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Robert D. Berghage Jr.

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## MODELING STEM ELONGATION IN THE POINSETTIA

Bу

Robert D. Berghage Jr.

## A DISSERTATION

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Horticulture

#### ABSTRACT

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## MODELING STEM ELONGATION IN THE POINSETTIA

By

Robert D. Berghage

A dynamic computer simulation model describing type of pinch, timing of the pinch relative to flower initiation, and poinsettia stem elongation in response to temperature was developed. The relationships between pinching technique and lateral shoot growth, and between temperature and plant development and internode elongation were quantified to provide the basis for this model.

Pinching technique influenced the release of lateral shoots from correlative inhibition, the rate of initial lateral shoot elongation, and the elongation of the primary stem. Lateral shoot elongation was delayed and reduced and the primary stem continued to elongate when immature leaves were left on the plant at pinching resulting in taller, narrower plants at anthesis than in plants where immature leaves were removed.

Plant developmental rates were influenced by prevailing temperatures. Both day temperature (DT) and night temperature (NT) had equal effects on the rate of leaf unfolding (based on time and temperature). The rate of leaf unfolding was a curvilinear function of temperature with a maximum at about 25C. In contrast, flower initiation



responded primarily to night temperature with NT above 23C delaying flower initiation. Flower development to visible bud was correlated with integrated prevailing temperatures below 23C and could be described using leaf unfolding rates. Flower development from visible bud to anthesis was also correlated with integrated prevailing temperatures.

Internode length was a function of the relationship between nodal position, day and night temperature (DIF = DT-NT), average temperature, and flower development. The first internode on a lateral shoot elongated more and matured faster than subsequent internodes. Final internode length in vegetative plants was primarily a function of DIF and to a lesser extent average temperature. Final length of an internode in a reproductive plant decreased exponentially in nodes closer to the inflorescence. Internode elongation was described using a 4 parameter Richards nonlinear function.

The model was validated using plants grown with a variety of temperature and pinching date combinations. The model accurately predicted the dynamic effects of temperature on stem elongation and proved to be robust in predicting stem elongation under a wide array of temperature and pinching date combinations.

#### ACKNOWLEDGEMENTS

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The paper format was adopted for this dissertation in accordance with departmental and university regulations. Section I has been accepted for publication in the <u>Journal of the American Society for Horticultural</u> <u>Science</u> in 1989, section II and III are to be submitted to the <u>Journal of</u> <u>the American Society for Horticultural Science</u>, and section IV is to be submitted to <u>Hortscience</u>.

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#### INTRODUCTION

The poinsettia has become the most important commercially produced pot plant in the USA based on number and value of plants produced in a year. The growth in popularity of the poinsettia over the last 25 years is largely a result of three factors, the development of free branching cultivars, the development of cultivars which retain their leaves and bracts, and the development of growth retardants for height control. The increasing public concern with chemicals in the environment make it prudent for commercial poinsettia producers to reduce their reliance on chemicals for height control. To reduce our reliance on chemicals for height control we must develop a thorough understanding of the factors which influence plant height, and we must quantify how each of these factors can be manipulated to control plant stem elongation.

The poinsettia is a short day plant which flowers naturally in late November and early December in the northern hemisphere due to the decreasing daylength. In commercial production, the poinsettia is generally propagated by cuttings in the summer, which are then grown on in the fall and flowered for sale between Thanksgiving and Christmas. The most common production unit is a single cutting planted in a 1200 cm<sup>3</sup> pot and pinched (decapitated) in the early fall to induce lateral branching producing 5 to 6 branches and 5 to 6 blooms.

In a determinant plant species such as the poinsettia, a lateral

shoot will terminate in a flower. The total height of a pinched poinsettia will be a combination of the height of the pot, and the sum of the lengths of the primary stem below the lateral shoots and the length of the lateral shoots. The length of the lateral shoots and the primary stem is a function of the number of internodes and the length of each internode.

The objective of this study was to determine how pinching technique and temperature in the greenhouse influence both internode number and internode length in commercial poinsettia production. Developing and applying quantitative relationships between these factors and plant stem elongation will provide a powerful tool to aid in the control of poinsettia plant height.



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PINCHING TECHNIQUE INFLUENCES LATERAL SHOOT DEVELOPMENT IN POINSETTIA Subject Category: Production and Culture Pinching Technique Influences Lateral Shoot Development in Poinsettia

Robert D. Berghage, Royal D Heins, Meriam Karlsson, John Erwin, and William Carlson

# Department of Horticulture Michigan State University East Lansing, Mi. 48824

<u>Additional Index Words</u>: <u>Euphorbia pulcherrima</u>, lateral bud development, stem elongation, apical dominance, correlative inhibition.

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Abstract Lateral shoot growth and plant morphology of poinsettia (Euphorbia pulcherrima Willd.) were influenced by the pinching technique used for apical meristem removal. Plants were pinched in one of four ways: 1) soft (removal of the apical meristem plus stem and leaf tissue associated with leaves two cm or less in length): 2) medium (removal of the apical meristem plus stem and leaf tissue associated with leaves up to seven cm in length); 3) hard (removal of the apical meristem plus stem and leaf tissue associated with all immature leaves); and 4) leaf removal (LR; soft pinch as defined above plus removal of all immature leaves but not the associated stem tissue). Initial growth of lateral shoots on soft and some medium-pinched plants was less than initial growth of lateral shoots on hard or LR- pinched plants. Shorter lateral shoots and longer primary stems at anthesis on soft-pinched plants resulted in vertical plant architecture. Hard and LR-pinched plants had a more horizontal plant architecture. The average height to width ratio of soft, hard and LRpinched plants at anthesis was 0.77, 0.68 and 0.63, respectively. Of 10 commercial cultivars tested in 1987, 48% of the inflorescences of softpinched plants developed below the bract canopy compared with 27% and 31% for hard and LR-pinched plants, respectively. These results show that the use of a soft pinch to increase inflorescence number in the bract canopy is not productive if immature leaves are left on the plant when pinching.

Lateral branching in poinsettia production is induced by removing the plant apex by decapitation (pinching). The amount of apical tissue removed during pinching is often based on the number of nodes that must

be left on the primary plant to produce a desired number of lateral branches (Berghage et al, 1987; Ecke, 1985). The tissue removed during pinching can vary from the apical meristem plus a very small amount of stem tissue to the apical meristem plus several cm of subtending stem and leaf tissue.

Small rapidly expanding leaves have been implicated as the major source of correlative inhibition in dicotyledonous plants (Hillman, 1984). The major source of lateral shoot inhibition in beans was the second and third rapidly expanding trifoliate leaves (two to five cm in length) (White et al, 1975). Still larger immature leaves in addition to the meristem and small leaves have been implicated in lateral bud inhibition in the poinsettia (Weiss and Shillo, 1988). The objective of this study was to determine the implications of pinching technique on poinsettia lateral- shoot growth and plant morphology at anthesis.

#### Materials and Methods

Rooted poinsettia cuttings ('Annette Hegg Dark Red' and 'V-14 Glory') were planted in 15.2 cm diameter 1200 cm<sup>3</sup> plastic pots 28 Aug. 1986. Five plants of each cultivar were given one of four pinching treatments on 10 Sept. Pinching treatments were defined as soft (removal of the apical meristem plus stem and leaf tissue associated with leaves two cm or less in length), medium (removal of the apical meristem plus stem and leaf tissue associated with leaves up to seven cm in length) and hard (removal of the apical meristem plus stem and leaf tissue associated with all immature leaves). The fourth pinching treatment, leaf removal (LR), was a soft pinch as defined above plus removal of all immature

leaves but not the associated stem tissue. Soft, medium, and hard pinches resulted in ca. 0.5, 1.0 to 1.5, and 2.0 to 3.0 cm of terminal stem tissue removal, respectively (Fig. 1).

The experiment was repeated in 1987 with the following cultivars 'Annette Hegg Dark Red', 'Annette Hegg Brilliant Diamond', 'V-14 Glory', 'Noel', 'Noel Pink and White', 'Frost', 'Improved Rochford', 'Super Rochford', 'White Rochford', 'Regal Velvet' and one experimental cultivar H365 (Pan-American plant company Parrish, Fl. 33564). The medium pinching treatment used in 1986 was omitted in 1987. In 1987, cuttings were planted on 21 Aug. and pinched on 7 Sept.

Plants were grown in a glass greenhouse under natural daylength (42° N latitude) with temperature setpoints of 20°C / 20°C / 24°C (DT/NT/vent) in 1986 and 17°C / 23°C (DT/NT) in 1987. A nutrient solution with 18:1:5 mM N:P:K and 1 micromolar Mo was applied at each irrigation.

In 1986, the lateral shoot length of seven consecutive lateral shoots on each plant was determined every three to five days using a digital caliper. Shoot one was defined as the lateral branch subtended by the uppermost fully expanded leaf at the time of pinching. Shoots two through seven were the laterals subtended by the second through seventh fully expanded leaves (Fig. 1). Branching studies normally number shoots acropetally. In this study we have numbered basipetally from the first fully expanded leaf at pinching. This was done to allow comparison, between pinching treatments, of lateral branches subtended by leaves of similar physiological and developmental stage. Shoot growth was monitored for 30 days following the pinch. In 1987, lateral shoot length of all lateral shoots on 'Annette Hegg Dark Red' was determined weekly through

anthesis (77 days following pinch). Shoot numbering in 1987 was as described above for shoots one to (n) where n was the number of lateral shoots subtended by fully expanded leaves at pinching. Lateral shoots developing from nodes subtended by immature leaves at pinching (soft and LR-pinched plants) were designated basipetally by the letters a through e (Fig. 1).

Anthesis date, plant height (from the top of the pot to the top of the plant), plant width (the average of two measurements made from above the plant measuring at the widest point from leaf tip to leaf tip and then again at a right angle to the original measurement), total number of lateral shoots, and the number of inflorescences contributing to the bract canopy were recorded in 1987. An inflorescence was considered to contribute to the bract canopy display if more than an estimated 30% of the bract area was visible from above the plant and the cyathia were not more than six cm below the outer edge of the bract canopy. The outer edge of the bract canopy was defined as a rough hemisphere extending down from the top of the plant and encompassing the outer edge of the plant on all sides.

The experiments were conducted using a complete randomized design with five replications in 1986 and 10 replications in 1987. Statistical analysis of the 1986 shoot length data (30 days after pinching) and 1987 final plant measurements (collected at anthesis) was by analysis of variance. There was no significant shoot length interaction between pinching treatment and lateral shoot position for lateral shoots one to seven in 1986 or one to eight in 1987 so growth rate was analyzed across these lateral shoots on each plant. The growth rate data were analyzed

using a repeated measures model with BMDP 2V PC software.

#### Results

Growth of a lateral shoot during the first 30 days following pinching was influenced by pinching technique (the number of immature leaves left on the plant) and the position of the lateral shoot on the plant. Lateral shoot length of all soft and some medium-pinched plants (ca. five and two immature leaves left on the plant, respectively) was different than in hard or LR-pinched plants (no immature leaves left on the plant) (Table 1). There was no difference in lateral shoot length between hard and LR-pinched plants. Lateral shoots four and six of medium-pinched plants were shorter than the same shoots in hard or LRpinched plants, while lateral shoots one, two, three, five and seven were not.

Within a pinching treatment, the position of the lateral shoot on the primary stem influenced lateral shoot growth. Elongation of lateral shoots four, five, and six was reduced compared to lateral shoots one, and two in medium-pinched plants (Table 1). Although not statistically significant the trend of reduced lateral shoot growth of lateral shoots four, five, and six was also observed in soft-pinched plants and to a lesser extent in hard-pinched plants.

Plants which received a soft pinch had a significantly lower lateral shoot growth rate (average of shoots 1-8) from 20 to 35 days after pinching than plants given a hard or LR pinch (Fig. 2). The growth rates of lateral shoots on plants given a hard or LR pinch were statistically identical. Lateral shoot growth rate of soft-pinched plants increased slowly to a maximum of 0.3 cm day<sup>-1</sup> about 55 days after pinching while lateral shoot growth rate in hard or LR-pinched plants increased rapidly to a peak of about 0.45 cm day<sup>-1</sup> 35 days after pinching (Fig. 2). Lateral shoot growth rate of all plants was similar 40 to 80 days after the pinch.

Due to the initial slower growth rate of lateral shoots one to eight in soft pinched plants (Fig. 2), lateral shoots of these plants were generally shorter at anthesis than those of hard or LR- pinched plants (Table 2). There was no significant interaction between pinching treatment and lateral shoot position for lateral shoots one to eight. However, a significant interaction existed between shoot position a to e and soft vs. LR pinching treatments (lateral shoots a to e did not exist on hardpinched plants). Lateral shoot length increased as shoot position increased basipetally from position a to e in LR-pinched plants (Table 2). There was no significant difference in shoot length for shoots a through e in soft-pinched plants.

Primary stems in plants given a soft or LR pinch were longer at anthesis than plants given a hard pinch for all cultivars except 'Regal Velvet' and 'H365' (Table 3). The increase in primary stem length in soft and LR-pinched plants was due to elongation of the four to five apical internodes of the primary stem. These internodes were removed at pinching on the hard-pinched plants. Elongation of the four to five apical internodes was less in LR-pinched plants than in soft-pinched plants.

The differences in primary and lateral stem growth caused by pinching produced changes in the relationship between plant height and width at anthesis (Table 3). The ratio of height to width was greatest in the soft-pinched plants averaging (0.77) for the 11 cultivars,

intermediate in hard-pinched plants averaging (.68), and lowest in the LRpinched plants averaging (0.63). There was no statistical interaction between pinching treatments and cultivar.

The number of inflorescences contributing to the bract canopy display was influenced by pinching technique (Table 3). Averaged over all plants given a soft pinch; 48% of the primary stem nodes did not give rise to lateral inflorescences contributing to the bract canopy display. Twenty-seven percent and 31% of the potential inflorescences of hard and LR-pinched plants failed to contribute to the bract canopy display. While there were four to five more nodes on the primary stem of a soft-pinched plant than a hard-pinched plant, these additional nodes produced on average less than one additional inflorescence in the bract canopy display (Table 3). There were between two and three more inflorescences in the bract canopy display of LR-pinched plants than hard-pinched plants.

The influence of pinching treatment on time to anthesis was cultivar specific (Table 3). In general, anthesis was earliest in soft- pinched plants, occurring as much as 14 days earlier in LR-pinched 'V-14 Glory' plants. There were no significant differences in time to anthesis between hard-pinched and LR- pinched plants.

#### Discussion

There is no general consensus as to the mechanism(s) of apical dominance (Hillman, 1984; Martin, 1987). It is, however, generally agreed that the source of apical dominance is the terminal portion of the plant shoot and more specifically the very young leaves associated with the apex

(Hillman, 1984; Martin, 1987). The relative contribution of different plant tissues to apical dominance appears to be species specific. The contribution of larger immature leaves is negligible compared with the apical bud in the rose (Zieslin and Halevy, 1976). Larger immature leaves contribute to axillary bud inhibition in the poinsettia (Weiss and Shillo, 1988).

The mechanism by which the larger immature leaves in the poinsettia exert a major influence on apical dominance is unknown. The involvement of auxin content and transport has been suggested (Weiss and Shillo, 1988). Exogenous auxin applied to the petiole stub of excised poinsettia leaves resulted in suppression of lateral bud growth. The total endogenous auxin content in the young leaves of poinsettia was reported to be higher than that in the apical bud, however, the specific content of endogenous auxin was greater in the apical bud than in the leaves (Weiss and Shillo, 1988).

Another possible mechanism involves the water potential of lateral buds. Release of the cotyledonary bud in peas from apical dominance following decapitation has been shown to be correlated to a rapid change in the water potential of the cotyledonary bud (Cottignies and Jennane, 1988). The authors suggested that the thin vascular connections between the cotyledonary bud and the much larger main stem vascular system function as a "vacuum pump" maintaining a hydraulic deficit in the bud. This vacuum pump is broken when the plant is decapitated resulting in hydration of the cotyledonary bud (Cottignies and Jennane, 1988). In this model, the expanding immature leaves of the poinsettia would serve to maintain the integrity of the "vacuum pump" and hence the growth

restricting hydraulic deficit in the lateral buds would be retained in soft-pinched plants.

Ethylene has also been implicated as a factor contributing to the release of lateral buds from apical dominance. Restricted apical shoot growth mediated by ethylene has been suggested as a cause for release from apical dominance in <u>Phaseolus</u> (Hillman and Yang, 1979). In <u>Pharbitis</u>, mechanical perturbation (Prasad and Cline, 1985) or inversion of the apical growing region of the shoot (Prasad and Cline, 1986) result in a decrease in growth rate, the evolution of ethylene and subsequent release from apical dominance. It is likely that the LR pinching treatment in this study resulted in the formation of wound ethylene. However, since growth rates of lateral buds in LR-pinched plants was not different than those for hard-pinched plants it is unlikely that the difference in growth between LR and soft-pinched plants was due to wound ethylene associated with the LR pinching treatment.

The effect of lateral shoot position on lateral shoot growth observed in medium-pinched plants and to a lesser extent in soft-pinched plants supports the hypothesis that there is an interaction between lateral bud developmental stage and sensitivity to correlative inhibition (Cutter, 1975). It is also likely that stress in propagation results in reduced growth of some lateral buds (Grueber and Wilkins, 1988). Reduced growth of vegetative lateral buds originating from the middle nodes (four, five and six) of a nine node primary stem (numbered from the bottom) has been previously reported in the poinsettia (Grueber and Wilkins, 1988).

Light quality (red to far-red ratio) has also been shown to influence lateral bud activity. Exposing plants to light with a high red

to far-red ratio increases lateral bud activity and growth in tobacco, tomato, Chenopodium, and chrysanthemum (Kasperbauer, 1971: Tucker, 1975; Holmes and Smith, 1977; Heins and Wilkins, 1979). Shading unpinched poinsettia plants results in reduced lateral branching (Hagen and Moe, 1981). There is a high probability of lateral bud shading by large leaves left on the plant at pinching in plants which receive a soft or medium pinch. Shading by these large primary leaves could be expected to decrease the red to far-red light ratio under the canopy (Holmes and Smith, 1977). It is possible that the reduced growth observed in the middle lateral shoots (four, five and six) in soft-pinched and medium pinched plants compared with hard or LR-pinched plants was the result of reduced initial growth caused by correlative inhibition and shading by the large primary leaves.

