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A NEW APPROACH TO THE ANALYSIS OF THE EFFECTS OF DAY AND NIGHT TEMPERATURES ON PLANT GROWTH AND MORPHOGENESIS

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SYSOYEVA M. I., KHARKINA T. G. and MARKOVSKAYA E. F. *A new approach to the analysis of the effects of day and night temperatures on plant growth and morphogenesis.* BIOTRONICS **30**, 93–102, 2001. Contradictory results on the effects of day and night temperatures on plant growth and development have been reported in the literature. This is partly due to the lack of unified approach to data analysis and interpretation of results. In the present paper a method for quantifying the effect of day and night temperatures, their difference (DIF) and average daily temperature (ADT) on plant growth and development is described. The proposed method is based on the model calculations and subsequent analysis of isopleth plots developed from the equations. It enables an easier and more precise analysis of the plant response to varying day and night temperatures in terms of their absolute values and their difference. The method was verified on cucumber, lily, petunia and sweet pepper.

Key words: day and night temperatures; plant height; internode length; cucumber, lily, petunia, sweet pepper.

INTRODUCTION

As long ago as 1944, Went (*12*) concluded that day temperature (DT) and night temperature (NT) had separate effects on stem extension in tomato and that the temperature optimum for day response was higher than that for night response. He believed that this was probably general in higher plants and introduced the term 'thermoperiodicity' to describe the response of plant growth and fruiting to fluctuating DT and NT.

Erwin et al. (*2*) have shown that it is the difference between day temperature and night temperature (DIF) rather than the absolute day and night temperatures which is important in determining stem growth. Since then, many other researchers have come to a similar conclusion, and there is a considerable bibliography on the topic (*1, 9*). Commercial growers are now increasingly using DIF temperature regimes to manipulate plant height, petiole length, lateral branching, shoot and leaf orientation, and leaf pigmentation.

Later Langton and Cockshull (*7*) have shown on tomato and chrysanthemum which were regarded as showing a strong DIF response (*9*) that extension growth in these two species responded to the absolute day and night temperatures rather than to DIF. They also re-appraised published data sets for petunia (*6*), fuchsia (*3*) and lily (*2*), which gave support to the concept of DIF and found that models based on DIF 'work' only when DT and NT have opposite effects on extension growth as in lily and fuchsia (*8*). Taking all five species together, they concluded that while DIF is a concept that provides growers with a simple and effective way of appreciating growth responses to temperature it is, nevertheless, an artefact that lacks real biological significance. Extension growth responses are determined by absolute DT and NT (*8*). These findings support Went's view (*12*) that stem extension is determined by two distinct sets of responses to temperature, one to DT and one to NT.

Thus, experimental results and their interpretations are very contradictory, which raises doubts about the importance of DIF or absolute day and night temperatures. We believe that differences in the experimental design and the lack of a widely used system for quantifying the effect of day and night temperatures on plant growth make the interpretation of results more difficult. Moreover, the two-dimensional graphs that are usually used by researchers are difficult to analyse when DIF results are under discussion.

In the present paper, we propose a method that allows to quantify the separate effects of day and night temperatures, DIF and average daily temperature (ADT) on plant growth and development.

MATERIAL AND METHODS

Cucumber seeds (*Cucumis sativus* L., cv. Alma-Atinsky 1) were germinated at 30°C and then seedlings were grown at 23°C until the cotyledons unfolded. After that, seedlings were selected for uniformity and placed in growth chambers. The experimental design included the following combinations of day (*DT*) and night (*NT*) temperatures (*DT/NT*): 15/15, 15/25, 15/35, 25/15, 25/25, 25/35, 35/15, 35/25, 35/35°C. All combinations of alternating temperatures were obtained by moving plants between growth chambers at the end of each 12-h light and dark period. Plants were grown in ceramic pots with sand and treated with Knop nutrient solution based on 1 g l^{-1} $Ca(NO_3)_2$, 0.25 g l^{-1} KH_2PO_4, 0.25 g l^{-1} $MgSO_4\,7H_2O$, 0.25 g l^{-1} KNO_3, trace quantity of $FeSO_4$ and pH 6.2-6.4. There was one plant per pot. Irradiance was maintained at 100 Wm^{-2} supplied 12 h/day by high pressure mercury lamps. Plants were grown at a CO_2 concentration of 0.03% and a relative air humidity of 60%.

