

# Quantification of Temperature Effects on Stem Elongation in Poinsettia

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**Abstract.** Elongation characteristics of each internode on a lateral shoot of poinsettia (*Euphorbia pulcherrima* Klotz) 'Annette Hegg Dark Red' were determined from pinching through anthesis for plants grown with 36 day/night temperature (DT/NT) combinations between 16 and 30C. The Richards function was used to describe the elongation of each internode. The first internode developing on a lateral shoot was longer and matured faster than subsequent internodes. The length of the first internode was a function of the difference between day and night temperatures (DIF = DT - NT). Subsequent internodes elongated uniformly in the absence of flower initiation. In the absence of flower initiation, the length of an internode, after the first, was a function of DIF. Internodes were shorter as proximity to the inflorescence increased. Internode length after the start of short days was a function of DIF and the visible bud index where visible bud index = [(days from pinching to the day an internode began to elongate - days from pinching to the day of the start of flower initiation)/the number of days from pinching to visible bud]. A poinsettia lateral shoot elongation model was developed based on the derived functions for internode elongation. The model predicted lateral shoot length within one standard deviation of the mean for plants grown in a separate validation study with 16 combinations of DT/NT. The model allows the prediction of lateral shoot length on any day from pinching through anthesis based on temperature, the number of nodes on the lateral shoot, the time each internode on the lateral shoot began elongating, and the visible bud index at the start of elongation of each node.

One of the major problems in commercial poinsettia production is the control of plant height. The use of growth regulating chemicals has provided a means to control plant height. However, increasing public concern with chemicals in the environment makes it prudent for commercial poinsettia plant producers to "reduce their reliance on all classes of chemicals. To reduce the reliance on chemicals for plant height control, a thorough understanding of the factors that influence stem elongation is needed together with information on how manipulation of these factors can be used to control stem elongation.

The influence of temperature on plant stem elongation has been the object of much study. Went (1957) provided an excellent review of the general influence of temperature on stem elongation. He observed that plants grown with cooler DT than NT were shorter than plants grown with a warmer DT than NT. A lack of understanding of the implications of this observation prevented commercial application until the late 1980s. Erwin et al. (1989) quantified the influence of temperature on morphogenesis of *Lilium longiflorum*. In particular, they found that the effects of DT and NT on stem elongation could be described quantitatively using the difference between day and night temperatures (DIF = DT - NT). Stem elongation increased as DIF increased. Similar relationships have been reported for chrysanthemum (Karlsson et al., 1989), fuchsia (Erwin and Heins, 1988), and poinsettia (Berghage, 1988). This appears to be a general growth response found in most plant species (Moe and Heins, 1989).

The objective of this research project was to quantify the influence of temperature on internode elongation in the poinsettia and subsequently develop a computer simulation model.

## Materials and Methods

Rooted 'Annette Hegg Dark Red' cuttings were planted in 1200-cm<sup>3</sup> plastic pots 28 Aug. 1986 and placed in a 23C constant temperature glass greenhouse. A nutrient solution with 18N-1P-8K (mM) and 1 μM Mo was applied at each irrigation. On 10 Sept., 360 uniform plants were pinched to about six nodes and moved to glass greenhouses with temperature set-points of 14, 17, 20, 23, 26, and 29C. Plants were moved between greenhouse sections starting at 0800 and 1730 HR to provide 36 temperature treatment combinations. Plants held at constant temperature were moved from one location to another within the greenhouse. Any lateral shoots that had formed below the five uppermost lateral shoots were removed 2 weeks after pinching. Starting on 28 Sept., black cloth was pulled at 1800 and 0800 HR immediately after and before the plants were moved, respectively. The 14-hr artificial nyctoperiod was continued until the experiment was terminated on 15 Dec.