The change in the pattern of growth which occurred 35 to 40 days after pinching (Fig. 2) corresponded approximately to the appearance of first bract color associated with reproductive development. We have observed that elongation of poinsettia internodes is greatly reduced in internodes subtended by colored leaves or bracts (unpublished data). It is not clear whether this reduction of internode elongation was linked with the development of bract color or cyathia development. However, the result was usually a growth rate curve skewed in favor of more rapid growth before bract color and cyathia development (i.e. hard and LRpinched plants). In contrast the growth rate curve observed in softpinched plants was skewed to the right (in favor of more rapid growth later in development) as might be expected due the delay in lateral shoot growth attributed to apical inhibition. The fact that the growth rate of

lateral shoots on the soft-pinched plants never reached the maximum growth rate of hard and LR-pinched plants was likely due to bract color and flower development. Thus the shape of the growth rate curves presented in figure 2 appear to be highly dependent on both the type of pinch used and the time of floral initiation.

Grueber and Wilkins (1988) observed that lateral shoot development in poinsettia is correlated with the size of the leaf subtending the lateral shoot. This correlation is possibly a reflection of the carbohydrate status of the developing shoot. A large vigorous leaf has the potential to supply more carbohydrates to an associated lateral shoot than a small less vigorous leaf. The young leaves left on the soft-pinched plants at pinching grew to a large size compared with leaves lower on the primary stem, and the lateral shoots which these leaves subtended grew more vigorously. In LR-pinched plants where subtending leaves were removed, growth of the upper two or three lateral shoots (a-c) was less vigorous (Table 2).

Short lateral shoots, increased vigor of the upper lateral shoots (a-e) and increased growth of the primary stem combined in soft- pinched plants to produce plants with vertical architecture and three to five dominant lateral shoots originating from the upper portion of the primary stem. LR-pinched plants had a more horizontal architecture with lateral shoots reaching a relatively uniform total height.

Pinching induced differences in plant architecture influenced the tendency for an inflorescence to develop beneath the bract canopy display. The taller primary stem in soft-pinched plants increased the vertical displacement between lower lateral shoots and the top of the plant. Lower

and middle lateral shoots (one to eight) did not elongate enough to consistently contribute to the bract canopy display of soft-pinched plants resulting in fewer inflorescences in the bract canopy display compared to LR- pinched plants. This was true for all the cultivars tested (Table 3). These results indicate that using a soft pinch to increase inflorescence number is ineffective unless immature leaves are removed.

The plant architecture and increased bract canopy display inflorescence number associated with the LR pinching technique made these plants aesthetically more pleasing than soft or hard-pinched plants. We know of several large poinsettia producers which are currently implementing this technique to improve final plant appearance.

Two explanations for earlier anthesis in soft-pinched plants can be proposed. Photosynthates contributed by the large leaves which developed from the immature leaves retained on the soft-pinched plants may have allowed faster development of the associated lateral shoots. Alternately, the young leaves in the poinsettia may act in flowering by increasing the sink strength of the apex, directing metabolites from the lower parts of the plant and promoting earlier flowering (Weiss and Shillo, 1988).

The results of these experiments indicate that not only the number of nodes left on the mother plant, but also the nature of the tissue left behind should be considered when pinching poinsettias. Removal of immature leaf blades promotes rapid uniform lateral shoot development and increased inflorescence number in the canopy. This can be achieved either through the use of a hard pinch or through a soft pinch with concomitant leaf blade removal.

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Figure. 1. Pinching treatments and lateral shoot position labels. Lateral shoot number one defined as the lateral shoot subtended by the uppermost fully expanded leaf at pinching. Shoots two through eight were the lateral shoots subtended by the second through the 8<sup>th</sup> fully expanded leaf at pinching. Pinching treatments were; soft (removal of the apical meristem plus stem and leaf tissue associated with leaves two cm or less in length); hard (removal of the apical meristem plus stem and leaf tissue associated with all immature leaves); and leaf removal (LR) (soft pinch as defined above plus removal of all immature leaves but not the associated stem tissue).



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Figure. 2. Effect of pinching technique on average lateral shoot growth rate of shoots one to eight (cm day<sup>-1</sup>), and analysis of variance for 'Annette Hegg Dark Red' in 1987, from pinching to anthesis. Lateral shoot number one defined as the lateral shoot subtended by the uppermost fully expanded leaf at pinching. Shoots two through eight were the lateral shoots subtended by the second through the 8<sup>th</sup> fully expanded leaf at pinching. Pinching treatments were; soft (removal of the apical meristem plus stem and leaf tissue associated with leaves two cm or less in length); hard (removal of the apical meristem plus stem and leaf tissue associated with all immature leaves); and leaf removal (LR) (soft pinch as defined above plus removal of all immature leaves but not the associated stem tissue).



Table 1. Effect of pinching technique on lateral shoot length (cm) of 'Annette Hegg Dark Red' 30 days after pinching in 1986. Lateral shoot number one defined as the lateral shoot subtended by the uppermost fully expanded leaf at pinching. Shoots two through seven were the lateral shoots subtended by the second through the 7<sup>th</sup> fully expanded leaf at pinching. Pinching treatments were; soft (removal of the apical meristem plus stem and leaf tissue associated with leaves two cm or less in length); medium (removal of the apical meristem plus stem and leaf tissue associated with leaves up to seven cm in length); hard (removal of the apical meristem plus stem and leaf tissue associated with all immature leaves); and leaf removal (LR) (soft pinch as defined above plus removal of all immature leaves but not the associated stem tissue).

Lateral shoot		Pinching	Treatment	
position	Soft	Medium	Hard	LR
1	5.8 <sup>z</sup>	8.3	8.5	8.2
2	5.1	8.4	9.8	9.2
3	4.5	7.7	9.5	8.7
4	3.0	4.3	7.8	9.8
5	2.8	4.2	7.3	6.9
6	3.3	4.8	8.1	8.6
7	5.9	10.5	10.3	10.5
Analysis of Variance				
Source	F			
Pinch type	12.9***			
Soft vs. medium pinch	15.8***			
Soft vs. hard pinch	46.5***			
Soft vs. LR pinch	53.8***			
Medium vs. hard pinch	8.3***			
Medium vs. LR pinch	10.1***			
Hard vs. LR pinch Error A	0.0(NS)			
Shoot position. Pinch*	5.2***			
Shoot position Error B	0.7(NS)			
LSD <sub>(.05)</sub>	3.2			

z Significantly different than hard and LR at the 5% level using single degree of freedom contrast.

\*\*\*,ns significance at 0.1%, not significant at 5% respectively

Table 2. Effect of pinching technique on lateral shoot length (cm) at anthesis of 'Annette Hegg Dark Red' in 1987. Lateral shoot number one defined as the lateral shoot subtended by the uppermost fully expanded leaf at pinching. Shoots two through eight were the lateral shoots subtended by the second through the  $8^{th}$  fully expanded leaf at pinching. Shoots a to e defined as lateral shoots subtended by immature leaves at pinching labeled basipetally from a (uppermost) to e. Pinching treatments were; soft (removal of the apical meristem plus stem and leaf tissue associated with leaves two cm or less in length); hard (removal of the apical meristem plus stem and leaf tissue of the apical meristem plus removal of the apical associated with all immature leaves); and leaf removal (LR) (soft pinch as defined above plus removal of all immature leaves but not the associated stem tissue).

Lateral shoot	Pi	inching treatme	<u>ent</u>	
position	Soft	Hard	LR	
a	13.8		8.8	
b	15.8		14.5	
С	15.6		17.4	
d	14.3		18.4	
е	15.4		20.6	
1	14.4	23.4	21.9	
2	14.3	22.3	21.8	
3	12.4	22.0	18.2	
4	11.7	19.2	16.1	
5	11.1	18.8	14.3	
6	12.3	18.1	18.3	
7	12.3	12.6	12.5	
8	18.4	16.3	18.7	
Analysis of Variance	Shoot	tsa-e	Shoots 1 - 8	
Source	F	:	F	
Pinching type Error A		.8(NS)	10.2***	
Shoot position Pinch *	21.	.8***	4.7***	
Shoot position Error B	8.	.6***	1.5(NS)	
LSD <sub>(.05)</sub>	2.	0	4.1	

\*\*\*, ns significance at 0.1%, and non significance at 5% respectively

Table 3. The effect of pinching technique on the number of days to anthesis, height to width ratio, primary shoot length, primary shoot node number, the number of inflorescences in the bract canopy display, and the % lateral shoots not contributing to the bract canopy display for poinsettia in 1987. Pinching treatments; soft (removal of the apical meristem plus stem and leaf tissue associated with leaves two cm or less in length); hard (removal of the apical meristem plus stem and leaf tissue associated with all immature leaves); and leaf removal (LR) (soft pinch as defined above plus removal of all immature leaves but not the associated stem tissue). Lateral shoots (%) not contributing to bract canopy display calculated as (average total nodes on primary stem average inflorescences in the bract canopy)/(average total nodes on the primary stem).

		Days from	Height to	Primary	Total nodes	Inflorescen	ces	X laterals not
	Pinch	pinch to	width	stem	on primary	in the		contributing to the
Cultivar	type	anthesis	ratio	length(cm)	stem	bract can	Удо	bract canopy
Annette Hegg	Soft	48	.85	19.9	F	13.5	6.3	53
Dark Red	Hard	51	.85	10.9		8.4	5.5	35
	LR	56	.74	16.7	-	13.6	8.2	40
Annette Hegg	Soft	48	62.	17.3	·	12.7	6.3	50
Brilliant	Hard	53	89.	10.4		7.5	5.7	24
	LR	54	.67	14.3	-	11.9	8.7	27
V-14	Soft	<b>%</b>	74	15.4	·	11.9	7.6	36
Glory	Hard	78	.59	6.9		7.4	6.3	15
	LR	80	.55	11.9		11.3	8.9	21
Super	Soft	48	.87	19.6	·	13.1	7.6	42
Rochford	Hard	53	Б.	11.7		8.2	6.8	17
	LR	52	.70	15.5	Ţ	13.2	8.2	38
Improved	Soft	52	.89	18.5	·	13.3	5.7	57
Rochford	Hard	58	٤.	11.0		8.0	5.4	32
	LR	58	.67	14.9		12.8	8.5	33
White	Soft	42	.82	17.4	Ţ	13.7	7.0	49
Rochford	Hard	45	٤.	10.6		8.3	6.8	18
	LR	48	.67	14.6		12.3	8.1	34
Noel	Soft	52	89.	12.1	·	12.2	8.0	34
	Hard	52	.55	7.5		7.7	6.8	12
	LR	58	.59	11.2	Ţ	12.7	9.3	27

Table 3.

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el	Soft	59	.74	12.8	12.8	7.4	74
nk and	Hard	60	.61	7.5	8.4	7.0	17
ite	LR	59	.59	9.9	11.8	10.3	13
ost	Soft	54	.65	14.8	14.6	7.6	48
	Hard	54	.63	8.7	9.4	5.4	42
	LR	54	.54	12.3	12.0	9.4	22
gal Velvet	Soft	55	52.	10.9	11.8	3.3	72
	Hard	61	.67	9.0	9.3	3.8	56
	LR	61	.59	9.6	11.5	4.3	62
365	Soft	51	.70	12.5	13.2	8.0	39
	Hard	76	<b>%</b>	9.0	9.6	7.2	33
	LR	50	.60	11.5	13.4	9.4	30
alysis of Va	riance						
urce		Ŀ	Ľ.	u.	u.	u.	
ltivar		<b>60.4**</b>	11.7***	42.5***	5.7***	10.6***	
nch		29.8***	35.4***	245.0***	352.0***	54.4***	
٩		3.1***	(SN)7.	3.0***	1.8*	1.0(NS)	
Error							
D, 01)		4.65	0.120	1.9	0.70	1.7	

\*,\*\*\*,ns significance at 5%, .1%, and nonsignificant at 5% respectively Statistics not presented on % laterals not contributing to the canopy since this column was derived from total nodes on the primary stem and inflorescences in the bract canopy

### SECTION II

# QUANTIFYING TEMPERATURE-DRIVEN LEAF UNFOLDING AND FLOWER DEVELOPMENT RATES IN THE POINSETTIA

Quantifying temperature-driven leaf unfolding and flower development rates in the poinsettia.

Robert D. Berghage and Royal D. Heins

## Department of Horticulture, Michigan State University, East Lansing, MI 48824.

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Abstract. Lateral shoot leaf unfolding and flower development rates were determined for poinsettia plants grown with 36 day and night temperature combinations ranging from 15 to 29C in 1986 and 21 day and night temperature combinations ranging from 15 to 24C in 1987. The rate of unfolding of the first three leaves on a lateral shoot following pinching was atypical of the rate of appearance of subsequent leaves on the lateral shoot. Leaf unfolding was therefore described using two functions; 1: The time (in days) from pinching to the appearance of the first three leaves (LAG) 2: The subsequent leaf unfolding rate (LUR). Both the LAG and LUR were temperature dependent with maxima at about 26C. A function with average daily temperature (ADT), day temperature  $(DT^2)$  and night temperature  $(NT^2)$  provided the best least squares model for LAG and LUR. The ratio the  $DT^2$  to  $NT^2$  model coefficients was similar to the ratio of day length to night length suggesting that there was no difference between the effect of day temperature and night temperature on LAG or LUR. Since day and night temperature had equal effects an hourly rate of hLAG or hLUR was estimated. The resulting function allows estimation of a daily leaf unfolding rate in a greenhouse with fluctuating temperatures. The number of leaves formed below the inflorescence and the time from the start of short days to visible bud were described as functions of leaf unfolding rates for plants grown with NT less than 26C. Flower development from visible bud to anthesis was influenced primarily by ADT for plants with NT less than 26C. Increasing ADT decreased time from visible bud to anthesis. Functions developed for LAG, LUR, leaf number, time to visible bud, and the time from visible bud to anthesis were combined to develop a two stage temperature-driven poinsettia development model based on leaf

unfolding rates before visible bud, and flower development rates from visible bud to anthesis.

The computer controlled greenhouse is rapidly becoming a reality in commercial pot plant production. Computer control not only provides a degree of environmental control which was unattainable 10 years ago, but also can be used to gather and interpret large quantities of information regarding past and present conditions in the greenhouse. To maximize the opportunities presented by this technology it is necessary to have a thorough understanding of generative and morphological responses of the plant to the environment.

In commercial poinsettia production plants are grown vegetatively for a period prior to flower initiation. The length of the vegetative growth period is generally determined by grower experiences with previous poinsettia crops. Flower initiation occurs either naturally near the end of September in the northern hemisphere, or is induced early by the grower providing artificial short day conditions. In either case growing temperatures are generally determined by previous experience rather than a quantitative understanding of the influence of temperature on plant development.

Leaf unfolding rates in many plant species increase as average temperature increases (Friend et al, 1962; Tollenaar et al, 1979; Karlsson et al, 1988; 1989). The relationship between leaf unfolding and average daily temperature was approximately linear for temperatures between 10 and 30C in the chrysanthemum (Karlsson et al, 1989) and the Easter lily (Karlsson et al, 1988). Since the Easter lily and the chrysanthemum are grown commercially within this temperature range a simple linear function can be used to predict leaf unfolding (Karlsson et al 1988). Although not reported in these studies, it is inevitable that at some point above 30C the rate of leaf unfolding will decline as the temperature optima is exceeded and high temperature stress is induced. Optimal temperatures for growth vary between and within species. For example, temperature optima ranging from about 25C to near 40C have been reported for different Chlorella species (Fogg, 1969) and in Arabadopsis, different races show differential growth responses above 30C (Langridge and Griffing, 1959).

Flower development from visible bud to anthesis also responds to ADT. The rate of flower development (1/Days to flower) increases as ADT increases. For example once the chilling requirement has been met, the daily average rate of development as a percentage increases as average temperature increases in Prunus (Werner et al, 1988). As with leaf unfolding the rate of flower development in response to temperature is curvilinear. Flowering occurs most rapidly when ADT is about 16 to 20C in the chrysanthemum with the optimum temperature dependant on both preceding and prevailing temperatures. (Karlsson et al, 1989). Flower development from visible bud to anthesis in the Easter lily was curvilinear in response to increasing temperature with an optimum at about 24 to 25C (Erwin personal communication).

Using developmental rate functions to monitor and control plant development has great potential for greenhouse application. Quantitative relationships between temperature and the rate of leaf unfolding (Karlsson et al, 1988) and leaf counting (Wilkins and Roberts, 1969) provide the basis for the prediction and control of the Easter lily development in commercial greenhouse. Developing similar relationships for the poinsettia would provide the ability to predict and control leaf number prior to flower initiation allowing the production of a more uniform and consistent crop from year to year. A leaf unfolding model for the poinsettia would also be useful in controlling time to visible bud after flower initiation has occurred. Combined with a model of development from visible bud to anthesis, these functions would provide the commercial poinsettia grower with a powerful production management tool. This study was undertaken to provide the quantitative information needed to develop a model of temperature-driven leaf unfolding and flower development rates in the poinsettia.

#### Materials and Methods

Rooted 'Annette Hegg Dark Red' cuttings were planted in  $1200 \text{ cm}^3$ plastic pots 28 Aug. 1986 and placed in a 23C constant temperature glass greenhouse. A nutrient solution with 18:1:8 mM N:P:K and 1  $\mu$ M Mo was applied at each irrigation. On 10 September 360 uniform plants were decapitated (pinched) to about 6 nodes and moved to glass greenhouses with temperature setpoints 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. About 30 minutes were required to move all the plants each morning and evening. Constant temperature treatment plants were moved from one location to another within the greenhouse. Two weeks after pinching any lateral shoots which had formed below the five uppermost lateral shoots were removed. Starting on 28 September, an opaque

blackout curtain was pulled at 1800 hr immediately after the plants were moved and retracted at 0800 hr before the plants were moved. The 14 hr artificial nyctoperiod was continued until the experiment was terminated on 15 December.

The number of leaves unfolded on the second lateral shoot below the pinch was recorded every three to four days. The date of first visible bud, and anthesis were recorded for each plant.

The experiment was repeated in 1987. Plants were potted on 21 August and pinched on 7 September. After pinching, plants were grown in a common greenhouse environment with constant temperature setpoints of 20C heat and 23C vent. Plants received night interruption lighting with  $10\mu$ mol m<sup>-2</sup>s<sup>-1</sup> PPF from incandescent lights from 2200 hr to 0200 hr each night to prevent flower initiation. Plants were moved to glass greenhouses with temperature setpoints of 14, 17, 20, and 23C on October 1. Plants were moved at 0800 and 1730 hr to provide 16 day and night temperature treatment combinations. An opaque blackout curtain was closed at 1800 hr immediately after plants were moved and retracted at 0800 hr prior to moving plants. Leaf number, the date of first visible bud, and anthesis were recorded as in 1986.

