey square). Solid lines represent linear regressions on the data: A, $y = 18.07 + 0.578x$, $R^2 = 0.95$; B, $y = 17.00 + 0.546x$, $R^2 = 0.89$; C, $y = 14.88 + 0.704x$, $R^2 = 0.62$; D, $y = 14.74 + 0.388x$, $R^2 = 0.32$.

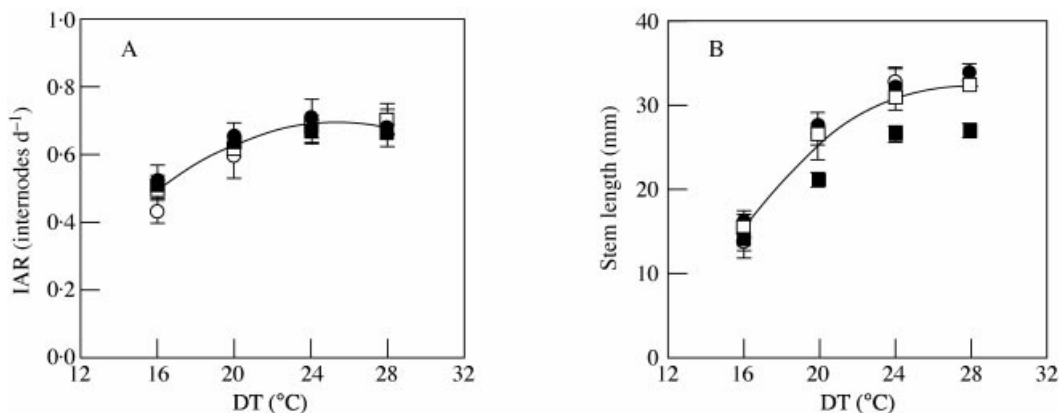


FIG. 6. IAR (A) and stem length formed during the experiment (B) as a function of day temperature (DT) in chrysanthemum 'Reagan Improved'. Symbols represent 16 day and night temperature combinations, with a night temperature of 16 °C (open circles), 20 °C (open squares), 24 °C (closed circles) and 28 °C (closed squares). Regression curves: A, $y = -0.0022x^2 + 0.113x - 0.75$, $R^2 = 0.88$; B, $y = -0.146x^2 + 7.82x - 72.9$, $R^2 = 0.88$. Vertical bars indicate s.e.m. ($n = 2$) when larger than symbols.

22 °C, both derivatives had approximately the same absolute value and opposite sign. DIF values calculated within an interval of DT and NT combinations close to 22 °C therefore gave a good fit to the predicted internode length (Fig. 5A and B). DT and NT combinations in the range of 18–24 °C resulted in the best fit ($R^2 = 0.95$) between these two variables (Fig. 5A), followed by the studied temperature range (16–28 °C) where DIF could explain 89 % of the variance (Fig. 5B).

DIF showed a poor relationship with the predicted final internode length for combinations of DT and NT ranging between 12 and 22 °C (Fig. 5C), and between 22 and 32 °C (Fig. 5D). For these temperature ranges, plants growing under the same DIF would have a very different predicted internode length. For instance, at 0 °C DIF, the predicted internode length varied between 8 mm (12 °C DT/12 °C NT) and 19 mm (22 °C DT/22 °C NT) (Fig. 5C). Although a significant ($P < 0.001$) positive linear trend was observed for both temperature ranges (Fig. 5C and D), a lower DIF did not always result in shorter internodes. For example, the predicted internode length for plants grown at 18 °C DT/22 °C NT (–4 °C DIF) was 88 % larger than for plants grown at 12 °C DT/12 °C NT (0 °C DIF).

Effect of temperature on internode appearance rate and stem length

Internode appearance rate (IAR) was calculated using the slope of the linear relationship between number of internodes and time (from 0 to 21 d after treatments started). A quadratic response to DT could explain 88 % of the variance observed in IAR (Table 2). IAR increased with DT up to an optimum at 25.7 °C. At this temperature, predicted IAR was 43 % higher than for plants grown at 16 °C DT. A further increase in DT, up to 28 °C, had a minor effect on this rate (Fig. 6A). MT and DIF also had a significant influence on IAR, but a lower percentage of variance was explained by these variables (Table 2).

The stem length formed during the experiment (final stem length – initial stem length) was significantly influenced by DT, DIF and MT, but a quadratic model using DT only explained the largest proportion of the variance (88 %) (Table 2). Increasing DT from 16 to 24 °C caused stem length to double, but a further increase had only a minor effect. However, this model overestimated the stem length of plants grown at 28 °C NT (Fig. 6B).