The length of each internode on the second lateral shoot below the pinch was measured to the nearest 0.01 cm, using a digital caliper every 3 to 4 days starting on the 5th day after the pinch. Measurements were made from leaf axil to leaf axil. Internode lengths were recorded to the nearest 0.01 cm. An internode was measured when it was longer than 0.15 cm (this was the smallest internode that could be reliably measured). DIBE was defined as the number of days from pinching to the day the internode attained a measurable length. Although the poinsettia is largely an alternate-leaved plant, =10% to 15% of the internodes fail to elongate, resulting in apparently opposite leaves. The formation of opposite leaves was not related to the temperature treatments. Where leaves were apparently opposite, one leaf was marked to assure consistency in internode measurements. Lateral shoot length was calculated by summing the measured lengths of each of the internodes on the lateral shoot.

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Abbreviations: ADT, average daily temperature; DIF, DT - NT; DIBE, days from pinching to day internode started to elongate; DT, day temperature; N, total number of internodes below inflorescence; NT, night temperature; VB, date of first visible bud; VBI, visible bud index.

VB was recorded for each plant. VBI for each internode was calculated as:

$$VBI = [(DIBE) - (SD)]/(VB) \quad [1]$$

where SD is the date of the start of short days. VBI for a vegetative plant was set to 0.

VBI was used as a measure of the temporal proximity of the appearance of an internode to the appearance of a visible flower bud. Calculated VBI ranged from zero to one for internodes that appeared between the start of flower initiation and visible bud, and was >1 for internodes that became measurable after VB.

Greenhouse temperatures were recorded with a datalogger using iron-constantan thermocouples. Two-hour temperature averages were calculated from measurements made at 10-sec intervals. Average DT and NT for each greenhouse section were calculated from these data and used in all regression analyses.

A Richards function (Richards, 1969) of the form:

$$IL_t = P_1 (1 + P_2 e^{P_3 - P_4 t})^{-\frac{1}{P_4}} \quad [2]$$

(where IL is the internode length,  $P_{1-4}$  are estimated parameters, and t is time after pinching, in days) was fitted to the data from each of the first six internodes on the second lateral shoot below the pinch on plants from each of the 36 temperature combinations. The pseudo  $R^2$  [ $1.0 - (\text{residual sums of squares}) / ((N - 1) \text{ variance})$ ] (Ralston, 1988) for each fitting of the Richards function ranged from 0.945 to 0.999.

The Richards function has previously been used to describe individual leaf growth (France and Thornley, 1984; Cao et al., 1988), plant diameter, and stem elongation (Larsen, 1988, 1989). In the Richards function,  $P_1$  is the asymptote (final internode length),  $P_2$  determines when the function begins to increase (on the time axis),  $P_3$  determines the rate of increase, and  $P_4$  determines the inflection point (Hunt, 1982). The BMDP AR subroutine (BMDP Statistical Software, Los Angeles, Calif.) was used to determine the minimum least squares model for the Richards functions and the exponential model for  $P_1$ . The linear model of  $P_1$  was obtained with stepwise regression using the BMDP 2R subroutine.

Parameter estimates from the Richards functions describing the first five internodes from all 36 temperature combinations were used in multiple linear regression analysis relating function parameters  $P_2$  and  $P_3$  to DT, NT, DIF, ADT, DIBE, and VBI. Multiple linear regressions were performed with the Systat MGLH subroutine (Systat, Evanston, 111.).

The Richards function parameters ( $P_1$ ), ( $P_2$ ), and ( $P_3$ ) and their temperature-dependent functions for the first internode were different than those for subsequent internodes. Regression functions were developed to describe the first internode and subsequent internodes independently, because growth of the first internode differed from that of subsequent internodes (Figs. 1 and 2).

The parameter  $P_1$  was not significantly influenced by temperature treatments so a constant value of  $P_1$  was used in the model.  $P_4$  was, however, significantly influenced by internode position; therefore, the mean value of all the estimates of  $P_4$  for each internodal position was used as the estimate of  $P_1$ . For internodes 1 to N in the stem elongation model (where N is the total number of internodes below the inflorescence) these means were 0.8, 1.1, 1.4, 1.2, 0.8, . . . 0.8.