Since temperature treatments in 1987 did not begin until the start of short days, a companion experiment was conducted to provide additional information on leaf unfolding rates from pinching to the start of short days. Ten plants from the 1987 planting were placed in each of five greenhouses with temperature setpoints of 14, 17, 20, 23, and 26C immediately after pinching. These plants were not moved. Incandescent night interruption lighting was provided from 2200 hr to 0200 hr to

prevent flower initiation. Leaf number on the second lateral shoot below the pinch was recorded every three days from 7 to 29 September.

A second group of plants from the 1986 planting was used in an experiment to determine the minimum number of leaves which would unfold below the inflorescence in the poinsettia. Plants were placed under 10 hr photoperiods (0800 to 1800 hr) 0, 2, 4, 6, 8, 10, 12, or 14 long days after pinching. Plants were grown in a greenhouse with temperature setpoints of 20C DT and NT. Incandescent night interruption lighting from 2000 to 0200 hr was used to prevent flower initiation prior to the start of short days. The number of leaves unfolded below the inflorescence, date of first visible bud, and date of anthesis were recorded.

A leaf was recorded as unfolded when it was greater than one cm in length and had reflexed to at least 45° from the lateral shoot axis. The three bract leaves which form a whorl below the primary cyathium (Struckmeyer and Beck, 1960) were not counted as leaves in this study. Subsequent reference to leaves below the inflorescence refer only to leaves formed below this whorl of three bracts.

Due to the pattern of leaf unfolding observed in these experiments separate model functions were developed to describe: 1) the time from pinching to the appearance of the first three leaves (LAG), and 2) the subsequent leaf unfolding rate (LUR). LAG (in days) was determined from the leaf number data for each plant. LUR for each plant was estimated using a linear regression of leaf number vs time. The rates of leaf unfolding obtained from these linear regressions were used to estimate a multiple linear regression relating leaf unfolding rates to greenhouse temperature. Greenhouse temperatures were recorded with a datalogger linked to iron-constantan thermocouples. Two hour integrated averages of temperature measurements made at ten second intervals were used to determine average day and night temperatures for each greenhouse section. Actual average greenhouse temperatures were used in all regression analyses.

Regression and multiple linear regression were performed with Systat MGLH, and BMDP 9r (all possible subsets) and 2r (stepwise) regression subroutines. Selection of models was based on Mallows cp,  $R^2$ , F, partial F, and t of the coefficients. In cases where multiple models were found to be approximately equivalent based on these selection criteria, the simplest model was selected. For example in models where  $DT^2$  or  $NT^2$  were selected models with  $DT^3$  and  $NT^3$  provided an approximately equivalent description of the data. Analysis of variance on leaf number data was conducted using the BMDP 2v subroutine.

#### Results and Discussion

Leaf unfolding in the poinsettia followed a distinct pattern after pinching. There was a lag between pinching and the appearance of the first leaf with the next one to two leaves often appearing rapidly, and sometimes simultaneously. The rate of leaf unfolding slowed to a steady rate after these first three leaves had unfolded (Figure 1). This developmental pattern occurred in plants grown in all 52 greenhouse temperature combinations examined in 1986 and 1987. Because of this pattern separate regression functions were developed to describe; 1) the time (in days) from pinching to the appearance of the first three leaves (LAG); and 2) the subsequent leaf unfolding rate (LUR).

LAG was negatively correlated with temperature. As average temperature increased from about 18 to 29C LAG decreased about 7 days (Figure 2). In contrast to the chrysanthemum where leaf unfolding could be estimated with a linear function of ADT between 10 and 30C (Karlsson 1989), LAG to 3 leaves in the poinsettia was clearly curvilinear between 18 and 30C (Figure 2). LAG decreased rapidly as either DT or NT increased from 18 to about 23C, while from 26 to 29C little or no change in LAG was observed (Figure 2). This trend occurred as either DT or NT was increased, suggesting that the response to temperature was the same for both day and night temperature (Table 1). A least squares regression model with 3 terms ADT.  $DT^2$  and  $NT^2$  was selected to describe LAG. The coefficients for the squared DT and NT terms in the least squares model were 0.01989 for DT and 0.0280 for NT. The ratio between these coefficients corresponds almost exactly to the ratio of hours of DT to hours of NT in this experiment, 0.710 and 0.714 respectively. A regression model fitted with DT and NT weighted to the equivalent of 12 hours each had equal coefficients for  $DT^2$ and  $NT^2$ . This suggests that as reported for leaf unfolding in the chrysanthemum and the Easter lily (Karlsson et al, 1989;1988) day temperature and night temperature have equal and equivalent effects on LAG in the poinsettia. More simply stated, the rate of development of the first three leaves in the poinsettia is a response to the absolute magnitude of the prevailing temperature.

The reciprocal of the number of days required to unfold 3 leaves gives the rate per day for the unfolding of these first three leaves (rLAG)(Table 1). A base temperature of about 10C and a maximum rLAG of about 0.09 leaves per day at 28C were estimated based on extrapolations of this function.

The rate of leaf unfolding after the first three leaves (LUR) increased as either day temperature or night temperature increased (Table 2). The lowest average rate of leaf unfolding observed was 0.132 leaves per day with ADT 15.3C in 1987. The highest average rate of leaf unfolding observed was 0.245 with ADT 27.8 (DT 24.5 and NT 30.1C) in 1986. These rates are comparable to the rates reported for unpinched poinsettia plants by Zakkour (1989). With plants grown in growth chambers she found that the rate of leaf unfolding was about 0.16 leaves per day at 18C and about 0.23 leaves per day at 24C when PPF was 400 micromol  $m^{-2}s^{-1}$ . With higher light (800 micromol  $m^{-2}s^{-1}$  she reported slightly higher rates (0.17 and 0.26 leaves per day respectively). Karlsson (1989) in contrast found no effect of PPF on leaf unfolding rates with increased PPF reported by Zakkor (1989) may have been the result of increased leaf temperature of the plants with high light levels.

As with LAG, the best least squares regression model for LUR contained three terms ADT,  $DT^2$  and  $NT^2$ . Predicted leaf unfolding rates ranged from 0.13 leaves per day at 15C ADT to 0.22 leaves per day at 25C ADT (Figure 3a). The ratio between the coefficients for DT and NT was 0.66 and compared favorably with the 0.71 ratio between day length and night length (Table 2). It is likely that as observed with LAG, day and night temperature influence the rate of leaf unfolding equally and independently. The maximum predicted leaf unfolding rate occurs at a temperature of about 25C.

Extrapolating the function derived for leaf unfolding also provides an estimated base temperature of about 10C. Base temperatures of about 10C for mainstem leaf production have been experimentally estimated for a number of plant species including jimsonweed, velvetleaf, pigweed, cocklebur, soybean, peas and sunflower (Alm et al , 1988).

Experimentally estimated base temperatures are often used to develop degree day models to predict leaf development. Although temperature-driven leaf development rates have been generally found to be curvilinear, a simple linear response is usually used in model development (ALM et al, 1989). With a simple linear model, the thermal units (degree days) required per leaf is the reciprocal of the slope of the line relating the rate of leaf unfolding to average temperature. The number of leaves on a plant can then be estimated as the number of accumulated heat units (ADT the base temperature) divided by the heat units required per leaf. This approach is only adequate when temperatures are generally below the curvilinear portion of the temperature response curve. Leaf number will be over estimated at higher temperatures. Since greenhouse temperatures often exceed 25C when poinsettias are grown a linear degree day model would be inappropriate. Furthermore, since extrapolation beyond the data was required to estimate the base temperature, the precision of the estimate can not be assured. Since the estimated base temperature influences how fast thermal units are accumulated, small errors in base temperature estimation can result in large errors in predicted plant development over time (Arnold, 1959). For these reasons, curvilinear models were selected to describe leaf appearance in the poinsettia.

The total number of leaves unfolded below the inflorescence on the

second lateral shoot in 1986 was dependent on the day and night temperature treatments (Table 3). Leaf number increased as either day or night temperature increased. The differences in leaf number could be attributed to two factors. Flower initiation was delayed or prevented in plants with night temperature setpoints of 26 or 29C. Plants grown with a 29C DT and NT failed to produce flower buds and continued to unfold leaves throughout the experiment. Plants grown with a 29C NT and DT from 14 to 26C produced flower buds which failed to develop to anthesis, and plants grown with NT in excess of 25C never developed normal bracts or pigmentation.

Regardless of day temperature, plants in this study grown with night temperature below 25C developed flower buds and bracts suggesting that the delay or prevention of flowering by high temperature was more strongly related to the night temperature than the day temperature. Delay of flower initiation by high night temperatures (Langhans and Miller 1963), high constant temperatures (Larson and Langhans, 1963) or by the relationship between day and night temperatures (Kristoffersen, 1969) have been reported. In this study night temperature had a dominant effect on flower initiation. Day temperature also had an effect although it was much smaller. The lack of a large flower initiation response to the relationship between day and night temperature in this study may have been due to the short (10 hr) photoperiod used. With shorter photoperiods sensitivity of poinsettia flower initiation to temperature is reduced (Kristoffersen, 1969).

The second factor causing increased leaf number with increased temperature setpoint was the effect of temperature on LAG and LUR before

flower initiation. Plants with warmer temperatures had more leaves unfolded before flower initiation and hence had more total leaves below the inflorescence.

In 1987 were temperature treatments and short days were started concurrently, and where night temperatures did not exceed 23C, plants grown at 23C unfolded about one more leaf after the start of short days than plants grown at 15C (Table 3). The predicted LUR for 23C and 15C were 0.216 and 0.113 respectively. At 23C, 4.5 days were predicted to be required to form one leaf while at 15C nine days were predicted. Thus if flower initiation for both plants required about nine days to be completed one more leaf would be expected on plants grown with 23 than 15C simply as a result of increased LUR at higher temperatures.

Struckmeyer and Beck (1960) reported that primary cyathium formation would occur with eight or less short days with the cultivar 'Ruth Ecke'. While as few as five to as many as 20 inductive photoperiod cycles were required for primary cyathia formation in 'Annette Hegg' poinsettias (Christensen, 1975). The reported differences in the number of short days needed to produce a primary cyathium may in part due to the dependence of poinsettia flower initiation on both temperature and photoperiod (Larson and Langhans, 1963; Kristofferssen, 1969; Grueber, 1985). Goddard (1961) observed that poinsettia plants grown in 1959 changed from vegetative development directly to reproductive development seven days after the start of short days, while in 1958 a transition period of up to two weeks occurred prior to microscopically observable primary cyathium development. Goddard attributed these differences to shorter photoperiods and warmer night temperatures in 1959. Microscopic visible bud formation was also reported in 12 to 24 days, depending on the temperature and photoperiod for 'Barbara Ecke Supreme' (Larson and Langhans, 1961). It is, in any case, important to note as emphasized by, Langhans and Miller (1960), that the appearance of a visible flower bud represents not only flower initiation but also early flower development. The increase in leaf number observed with increasing temperature in 1987 can therefore be explained simply as the result of the development of additional leaf primordia predicted by increased LUR at warmer temperatures given nine or more days from the start of short days to the differentiation of the primary cyathium.

Poinsettia plants grown in 1987 developed 6.4 to 7.7 leaves below the whorl of three leaves subtending the primary cyathium after the start of short days (Table 4). This is in general agreement with previously reported leaf numbers. Kofranik and Hacket (1965) found 10-11 microscopic leaves and 7 to 8 macroscopic leaves on single stem 'Paul Mikkelsson' poinsettias at the start of short day treatments, and about 20 leaves below the inflorescence at visible bud. They included in this number the three bracts found immediately below the primary cyathium. Thus, about nine leaves (not counting the whorl of three immediately subtending the primary ciathium) unfolded on these plants from the start of short days until visible bud. Shanks (1969) and Christensen (1975) both reported an average of seven to eight microscopic leaves in the poinsettia apical bud. With four to five fully expanded leaves at the start of short days, single stem 'Annette Hegg' poinsettias developed 16 leaves below the inflorescence including the whorl of three below the primary cyathium (Christensen, 1975). Assuming that two to three of the nine macroscopic

leaves reported by Christensen were immature but unfolded (by the definition used in this study) then six to seven leaves below the three subtending the primary cyathium would have unfolded after the start of short days.

If about eight leaf primordia are present in the vegetative poinsettia bud (Shanks, 1969; Christensen, 1975) then the minimum number of leaves which must unfold (excluding the uppermost three) would be about five. Poinsettia plants pinched and placed immediately under short days developed an average of 5.3 leaves (Table 5).

Based on the above discussion, an estimate of the number of days required to complete flower initiation was calculated by subtracting five from the number of leaves formed after the start of short days and dividing this result by the predicted leaf unfolding rate. An average of 11 days (range of seven to 14) from the start of short days to the completion of flower initiation (cassation of leaf unfolding) was calculated for plants in the 1987 experiment. This predicted time for primary cyathium differentiation is in agreement with previous estimates obtained by morphological examinations of the apical bud (Larson and Langhans, 1963a; 1963b; Goddard, 1959; Christensen 1975).

Final leaf number on a flowering poinsettia lateral shoot can then be estimated as; the leaf number at the start of short days plus five, plus the predicted number of leaves which would unfold in the time required to complete flower initiation. Based on this method of estimation the start of flower initiation of plants grown in the 1986 experiment occurred about September 24 for plants with day and night temperatures below  $26^{\circ}C$  (Table 4). This date is within the range of dates for natural

flower initiation reported in the literature (Kiplinger, 1955; Gartner and McIntyre, 1957).

Since visible bud should occur when all the leaves below the bud have unfolded, it should be possible to predict the time from the start of short days to visible bud based on the number of leaves unfolded after the start of short days, and the leaf unfolding rate. The predicted date of visible bud was consistantly greater than the observed visible bud date when this was attempted. Examination of the leaf number data on the visible bud date for each plant indicated that the reason for this overestimation was that the last leaf was not unfolded (by the definition used in this study) at the visible bud date. Subtracting one from the estimated leaf number left to unfold after the start of short days resulted in close agreement ( $R^2 = 0.96$ ) between predicted and observed visible bud dates (Table 6).

The time to visible bud was not influenced by the number of long days before the start of short days (Table 5). This concurs with data reported by Gartner and McIntyre (1957) where bud set was delayed by about the same number of days as was the start of short days. While the same number of days were required to reach visible bud in plants given from 0 to 14 long days, final leaf number in these plants varied from 5.3 to 10.1. Plants given less than 8 long days at  $20^{\circ}$ C had no leaves unfolded at the start of short days, however final leaf number increased from 5.3 to 8.8 (Table 5). The three leaf stage was reached after about 12 to 14 long days. With plants which had unfolded one or more leaves (eight or more long days prior to the start of short days) predicted visible bud dates (based on actual leaf number unfolded after the start of short days) were

in close agreement with the recorded visible bud dates. Visible bud date was however, underestimated in plants given less than 8 long days before the start of short days. This indicates that either rLAG, LUR or both were decreased in plants placed under short days before the first leaf had unfolded. Therefore, the functional relationships between LUR, final leaf number and visible bud outlined in this report are only valid after the first leaf has appeared. The functions can still be used to predict visible bud date where no leaves have unfolded before the start of short days however, final leaf number will be overestimated.

Time from visible bud to anthesis was also influenced by temperature. Fewer plants given low temperatures (14 and 17C) or high night temperatures (26 and 29C) reached anthesis than those receiving more moderate temperatures (Table 7). This is not surprising since low temperature delays flower development (Langhans and Miller, 1960) and high night temperatures delay flowering through delayed flower initiation (Langhans and Miller, 1960; Larson and Langhans 1963; Kristoffersen 1975). None of the plants receiving a 29C night temperature, 14C constant temperature, or 14 DT and 17C NT reached anthesis in the course of this experiment (Table 7).

Time from visible bud to flower was not equally dependent on day and night temperature. With high night temperatures (26C in 1986 and 23C in 1987) day temperature had no effect on time from visible bud to anthesis. It is not possible to determine from these experiments whether the observed high temperature delays in time from visible bud to anthesis were a response to preceding or prevailing temperatures. Therefore to avoid potential complications with known effects of high temperatures on

flower initiation, plants grown with temperatures in excess of 25C in 1986 and 22C in 1987 were excluded from further analysis.

The number of days from visible bud to anthesis ranged from in excess of 40 with cool temperatures (18C DT and 15C NT to about 20 days with 26C DT and 24C NT. With the cultivar 'Barbara Ecke Supreme' Gartner and McIntyre (1959) reported about 40 days from visible bud to anthesis with a 15C NT and about 35 days at 21C NT (no DT was reported). The number of days from short days to anthesis was reported for various temperatures from 15C to 21C with the cultivar 'Paul Mikkelsen'. Time to anthesis ranged from 53 days at 21C to 74 days with 15C DT and 18C NT (Kristoffersen, 1969). This compares with 73 days for plants grown with 17C DT and NT and 55 days for plants grown in greenhouses with 23C DT and 20C NT setpoints in 1987.

A regression model with two terms, ADT and  $ADT^2$  provided the best description of the number of days from visible bud to anthesis (Table 7). This function was nearly linear, and in fact the  $ADT^2$  model term was not significant for a regression of the rate of development (1/days from visible bud to anthesis). Since temperature control is not generally a problem late in poinsettia development in northern latitudes (from visible bud to flower), a simple linear model was selected to predict the rate of flower development.

The predicted number of days from visible bud to anthesis approached a maximum at about 25C. That all three temperature-driven developmental rate functions developed for the poinsettia in this study provide an estimated maximum rate at about 25C suggests that there is a common underlying physiological basis for this optimum in the poinsettia. The predicted base temperature for flower development from visible bud to anthesis was about 12.5C using the quadratic function. Since many of the plants grown at cooler temperatures did not reach anthesis during the course of this experiment, this estimated base temperature is uncertain. However higher base temperatures for flower development than for leaf unfolding have been reported (ALM, 1989).

A two stage developmental model for the poinsettia can be constructed using the functions reported in this study. The first stage is the vegetative growth stage. Development in this stage is open ended up to the development of 30 leaves. This stage terminates naturally at about 30 leaves because the poinsettia will develop primary cyathia (split) under long day conditions after about 30 leaves have unfolded (Christensen, 1975). The vegetative stage of poinsettia development is described by the leaf number, and leaf number is in turn estimated with two functions one for LAG and a second for subsequent LUR.

The second stage represents reproductive development. This stage is characterized by the time from the start of short days to visible bud and the time from visible bud to anthesis. The time from the start of short days to visible bud is estimated as a function of LUR while the time from visible bud to anthesis is estimated with a separate function.