Ten plants were collected from each temperature regime at the same growth stage of 1 complete leaf. Plant height and leaf petiole length were measured. Each treatment was repeated three times.

Based on the fact that various physiological processes have parabolic dependencies on environmental factors (*5, 10*), quadratic regression equations were fitted to the data to describe the dependencies of growth variables (*GV*) on *DT* and *NT*.

$$GV=A_1+A_2\times DT+A_3\times NT+A_4\times DT^2+A_5\times NT^2+A_6\times(DT\times NT)$$

where A_1–A_6 are the coefficients.

Subsequent analyses were based on the model calculations and development of isopleth plots from the equations to show the response of plant variables to varying *DT* and *NT*.

Isopleths are the isolines of a growth variable displaying it as a function of *DT* and *NT*. To construct isopleth plots maximum or minimum of growth variables were calculated from the equations and spacing between isolines was chosen as the percentage of the maximum value. Every isopleth shows limits of the range of day and night temperatures that gives predicted value of growh variable within its maximum or minimum value, the degree of deviation being specified. The analysis of the arrangement of the isopleths in the space of DT

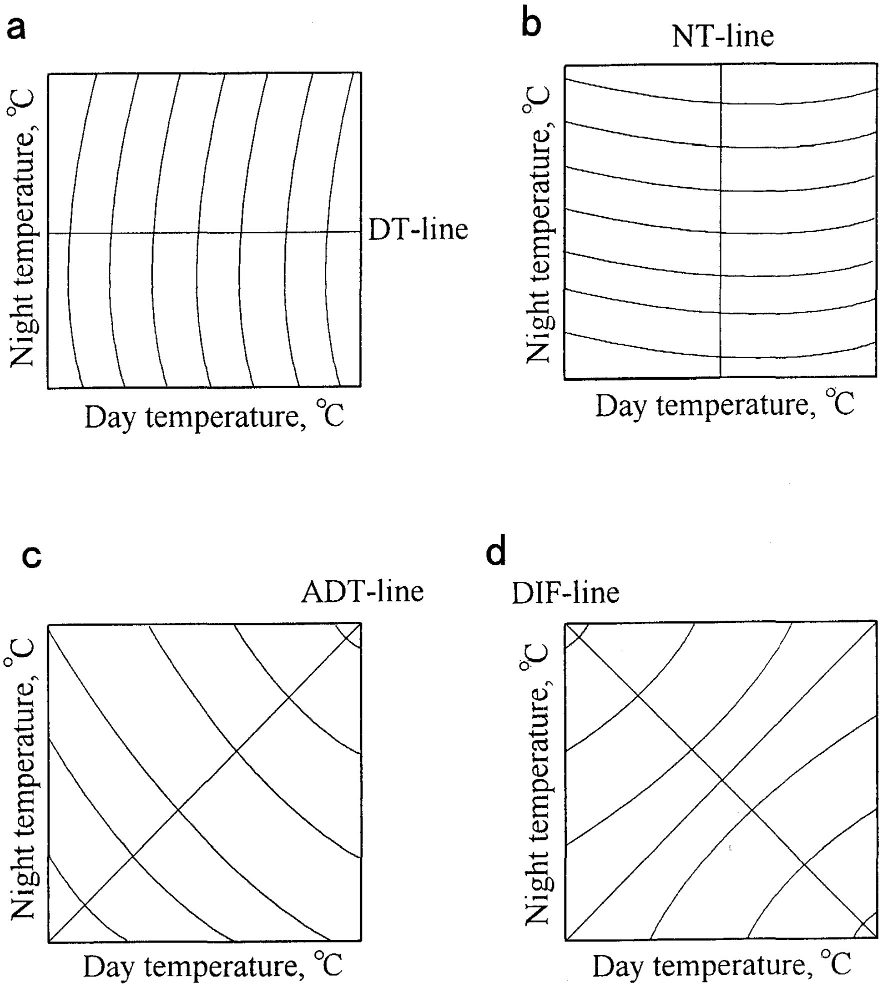

Fig. 1. Schematic diagram of model isopleth plots showing the cases when the variable is more affected by day temperature (DT) (a), night temperature (NT) (b), average daily temperature (ADT) (c) or difference between day and night temperatures (DIF) (d).

and NT values allows to estimate and compare the effects of DT, NT, ADT and DIF on growth variable by counting the number of isolines intersected by DT–, NT–, ADT– and DIF–lines (Fig. 1). For example, if more isolines intersected by DT–lines (Fig. 1a) or NT–lines (Fig. 1b) it means that the variable is more affected by DT or NT, respectively. The same is with ADT (Fig. 1c) and DIF (Fig. 1d).