Equations developed for  $P_1$ ,  $P_2$ , and  $P_3$  are given below. The Subscript (1) indicates the equation was developed for internode

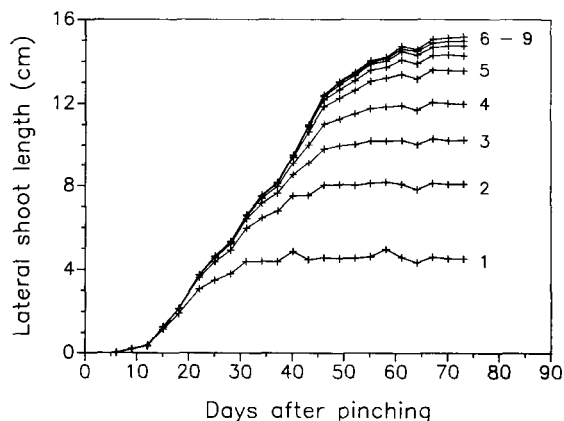


Fig. 1. Total lateral shoot elongation as the sum of individual internodes on the second lateral shoot below the pinch for 'Annette Hegg Dark Red' poinsettia grown with 20C DT and NT. Numbers on right indicate nodes on the lateral shoot, 1 being the proximal node. Internode length is the distance between the curves (nodes).

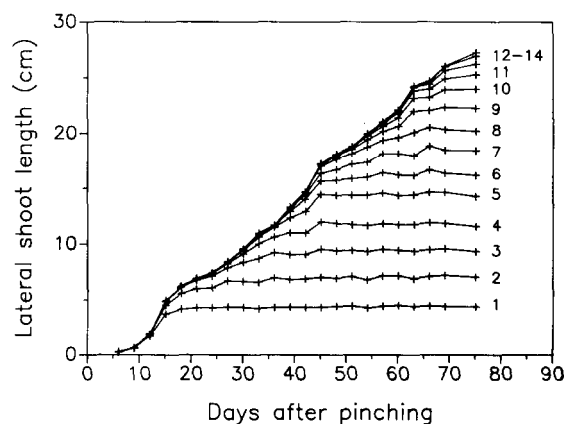


Fig. 2. Total lateral shoot elongation as the sum of individual internodes on the second lateral shoot below the pinch for 'Annette Hegg Dark Red' poinsettia grown with 29C DT and NT. Numbers on right indicate nodes on the lateral shoot, 1 being the proximal node. Internode length is the distance between the curves (nodes).

one; (2-N) indicates the function developed for internodes two through N.

$$P_{1(1)} = 4.647 + 0.111 (DIF) + 0.00348 (DIF^2) \quad [3]$$

$$P_{1(2-N)} = (-270.8 + 13.164 (DIF) + 0.25293 (DIF^2) - 17.572 (DIF) (VBI) + 50.73 (ADT) - 1.115 (ADT^2))^{-0.3738 (2VBI) - 0.572 (2VBI)(VBI^2)} \quad [4]$$

$$P_{2(1)} = -1.311 + 3.875 (P_4) + 0.115 (DIBE) + 0.052 (DIF) \quad [5]$$

$$P_{2(2-N)} = -4.69 + 3.742 (P_4) + 0.126 (DIBE) + 0.065 (DIF) + 0.146 (ADT) \quad [6]$$

$$P_{3(1)} = -0.408 + 0.106 (P_2) + 0.022 (ADT) \quad [7]$$

$$P_{3(2-N)} = -0.0408 + 0.311 (P_2) - 0.00024 (P_2) (DIBE) - 0.00213 (DIBE) + 0.00549 (ADT) + 0.04775 (VBI) \quad [8]$$

Equations 2 through 8 form a static (with regard to temperature) model that can be used to predict internode length with a given DT and NT. Summing the lengths of each internode provides an estimate of the total lateral shoot length. DT and

NT must be held constant throughout the simulation because direct output from the Richards function is used in this model to predict internode length.