Stem length was closely related to IAR ($R^2 = 0.82$) and to a lesser extent with final length of internode 10 ($R^2 = 0.71$). These two variables together explained 97 % of its variability.

Effect of movement on stem length

The daily movement between growth chambers that was imposed on the plants had no significant effect ($P = 0.097$) on stem length formed during the experiment under the temperature conditions tested (16, 20, 24 and 28 °C, constant DT and NT).

DISCUSSION

Within the experimental temperature range of 16–28 °C, a positive linear relationship between DIF and internode length was observed when internodes had reached their final size (Fig. 2B). In contrast to the assumption of Langton and Cockshull (1997a), it was shown that internode lengths recorded in early stages of development do not bear a close relationship to final internode lengths (Fig. 3). A possible reason for these findings is the fact that internodes from plants grown under different temperature combinations were at different stages of elongation at day 10 (Figs 1 and 3). For instance, 10 d after the treatments started, internode 10 from plants grown at 20 °C DT/16 °C NT had reached only 28 % of its final length, whereas at 20 °C DT/28 °C NT it had reached 47 % of its final length (Fig. 1B). This is a result of different durations of elongation period and

different rates of internode elongation. Hence, the conclusion of Langton and Cockshull (1997a) that internode elongation is not related to DIF may be invalidated by the short duration of their experiment (10 d).

Besides the stage at which internodes were measured, the range of temperatures also played a major role in the relationship with DIF. The predicted final internode length, based on a quadratic model for both DT and NT [eqn (1)], showed a positive relationship with DIF (Fig. 5). However, a close relationship existed only within a certain temperature interval (Fig. 5A and B) when the positive effect of DT on final internode length was compensated by a similar negative effect of NT (Fig. 4), resulting in equal length at the same DIF. For temperature combinations outside that range (10–22 °C and 22–34 °C), predicted final internode length showed a poor relationship with DIF (Fig. 5C and D).

These results clearly demonstrate that the DIF concept is valid only if the effects of DT and NT on internode length have similar magnitudes and opposite signs. This leads to a conclusion similar to that drawn by Pearson *et al.* (1995) who reported that plants do not respond to DIF itself but to the combination of the independent effects of temperature during the day and night periods.

In previous studies on pot chrysanthemum, stem length was closely related to DIF (e.g. Karlsson *et al.*, 1989; Cockshull *et al.*, 1995) because plants were grown under short day conditions, without a period of long days. Consequently, stem elongation was mainly the result of internode elongation alone since all the internodes had been previously formed. To analyse the effect of temperature on stem elongation of cut chrysanthemum, attention should also be paid to its influence on the number of internodes. For many plant species, including chrysanthemum, leaf unfolding rate (equal to IAR) has been reported to increase linearly with MT (Karlsson *et al.*, 1989; Challa *et al.*, 1995). However, in the present study, IAR showed an optimum response to MT, and an even stronger one to DT alone (Table 2; Fig. 6A). Larsen and Hidén (1995) were also unable to find a simple linear relationship between MT and leaf unfolding rate in chrysanthemum. These differences may be due to a cultivar effect.

Stem length formed during the experiment showed a closer relationship to DT than to DIF (Table 2). If stem length were dependent only on final internode length (mainly controlled by DIF), then plants grown at the same DIF, regardless of the actual DT and NT, would have a similar stem length. However, at the end of the experiment, plants had not reached their final stem length. Several internodes (above internode 10) were not fully elongated, but the number of internodes was already defined in all treatments except 28 °C NT combinations, where the apical flower bud was still not visible. This could explain why stem length showed a closer relationship with IAR ($R^2 = 0.82$) than with final length of internode 10 ($R^2 = 0.71$). Thus, it is expected that the response of final stem length to temperature would have been different. In general, as more internodes become fully elongated, the relationship between final stem length and DIF should improve.

Considering that chrysanthemum is commonly grown at temperatures between 17 and 23 °C and that the daily

movement imposed on the plants did not affect stem length, these results can be extrapolated to commercial growing conditions. Although the DIF concept is simply a different parameterization of the distinct responses to DT and NT (Langton and Cockshull, 1997a) it can still be a valid tool in the manipulation of final internode length. However, the use of different chrysanthemum cultivars (Hansen *et al.*, 1996) or different growing conditions (Myster and Moe, 1995) should be taken into account when evaluating the effectiveness of DIF. For instance, Myster and Moe (1995) suggested that there is a higher sensitivity of stem elongation to temperature fluctuations during the short day period rather than the long day period for several pot plants.