Two approaches which differ in the time period used for integration of the rate functions can be used in applying these functions to describing temperature-driven development in the poinsettia. The first is a daily approach using observed average day temperature and observed average night temperature with the derived functions. No alteration of the functions is required for a 10 hour day and 14 hour night. If different

day and night lengths are desired the function can be modified as follows:

1. LAG= -.099+.0123((ADL(DT))+(ANL(NT))/24)-.000085(ADL/10)DT-.000118(ANL/14)NT

2. LUR= -.347+.046((ADL(DT))+(ANL(NT))/24)-.000373(ADL/10)DT-.000564(ANL/14)NT

3. rVBtoA = -.0177+.002577(ADT) (for NT<24 and DT<30°C)

Where ADL = Actual day length ANL = Actual night length

Modification of the LAG and LUR functions for various day lengths is possible assuming the relative influence of DT or NT is a function of the day length or the night length respectively. Changing the daylength changes the shape of the temperature response surface for both LAG and LUR. At equal day and night lengths the LUR temperature response surface is concentric around the optimum (Figure 3a). The surface is stretched along the DT axis (Figure 3b) with shorter days than nights, and with longer nights than days, the surface is stretched along the NT axis (Figure 3c). The relative position of the optimum is determined by the ratio between the  $DT^2$  and  $NT^2$  coefficients in the model. Since the ratio of the predicted coefficients was slightly less than the ratio of day length to night length the optimum is shifted to a higher DT than NT. If the effects of DT and NT are presumed to be equal, the center of the

optimum range would be shifted to 25C DT and NT (Figure 3d).

The presumtion of equal DT and NT effects makes possible a modification of the model rate functions to provide an estimate of hourly rates of development. For the LAG and LUR functions the DT and NT coefficients are combined to provide average temperature functions. The average temperature functions when divided by 24 provide an estimated hourly developmental rate. Integrated over a 24 hour period the hourly rates give a daily rates for each of the developmental rate functions.

Daily rates calculated from hourly rate functions are:

4. 
$$rLAG = \sum_{24}^{h=1} (52.1-2.797T_h + .0479T_h^2)/24$$

5. LUR = 
$$\sum_{24}^{h=1} (-.347+.046T_{h}-.000837T_{h}^{2})/24$$

h-1

6. rVBtoA = 
$$\Sigma_{2}^{(n-1)}$$
 .0177+.002577T<sub>h</sub> (for NT<24 and DT<30°C)  
24

Where  $T_{h}$  = the average temperature for hour (h)

The development of a poinsettia is then estimated using functions 1 to 3 or 4 to 6 as follows.

Leaf number is estimated by;

7. 
$$LAG_{index} = \int_{rLAG(x)dx}^{d}$$

for LAG<sub>index</sub> < 1  
Leaf 
$$\# = 0$$
  
8. for LAG<sub>index</sub> > 1 and leaf  $\# < N$   
Leaf  $\# = 3 + \int_{d}^{d} LUR(x) dx d_{LAG}$   
For leaf  $\# > N$   
Leaf  $\# = 3 + \int_{d}^{d} LUR(x) dx d_{LAG}$   
For leaf  $\# > N$   
Leaf  $\# = N$   
Where d = The number of days following pinching.  
d\_{LAG} = The day of the end of the LAG (i.e. LAG<sub>index</sub> = 1).  
N = The number of leaves formed on the lateral  
shoot below the inflorescence. This is given as 30  
if plants are maintained under long days or is  
calculated by the flower induction transition  
calculation given below.  
Reproductive development is predicted as follows:  
Transition to flowering (estimating N):  
9. For SD=1 to I  
N = 5 +  $\int_{d}^{d} LUR(x) dx d_{SD}$   
Where SD = The number of days from the start of shortdays.  
I = The number of days from the start of short days.  
I = The number of days from the start of short days.  
I = The number of lays from the start of short days.  
I = The number of lays from the start of short days.  
I = The number of lays from the start of short days.  
I = The start of short days  
Start of short days to visible bud:  
10. For SD > I  
and VB<sub>index</sub> < 1  
H. Leaf  $\#_{SD} = \int_{d,UR}^{d} (x) dx d_{SD}$ 

11.

Where Leaf  ${\rm \#}_{\rm SD}$  = The number of leaves unfolded after the Start of short days.
Visible bud to anthesis: For VB. > 1

12.

$$A_{index} = \begin{cases} d \\ frVBtoA(x)dx \\ d_{vB} \end{cases}$$

Where  $d_{vB}$  = The predicted visible bud day.

Visible bud is predicted to occur when  $VB_{index} = 1$  and anthesis is predicted to occur when  $A_{index} = 1$ .

These functions are assembled to form a poinsettia development model shown in figure 4. The time unit used for overall integration in this model is one day, however the individual rate functions can be integrated at a more rapid rate (one hour) within the general structure if this is desired.

The use of the hourly integrated rate functions rather than daily rate functions hold the promise of allowing more accurate prediction of daily rates of plant development where temperature fluctuates above and below the developmental optimum. This is often the case in greenhouses in the summer where it is not uncommon for temperatures to exceed 30°C for several hours on a hot sunny day.

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Nigh	t		0	ay temp	erature			
temp setp	erature oint	14	17	Setp 20	oint 23	26	29	AVT
14	1986 1987	17.0 19.4	16.9	16.3	14.7	15.2	14.3	17.3 18.3
17	1986 1987	15.7	16.6 15.1	15.3	15.1	13.9	14.6	19.0 19.3
20	1986 1987	15.0	15.0	14.5 12.8	14.3	13.9	12.8	21.2 21.9
23	1986 1987	14.0	14.0	12.7	13.0 11.8	12.8	15.0	24.0 23.6
26	1986 1987	13.4	13.3	12.4	11.9	12.0 10.4	12.2	26.6 27.7
29	1986	13.7	12.6	12.2	12.0	11.9	12.1	29.5
AVT	1986 1987	19.0 18.3	20.1 19.3	21.7 21.9	24.5 23.6	26.7 27.7	30.1	
Regr	ession An	alysis			rlA	6 to 3	leaves (1	/1 46)
Vari Cons ADT DT <sup>2</sup> NT <sup>2</sup>	able tant	Coefficie 52.1 ** -2.797 ** 0.0199 ** 0.0280 **	ent ** ** **		Var Con ADT DT <sup>2</sup> NT <sup>2</sup>	iable stant	Coeffi -0.098 0.0123 -0.00008 -0.00011	cient 9 *** 2 *** 5 *** 8 ***
Raw N R <sup>2</sup> .! F	data 397 571 ***	Means 41 .809 ***			Raw N R <sup>2</sup> F	Data 397 .551 ***	Mea .7 *	ns 41 87 **

Table 1. Number of days from pinching to the appearance of the third leaf in <code>`Annette Hegg Dark Red'</code> poinsettias on the second lateral shoot below the pinch. Average greenhouse day and night temperatures (AVT) are presented as well as the greenhouse setpoint temperatures.

\*\*\* Significance at .01 (t for coefficients or F for regressions)

Table 2. Average leaf unfolding rate in 1986 and 1987 for `Annette Hegg Dark Red'. Rates were determined for each plant (10 replications per treatment) by regressing leaf number with time.  $R^2$  for individual regressions varied from .8 to .99. Actual average greenhouse temperatures (AVT) are given for the average time from the appearance of the third leaf to visible bud or the termination of the experiment, whichever came first.

Nigh	t erature			Day ter	nperatur	е		
setp	pint	14	17	20	23	26	29	AVT
14	1986 1987	0.141 0.132	0.178 0.155	0.163 0.160	0.171 0.169	0.214	0.166	16.2 14.8
17	1986 1987	0.161 0.148	0.197 0.172	0.202 0.174	0.220 0.195	0.205	0.202	19.0 16.8
20	1986 1987	0.194 0.181	0.187 0.189	0.209 0.211	0.199 0.197	0.225	0.180	21.2 19.5
23	1986 1987	0.207 0.188	0.203 0.200	0.201 0.196	0.229 0.209	0.218	0.245	24.5 22.8
26	1986	0.207	0.191	0.192	0.205	0.214	0.205	26.7
29	1986	0.181	0.177	0.181	0.190	0.208	0.234	29.5
AVT	1986 1987	16.7 16.0	19.5 18.0	21.7 20.0	24.5 22.3	26.7	30.1	
Regri Vari Cons ADT DT <sup>2</sup> NT <sup>2</sup>	ession a able tant	nalysis Coefficie -0.3472 0.0460 -0.000373 -0.000564	ent *** *** ***		1			
Raw I N 6 R <sup>2</sup> . 4 F	Data 41 420 ***		Means N 52 R <sup>2</sup> .711 F ***					

Nigh	t erature			Day	tempera Setpoin	ture t		
setp	oint	14	17	20	23	26	29	AVT
14	1986 1987	7.0 10.6	8.7 11.2	7.8 11.0	8.6 11.4	9.7	10.0	16.2 14.8
17	1986 1987	7.9 11.1	8.4 11.0	8.4 10.9	9.6 11.8	10.1	10.1	19.0 16.8
20	1986 1987	8.0 11.2	8.2 10.6	8.9 11.6	9.0 11.9	10.3	10.6	21.2 19.5
23	1986 1987	9.8 10.9	10.0 11.3	9.9 11.7	10.7 11.6	10.7	10.6	24.5 22.8
26	1986	11.0	10.7	11.1	11.2	11.1	11.7	26.7
29	1986	11.8	11.7	13.1	14.9	16.3	18.4	29.5
AVT	1986 1987	16.7 16.0	19.5 18.0	21.7 20.0	24.5 22.3	26.7	30.1	
Ana1 1986	ysis of v Data	ariance			198	7 Data		
Sour	ce	F			Sou	rce	F	
NT DT*N	т	***			NT DT*I	NT	NS NS	

Table 3. Average lateral shoot leaf number of the second lateral shoot below the pinch of 'Annette Hegg Dark Red' poinsettias grown with greenhouse temperatures between 15 and 30°C in 1986. Plants were pinched 9/10 and a 14 hour nyctoperiod was maintained from 9/28 to 12/15.

\*\*\*,\*\* significance at .001 and .01 respectively.

Table 4. Observed and predicted number of leaves formed after the start of short days in 1987, and after 9/24 in 1986 on the second lateral shoot below the pinch in poinsettia. The whorl of three leaves directly below the primary cyathium are not included. Plants received night interruption lighting from 2000 to 0200 hr from incandescent lights until 10/1 when blackcloth was pulled at 0800 and 1800 to provide a 10 hr photoperiod. In 1986 plants were under natural photoperiods (42° N Latitude) until 9/28 when blackcloth was pulled at 0800 and 1800 to provide a 10 hr photoperiod.

Nigh	t erature			Day tem Set	peratur point	е		
setp	oint	14	17	20	23	26	29	AVT
14	1986 1987	6.1 6.4	7.7 6.7	6.4 7.3	6.5 7.1	7.7	8.0	16.2 14.8
17	1986 1987	6.0 6.6	7.3 7.0	6.4 6.7	7.2 7.6	7.7	7.6	19.0 16.8
20	1986 1987	5.8 6.8	6.2 6.4	6.8 7.7	6.2 7.3	7.7	7.7	21.2 19.5
23	1986 1987	7.4 6.8	7.1 7.2	6.9 7.5	7.4 7.4	7.6	7.4	24.5 22.8
26	1986	8.1	7.7	7.7	7.6	7.5	8.0	26.7
29	1986	8.8	8.6	9.3	11.1	12.3	14.3	29.5
AVT	1986 1987	16.7 16.0	19.5 18.0	21.7 20.0	24.5 22.3	26.7	30.1	
Anal	ysis of v	ariance			109	7 Data		
Sour	ce	F			Sou	rce	F	
DT		***			DT		*** NC	
DT*N	т	***			DT*	NT	NS	

\*\*\*,NS significance at .001 and not significant at .05 respectively.

Table 5. Number of leaves and number of days from the start of short days to visible bud in `Annette Hegg Dark Red' poinsettias pinched and given 0,2,4,6,8,10,12 or 14 long days prior to placing under 10 hr photoperiod with blackcloth pulled at 0800 and 1800 hr in 1986. Plants were grown in a greenhouse with temperature setpoints of 20°C for both day and night.

Number of									
long days	0	2	4	6	8	10	12	14	
after pinching									
Lateral shoot									
Leaf number	5.3	6.6	7.0	7.8	8.8	8.5	9.6	10.1	
Number of days									
to visible bud	32.7	32.2	31.1	33.0	31.2	33.3	32.1	30.7	
Analysis of vari	ance								
Variable		F							
Leaf number		***							
Days to VB		NS							

\*\*\*,NS Significance at .001 and nonsignificant at .05 respectively.

Table 6. Observed and predicted number of days from the start of short days to visible bud in `Annette Hegg Dark Red' grown with 16 day and night temperature combinations in 1987.

Nigh temp	t erature		Day t se	emperatu tpoint	re	
setp	oint	14	17	20	23	AVT
14	observed	45.8	38.7	38.1	34.6	14.8
	predicted	40.0	37.5	35.9	34.7	
17	observed	39.1	35.0	34.6	31.4	16.8
	predicted	36.7	34.7	33.4	32.4	
20	observed	34.2	32.1	30.0	29.2	19.5
	predicted	34.1	32.5	31.4	30.6	
23	observed	33.9	30.2	31.7	30.3	22.8
	predicted	32.9	31.4	30.4	29.7	
AVT		16.0	18.0	20.0	22.3	

Correlation Coefficient (Observed vs. Predicted) = .96

Predicted leaves left to unfold after the start of short days determined as follows:

Leaves = ((LUR)(I)+C))/LUR

- Where I = The number of days between the start of short days and the completion of flower initiation (estimated to be 11).
  - LUR = The predicted leaf unfolding rate based on the day and night temperatures.
    - C = A constant (4:(8-3-1)determined by the number of microscopic leaves in the bud less four, since the last three leaves which form a whorl beneath the primary ciathium were not counted and the bud becomes visible before the last counted leaf unfolded by the definition used in this study.

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No.  1986	setpoint	aJu	14	17	50 70	23 23	26	29	AVT
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	4	1986 1987	(0) (0)	40.0 (2) 46.0 (2)	37.6 (7) 37.4 (6)	33.8 (6) 30.0 (10)	25.8 (10)	24.6 (10)	15.6 15.1
20  198  34.1  (9)  31.2  (10)  29.4  (10)  27.8  (10)  27.8  (10)  27.0  (10)  27.0  (10)  27.0  (10)  27.0  (10)  27.0  (10)  27.0  (10)  27.0  (10)  27.0  (10)  27.0  (10)  27.0  (10)  27.0  (10)  27.0  (10)  27.0  (10)  27.0  20.	17	1986 1987	39.2 (7) (0)	33.4 (9) 38.4 (6)	32.1 (10) 32.6 (10)	29.6 (10) 27.2 (10)	22.8 (10)	23.4 (10)	19.1
23  1986  23.0 (10)  25.4 (10)  25.1 (10)  22.6 (9)  20.0    26  1986  28.1 (10)  26.1 (10)  26.1 (10)  26.4 (9)  28.0    26  1986  28.2 (7)  26.6 (8)  28.4 (10)  28.4 (10)  28.5    29  1986  (0)  (0)  (0)  (0)  (0)  (0)    AVI  1966  (0)	20	1986 1987	34.1 (9) 36.2 (10)	31.2 (10) 30.0 (10)	29.4 (10) 28.6 (10)	27.8 (10) 24.4 (10)	22.0 (10)	23.1 (10)	21.4
26  198  29.2  (7)  28.6  (8)  28.6  (7)  28.4  (6)  28.5    29  1966   (0)   (0)   (0)   (1)   (1)  28.4  (5)  28.5  28.5    AVT  1986  15.7  19.2  21.4  24.5  26.7  26.7    Mor  1986  15.7  19.0  20.2  21.4  24.5  26.7    Regression Analysis  19.2  20.2  20.2  21.4  24.5  26.7    Regression Analysis  0.2  30.2  20.2  21.4  24.5  26.7    Regression Analysis  0.2  30.2  20.2  21.4  20.7  24.7    Regression Analysis  0.3  30.2  30.2  30.2  30.2  30.7  30.7    Regression Analysis  0.3  30.2  30.2  30.2  30.2  30.2  30.2  30.2  30.2  30.2	23	1986 1987	28.0 (10) 28.0 (10)	25.4 (10) 29.1 (10)	25.1 (10) 26.1 (10)	22.6 (9) 29.3 (10)	20.0 (10)	20.2 (10)	24.4
29  1986  (0)	26	1986	28.2 (7)	26.6 (8)	28.8 (7)	28.4 (6)	28.5 (9)	25.0 (3)	26.7
MI  1966  15.5  19.2  21.4  24.5  26.7    Represention Analysis  15.7  18.0  20.2  22.7  24.5  26.7    Days from Visible bol to Anthesis  16.0  20.2  21.4  24.5  26.7    Days from Visible bol to Anthesis  6.0  20.2  20.2  21.4  20.6    Orielable  Contraction  -9.55  -0.0  25.4  0.0  10.1    Dir  0.172  0.1722  0.1722  0.0  20.7  20.7  20.7  20.7    Model  0.1722  0.1722  0.1722  0.1722  0.1  0.1  20.6  20.7	59	1986	(0)	(0)	(0)	(0)	(0)	(0)	29.5
Regression Analysis Regression Analysis Coronality of Confriction Confriction (Crothen Constant 953, 001 001 0.1722 0.1722 001 84 data 86 data 86 data 86 data 61 data 2012 0.1722 0.1722 001 84 data 33 data 86 data 30 data 202 84 272 85 35 86 data 86 data 202 86 272 85 35 86 data 86 data 202 86 272 85 86 data 86 data 202 86 272 86 data 86 data 202 86 273 86 data 202 87 273 86 data 202 87 273 86 data 202 86 273 86 data 202 87 273 86 data 202 87 273 86 data 202 86 273 86 data 202 87 273 86 data 202 87 273 86 data 202 87 273 87 273 87 273 87 273 87 273 87 273 88 data 202 87 273	AVT	1986	15.5 15.7	19.2 18.0	21.4 20.2	24.5 22.7	26.7	29.5	
Construction  Coefficient  Variable    Constant  19.0,5  Constant  Variable    Constant  19.0,5  Constant  Variable    Constant  19.0,5  Constant  Variable    Op12  0,1722  9.1722  An    Add  data  Maximum  Maximum    Rev data  Maximum  Maximum  Zd2    Rev data  Maximum  Zd2  Maximum    Rev data  Maximum  Zd2  Maximum    Rev data  Maximum  Zd2  Maximum  Zd2    Rev data  Maximum  Zd2  Maximum  Zd2    Rev data  Maximum  Zd2  Maximum  Zd2	Regressi Days fro	on Analysis m Visible bud t	to Anthesis			Rate	of development f	rom visible bud to	anthesis
Constant 130.2 Constant 130.2 Constant 0.012 0.1722 ••• 0.1722 ••• 0.1722 ••• 0.1722 ••• 0.1722 ••• 0.1 Constant 0.1 Const	Variable			Coefficient		Vari	able	Coeffic	cient
Ruu 2013 Montos Ruu 2013 3 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	Constant ADT ADT <sup>2</sup>			-9.534 *** 0.1752 ***		ADT	1 and 1	.0025	***
	Raw data N2 262 R <sup>2</sup> .742 F ***			Means 33 .850		R N R A	data 262 .753	Means 33 .861	

\*\*\* significance at .001 for F for regressions and t for individual coefficients.