A dynamic model was constructed using Euler integration to allow estimation of the effects of changes in the DT and NT on a daily basis. This was done by integrating the output of the first derivative of the Richards function (assuming that the effect of temperature were instantaneous with no carryover from one day to the next). The amount of elongation predicted for a given time interval (i.e., rate/day) was estimated and the output was summed with respect to time. This can be illustrated as follows.

$$L_{(t+DT)} = L_{(t)} + \int_t^{t+DT} (R(x)) dx \quad [9]$$

where L is the internode length, DT is the time step used in the model (1 day), and R is the Richards function using parameters estimated with Eqs. 3 through 8. This model is based on a fixed (1 day) timestep derived from data for internode elongation for each internode from pinching to anthesis. Without modification, this model predicts resumption of internode elongation in a mature internode if temperature is changed. The time input to the Richards function was adjusted to reflect the maturity of an internode to eliminate this error. Maturity of an internode was calculated based on the fraction of the total potential elongation that was predicted to occur in the time interval  $t + DT$ . These fractions were summed at each iteration of the model to provide a maturation index for each internode that ranged from 0 (elongation had not yet begun) to 1 (internode elongation complete). The time input for the Richards function ( $t$ ) was then adjusted based on the maturity index. For example, if the solution to the integral part of Eq. 9 was 1 cm and  $P_i$  was 4 cm, then the internode would have completed 25% of its total potential elongation in that iteration of the model. The maturation index for that internode would be 0.25. If DIBE was 4, then the time input ( $t$ ) for the next iteration of the model would be calculated by solving the Richards function (Eq. 2) for ( $t$ ) based on an internode that had completed 25% of its elongation [ $IL_i = 0.25(P_i)$ ]. For internode 1 at 16C DT and NT,  $t$  would thus be 18 for the next iteration, and at 23C DT and NT,  $t$  would be 9.

The number of internodes present, DIBE, and VBI are constants in this model. These terms could, however, be estimated based on the output of a developmental rate model for the poinsettia (Berghage, 1989).

A study was conducted in 1987 to validate the model. Plants were potted on 21 Aug. and pinched on 7 Sept. Plants were grown in a common greenhouse environment after pinching, with heating beginning at 20C and ventilation beginning at 23C. Plants received night interruption lighting with incandescent lights from 2200 HR to 0200 HR each night to prevent flower initiation. Plants were placed in glass greenhouses on 1 Oct. with temperature setpoints of 14, 17, 20, and 23C. Plants thereafter were moved at 0800 and 1730 HR to provide 16 DT/NT combinations. An opaque blackout curtain was closed at 1800 HR immediately after plants were moved and retracted at 0800 HR before plants were moved. Data were collected as in 1986.

## Results and Discussion

Lateral shoot elongation in poinsettia followed a sigmoid pattern similar to that observed for the chrysanthemum (Heins et al., 1988). There was a lag following pinching where stem elongation occurred slowly. The lag phase was followed by a rapid elongation phase and then a slower terminal growth stage

approaching an asymptote as plants reached anthesis at =65 days (Fig. 1). This general pattern was observed in all plants where flower initiation occurred (i.e., visible buds were observed). A different pattern of growth was observed in plants grown with a 29C DT and NT (Fig. 2). Flower initiation was prevented in these plants due primarily to the high night temperature (Langhans and Miller, 1960; Berghage, 1989). In plants where flower initiation was prevented, both the lag phase and the rapid elongation phase were observed; however, there was no terminal growth phase, and elongation continued at a steady rate until the experiment was terminated (Fig. 2).

Lateral shoot elongation patterns can be explained by examining the elongation of the individual internodes. The elongation of each internode followed a sigmoid pattern. In plants where flower initiation did not occur, new internodes continued to appear throughout the experiment (Fig. 2). The first internode to appear after pinching was longer and matured at a more rapid rate than subsequent internodes. The internodes that developed after the first all elongated at about the same rate and grew to about the same final length.