For an additional check on the validity of the suggested method, the data published by Grimstad and Frimanslund (*4*) for cucumber (*Cucumis sativus* L., cv. Farbiola), Erwin et al. (*2*) for lily (*Lilium longiforum* Thunb., cv. Croft), Kaczperski et al. (*6*) for petunia (*Petunia*×*hybrida* cv. Snow Cloud) and Si and Heins (*11*) for sweet pepper (*Capsicum annuum* L., cv. Resistant Giant no. 4) were analysed.

RESULTS

We applied the approach described above in investigating the effects of day and night temperatures, as well as DIF and ADT on young cucumber plants and calculated the regression equation for leaf petiole length. Isopleth plots were developed from the equation to show the response of leaf petiole length to varying DT and NT (Fig. 2). The arrangement of the isopleths as concentric circles shows that leaf petiole length is affected by both absolute day and night temperatures as well as by ADT and DIF. However, the conclusion can be made that ADT has slightly stronger effect on leaf petiole length than DIF as the ADT –line intersects more isolines than the DIF–line does.

We have not included plant height in the analysis, as in our experiments plants were grown in identical conditions until the stage of unfolded cotyledons and consequently at the stage of one complete leaf the variation of hypocotyl length was insignificant.

According to data on plant height of cucumber plants published by Grimstad and Frimanslund (*4*), we constructed a quadratic regression equation of temperature dependence of plant height and developed isopleth plots of plant height for varying combinations of DT and NT (Fig. 3). It is evident that plant height is affected more by DT than NT and more by ADT than DIF. Furthermore, drawn DT–lines 1 and 2 show that the effect of DT is more pronounced at higher night temperatures, and the effect of NT at higher day temperatures. At lower DT and NT the DIF–lines (for example DIF–line 2) are almost parallel to isopleths that testifies to the lack of DIF effect on plant height.

According to the data on the effect of diurnal temperatures on the growth of lily (*2*), petunia (*6*) and sweet pepper (*11*), we constructed quadratic regression equations of temperature dependencies of growth variables for each crop and developed isopleth plots of plant growth variables for varying combinations of DT and NT (Figs. 4 and 5).

As shown in Fig. 4a plant height of lily is strongly affected by DIF and not affected by ADT as the ADT–lines are almost parallel to the isolines. Fig. 4b shows that leaf length of lily depends very much on NT and very little on DT