CONCLUSIONS

The response of chrysanthemum final internode length to temperature is strongly related to DIF, but this response is simply the result of independent and opposite effects of day and night temperatures. It is concluded that although the DIF concept does not have a biological meaning, it can be a good predictor of final internode length of chrysanthemum within a temperature range of 16–28 °C.

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LITERATURE CITED

- Bertram L, Karlsen P. 1994. Patterns in stem elongation rate in chrysanthemum and tomato plants in relation to irradiance and day/night temperature. *Scientia Horticulturae* **58**: 139–150.
- Carvalho SMP, Heuvelink E. 2001. Influence of greenhouse climate and plant density on external quality of chrysanthemum (*Dendranthema grandiflorum* (Ramat.) Kitamura): First steps towards a quality model. *Journal of Horticultural Science and Biotechnology* **76**: 249–258.
- Challa H, Heuvelink E, van Meeteren U. 1995. Crop growth and development. In: Bakker JC, Bot GPA, Challa H, van de Braak NJ, eds. *Greenhouse climate control: an integrated approach*. Wageningen: Wageningen Pers, 62–84.
- Cockshull KE, Langton FA, Cave CRJ. 1995. Differential effects of different DIF treatments on chrysanthemum and poinsettia. *Acta Horticulturae* **378**: 15–25.
- Erwin JE, Heins RD. 1995. Thermomorphogenic responses in stem and leaf development. *HortScience* **30**: 940–949.
- Erwin JE, Heins RD, Karlsson MG. 1989. Thermomorphogenesis in *Lilium longiflorum*. *American Journal of Botany* **76**: 47–52.
- Hansen HT, Hendriks L, Ueber E, Andersen AS. 1996. Effect of a low temperature period (Drop) during different periods on morphogenesis of *Dendranthema* 'Surf', Fuchsia 'Beacon', Verbena 'Karminrosa', and *Pelargonium* 'Pulsar Red'. *Gartenbauwissenschaft* **61**: 188–196.
- Heuvelink E. 1989. Influence of day and night temperature on the growth of young tomato plants. *Scientia Horticulturae* **38**: 11–22.
- Jacobsen L, Amsen MG. 1992. The effect of temperature and light quality on stem elongation of chrysanthemum. *Acta Horticulturae* **305**: 45–50.
- Karlsson MG, Heins RD. 1994. A model of chrysanthemum stem elongation. *Journal of the American Society for Horticultural Science* **119**: 403–407.
- Karlsson MG, Heins RD, Erwin JE, Berghage RD, Carlson WH, Biernbaum JA. 1989. Temperature and photosynthetic photon flux

- influence chrysanthemum shoot development and flower initiation under short-day conditions. *Journal of the American Society for Horticultural Science* **114**: 158–163.
- Khattak AM, Pearson S.** 1997. The effects of light quality and temperature on the growth and development of chrysanthemum cvs Bright Golden Anne and Snowdon. *Acta Horticulturae* **435**: 113–121.
- Langton FA.** 1998. Regulation of stem extension by temperature. In: Cockshull KE, Gray D, Seymour GB, Thomas B, eds. *Genetic and environmental manipulation of horticultural crops*. New York: CABI Publishing, 191–203.
- Langton FA, Cockshull KE.** 1997a. Is stem extension determined by DIF or by absolute day and night temperatures? *Scientia Horticulturae* **69**: 229–237.
- Langton FA, Cockshull KE.** 1997b. A re-appraisal of DIF extension growth responses. *Acta Horticulturae* **435**: 57–64.
- Larsen RU, Hidén C.** 1995. Predicting leaf unfolding in flower induced shoots of greenhouse grown chrysanthemum. *Scientia Horticulturae* **63**: 225–239.
- LePage I, DeJong J, Smeets L.** 1984. Effect of day and night temperatures during short photoperiods on growth and flowering of *Chrysanthemum morifolium* Ramat. *Scientia Horticulturae* **22**: 373–381.
- Myster J, Moe R.** 1995. Effect of diurnal temperature alternations on plant morphology in some greenhouse crops: a mini review. *Scientia Horticulturae* **62**: 205–215.
- Pearson S, Hadley P, Wheldon, AE.** 1995. A model of the effect of day and night temperatures on the height of chrysanthemums. *Acta Horticulturae* **378**: 71–79.
- Went FW.** 1944. Plant growth under controlled conditions. II. Thermoperiodicity in growth and fruiting of the tomato. *American Journal of Botany* **31**: 135–150.