The number of internodes below the inflorescence was limited in plants where flower initiation occurred. Again, the first internode was longer and matured at a faster rate than subsequent internodes. Whereas each of the internodes that developed after the first one elongated at about the same rate, final internode length was greatly reduced in internodes closer to the inflorescence (Fig. 1).

The pattern of stem elongation thus depended on internode number, length, and position on a reproductive plant. Internode number and length varied among plants grown under the various temperature regimes. Internode number was influenced by the effects of temperature on leaf unfolding and flower initiation.

Leaf unfolding rates in the poinsettia increase as average temperature increases up to  $\approx 25C$  and the number of leaves formed before flower initiation determines the final number of leaves on a lateral shoot (Berghage, 1989). The poinsettia is an alternate-leaved plant, with an occasional internode (10% to 15%) that fails to elongate. The number of leaves formed on a lateral shoot can thus be described as a function of the number of nodes on the lateral shoot (Fig. 3). Therefore, increased average temperature between pinching and flower initiation results in more leaves unfolded before flower initiation and hence more nodes (and internodes) on a lateral shoot.

Internode number was also influenced by the effects of temperature on flower initiation. High NT are known to delay flower

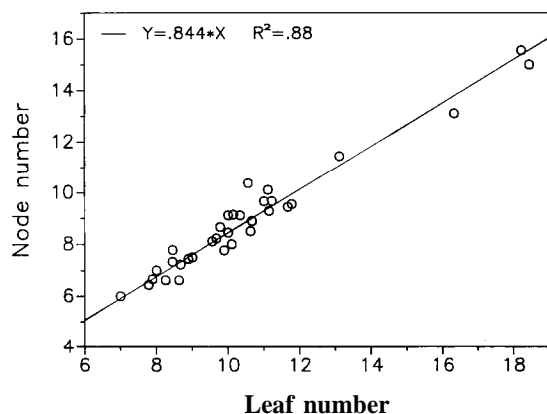


Fig. 3. Node number vs. leaf number for 'Annette Hegg Dark Red' poinsettia grown with 36 DT and NT combinations in 1986. Node number = leaf number  $\times$  0.844.  $R^2 = 0.89$ .

initiation in poinsettia (Langhans and Miller, 1960; Larson and Langhans, 1963; Kristofferson, 1969). Delayed flower initiation in plants grown with  $NT > 25C$  resulted in more leaves on these plants (Berghage, 1989).

Final internode length was influenced by the relationship between DT and NT. The results of multiple linear regression analysis indicated that DIF described much of the variability in final internode length observed in this experiment (Fig. 4); The length of the first internode depended only on DIF, which accounted for 68% ( $R^2 = 0.68$ ) of the variability. The length of subsequent internodes (two through N) depended on DIF and VBI ( $R^2 = 0.84$ ).

The observed effects of VBI on internode length were suggestive of an exponential function (Fig. 5). An exponential function tested using the same terms contained in the multiple linear regression model provided a better description of the data than the linear regression model (the residual sums of squares were = 13% less than in the linear model). However, this exponential model did not adequately predict the lateral shoot length of plants grown in the validation study ( $R^2 = 0.51$ ). Multiple linear regression of ADT and the predicted and observed lateral shoot lengths for plants in the validation study suggested that the unaccounted-for variability was related to ADT ( $R^2 = 0.87$ ).

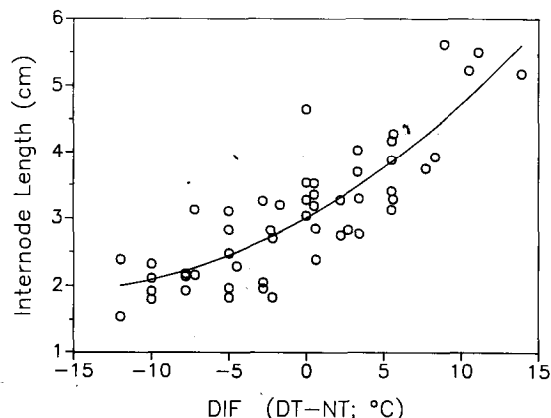


Fig. 4. Relationship between DIF and length of internodes on the second lateral shoot of poinsettia 'Annette Hegg Dark Red' grown with 36 DT/NT combinations. Data shown are for all nodes after the first with a VBI of 0 for each of the temperature treatments.