Figure 1. Leaf number on the second lateral shoot of `Annette Hegg Dark Red' poinsettia plants grown with 20C DT and NT temperature setpoints in 1986 and 1987.





Figure 2. Time required from pinching to unfold the first three leaves (LAG) on the second lateral shoot below the pinch in 'Annette Hegg Dark Red' poinsettia grown with 41 day and night temperature combinations in 1986 and 1987. LAG = 52.1 - 2.797\*average daily temperature (ADT) + 0.0199\*Day temperature squared ( $DT^2$ ) + .0280\*Night temperature squared ( $NT^2$ ) R<sup>2</sup>=.81.





Figure 3. Isopleth plots of predicted leaf unfolding rates (LUR) for 'Annette Hegg Dark Red' poinsettias grown with various day and night temperature combinations. a: Isopleth of predicted leaf unfolding rates for a 10HR day and 14HR night based on a regression of 52 DT and NT combinations between 14.8 and 30.1C in 1986 and 1987. b: estimated LUR adjusted for a 12HR day. c: estimated LUR adjusted for a 14HR day. d: estimated LUR for a 12HR day with DT<sup>2</sup> and NT<sup>2</sup> coefficients adjusted to reflect equal response to DT and NT.



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Figure 4. Schematic diagram of a plant development model for the poinsettia.



SECTION III

QUANTIFYING TEMPERATURE-DRIVEN STEM ELONGATION IN THE POINSETTIA

Subject Category: Growth and Development

Quantifying temperature-driven stem elongation in the poinsettia.

Robert D. Berghage and Royal D. Heins.

Department of Horticulture. Michigan State University. East Lansing. MI 48824.

<u>Additional index words</u>. Internode elongation, Richards function, nonlinear regression, <u>Euphorbia pulcherrima</u>.

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Abstract. The elongation of each internode on a lateral shoot of poinsettia 'Annette Hegg Dark Red' was determined from pinching through anthesis for plants grown with 36 day and night temperature (DT and NT) combinations between 16 and 30C. A 4 parameter Richards nonlinear function was used to describe the elongation of each internode. The first internode 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). The rate of development (time to maturation) of the first internode was a function of average daily temperature. Subsequent internodes developed uniformly in the absence of flower In the absence of flower initiation the length of an initiation internode after the first was a function of DIF, and the developmental rate was primarily a function of ADT. Following flower initiation, internode length decreased exponentially as flower buds developed. Internode length after the start of short days was a function of DIF, and the visible bud index where visible bud index = (date internode elongation began - date of the start of flower initiation) / date of visible bud. A poinsettia lateral shoot stem elongation model was developed based on the derived functions for internode elongation. The model predicted lateral shoot length within 1 standard deviation of the mean for plants grown in a separate validation study with 16 day and night temperature combinations. 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, when each node started to elongate, and the visible bud index at the start of elongation of each node.

One of the major constraints in commercial poinsettia production is the control of plant height. Advances in the use of growth regulating chemicals have provided a means to control plant height, however, increasing public concern with chemicals in the environment make 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, we must develop a thorough understanding of the factors which influence stem elongation, and we must quantify 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. Unfortunately, as is often the case, the technology of the time did not provide the means for practical application of this information. The commercial application of cool days and warm nights to limit stem elongation had to wait for two developments. The first was the introduction of greenhouse thermal blankets in response to increasing energy costs in the 1970's, and the second was the introduction of greenhouse climate control computers. The use of a thermal blanket made it economically feasible to have a warmer night temperature than day temperature (Erwin et al. 1988), and the greenhouse environmental control computer provided the means for precise control of the temperature and the impetus for quantifying the effects of temperature on plant growth and development.

Erwin et al (1989) quantitatively described the influence of

temperature on morphogenesis of <u>Lilium longiflorum</u>. In particular, they found that the effects of day and night temperature on stem elongation could be quantitatively described using the difference between day and night temperatures (DIF = DT-NT). Stem elongation increased as DIF increased. The relationship between DIF and stem elongation has been reported for chrysanthemum (Karlsson et al, 1989), fuchsia (Erwin and Heins, 1988), poinsettia (Berghage and Heins, 1988), and in fact 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 to use these quantitative relationships to develop a computer simulation model of stem elongation.

## Materials and Methods

Rooted 'Annette Hegg Dark Red' cuttings were planted in  $1200 \text{ cm}^3$ plastic pots 28 Aug. 1986, and placed in a 23C constant temperature glass greenhouse. A nutrient solution with 18:1:8 mM N:P:K and 1  $_{\mu}$ M Mo was applied at each irrigation. On 10 September, 360 uniform plants were pinched to about 6 nodes and moved to glass greenhouses with temperature setpoints 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. About 30 minutes were required to move all the plants each morning and evening. Constant temperature treatment plants were moved from one location to another within the greenhouse. Any lateral shoots which had formed below the five uppermost lateral shoots were removed two weeks after pinching. Starting on 28 September, an opaque blackout curtain was pulled at 1800 HR immediately after the plants were moved and retracted at 0800 HR before the plants were moved. The 14 HR artificial nyctoperiod was continued until the experiment was terminated on 15 December.

The length of each internode on the second lateral shoot below the pinch was measured using a digital caliper every three to four days starting on the 5<sup>th</sup> 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 greater than 0.15 cm in length (this was the smallest internode which could be reliably measured). Although the poinsettia is largely an alternate leaved plant, about 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 in order to assure consistency in internode measurements. The date of first visible bud was recorded for each plant. Visible bud index (VBI) for each node was calculated as (VBI= (Date of internode appearance (i.e. 0.15 cm) - date of short days) / date of visible bud).

Greenhouse temperatures were recorded with a datalogger linked to iron-constantan thermocouples. Two hour integrated averages of temperature measurements made at ten second intervals were used to determine average day and night temperatures for each greenhouse section. Actual average greenhouse temperatures were used in all regression analyses.

A four parameter Richards' function (Richards, 1959;1969) of the

form; Internode length at time T =  $P_1*(1+P_2*exp(P_2-P_3*T))^{(-1/P_4)}$  (where  $P_{1-4}$  are estimated parameters and T is time in days) and a three parameter Gompertz function (France and Thornley, 1984) of the form; Internode length at time T =  $P_1*exp(-P_2*exp(-P_3*T))$  (where  $P_{1-3}$  are estimated parameters and T is time in days) were fitted to the data from each of the first 6 internodes on plants from each of the 36 temperature treatment combinations. The four parameter Richards function was selected to describe internode elongation because it provided a consistantly lower residual sums of squares than the Gompertz function. Psuedo  $R^2$  for the Richard function estimates ranged from .945 to .999. The psuedo  $R^2$  was calculated as (1.0- (residual sums of squares)/((N-1) variance) (Ralston, 1988).

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, Inc. Los Angeles, CA 90025) was used to determine the minimum least squares model for the Richards and Gompertz functions and the mixed linear and 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 functions describing first 5 internodes from all 36 temperature treatment combinations were used in multiple linear regression analysis relating function parameters  $P_2$  and  $P_3$  to DT,

NT, DIF, ADT, and VBI. Multiple linear regressions were performed with the Systat MGLH, subroutine (Systat Inc, Evanston, 111.).

The inflection point parameter  $P_4$  was significantly influenced by node position but not temperature treatments. Constant values (means) of 0.8, 1.1, 1.4, 1.2, 0.8, ... 0.8 were used as estimates of  $P_4$  for nodes 1 to N in the stem elongation model (where N is the total number of nodes below the inflorescence).

A validation study was conducted in 1987. Plants were potted on 21 August and pinched on 7 September. Plants were grown in a common greenhouse environment with constant temperature setpoints of 20C heat and 23C vent after pinching. Plants received night interruption lighting with incandescent lights from 2200 hr to 0200 hr each night to prevent flower initiation. On October 1 plants were moved to glass greenhouses with temperature setpoints of 14, 17, 20, and 23C. Plants were moved at 0800 and 1730 hr to provide 16 day and night temperature treatment combinations. An opaque blackout curtain was closed at 1800 hr immediately after plants were moved and retracted at 0800 hr prior to moving plants. lateral shoot length was recorded as in 1986.

## Results and Discussion

Stem elongation in the poinsettia followed a general sigmoidal curve very similar to that observed for the chrysanthemum (Heins et al, 1988). Stem elongation could be generally described as occurring in three stages. Following pinching there was lag where stem elongation occurred slowly followed by a rapid elongation phase, and then a slower terminal growth stage approaching an asymptote as plants reached anthesis (Figure 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 (Figure 2). Flower initiation was prevented in these plants due primarily to the high night temperature (Langhans and Miller, 1963; 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 75 days after pinching (Figure 2).

The reasons for this difference in elongation pattern can be explained by examining the pattern of elongation of the individual internodes. The elongation of each internode followed a sigmoid curve (Sachs, 1882). In plants where flower initiation did not occur, new nodes continued to appear throughout the experiment. The first node to appear after pinching was longer and matured at a more rapid rate than subsequent nodes. The nodes which developed after the first all elongated at approximately the same rate and grew to about the same final length (Figure 2).

In plants where flower initiation occurred, the number of internodes below the inflorescence was limited. Again the first internode was longer and matured at a faster rate than subsequent internodes. While each of the internodes which developed after the first elongated at about the same rate, their final length was greatly reduced in nodes closer to the inflorescence (Figure 1).

The pattern of overall stem elongation was thus, dependent on internode number, internode length, and internode position on a

reproductive plant. Both internode number and internode length varied between plants grown under the different temperature regimes. Internode number was influenced by the effects of temperature on both leaf unfolding, and flower initiation. Leaf unfolding rates in the poinsettia increase as average temperature increases up to about 25C (Berghage et al 1989). The poinsettia is an alternate leaved plant, with an occasional internode (10 to 15%) which fails to elongate. The number of internodes formed on a lateral shoot can thus be described as a function of the number of leaves formed on the lateral shoot (Figure 3). Since the number of leaves formed before flower initiation determines the number of leaves on a lateral shoot (Berghage, 1989), and increased average temperature increases the number of leaves unfolded in a given period of time, it is not surprising that plants grown with cooler temperatures would have fewer internodes than plants grown at warmer temperatures.

Internode number was also influenced by the effects of temperature on flower initiation. High night temperatures are known to delay flower initiation in the poinsettia (Langhans and Miller, 1960; Larson and Langhans, 1963; Kristoffersen, 1969). Delayed flower initiation in plants grown with high night temperatures (above 25C) resulted in increased leaf number in these plants (Berghage, 1989).

Final internode length was influenced by temperature. Linear regression analysis of the final internode length indicated that much of the variability in final internode length observed in this experiment could be described by the relationship between the DT and NT (DIF) (Figure 4). The length of the first internode was described by a regression model with linear and quadratic terms for DIF (Table 2). The length of

subsequent internodes (two through N) were described with a single linear regression model containing linear quadratic and first order interaction terms for DIF and VBI (Table 2). When VBI is held to zero in the function for nodes two through N, the major difference in predicted node length between the first internode and subsequent internodes is due to the difference in the constant for the two functions (4.6 vs. 3.0, respectively).

The observed effects of VBI on node length were suggestive of an exponential function (Figure 5), so a mixed linear and exponential function was tested using the same terms contained in the multiple linear regression model. This mixed linear and exponential model provided a better description of the data than the linear regression model; (the residual sums of squares were about 13% less than in the linear model). However, this mixed linear and exponential model did not adequately predict the lateral shoot length of plants grown in the validation study  $(R^2=.51)$ . Multiple linear regression of temperature and the predicted and observed lateral shoot lengths for plants in the validation study suggested that much of the unaccounted for variability was related to linear and quadratic effects of average temperature ( $R^2$ =.87). Adding linear and guadratic ADT terms to the linear part of the mixed model resulted in a reduction of the residual sums of squares of 20% and 9% compared with the linear, and mixed linear and exponential models without ADT terms (Table 1). The mixed linear and exponential model with ADT terms predicted lateral shoot length of the plants grown in the validation study within about 1 standard deviation for all but 2 treatments (Table 2).

Because of the complex interrelationships observed between

temperature, internode number, internode length, and reproductive status, a single internode model was selected for predicting poinsettia stem elongation. Although a model of whole lateral shoot elongation could be developed, a model of this form would be considerably less versatile than one based on individual internodes. This reduced versatility for a whole stem model comes about as a result of the potential variability in both temperature during and length of the vegetative phase of poinsettia growth. A longer vegetative growth period prior to flower initiation or a higher temperature during this period would result in increased leaf and internode number. An increased internode number would 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. Linear regression of the parameter estimates from Richards functions describing internodes of plants grown in the 36 day and night temperature combinations indicated that these parameters were correlated with the temperature treatments. The rate constant of the Richards function ( $P_3$ ) was correlated with ADT. As ADT increased so did the rate parameter. The predicted effect of average temperature on the rate constant of the first internode was much greater than the same

coefficient for subsequent internodes (Table 3).

The rate constant parameter  $(P_3)$  was also highly correlated with the second parameter of the function  $(P_2)$ . For a given set of data there are a family of solutions for the Richards function based on reciprocal changes in each of the curve shaping parameters  $(P_{2-4})$ . The number of solutions which adequately fit the data depends on the variance of the data set. In order to account for this interrelationship between the parameters, it was necessary to link the functional estimate of  $P_3$  to  $P_2$ and the estimate of  $P_2$  to  $P_4$ . The first parameter  $P_1$  was not dependant on  $P_2$ ,  $P_3$ , or  $P_4$ .

The rate  $(P_3)$ , shape  $(P_2)$  and length  $(P_1)$  parameters and their temperature dependant functions for the first internode were different than those for subsequent internodes. Because growth of the first internode was different than that of subsequent internodes (Figure 1 and 2) a separate regression function was developed to describe each parameter for the first internode (Table 1 and 3). Richards function parameters for subsequent internodes were similar when adjusted for plant development. The parameters for all the internodes after the first on a lateral shoot could be estimated with a single function for each parameter.

The shaping parameter  $P_2$  which reflects how the curve is shifted on the time axis was primarily a function of when the internode began to elongate (defined as when the internode reached 0.15 cm) and the inflection point parameter ( $P_4$ ). The shaping parameter  $P_2$  was also significantly influenced by DIF and ADT (Table 3).

The rate constant  $(P_3)$  was primarily a function of ADT and the shaping parameter  $(P_2)$  with smaller contributions from VBI, the date the
internode began to elongate and an interaction between the date the internode began to elongate and the shaping parameter  $(P_{-})$  (Table 3).

The inflection point parameter  $(P_4)$  was significantly related to node number but not the temperature treatments. This parameter was on average higher for nodes two to four, with estimates for nodes one five and six being roughly equal. Since no temperature effects were observed, a constant for each internode was used to estimate this parameter in the model.

A static (with regard to temperature) model can be constructed directly from the equations in Tables 1 and 3 and the Richards function. This model will, for a given day and night temperature, predict the height of each internode on the second lateral shoot on any given day. Summing the lengths of each internode provides an estimate of the total lateral shoot length. Because direct output from the Richards function is used in this model to predict internode length, day and night temperature must be held constant throughout the simulation.

A dynamic model can be constructed to allow estimation of the effects of changes in the day and night temperature on a daily basis. The model can be made into a dynamic simulation by integrating the output of the first derivative of the Richards function (assuming that the effects of temperature are instantaneous with no carryover from one day to the next). This can be accomplished by determining the amount of elongation predicted for a given time interval (i.e rate / day) and then summing the output with respect to time. This can be expressed as follows:

1. 
$$Lt = \sum_{i=0}^{t} L(T_i)$$

where the total length at time t (Lt) is equal to the sum of a series of partial lengths  $(L(T_i))$  where  $T_i$  is the time interval. The partial lengths for each time interval are calculated as;

2. 
$$L(T_{i}) = R(t) - R(t-1)$$

where R is the Richards function for the internode.

Since the rate of maturation of an internode is also dependant on temperature the relationship between internode elongation and internode maturation will not be conserved unless the relative maturation (maturation fraction) of each internode is also integrated over time. In practical terms the conservation of the relationship between internode elongation and maturation means that the model will not predict resumption of growth in an internode which has already ceased elongating. The integration of maturation is achieved by summing the partial internode maturation for each time interval  $(M(T_i))$  as shown above for internode elongation. The partial development for a time interval can be estimated as the ratio between the total predicted length of the internode and the partial length predicted for the given time interval.

3.  $Mt = \sum_{i=0}^{L} M(T_i)$ 

4.  $M(T_i) = P_1(t_i)/L(T_i)$ 

The part of the Richards function related to the maturation fraction is then solved for  $t_i$ .

5. 
$$M(T_i) = (1+P_2*exp(P_2-P_3*t_i)^{(1/P_4)})$$

The relative day for a given internode maturity and temperature combination  $(t_i)$  is then used as the time input for the Richards function to provide an estimate of the growth for the next day  $(t_{i+1})$ . This dynamic model accounted for 74% of the variability in the final lateral shoot length of plants grown in the validation study.

In either the static or the dynamic model, the number of internodes present, the date they begin to elongate and the VBI (visible bud index) are considered constants, however these terms can also be estimated based on the output of a developmental rate model for the poinsettia (Berghage, 1989). Combining these two models provides a powerful tool for understanding the possibilities and limitations of the use of temperature to control growth and development in the poinsettia.

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Figure 1. Lateral shoot elongation of the second lateral shoot below the pinch for `Annette Hegg Dark Red' poinsettia grown with 20C DT and NT temperature setpoints. Total shoot length is shown as the sum of the individual internodes.