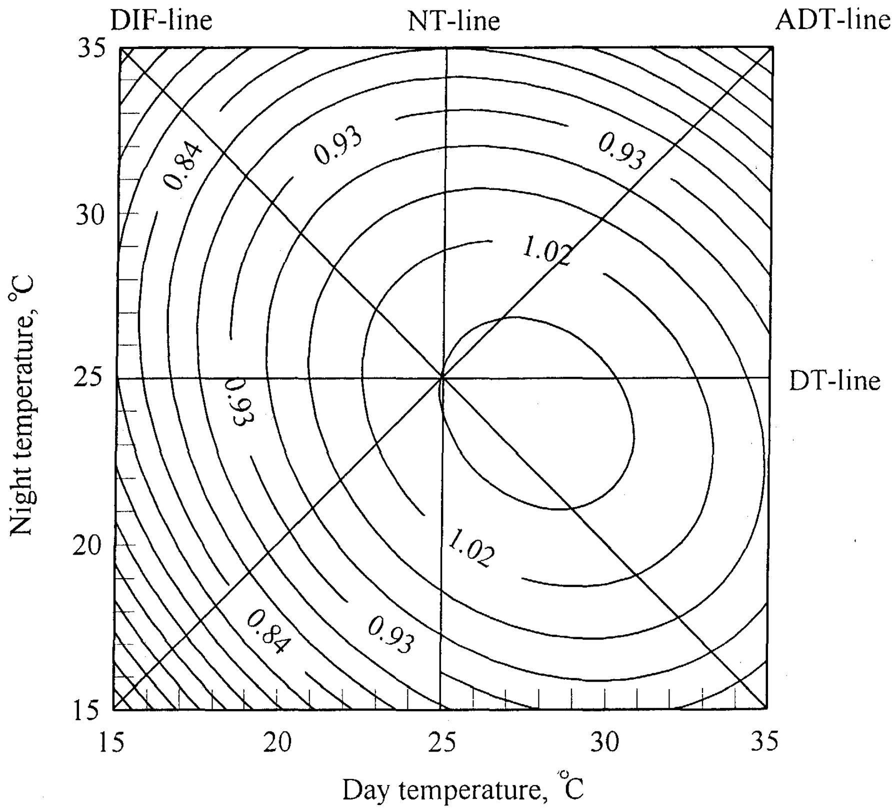

Fig. 2. Isopleth plots of leaf petiole length (cm) for varying combinations of day and night temperatures for *Cucumis sativus* L cv. Alma-Atinsky 1.
(leaf petiole length $= -1.67 + 0.11DT + 0.10NT - 0.0016DT^2 - 0.0017NT^2 - 0.0008\ DT\ NT$, $R^2 = 0.83$, S.D.* $= 0.06$).

as the isolines are almost parallel to DT axis. Nevertheless, if to consider the effects of DIF and ADT they are also present. The opposite effect of temperatures is observed in petunia internode length (Fig. 5), which is affected by DT and not affected by NT. A slight effect of NT is observed only at high DT over 25℃.

In sweet pepper plant height is affected strongly by ADT and almost not affected by DIF (Fig. 6a) while internode length is more affected by DT and DIF (Fig. 6b).

DISCUSSION

Figure 4a shows a classic example of DIF effect on plant height, when DT and NT have opposite effects on internode extension over a wide range of temperatures as it was reported by Erwin et al. (*2*) based on the analysis of

*S.D. –Standard deviation of regression. All equations are significant according to Fisher's test ($P<0.05$).

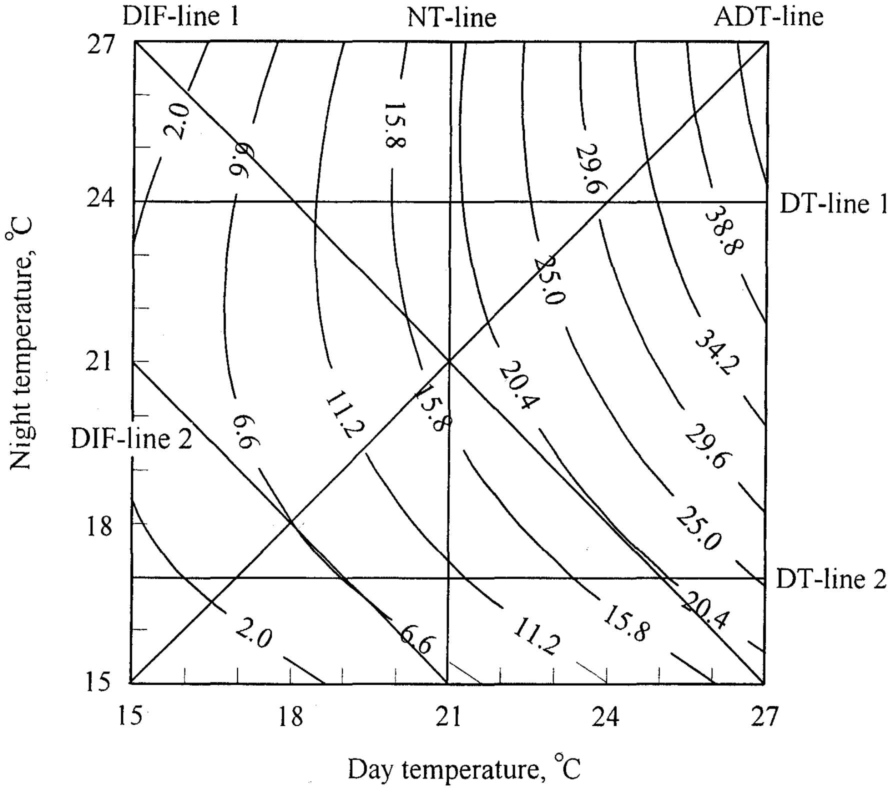

Fig. 3. Isopleth plots ofplant height (cm) for varying combinations of day and night temperatures for *Cucumis sativus* L. cv. Farbiola (data of Grimstad and Frimanslund, (*4*)).
(plant height$=-8.29-4.43DT+2.83NT+0.073DT^2-0.14NT^2+0.21DT\ NT$, $R^2=0.96$, S.D.$=3.15$).