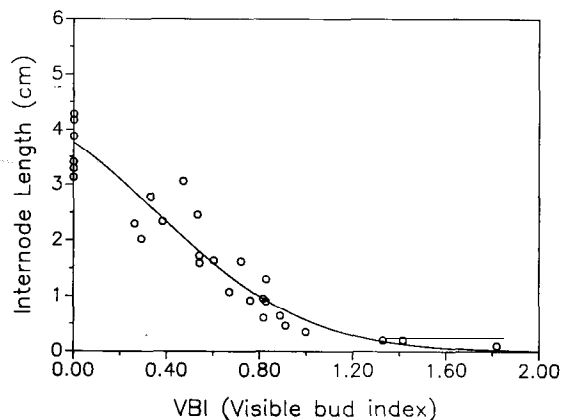


Fig. 5. Relationship between VBI and internode length for internodes on the second lateral shoot of poinsettia 'Annette Hegg Dark Red' grown with a DIF (DT - NT) of 5.5C.  $VBI = [Date\ internode\ began\ elongation\ (DIBE) - the\ date\ of\ the\ start\ of\ flower\ initiation] / date\ of\ visible\ bud$ .

Including ADT in the exponential model reduced the residual sums of squares 20% and 9% compared with the linear and exponential models, respectively, without ADT and resulted in a model that predicted lateral shoot length of the plants grown in the validation study to within one standard deviation for all but two treatments (Table 1).

The complex interrelationships between temperature, internode number, internode length, and reproductive status suggested that a single internode model should be used for predicting poinsettia stem elongation. A model of whole lateral shoot elongation would be considerably less versatile than one based on individual internodes due to the potential variability in the temperature during and the length of the vegetative phase of poinsettia growth. A longer vegetative growth period before flower initiation or a higher temperature during this period would result in increased leaf and internode number and substantially change the pattern of lateral shoot elongation. For a whole shoot model to account for all the possible permutations of time and temperature during the vegetative phase, a large number of the possible combinations would need to be tested individually. A single internode model in conjunction with a developmental rate model (Berghage, 1989) would allow prediction of stem elongation for any temperature and time combination simply by increasing the number of internodes contributing to the model.

For a single internode stem elongation model to be effective, there must be underlying trends in the parameter estimates for the nonlinear growth functions. The final internode length ( $P_1$ ) increased as DIF increased, decreased as VBI increased, and was also related to ADT.

The parameter  $P_3$ , which reflects how the curve is shifted on the time axis, increased as DIBE and DIF increased for the first internode ( $R^2 = 0.80$ ) and also increased as ADT increased for internodes two through N ( $R^2 = 0.83$ ). The rate parameter of the Richards function ( $P_3$ ) increased with increasing ADT for internode 1 ( $R^2 = 0.97$ ) and for internodes two through N was also correlated with DIBE and VBI ( $R^2 = 0.96$ ). The parameters of the Richards functions estimated for internode elongation of plants grown with various combinations of DT and NT were thus interrelated as functions of temperature (DIF and ADT) and time (DIBE and VBI).

The model constructed based on these relationships accounted for 74% of the variability in final lateral shoot length of plants grown in the validation study (Table 1). Estimated total lateral shoot length was within one standard deviation of observed lateral shoot length for all but two temperature combinations in the validation study.

The first objective of this study was to quantify the influence of temperature on stem elongation in the poinsettia. The information generated in accomplishing this objective has implications beyond developing a simulation model. Understanding the impact of DIF on stem elongation allows the poinsettia grower to select a temperature regime based on desired internode elongation. Longer internodes can be obtained by increasing DIF and shorter internodes by decreasing DIF (Fig. 4). The quadratic nature of the response provides for a greater relative decrease in internode length by changing the greenhouse temperature from a positive DIF to a zero DIF, than by an equivalent decrease in DIF from zero to a negative value. Thus, a poinsettia grower wishing to limit reliance on chemical growth regulators would be well-advised to avoid greenhouse temperature regimes with a large positive DIF.