Figure 2. Lateral shoot elongation of the second lateral shoot below the pinch for `Annette Hegg Dark Red' poinsettia grown with 29C DT and NT temperature setpoints. Total shoot length is shown as the sum of the individual internodes.





Figure 3. Node number vs. leaf number for 'Annette Hegg Dark Red' poinsettia grown with 36 day and night temperature combinations in 1986. Node number = Leaf number \* .844.  $R^2$  = .88.



Node number



Figure 4. Relationship between DIF and internode length of internodes on the second lateral shoot of poinsettia 'Annette Hegg Dark Red' grown with 36 day and night temperature combinations. Data shown is for all nodes after the first with a VBI of 0 for each of the temperature treatments. Prediction line is based on a mixed linear and exponential model of internode length (Table 1).





Figure 5. Relationship between Visible bud index (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 elongation began (internode < 0.15 cm long) - the date of the start of flower initiation) / date of visible bud. Prediction line is based on a mixed linear and exponential model of internode length (Table 1).





Table 1. Prediction equations for final internode length  $(P_1)$  on the second lateral shoot below the pinch in poinsettia.

\_\_\_\_\_ Internode 1. Length =  $C + B_* DIF + B_* DIF^2$  $R^2 = .684$ F = 35.7 \*\*\* Internode 2 - N (Where N is the number of nodes below the inflorescence) Linear Model Length = C +  $B_1*DIF + B_2*DIF^2 + B_3*VBI + B_4*VBI^2 + B_5*DIF*VBI$  $\begin{array}{rcl} C &=& 3.005 & *** \\ B_1 &=& 0.1157 & *** \\ B_2 &=& 0.00295 & *** \end{array}$ R<sup>2</sup> .839 F 244.5 \*\*\* -Residual SS = 4650 N 240 -Mixed Linear and Exponential Model Length = (C +  $B_1$ \*DIF +  $B_2$ \*DIF<sup>2</sup> +  $B_3$ \*DIF\*VBI) +  $B_4$ \*ADT +  $B_5$ \*ADT<sup>2</sup>) \* exp(P<sub>1</sub>\*(VBI\*2) + P<sub>2</sub>\*(VBI\*2)\*vbi<sup>2</sup>) Psuedo  $R^2 = .871$ C = -270.8 B. = 13,164 Residual SS = 3732 Ν 240 \_\_\_\_\_ \*\*\* Significant at .001 for F of linear regressions and t of linear regression coefficients.

Psuedo  $R^2$  for mixed model = 1.0-(residual ss/(N-1\*variance))

Table 2. Predicted and observed lengths of the second lateral shoot below the pinch for poinsettia 'Annette Hegg Dark Red' grown in 16 day and night temperature combinations in 1987. Predicted lengths based on a mixed linear and exponential stem elongation model developed using plants grown with 36 day and night temperature combinations in 1986.

*****					
ature nt	14	Day temperat setpoint 17	ture 20	23	bserved temp
Observed	14.4 ± 1.8	16.2 ± 2.0	16.2 ± 1.4	19.6 ± 2.6	5 14.8
Predicted	14.5	16.8	18.9	21.1	
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	
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	
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	
ed ature 16.0	18.0	20.0	22.3		
	ature nt Dbserved Predicted Dbserved Predicted Dbserved Predicted Dbserved Predicted ed ature 16.0	ature nt 14   Dbserved $14.4 \pm 1.8$ Predicted $14.5 \pm 1.8$ Dbserved $15.5 \pm 1.8$ Predicted $15.0 \pm 1.8$ Dbserved $14.7 \pm 2.6$ Dbserved $14.3 \pm 1.6$ Predicted $15.4 \pm 1.6$ Dbserved $14.3 \pm 1.6$ Predicted $15.1 \pm 1.6$	Day temperal setpoint   ature tt 14 Day temperal setpoint   11 17   Dbserved 14.4 $\pm$ 1.8 16.2 $\pm$ 2.0   Predicted 14.5 16.8   Dbserved 15.5 $\pm$ 1.8 17.0 $\pm$ 2.6   Predicted 15.4 17.0   Dbserved 14.7 $\pm$ 2.6 16.1 $\pm$ 2.2   Predicted 15.4 17.2   Dbserved 14.3 $\pm$ 1.6 16.4 $\pm$ 1.6   Predicted 15.1 16.5   ed ature 16.0 18.0 20.0	Day temperature setpoint Day temperature setpoint   14 17 20   Dbserved 14.4 $\pm$ 1.8 16.2 $\pm$ 2.0 16.2 $\pm$ 1.4   Predicted 14.5 $\pm$ 1.8 17.0 $\pm$ 2.6 17.4 $\pm$ 1.6   Observed 15.5 $\pm$ 1.8 17.0 $\pm$ 2.6 17.4 $\pm$ 1.6   Predicted 15.4 17.2 19.0 $\pm$ 2.0   Dbserved 14.3 $\pm$ 1.6 16.4 $\pm$ 1.6 17.7 $\pm$ 1.7   Predicted 15.1 16.5 17.6   Dbserved 14.3 $\pm$ 1.6 16.4 $\pm$ 1.6 17.7 $\pm$ 1.7   Predicted 15.1 18.0 20.0 22.3	Day temperature setpoint Day temperature setpoint Operative setpoint

 $R^2$  Predicted vs observed = .74, Linear regression coefficient = 1.018



Table 3. Prediction equations for curve shaping parameters  $P_2$  and  $P_3$  for Richards function models of internodes of the second lateral shoot of plants grown with 36 day and night temperature combinations. Richards function given as; Length at time T = Final length \*  $(1+P_2*exp(P_2-P_3*T))**(-1/P_4)$ .

Internode 1 Ρ,  $P_2 = C + B_1 * P_1 + B_2 * DIEB + B_7 * DIF$  $R^2 = .799$ C = -1.311 \*\*\* B. = 3.875 \*\*\*  $B_2^1 = 0.115 *** B_3^2 = 0.052 ***$ Internode 2 - N (Where N = the number of nodes below the inflorescence)  $P_2 = C + B_1 * P_4 + B_2 * DIEB + B_3 * DIF + B_4 * ADT$  $R^2 = .831$ C = -4.69 \*\*\*B<sub>1</sub> = 3.742 \*\*\*  $B_2 = 0.126 ***$  $B_3 = 0.065 ***$  $B_4 = 0.146 ***$ Ρ, Internode 1  $P_{z} = C + B_{1}*P_{2} + B_{2}*ADT$  $\begin{array}{rcl} C &=& -0.408 & *** \\ B_1 &=& 0.106 & *** \\ B_2 &=& 0.022 & *** \end{array}$  $R^2 = .966$ Internode 2 - N (Where N = the number of nodes below the inflorescence)  $P_z = C + B_1 * P_2 + B_2 * P_2 * DIEB + B_z * DIEB + B_\ell * ADT + B_s * VBI$  $R^2 = .963$ C = -0.0408 \*\*\*B, = 0.3110 \*\*\*  $B_{2} = -0.00024 ***$ B<sub>3</sub><sup>2</sup> = -0.00213 \*\*\*  $B_4^3 = 0.00549 ***$  $B_{s}^{4} = 0.04775 ***$ \*\*\* Significant t at 0.001 for regression coefficients DIEB = Day internode elongation begins (defined as internode 0.15 cm in

length)

SECTION IV

A DYNAMIC COMPUTER SIMULATION MODEL OF

Subject Category: Growth and development

A dynamic computer simulation model of lateral shoot length and plant height in poinsettia.

Robert D. Berghage and Royal D. Heins

# Department of Horticulture, Michigan State University, East Lansing, MI 48824

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Abstract. A dynamic computer simulation model to predict stem elongation in response to temperature was constructed for the poinsettia. This model was developed with two basic components; a model to predict the influence of temperature on developmental rate, and a model to predict the influence of temperature on stem elongation. The model was validated in three ways. 1) The basic ability of the model to predict stem elongation from pinch to anthesis was tested using plants grown with a 23C day temperature (DT) and a 17C night temperature (NT) or a 17C DT and 23C NT. 2) The dynamic nature of the model was tested using plants moved between a 23C DT and 17C NT greenhouse and a 17C DT and 23C NT greenhouse for 1 week 35 days after pinching, and 3) the robustness of the model was tested using plants grown with 39 combinations of pinch date, temperature from pinching to October 1, and temperature from October 1 to anthesis. The model was found to be accurate, dynamic and robust. The model was used to predict maximum and minimum plant heights for plants grown with a range of cultural conditions. These maxima and minima provide an estimate of the potential range of poinsettia stem elongation which can be used to help predict where commercial problems in poinsettia height control may occur.

Height control is a major concern in commercial production of the poinsettia. Height control is generally achieved using growth retardants, or more recently by manipulating the difference between day and night temperature (DIF = day temperature (DT) - night temperature (NT)) (Erwin et al, 1989). In either case a quantitative understanding of how temperature influences the way the plant develops is important to allow

the precise control of plant height needed to meet increasingly strict commercial plant production specifications.

The height of a poinsettia plant at anthesis is the total of the pot height, the length of the primary stem up to the point where lateral shoots originate, and the length of the longest lateral shoots. In a pinched plant, the length of the primary stem is dependant in part on the pinching technique used (Berghage et al, 1989). The length of the primary stem is essentially fixed if a hard pinch is used since all immature internodes on the primary stem are removed in the pinch. If a soft pinch is used, the primary stem will continue to elongate following the pinch. The elongation of the primary stem in soft pinched plants combined with long lateral shoots originating from the axils of the uppermost leaves of the primary stem results in a taller plant than a hard pinched plant. If immature leaf blades are removed in plants given a soft pinch, primary stem elongation will be reduced as will the length of the uppermost lateral shoots resulting in a total plant height approximately equal to that of a hard pinch (Berghage et al 1989). Pinching technique can also influence node number since the use of a soft pinch delays initial lateral shoot growth (Berghage et al, 1989).

The length of a shoot is ultimately a function of the number of internodes and the length of each internode. Since the poinsettia is an alternate leaved determinant plant, the number of internodes on a lateral shoot will depend on the number of leaves (nodes) formed before flower initiation. The rate of leaf unfolding in the poinsettia is a curvilinear function of absolute temperature with a maximum leaf unfolding rate at about 25C (Berghage et al, 1990). Thus, increasing temperature to 25C, or



increasing the time between pinching and flower induction will increase leaf (node) number.

The influence of temperature on flower initiation can also affect leaf (node) number. High temperatures above 23C (particularly at night) delays flower initiation resulting in increased leaf (node) number compared with plants grown with cooler temperatures (Larson and Langhans, 1960; Langhans and Miller, 1963; Kristofferson, 1969; Berghage, 1989).

Internode length in the vegetative poinsettia is influenced by the node position, DIF (DT-NT) and average daily temperature (ADT) (Berghage, 1989). Internode length in reproductive poinsettia plants is also influenced by flower development. Floral development at the time an internode can first be measured (0.15 cm) can be expressed for each internode as the visible bud index (VBI = (The date the internode began to elongate (beyond 0.15 cm) - the date of the start of flower initiation) / the date of visible bud). Internode length decreases exponentially as VBI increases (Berghage and Heins, 1990).

Computer simulation modeling offers the possibility of combining the relationships for the influence of temperature and pinching technique on stem elongation in the poinsettia. A model of plant growth can be used to "test" a large number of "treatments" in a short period of time and thereby increase our understanding of the total system. Of course, the output of a model is only as good as the model itself and predicted results must be validatied through greenhouse experiments. The development of computer models for plant growth also holds much promise for the future as interfaces for greenhouse climate control computers. A well constructed and tested model could eventually be relied upon to optimize control of the greenhouse environment based on past, present, and predicted future plant growth.

The objective of this study was to construct a model using previously developed functions that describe the effects of temperature and pinching technique on stem elongation in the poinsettia and to validate the models ability to predict poinsettia stem elongation.

# Materials and Methods

A computer simulation model (Figure 1) was constructed using quantitative functions for temperature-driven poinsettia development and temperature-driven internode elongation previously described (Berghage, 1989). The functions for poinsettia development were linked to the functions for internode elongation through the estimations of leaf number and visible bud index provided in the developmental rate model (Berghage and Heins, 1989). Leaf number potential during the lag phase (used to calculate VBI and total leaf number for plants where short days started before the lag phase was completed) was estimated as (LAGindex \* 3) (Berghage and Heins, 1989). The leaf number output at time (t) was used as an input to the internode elongation model to estimate the first day (D) of observable internode elongation for each internode. D for internode(i) was estimated as the time(t) (in days) when leaf number(i) = Node number / .85 ) The VBI was calculated for time (t) = (D) for each internode. To estimate the effects of a soft pinch on plant height the model was modified to include primary stem internodes for each of the immature leaves remaining on the plant following pinching. A further

modification for plants given a soft pinch was to delay the start of lateral shoot development by 10 days to account for delayed growth observed in these plants (Berghage et al, 1989). Total plant height was estimated as the sum of the pot height, the primary stem length, and the lateral shoot length.

Validation experiments were designed to examine the ability of the model to predict plant stem elongation. Three general tests of the model were undertaken. In each of these experiments greenhouse temperatures were recorded with a datalogger (Digistrip III, Kaye Instruments Co., New Bedford Conn.) linked to iron-constantan thermocouples. Two hour integrated averages of temperature measurements made at ten second intervals were used to determine average day and night temperatures for each greenhouse section for each day of the experiment. The integrated observed day and night temperature averages for each day were used as the temperature inputs for the model simulations for each validation experiment.

<u>Validation experiment 1.</u> This basic validation step was undertaken to determine how well does the model predict the elongation of plants from pinching through anthesis when grown with a positive DIF or a negative DIF. Rooted 'Annette Hegg Dark Red' cuttings were planted in 1200 cm<sup>2</sup> plastic pots and placed in a glass greenhouse with 23C DT and NT temperature setpoints. A nutrient solution with 18:1:8 mM N:P:K and  $1_{\mu}M$  Mo was applied at each irrigation. On 4 Sept., two weeks after planting, 20 plants were pinched and moved into one of 2 greenhouse sections with greenhouse temperature setpoints of 17C DT and 23C NT to provide a negative 6C DIF or 23C DT and 17C NT to provide a positive 6C DIF. Two

weeks after pinching an opaque blackout curtain was pulled at 1800mm and 0800mm to provide a 14mm nyctoperiod. Internode length of the second lateral shoot below the pinch was measured with a digital caliper every seven days. The observed day and night temperature averages (Figure 2) were used as temperature inputs for the simulation model. Lateral stem length was calculated using the model for each day for 80 days following pinching.

<u>Validation experiment 2.</u> Dynamic validation was done to deternine if the model could predict the effects of changing from a positive DIF to a negative DIF and visa-versa for 1 week. A second group of 10 plants was grown in each of the greenhouses used in experiment 1. These plants were treated the same way as those in experiment 1 until 35 days after pinching. Plants were moved from the positive DIF greenhouse to the negative DIF greenhouse and visa versa 35 days after pinching. One week later (42 days after pinching) the process was reversed and the plants were returned to the greenhouse of origin. Internode length of the second lateral shoot below the pinch was measured with a digital caliper every seven days. The observed day and night temperature averages (Figure 2) were used as temperature inputs for the simulation model. Lateral stem length was calculated using the model for each day for 80 days following pinching.

<u>Validation experiment 3.</u> Validation of model robustness was done to determine if the model could predict the final lateral shoot length of plants pinched on different dates and grown with different temperatures both before and after flower initiation. Rooted 'Annette Hegg Dark Red' cuttings were planted in 1200 cm<sup>3</sup> plastic pots on 16 Aug. 1988 and placed

in a glass greenhouse with 23C DT and NT setpoints. A nutrient solution with 18:1:8 mM N:P:K and  $1_{\mu}M$  Mo was applied at each irrigation. At various dates starting on 29 Aug., plants were given a hard pinch (Berghage et al, 1989) and moved into constant temperature glass greenhouses with setpoints at either 18, 21, 24, 30, or 35C. Plants in the 35C greenhouse died and were thus excluded from further analysis. Plants were grown in each of these greenhouses until 1 October when plants from each pinching date and temperature combination were placed in each of three temperature regimes; Positive DIF (21C DT and 17C NT), Zero DIF (19C DT and NT), or Negative DIF (16C DT and 20C NT). These temperature regimes after October 1 were selected to provide about the same average daily temperature while not exceeding 20C at night. A complete list of temperature and pinch date combinations is given in Table 1. Starting 1 October an opaque blackout curtain was pulled at 0800 and 1800 HR to provide a 14 HR nyctoperiod. The blackout curtain was used as a precaution against light pollution from neighboring greenhouses.

Leaf number and the length of the second lateral shoot below the pinch were determined at anthesis. The observed day and night temperature averages were used as temperature inputs for the simulation model. Final lateral stem length and total leaf number were calculated using the model for each pinch date and temperature treatment combination. In these simulations natural photoperiod flower initiation was considered to occur on or about 21 Sept. except for plants grown with greenhouse temperatures above 24C. Plants grown with greenhouse temperatures above 24C were considered to be heat delayed until temperatures were lowered on 1 October. Predicted and observed leaf number and lateral shoot length were compared using regression analysis.

# Results

The length of the second lateral shoot below the pinch in plants grown in the validation tests was consistently greater than the predicted length. The difference between predicted and observed lengths was about 25% on average. When the predicted lateral shoot lengths were multiplied by 1.3 for experiments 1 and 2 and 1.25 for experiment 3, regression analysis indicated a 1 to 1 relationship between (adjusted) predicted and observed lengths. All subsequent references to model output are to adjusted model output.

### Validation 1.

The model predicted both the rate and the total amount of lateral shoot elongation for plants grown with either a constant negative DIF (17C/23C DT/NT) or a constant positive DIF (23C/17C DT/NT) from pinching through anthesis (Figure 3). Predicted lateral shoot length was well within the standard deviations of the observed lateral shoot length for all but the first 2 observations for the positive DIF grown plants. Validation 2.

Dynamic changes in stem elongation resulting from moving plants from the positive DIF environment to the negative DIF environment for 1 week were accurately predicted by the model (Figure 4). A one week change from the positive DIF environment to the negative DIF environment resulted in a reduction of stem elongation for that week. When plants were then returned to the positive DIF environment elongation returned to a rate approximately equal to that of plants which were not moved. The model

output very closely predicted the reduced elongation observed in the week in which the plants were moved. Model output then nearly matched observed elongation from that point to anthesis.

The effects of moving plants from a negative DIF to a positive DIF were essentially a mirror image of the change from a positive DIF to a negative DIF. As predicted elongation increased during the week when the plants were moved from the negative DIF environment to the positive DIF environment. When plants were moved back to the negative DIF environment, elongation continued at about the same rate as observed in plants grown continuously in the negative DIF environment (Figure 5). Again the model output closely paralleled the observed plant growth.