response surface plots. Langton and Cockshull (*7*) re-appraised data sets published by Erwin et al. (*2*) and based on a significant linear DT×linear NT interaction concluded that effects of changing DT were more pronounced at low NT than at high NT, and that effects of changing NT were more pronounced at high DT than at low DT. These conclusions are graphically supported by the isopleth plot on Fig. 4a. Erwin et al. (*2*) reported that leaf length of lily was primarily influenced by NT and more by absolute DT and NT than DIF. As NT increased from 14 to 30℃ with a 14℃ DT leaf length decreased 32% (5.8 cm). DT had little influence on leaf length. To demonstrate these conclusions authors refer to the table and figure with three-dimensional response surface. We consider that isopleth plot on Fig. 4b incorporates information given in the table and on the graph.

Si and Heins (*11*) have shown that stem length, intemode length and other growth variables of sweet pepper were primarily functions of average daily temperature, i.e. DT and NT had similar effects on each parameter. Compared to ADT, DIF had a smaller but still statistically significant effect on stem and internode length. Authors have used two-way and one-way analysis of variance and had to refer to the tables and separate two-dimensional graphs

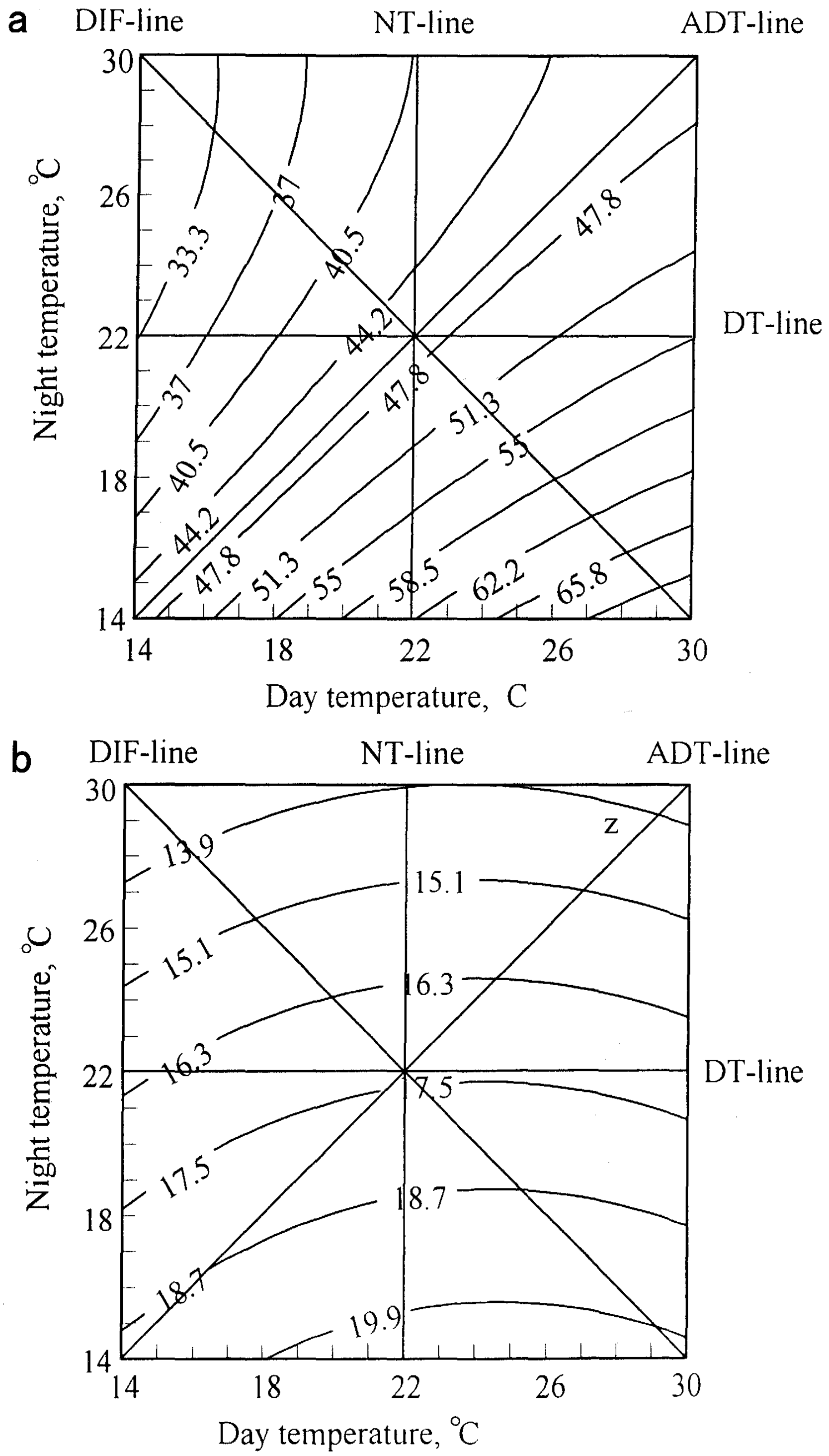

Fig. 4. Isopleth plots ofplant height (cm) (a) and leaf length (cm) (b) for varying combinations of day and night temperatures for *Lilium longiflorum* Thunb. cv. Croft (data of Erwin et al. (*2*)).
(plant height$=46.60+3.84DT-3.87NT-0.038DT^2+0.076NT^2-0.037DT\ NT$, $R^2=0.96$; S.D.$=0.95$) (leaf length$=16.25+0.67DT-0.22NT-0.013DT^2-0.003NT^2-0.002DT\ NT$, $R^2=0.94$, S.D.$=0.59$).

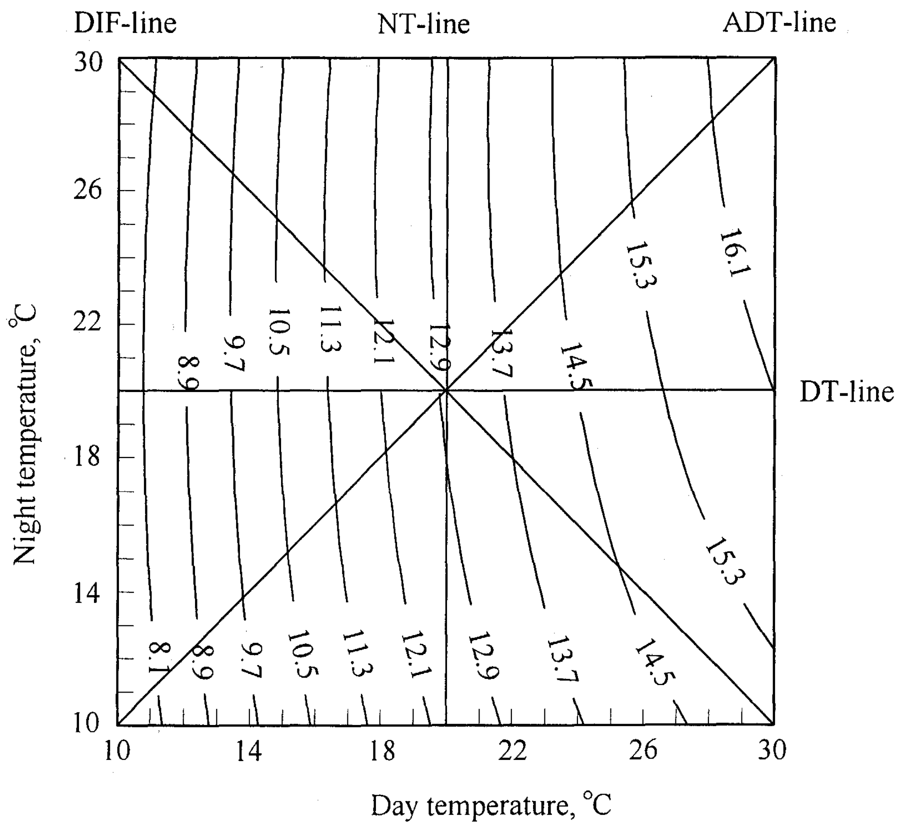

Fig. 5. Isopleth plots of internode length (mm) for varying combinations of day and night temperatures for *Petunia*×*hybrida* cv. Snow Cloud at 6.5 mol day^{-1} m^{-2} (data of Kaczperski et al. (*6*)).
(internode length $= -0.48 + 0.80DT + 0.08NT - 0.011DT^2 - 0.003NT^2 + 0.004DT\,NT$, $R^2=0.84$, S.D.$=0.13$).