The total length of a lateral shoot is a function of both the length of each internode and the number of internodes present.

Table 1. Predicted and observed lengths of the second lateral shoot below the pinch for poinsettia 'Annette Hegg Dark Red' grown in 16 day/night temperature combinations in 1987.<sup>a</sup>

Night temperature setpoint (°C)		Day temperature setpoint (°C)				Observed NT (°C)
		14	17	20	23	
<i>Length (cm)</i>						
14	Observed	14.4 ± 1.8	16.2 ± 2.0	16.2 ± 1.4	19.6 ± 2.6	14.8
	Predicted	14.5	16.8	18.9	21.1	
17	Observed	15.5 ± 1.8	17.0 ± 2.6	17.4 ± 1.6	21.9 ± 3.3	16.8
	Predicted	15.0	17.0	18.9	21.1	
20	Observed	14.7 ± 2.6	16.1 ± 2.2	19.0 ± 2.0	20.4 ± 3.2	19.5
	Predicted	15.4	17.2	18.4	20.3	
23	Observed	14.3 ± 1.6	16.4 ± 1.6	17.7 ± 1.7	22.2 ± 2.9	22.8
	Predicted	15.1	16.5	17.6	19.0	
Observed DT (°C)		16.0	18.0	20.0	22.3	

<sup>a</sup>R<sup>2</sup> predicted vs. observed = 0.74; linear regression coefficient = 1.018

Internodes that elongated after flower initiation (VBI > 0) were shorter than those elongating before flower initiation (Fig. 5). The formation of additional internodes before flower initiation could, therefore, have a major impact on total lateral shoot length, particularly on plants with few leaves. A poinsettia grower should thus manage both internode number (before flower initiation) and internode length (both before and after flower initiation) to optimize height control in the poinsettia.

Shorter internodes observed as VBI increased suggest that the potential for modifying total lateral shoot length with DIF would decrease in internodes elongating after flower initiation and would be small late in the development of the plant. The simulation model provides a means for examining this possibility. Increasing DIF in the simulation from -6C to +6C 6 weeks after flower initiation resulted in little change in predicted lateral shoot length. This result has since been confirmed experimentally (Berghage and Heins, 1988).

Examining the structure and response characteristics of the model provides further insight into the relative effectiveness of height control measures at various times in the development of the plant. Clearly, the total change in lateral shoot length in a time interval  $t + DT$  is a function of the number of internodes elongating during that time interval and the total elongation of each one. In the case of a change in DIF late in the development of the lateral shoot, most of the internodes have already ceased elongating. The internodes that still are elongating are strongly influenced by their proximity to the reproductive structures; hence, total lateral shoot elongation is small. Total predicted change in lateral shoot elongation in response to increasing DIF is also small early in the development of a lateral shoot (1 to 2 weeks after pinching). In this case, only the first internode has begun to elongate; hence, any response will be limited to this internode. A large response to increasing DIF is predicted 5 to 6 weeks after pinching. Several internodes are predicted to be elongating at this time and each will respond to the change in DIF, resulting in a relatively large cumulative change in lateral shoot elongation. Each of these possibilities has been confirmed (Berghage and Heins, 1988)

This model also has the potential for use in direct commercial applications. Many greenhouse growers are currently using "graphical tracking" (Heins and Carlson, 1990) as a tool in height control of poinsettia. This technique uses a static sigmoid curve to determine crop progress toward a desired height goal. Growers are currently limited to plotting and observing past

progress of the crop and then adjusting the environment to alter future growth. Our model could be used in conjunction with graphical tracking in a computer spreadsheet to predict the growth of a crop based on a variety of inputs, allowing the grower to make better decisions when temperature adjustments are required.

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