### Validation 3.

Observed lateral shoot lengths for plants grown in experiment 3 ranged from about 15 cm to 33 cm. Regression analysis of predicted vs. observed lateral shoot length for these plants indicated that 66% of the total variability in the observed lateral shoot length was predicted by the simulation model (Figure 6). The standard error on the intercept for observed lateral shoot lengths was 2.6 cm. This compares favorably with the standard deviations for individual treatment means of observed lateral shoot length, which averaged about 2.6 cm, and ranged from 0.9 cm to 6.3 cm.

Final leaf number on plants grown in experiment 3 ranged from 8 to 15. The simulation model predicted 88% of the variability in leaf number observed in this experiment (Figure 7). The standard error of the regression intercept for leaf number was 0.6 leaves.
## Discussion

The consistent difference between predicted and observed lateral shoot lengths suggested that there was some change between the treatments used to generate the model and those used to validate the model. The most obvious difference between these experiments was in the way the plants were handled. In the experiments used to develop the model, plants were moved between and within greenhouse sections twice each day. The plants in the validation experiments were moved much less frequently; a total of two time in experiment 2, once in experiment 3, and not at all with experiment 1. Regular physical manipulations (i.e. shaking) can reduce plant growth (Biddington and Dearman, 1985). It is therefore likely that elongation was reduced in the plants used to develop the model due to the daily movement of these plants. A constant multiplication factor was therefore added to the model to account for the observed differences between plants which were moved and those which were not.

The adjusted model accurately predicted the dynamic relationships between daily temperature and lateral shoot elongation. Furthermore the model proved to be robust in its ability to describe the effects of multiple cultural changes (i.e. pinching date and temperature regimes) on lateral shoot length. The success of the model in handling the various validation problems presented in this study support the general applicability of the model.

An interesting use of the model is to predict the minimum and maximum plant height for a range of cultural practices (Table 2). Where the predicted plant heights overlap plants of the same height could be produced using very different cultural strategies. One strategy to control height is to modify the temperature DIF between the extremes presented; plants of intermediate height could then be produced. A second strategy is to control leaf number. This can be accomplished because leaf number is a function of heat units accumulated before the start of short days (Berghage and Heins, 1989). Plants with different leaf numbers have different potential heights (Table 2). A third strategy is to modify the pinch type. A soft pinch will result in a taller plant all else being equal (Berghage et al, 1989). Combining these three strategies provides the ability to produce plants "to order" with a final height anywhere between a maximum and minimum for a given set of temperature and pinching conditions(in the example presented, between 71 and 35 cm). The model can be used to select different temperature and pinching options to produce plants of similar heights but grown with different temperature and pinching strategies.

Just being able to estimate the theoretical limits for poinsettia stem elongation should make it easier to grow plants of a desired height. As a general rule producing plants closer to the predicted limits would be more difficult than producing plants in the middle of the theoretical height range. This is because there would be more potential for correcting mistakes in the middle of the theoretical range. Growers who were aware of the theoretical height range in which their crop was being produced would be better able to anticipate potential problems in height control.

It is important to note however that although plants may be the same height, the perceived quality may not be the same. A plant given a soft pinch will be taller, however perceived quality may be lower (Berghage et al, 1989). Furthermore a plant with few leaves and longer internodes may





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appear more open and leggy than a plant with more leaves and shorter internodes.

It should further be noted that all the plants used to generate and validate this model were grown without the use of growth regulators to demonstrate the potential power of using temperature control to limit the need for growth regulators for comercial poinsettia production. A well managed poinsettia production program using temperature to control plant height and development should require little or no use of growth regulators.



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Table 1. Treatments used to examine the robustness (experiment 3) of the poinsettia stem elongation simulation model.

Pinch	Tem	peratu	re set	points
date	Pin	ch to	Octobe	er 1
8/29	18	21	24	30
9/6			24	'
9/7		21		30
9/10	18			
9/11			24	
9/12				30
9/15		21		
9/18			24	30

Table 2. Predicted total plant height (cm) for 'Annette Hegg Dark Red' poinsettia "grown" to produce 8,9,10,11, or 12 leaves on a lateral shoot with either a negative DIF (DT-NT) or a positive DIF and either a hard pinch or a soft pinch.

Number of	Hard Pinch			Soft Pinch					
a lateral shoot	DT 18	NT 21	DT 25	NT 18	DT 18	NT 21	DT 25	NT 18	
8	35		39		43		51		
9		38		42		47		57	
10	40		48		50		63		
11	44		52		53		66		
12	46		57		56		71		





Figure 2. Average day and night temperatures for greenhouses used in validation experiments 1 and 2. Setpoint temperatures were a: 23C DT and 17C NT and b: 17C DT and 23C NT.





Figure 3. Predicted and observed length (cm) of the second lateral shoot in `Annette Hegg Dark Red' poinsettia grown in greenhouses with setpoints of 23C DT and 17C NT or 17C DT and 17C NT.





Figure 4. Predicted and observed length (cm) of the second lateral shoot below the pinch of 'Annette Hegg Dark Red' poinsettia plants grown with 23C DT and 17C NT and moved to 17C DT and 23C NT for 1 week 35 days after pinching.





Figure 5. Predicted and observed length (cm) of the second lateral shoot below the pinch of `Annette Hegg Dark Red' poinsettia plants grown with 17C DT and 23C NT and moved to 23C DT and 17C NT for 1 week 35 days after pinching.







Figure 6. Predicted vs observed lateral shoot length (mm) of the second lateral shoot below the pinch in 'Annette Hegg Dark Red' poinsettia grown with various combinations of pinch date and temperature from pinching to October 1 and from October 1 to anthesis. Predicted lateral shoot lengths have been adjusted by a constant factor to account for differences in handling of the plants used to develop the model and those used in this experiment.





Figure 7. Predicted vs Observed leaf number for 'Annette Hegg Dark Red' poinsettia grown with various combinations of pinch date and temperature. Predicted leaf number was developed using a dynamic model of poinsettia development.



Observed lateral shoot leaf number



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## APPENDIX A

LOTUS 123 SPREADSHEET FORMULAS FOR A POINSETTIA STEM ELONGATION MODEL



## Appendix A. Lotus 123 Spreadsheet formula coding for a poinsettia stem elongation model

Cell Formulas for the headings and the first 4 lines of calculating cells. The fourth line of calculating cells is copied down the spreadsheet to provide cells to calculate the desired number of days in the simulation.

A1: 'sd B1: 'cf C1: 'sd to I E1: 'tln F1: 'Inld G1: 'pot ht H1: 'primary stem I1: 'pinch J1: 'immature leaves P1: 'parameters node R1: 1 X1: 'parameters node Z1: 2 AG1: 'parameters node AI1: 3 AP1: 'parameters node AR1: 4 AY1: 'parameters node BA1: 5 BH1: 'parameters node BJ1: 6 BQ1: 'parameters node BS1: 7 BZ1: 'parameters node CB1: 8 CI1: 'parameters node CK1: 9 CR1: 'parameters node CT1: 10 DA1: 'parameters node DC1: 11 DJ1: 'parameters node DL1: 12 A2: 14 B2: 1.3 C2: 11 E2: @VLOOKUP(A2+C2,E6..F80,1) F2: aVLOOKUP(A2,E6.,F80,1)-5 G2: 14 H2: 9 12:1 J2: 0 N2: 'db A3: (K96) E3: ' day G3: ' dt H3: ' nt 13: 'dif J3: 'adt N3: aVLOOKUP(0.2,86..E80,3) Q3: 'p4 R3: 0.8 x3: 'vbi

Y3: @IF(Z1>E2\*0.85.2.@VLOOKUP(Y4.A6..D80.3)) AG3: 'vbi AH3: @IF(AI1>E2\*0.85.2.@VLOOKUP(AH4.A6..D80.3)) AP3: 'vbi AQ3: @IF(AR1>E2\*0.85,2,@VLOOKUP(AQ4,A6..D80,3)) AY3: 'vbi AZ3: @IF(BA1>E2\*0.85,2,@VLOOKUP(AZ4,A6..D80,3)) BH3: 'vbi BI3: alf(BJ1>E2\*0.85.2.avLOOKUP(BI4.A6..D80.3)) 803: 'vbi BR3: @IF(BS2>E2\*0.85,2,@VLOOKUP(BR4,A6..D80,3)) 873: 'vbi CA3: @IF(CB1>E2\*0.85.2.@VLOOKUP(CA4.A6..D80.3)) C13: 'vbi CJ3: @IF(CK1>E2\*0.85.2.@VLOOKUP(CJ4.A6..D80.3)) CR3: 'vbi CS3: @IF(CT1>E2\*0.85,2,@VLOOKUP(CS4,A6..D80,3)) DA3: 'vbi DB3: @IF(DC1>E2\*0.85,2,@VLOOKUP(DB4,A6..D80,3)) DJ3: 'vbi DK3: @IF(DL1>E2\*0.85,2,@VLOOKUP(DK4,\$A6..\$D80,3)) A4: +D190 B4: 'lagi C4: 'leaf# D4: 'VBi K4: 'lateral length N4: 'vbi Q4: 'p1 R4: 'p2 \$4: 'p3 X4: 'dieb Y4: aVLOOKUP(2/0.85.C6., E80.2)-5 Z4: 'p4 AA4: 1.3 AG4: 'dieb AH4: @VLOOKUP(3/0.85.C6., E80.2)-5 A14: '04 AJ4: 1.4 AP4: 'dieb AQ4: @VLOOKUP(4/0.85.C6..E80.2)-5 AR4: 'p4 AS4: 1.2 AY4: 'dieb AZ4: @VLOOKUP(5/0.85,C6..E80,2)-5 BA4: 'p4 BB4: 1 BH4: 'dieb BI4: @VLOOKUP(6/0.85,C6..E80,2)-5 BJ4: 'p4 BK4: 0.9 BQ4: 'dieb BR4: @VLOOKUP(7/0.85,C6..E80,2)-5 BS4: 'p4 BT4: 0.9 BZ4: 'dieb CA4: @VLOOKUP(8/0.85,C6..E80,2)-5 CB4: 'p4 CC4: 0.9 CI4: 'dieb CJ4: aVLOOKUP(9/0.85,C6..E80,2)-5 CK4: 'p4 CL4: 0.9 CR4: 'dieb CS4: @VLOOKUP((CT1)/0.85,C6..E80,2)-5 CT4: 'p4 CU4: 0.8 DA4: 'dieb

DB4: @VLOOKUP((DC1)/0.85,C6..E80,2)-5 DC4: 'p4 DD4: 0.8 DJ4: 'dieb DK4: avLOOKUP((DL1)/0.85.\$C6..\$E80.2)-5 DL4: 'p4 DM4: 0.8 A5: 'day N5: @VLOOKUP(0.2, B6.. E80, 2) Z5: 'p1 AA5: 'p2 AB5: 'p3 AI5: 'p1 AJ5: 'p2 AK5: 'p3 AR5: 'p1 AS5: 'p2 AT5: 'p3 BA5: 'p1 BB5: 'p2 BC5: 'p3 BJ5: 'p1 BK5: 'p2 BL5: 'p3 BS5: 'p1 BT5: 'p2 BU5: 'p3 CB5: 'p1 CC5: 'p2 CD5: 'p3 CK5: 'p1 CL5: 'p2 CM5: 'p3 CT5: 'p1 CU5: 'p2 CV5: 'p3 DC5: 'p1 DD5: 'p2 DE5: 'p3 DL5: 'p1 DM5: 'p2 DN5: 'D3 A6: 0 B6: (-0.099+0.0123\*\$J6-0.000085\*\$G6^2-0.000118\*\$H6^2) C6: (@IF(B6<1,3\*B6,(-0.3472+0.046\*J6-0.000373\*G6^2-0.000564\*H6^2))) D6: aIF(E6<\$A\$2,0,(C6-\$F\$2)/(\$E\$2-\$F\$2-1)) E6: (A6) F6: (C6+5) G6: 21.1 H6: 20.9 16: (G6-H6) J6: ((G6\*10)+(H6\*14))/24 K6: (N6+W6+AF6+A06+AX6+BG6+BP6+BY6+CH6+CQ6+CZ6+D16) L6: (N6/Q6) M6: ((@LN((((L6)^(1/(-1/\$R\$3)))-1)/R6)-R6)/-S6) N6: (06) O6: (Q6\*(1+R6\*@EXP(R6-S6\*(\$E6-4)))^(-1/\$R\$3)) Q6: (464.7+11.099\*16+0.348\*16^2)\*\$B\$2 R6: ((-1.311+3.875\*\$R\$3+0.115\*\$N\$3+0.052\*16)) \$6: (-0.506257+0.106433\*R6+0.0241836\*J6) U6: (W6/Z6) V6: (E6) W6: (X6) X6: (Z6\*(1+AA6\*@EXP(AA6-AB6\*(\$E6-4)))^(-1/AA\$4)) z 6 (-270.8+13.16\*\$16+0.253\*\$16^2-17.57\*\$13\*Y\$3+50.73\*\$J6-1.115\*\$J6^2)\*@EXP(-0.3738\*(Y\$3+Y\$3)-0.5722\*(Y\$3+Y\$3)^2 )\*\$B\$2

AA6: ((-4.69+3.742\*AA\$4+0.126\*Y\$4+0.065\*\$16+0.146\*\$J6)) AB6: (-0.0408+0.0311\*AA6-0.00024\*AA6\*Y\$4-0.00213\*Y\$4+0.00549\*\$J6+0.04775\*Y\$3) AD6: (AF6/AI6) AE6: (\$E6) AF6: (AG6) AG6: (A16\*(1+AJ6\*@EXP(AJ6-AK6\*(\$E6-4)))^(-1/AJ\$4)) (-270.8+13.16\*\$16+0.253\*\$16^2-17.57\*\$13\*AH\$3+50.73\*\$J6-1.115\*\$J6^2)\*@EXP(-0.3738\*(AH\$3+AH\$3)-0.5722\*(AH\$3+AH \$3)^2)\*\$8\$2 AJ6: ((-4.69+3.742\*AJ\$4+0.126\*AH\$4+0.065\*\$I6+0.146\*\$J6)) AK6: (-0.0408+0.0311\*AJ6-0.00024\*AJ6\*AH\$4-0.00213\*AH\$4+0.00549\*\$J6+0.04775\*AH\$3) AM6: (AO6/AR6) AN6: (\$E6) A06: (AP6) AP6: (AR6\*(1+AS6\*@EXP(AS6-AT6\*(\$E6-4)))^(-1/AS\$4)) R 6 (-270.8+13.16\*\$16+0.253\*\$16^2-17.57\*\$13\*AQ\$3+50.73\*\$J6-1.115\*\$J6^2)\*@EXP(-0.3738\*(AQ\$3+AQ\$3)-0.5722\*(AQ\$3+AQ \$3)^2)\*\$8\$2 AS6: ((-4.69+3.742\*AS\$4+0.126\*AQ\$4+0.065\*\$16+0.146\*\$J6)) AT6: (-0.0408+0.0311\*AS6-0.00024\*AS6\*A0\$4-0.00213\*A0\$4+0.00549\*\$J6+0.04775\*A0\$3) AV6: (AX6/BA6) AW6: (\$E6) AX6: (AY6) AY6: (BA6\*(1+BB6\*@EXP(BB6-BC6\*(\$E6-4)))^(-1/BB\$4)) 6 (-270.8+13.16\*\$16+0.253\*\$16^2-17.57\*\$13\*A2\$3+50.73\*\$J6-1.115\*\$J6^2)\*@EXP(-0.3738\*(A2\$3+A2\$3)-0.5722\*(A2\$3+A2 \$3)^2)\*\$B\$2 BB6: ((-4.69+3.742\*BB\$4+0.126\*AZ\$4+0.065\*\$16+0.146\*\$J6)) BC6: (-0.0408+0.0311\*BB6-0.00024\*BB6\*AZ\$4-0.00213\*AZ\$4+0.00549\*\$J6+0.04775\*AZ\$3) BE6: (BG6/BJ6) BF6: (\$E6) BG6: (BH6) BH6: (BJ6\*(1+BK6\*@EXP(BK6-BL6\*(\$E6-4)))^(-1/BK\$4)) 6 (-270.8+13.16\*\$16+0.253\*\$16^2-17.57\*\$13\*B1\$3+50.73\*\$J6-1.115\*\$J6^2)\*@EXP(-0.3738\*(B1\$3+B1\$3)-0.5722\*(B1\$3+B1 \$3)^2)\*\$B\$2 BK6: ((-4.69+3.742\*BK\$4+0.126\*BI\$4+0.065\*\$I6+0.146\*\$J6)) BL6: (-0.0408+0.0311\*BK6-0.00024\*BK6\*BI\$4-0.00213\*BI\$4+0.00549\*\$J6+0.04775\*BI\$3) BN6: (BP6/BS6) BO6: (\$E6) BP6: (BQ6) BQ6: (BS6\*(1+BT6\*@EXP(BT6-BU6\*(\$E6-4)))^(-1/BT\$4)) s (-270.8+13.16\*\$16+0.253\*\$16^2-17.57\*\$13\*BR\$3+50.73\*\$J6-1.115\*\$J6^2)\*@EXP(-0.3738\*(BR\$3+BR\$3)-0.5722\*(BR\$3+BR \$3)^2)\*\$8\$2 BT6: ((-4.69+3.742\*BT\$4+0.126\*BR\$4+0.065\*\$16+0.146\*\$J6)) BU6: (-0.0408+0.0311\*BT6-0.00024\*BT6\*BR\$4-0.00213\*BR\$4+0.00549\*\$J6+0.04775\*BR\$3) BW6: (BY6/CB6) BX6: (\$E6) BY6: (876) BZ6: (CB6\*(1+CC6\*@EXP(CC6-CD6\*(\$E6-4)))^(-1/CC\$4)) D (-270.8+13.16\*\$16+0.253\*\$16^2-17.57\*\$13\*CA\$3+50.73\*\$J6-1.115\*\$J6^2)\*@EXP(-0.3738\*(CA\$3+CA\$3)-0.5722\*(CA\$3+CA \$3)^2)\*\$R\$2 CC6: ((-4.69+3.742\*CC\$4+0.126\*CA\$4+0.065\*\$16+0.146\*\$J6)) CD6: (-0.0408+0.0311\*CC6-0.00024\*CC6\*CA\$4-0.00213\*CA\$4+0.00549\*\$J6+0.04775\*CA\$3) CF6: (CH6/CK6) CG6: (\$E6) CH6: (CI6) CI6: (CK6\*(1+CL6\*@EXP(CL6-CM6\*(\$E6-4)))^(-1/CL\$4)) C 6 (-270.8+13.16\*\$16+0.253\*\$16^2-17.57\*\$13\*CJ\$3+50.73\*\$J6-1.115\*\$J6^2)\*@EXP(-0.3738\*(CJ\$3+CJ\$3)-0.5722\*(CJ\$3+CJ \$3)^2)\*\$B\$2 CL6: ((-4.69+3.742\*CL\$4+0.126\*CJ\$4+0.065\*\$I6+0.146\*\$J6)) CM6: (-0.0408+0.0311\*CL6-0.00024\*CL6\*CJ\$4-0.00213\*CJ\$4+0.00549\*\$J6+0.04775\*CJ\$3) CO6: (CQ6/CT6)