displaying the relationships between ADT and growth variables and between DIF and growth variables. Our Figs. 6a and b allow to make the same conclusions and moreover, to see that DIF has no effect on plant height at lower temperatures and slight effect at higher temperatures (Fig. 6a). As for the intemode length Fig. 6b shows that the statement that DT and NT had similar effect is not absolutely correct as it is seen that DT is more effective.

Kaczperski et al. (*6*) found that internode length increased quadratically as day temperature increased, and commented that DIF did not gave as great an effect as has been seen in other plants. Analysis of the location of isopleths on Fig. 5 allows to make rather extensive conclusions. Provided that internode length varies roughly from 8 to 17 mm with the day temperature and from 8 to 15 mm depending on DIF, it is not correct to state that DIF has slight effect. To conclude that NT has no effect on internode length in petunia is also not absolutely correct as it 'works' only at DT below 25℃ as it is seen on Fig. 5.

These examples show that proposed method for quantifying the effect of temperature treatments on plant growth by the analysis of isopleth plots developed from the equations enables an easier and more precise analysis of the

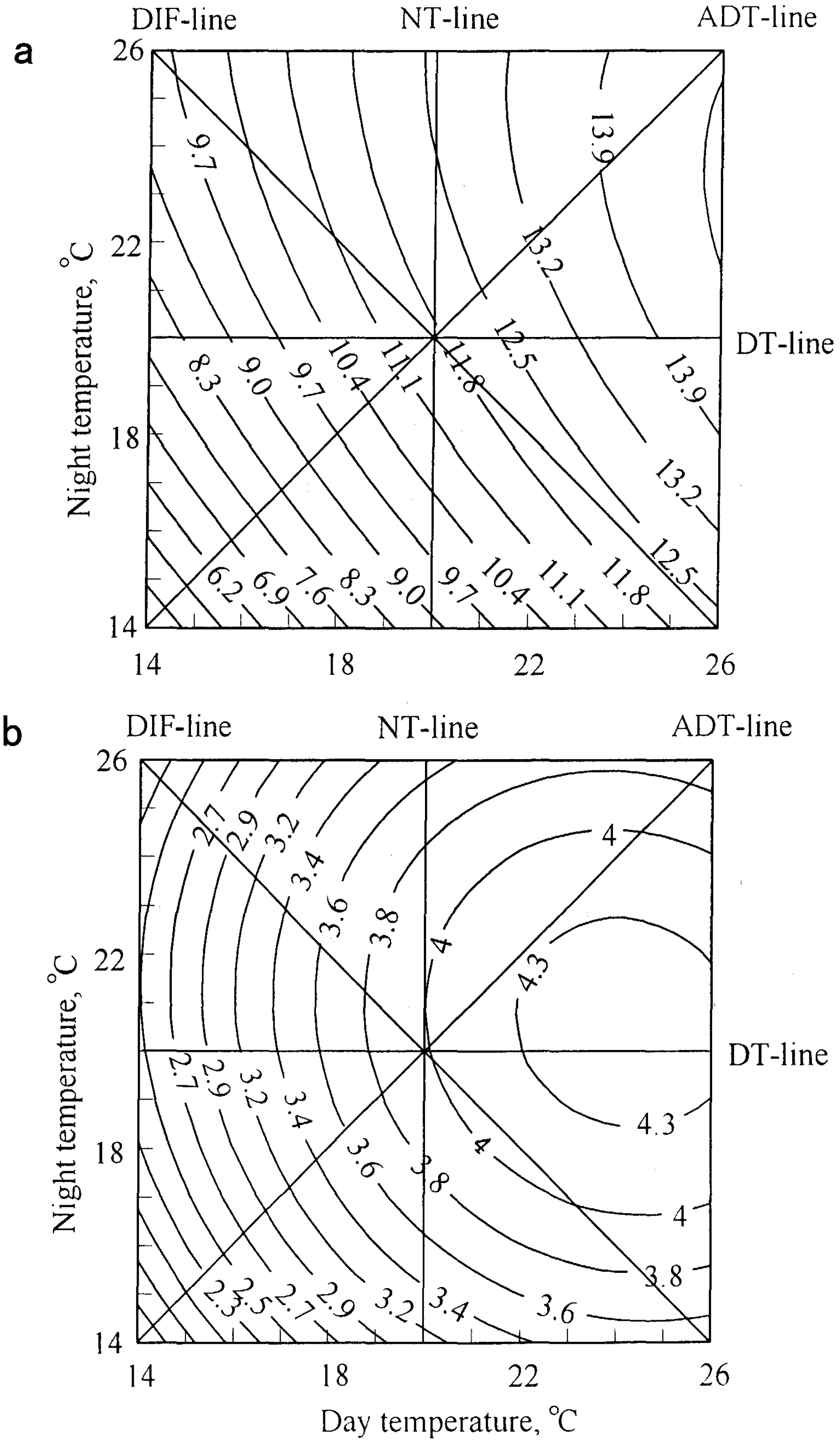

Fig. 6. Isopleth plots of plant height (cm) (a) and internode length (cm) (b) for varying combinations of day and night temperatures for *Capsicum annuum* L., cv. Resistant Giant no. 4 (data of Si and Heins (*11*)). (stemlenght$=-31.93+1.66DT+1.83NT-0.017DT^2-0.027NT^2-0.021DT\ NT$, $R^2=0.86$, S.D.$=0.87$; internode length$=-16.24+0.94DT+0.90NT-0.018DT^2-0.020NT^2-0.003DT\ NT$, $R^2=0.86$, S.D.$=0.34$).

effects of day temperature, night temperature, DIF and ADT on plant growth.

REFERENCES

1. Erwin J. E. and Heins R. D. (1995) Thermomorphogenic responses in stem and leaf development. *Horticultural Science* **30**, 940–949.
2. Erwin J. E., Heins R. D. and Karlsson M. G. (1989) Thermomorphogenesis in Lilium longiflorum. *American Journal of Botany* **76**, 47–52.
3. Erwin J. E., Heins R. D. and Moe R. (1991) Temperature and photoperiodic effects on *Fuchsia×hybrida* morphology. *Journal of American Society for Horticultural Science* **116**, 955–960.
4. Grimstad S. O. and Frimanslund E. (1993) Effect of different day and night temperature regimes on greenhouse cucumber young plant production, flower bud formation and early, yield. *Scientia Horticulturae* **53**, 191–204.
5. Ivory D. A. and Whiteman P. C. (1978) Effect of temperature on growth of five subtropical grasses. 1. Effect of day and night temperature on growth and morphological development. *Australian Journal of Plant Physiology* **5**, 131–148.
6. Kaczperski M. P., Carlson W. H. and Karlsson M. G. (1991) Growth and development of *Petunia×hybrida* as a function of temperature and irradiance. *Journal of American Society for Horticultural Science* **116**, 232–237.
7. Langton F. A. and Cockshull K. E. (1997a) Is stem extension determined by DIF or by absolute day and night temperatures? *Scientia Horticulturae* **69**, 229–237.
8. Langton F. A. and Cockshull K. E. (1997b) A reappraisal of DIF extension growth responses. *Acta Horticulturae* **435**, 57–64.
9. Myster J. and Moe R. (1995) Effect of diurnal temperature alternations on plant morphology in some greenhouse crops–a mini review. *Scientia Horticulturae* **62**, 205–215.
10. Seginer I. and Raviv M. (1984) Optimum night temperatures for greenhouse seedlings. *Scientia Horticulturae* **23**, 203–216.
11. Si Y. and Heins R. D. (1996) Influence of day and night temperatures on sweet pepper seedling development. *Journal of American Society for Horticultural Science* **121**, 699–704.
12. Went F. W. (1944) Plant growth under controlled conditions. II. Thermoperiodicity in growth and fruiting of the tomato. *American Journal of Botany* **31**, 135–150.