CP6: (\$E6)

CO6: (CR6) CR6: (CT6\*(1+CU6\*@EXP(CU6-CV6\*(\$E6-4)))^(-1/CU\$4)) т 6 (-270.8+13.16\*\$16+0.253\*\$16^2-17.57\*\$13\*C\$\$3+50.73\*\$16-1.115\*\$16^2)\*@EXP(-0.3738\*(C\$\$3+C\$\$3)-0.5722\*(C\$\$3+c\$ \$3)^2)\*\$B\$2 CU6: ((-4.69+3.742\*CU\$4+0.126\*CS\$4+0.065\*\$16+0.146\*\$J6)) CV6: (-0.0408+0.0311\*CU6-0.00024\*CU6\*CS\$4-0.00213\*CS\$4+0.00549\*\$J6+0.04775\*CS\$3) CX6: (CZ6/DC6) CY6: (\$E6) CZ6: (DA6) DA6: (DC6\*(1+DD6\*@EXP(DD6-DE6\*(\$E6-4)))^(-1/DD\$4)) D c (-270.8+13.16\*\$16+0.253\*\$16^2-17.57\*\$13\*DB\$3+50.73\*\$J6-1.115\*\$J6^2)\*0EXP(-0.3738\*(DB\$3+DB\$3)-0.5722\*(DB\$3+DB \$3)^2)\*\$B\$2 DD6: ((-4.69+3.742\*DD\$4+0.126\*DB\$4+0.065\*\$I6+0.146\*\$J6)) DE6: (-0.0408+0.0311\*DD6-0.00024\*DD6\*DB\$4-0.00213\*DB\$4+0.00549\*\$J6+0.04775\*DB\$3) DG6: (D16/DL6) DH6: (\$E6) DI6: (DJ6) DJ6: (DL6\*(1+DM6\*@EXP(DM6-DN6\*(\$E6-4)))^(-1/DM\$4)) n 6 (-270.8+13.16\*\$16+0.253\*\$16^2-17.57\*\$13\*DK\$3+50.73\*\$J6-1.115\*\$J6^2)\*@EXP(-0.3738\*(DK\$3+DK\$3)-0.5722\*(DK\$3+DK \$3)^2)\*\$B\$2 DM6: ((-4.69+3.742\*DM\$4+0.126\*DK\$4+0.065\*\$I6+0.146\*\$J6)) DN6: (-0.0408+0.0311\*DM6-0.00024\*DM6\*DK\$4-0.00213\*DK\$4+0.00549\*\$J6+0.04775\*DK\$3) A7: 1 B7: (B6+(-0.099+0.0123\*\$J7-0.000085\*\$G7^2-0.000118\*\$H7^2)) C7: (@IF(B7<1.3\*B7.C6+(-0.3472+0.046\*J7-0.000373\*G7^2-0.000564\*H7^2))) D7: @IF(E7<\$A\$2,0,(C7-\$F\$2)/(\$E\$2-\$F\$2-1)) E7: (A7) F7: (C7+5) G7: 24.2 H7: 19.7 17: (G7-H7) J7: ((G7\*10)+(H7\*14))/24 K7: (N7+W7+AF7+A07+AX7+BG7+BP7+BY7+CH7+CQ7+CZ7+D17) L7: (L6+((P7-07)/Q7)) M7: ((@LN((((L7)^(1/(-1/\$R\$3)))-1)/R7)-R7)/-S7) N7: (N6+(P7-07)) 07: (07\*(1+R7\*@EXP(R7-S7\*(\$E7-5)))^(-1/\$R\$3)) P7: (Q7\*(1+R7\*@EXP(R7-S7\*(\$E7-4)))^(-1/\$R\$3)) Q7: (464.7+11.099\*17+0.348\*17^2)\*\$B\$2 R7: ((-1.311+3.875\*\$R\$3+0.115\*\$N\$3+0.052\*17)) s7: (-0.506257+0.106433\*R7+0.0241836\*J7) U7: (U6+((Y7-X7)/Z7)) V7: (E7) W7: (W6+(Y7-X7)) X7: (Z7\*(1+AA7\*@EXP(AA7-AB7\*(\$E7-5)))^(-1/AA\$4)) Y7: (Z7\*(1+AA7\*@EXP(AA7-AB7\*(\$E7-4)))^(-1/AA\$4)) (-270.8+13.16\*\$17+0.253\*\$17\*2-17.57\*\$14\*Y\$3+50.73\*\$J7-1.115\*\$J7\*2)\*@EXP(-0.3738\*(Y\$3+Y\$3)-0.5722\*(Y\$3+Y\$3)\*2 )\*\$8\$2 AA7: ((-4.69+3.742\*AA\$4+0.126\*Y\$4+0.065\*\$I7+0.146\*\$J7)) AB7: (-0.0408+0.0311\*AA7-0.00024\*AA7\*Y\$4-0.00213\*Y\$4+0.00549\*\$J7+0.04775\*Y\$3) AD7: (AD6+((AH7-AG7)/AI7)) AE7: (\$E7) AF7: (AF6+(AH7-AG7)) AG7: (AI7\*(1+AJ7\*@EXP(AJ7-AK7\*(\$E7-5)))^(-1/AJ\$4)) AH7: (AI7\*(1+AJ7\*@EXP(AJ7-AK7\*(\$E7-4)))^(-1/AJ\$4)) 7 (-270.8+13.16\*\$17+0.253\*\$17^2-17.57\*\$14\*AH\$3+50.73\*\$J7-1.115\*\$J7^2)\*@EXP(-0.3738\*(AH\$3+AH\$3)-0.5722\*(AH\$3+AH \$3)^2)\*\$B\$2 AJ7: ((-4.69+3.742\*AJ\$4+0.126\*AH\$4+0.065\*\$I7+0.146\*\$J7)) AK7: (-0.0408+0.0311\*AJ7-0.00024\*AJ7\*AH\$4-0.00213\*AH\$4+0.00549\*\$J7+0.04775\*AH\$3) AM7: (AM6+((AQ7-AP7)/AR7)) AN7: (\$E7) A07: (A06+(AQ7-AP7))

AP7: (AR7\*(1+AS7\*@EXP(AS7-AT7\*(\$E7-5)))^(-1/AS\$4)) AQ7: (AR7\*(1+AS7\*@EXP(AS7-AT7\*(\$E7-4)))^(-1/AS\$4)) R 7 (-270.8+13.16\*\$17+0.253\*\$17^2-17.57\*\$14\*AQ\$3+50.73\*\$J7-1.115\*\$J7^2)\*BEXP(-0.3738\*(AQ\$3+AQ\$3)-0.5722\*(AQ\$3+AQ \$3)^2)\*\$B\$2 AS7: ((-4.69+3.742\*AS\$4+0.126\*AQ\$4+0.065\*\$17+0.146\*\$J7)) AT7: (-0.0408+0.0311\*AS7-0.00024\*AS7\*AQ\$4-0.00213\*AQ\$4+0.00549\*\$J7+0.04775\*AQ\$3) AV7: (AV6+((AZ7-AY7)/BA7)) AW7: (\$E7) AX7: (AX6+(AZ7-AY7)) AY7: (BA7\*(1+BB7\*@EXP(BB7-BC7\*(\$E7-5)))^(-1/BB\$4)) AZ7: (BA7\*(1+BB7\*@EXP(BB7-BC7\*(\$E7-4)))^(-1/BB\$4)) 7 (-270.8+13.16\*\$17+0.253\*\$17^2-17.57\*\$14\*AZ\$3+50.73\*\$J7-1.115\*\$J7^2)\*0EXP(-0.3738\*(AZ\$3+AZ\$3)-0.5722\*(AZ\$3+AZ \$3)^2)\*\$B\$2 BB7: ((-4.69+3.742\*BB\$4+0.126\*AZ\$4+0.065\*\$17+0.146\*\$J7)) BC7: (-0.0408+0.0311\*BB7-0.00024\*BB7\*AZ\$4-0.00213\*AZ\$4+0.00549\*\$J7+0.04775\*AZ\$3) BE7: (BE6+((B17-BH7)/BJ7)) BF7: (\$E7) BG7: (BG6+(BI7-BH7)) BH7: (BJ7\*(1+BK7\*@EXP(BK7-BL7\*(\$E7-5)))^(-1/BK\$4)) BI7: (BJ7\*(1+BK7\*@EXP(BK7-BL7\*(\$E7-4)))^(-1/BK\$4)) 7 (-270.8+13.16\*\$17+0.253\*\$17^2-17.57\*\$14\*B1\$3+50.73\*\$J7-1.115\*\$J7^2)\*@EXP(-0.3738\*(B1\$3+B1\$3)-0.5722\*(B1\$3+B1 \$3)^2)\*\$B\$2 BK7: ((-4.69+3.742\*BK\$4+0.126\*B1\$4+0.065\*\$17+0.146\*\$J7)) BL7: (-0.0408+0.0311\*BK7-0.00024\*BK7\*B1\$4-0.00213\*B1\$4+0.00549\*\$J7+0.04775\*B1\$3) BN7: (BN6+((BR7-BQ7)/BS7)) BO7: (\$E7) BP7: (BP6+(BR7-BQ7)) BQ7: (BS7\*(1+BT7\*@EXP(BT7-BU7\*(\$E7-5)))^(-1/BT\$4)) BR7: (BS7\*(1+BT7\*@EXP(BT7-BU7\*(\$E7-4)))^(-1/BT\$4)) R S 7 (-270.8+13.16\*\$17+0.253\*\$17^2-17.57\*\$14\*BR\$3+50.73\*\$17-1.115\*\$17^2)\*@EXP(-0.3738\*(BR\$3+BR\$3)-0.5722\*(BR\$3+BR \$3)^2)\*\$8\$2 BT7: ((-4.69+3.742\*BT\$4+0.126\*BR\$4+0.065\*\$I7+0.146\*\$J7)) BU7: (-0.0408+0.0311\*BT7-0.00024\*BT7\*BR\$4-0.00213\*BR\$4+0.00549\*\$J7+0.04775\*BR\$3) BW7: (BW6+((CA7-BZ7)/CB7)) BX7: (\$E7) BY7: (BY6+(CA7-BZ7)) BZ7: (CB7\*(1+CC7\*@EXP(CC7-CD7\*(\$E7-5)))^(-1/CC\$4)) CA7: (CB7\*(1+CC7\*@EXP(CC7-CD7\*(\$E7-4)))^(-1/CC\$4)) (-270.8+13.16\*\$17+0.253\*\$17^2-17.57\*\$14\*CA\$3+50.73\*\$J7-1.115\*\$J7^2)\*@EXP(-0.3738\*(CA\$3+CA\$3)-0.5722\*(CA\$3+CA \$3)^2)\*\$8\$2 CC7: ((-4.69+3.742\*CC\$4+0.126\*CA\$4+0.065\*\$17+0.146\*\$J7)) CD7: (-0.0408+0.0311\*CC7-0.00024\*CC7\*CA\$4-0.00213\*CA\$4+0.00549\*\$J7+0.04775\*CA\$3) CF7: (CF6+((CJ7-C17)/CK7)) CG7: (\$E7) CH7: (CH6+(CJ7-CI7)) CI7: (CK7\*(1+CL7\*@EXP(CL7-CM7\*(\$E7-5)))^(-1/CL\$4)) CJ7: (CK7\*(1+CL7\*@EXP(CL7-CM7\*(\$E7-4)))^(-1/CL\$4)) ĸ 7 (-270.8+13.16\*\$17+0.253\*\$17^2-17.57\*\$14\*CJ\$3+50.73\*\$J7-1.115\*\$J7^2)\*0EXP(-0.3738\*(CJ\$3+CJ\$3)-0.5722\*(CJ\$3+CJ \$31^21\*\$8\$2 CL7: ((-4.69+3.742\*CL\$4+0.126\*CJ\$4+0.065\*\$17+0.146\*\$J7)) CM7: (-0.0408+0.0311\*CL7-0.00024\*CL7\*CJ\$4-0.00213\*CJ\$4+0.00549\*\$J7+0.04775\*CJ\$3) CO7: (CO6+((CS7-CR7)/CT7)) CP7: (\$E7) CQ7: (CQ6+(CS7-CR7)) CR7: (CT7\*(1+CU7\*@EXP(CU7-CV7\*(\$E7-5)))^(-1/CU\$4)) CS7: (CT7\*(1+CU7\*@EXP(CU7-CV7\*(\$E7-4)))^(-1/CU\$4)) 0 т 7 (-270.8+13.16\*\$17+0.253\*\$17^2-17.57\*\$14\*C\$\$3+50.73\*\$J7-1.115\*\$J7^2)\*@EXP(-0.3738\*(C\$\$3+C\$\$3)-0.5722\*(C\$\$3+c\$ \$3)^2)\*\$B\$2 CU7: ((-4.69+3.742\*CU\$4+0.126\*CS\$4+0.065\*\$17+0.146\*\$J7)) CV7: (-0.0408+0.0311\*CU7-0.00024\*CU7\*CS\$4-0.00213\*CS\$4+0.00549\*\$J7+0.04775\*CS\$3)
CX7: (CX6+((DB7-DA7)/DC7)) CY7: (\$E7) CZ7: (CZ6+(DB7-DA7)) DA7: (DC7\*(1+DD7\*@EXP(DD7-DE7\*(\$E7-5)))^(-1/DD\$4)) DB7: (DC7\*(1+DD7\*@EXP(DD7-DE7\*(\$E7-4)))^(-1/DD\$4)) С 7 (-270.8+13.16\*\$17+0.253\*\$17^2-17.57\*\$14\*DB\$3+50.73\*\$J7-1.115\*\$J7^2)\*@EXP(-0.3738\*(DB\$3+DB\$3)-0.5722\*(DB\$3+DB \$3)^2)\*\$B\$2 DD7: ((-4.69+3.742\*DD\$4+0.126\*DB\$4+0.065\*\$I7+0.146\*\$J7)) DE7: (-0.0408+0.0311\*DD7-0.00024\*DD7\*DB\$4-0.00213\*DB\$4+0.00549\*\$J7+0.04775\*DB\$3) DG7: (DG6+((DK7-DJ7)/DL7)) DH7: (\$E7) D17: (D16+(DK7-DJ7)) DJ7: (DL7\*(1+DM7\*@EXP(DM7-DN7\*(\$E7-5)))^(-1/DM\$4)) DK7: (DL7\*(1+DM7\*@EXP(DM7-DN7\*(\$E7-4)))^(-1/DM\$4)) 7 D 1 (-270.8+13.16\*\$17+0.253\*\$17^2-17.57\*\$14\*DK\$3+50.73\*\$J7-1.115\*\$J7^2)\*@EXP(-0.3738\*(DK\$3+DK\$3)-0.5722\*(DK\$3+DK \$3)^2)\*\$8\$2 DM7: ((-4.69+3.742\*DM\$4+0.126\*DK\$4+0.065\*\$17+0.146\*\$J7)) DN7: (-0.0408+0.0311\*DM7-0.00024\*DM7\*DK\$4-0.00213\*DK\$4+0.00549\*\$J7+0.04775\*DK\$3) 48. 2 B8: (B7+(-0.099+0.0123\*\$J8-0.000085\*\$G8^2-0.000118\*\$H8^2)) C8: (aIF(B8<1,3\*B8,C7+(-0.3472+0.046\*J8-0.000373\*G8^2-0.000564\*H8^2))) D8: @IF(E8<\$A\$2,0,(C8-\$F\$2)/(\$E\$2-\$F\$2-1)) F8. (A8) F8: (C8+5) G8: 21.9 H8: 19.9 18: (G8-H8) J8: ((G8\*10)+(H8\*14))/24 K8: (N8+W8+AF8+A08+AX8+BG8+BP8+BY8+CH8+CQ8+CZ8+D18) L8: (L7+((P8-08)/98)) M8: ((@LN((((L7)^(1/(-1/\$R\$3)))-1)/R8)-R8)/-S8)+1 N8: (N7+(P8-08)) 08: (Q8\*(1+R8\*@EXP(R8-S8\*(M8-1)))^(-1/\$R\$3)) P8: (Q8\*(1+R8\*@EXP(R8-S8\*(M8)))^(-1/\$R\$3)) 98: (464.7+11.099\*18+0.348\*18^2)\*\$B\$2 R8: ((-1.311+3.875\*\$R\$3+0.115\*\$N\$3+0.052\*18)) \$8: (-0.506257+0.106433\*R8+0.0241836\*J8) U8: (U7+((Y8-X8)/Z8)) V8: ((@LN((((U7)^(1/(-1/AA\$4)))-1)/AA8)-AA8)/-AB8)+1 W8: (W7+(Y8-X8)) X8: (Z8\*(1+AA8\*@EXP(AA8-AB8\*(V8-1)))^(-1/AA\$4)) Y8: (Z8\*(1+AA8\*@EXP(AA8-AB8\*(V8)))^(-1/AA\$4)) z 8 (-270.8+13.16\*\$18+0.253\*\$18^2-17.57\*\$15\*Y\$3+50.73\*\$J8-1.115\*\$J8^2)\*@EXP(-0.3738\*(Y\$3+Y\$3)-0.5722\*(Y\$3+Y\$3)^2 >\*\$B\$2 AA8: ((-4.69+3.742\*AA\$4+0.126\*Y\$4+0.065\*\$18+0.146\*\$J8)) AB8: (-0.0408+0.0311\*AA8-0.00024\*AA8\*Y\$4-0.00213\*Y\$4+0.00549\*\$J8+0.04775\*Y\$3) AD8: (AD7+((AH8-AG8)/A18)) AE8: ((@LN((((AD7)^(1/(-1/AJ\$4)))-1)/AJ8)-AJ8)/-AK8)+1 AF8: (AF7+(AH8-AG8)) AG8: (A18\*(1+AJ8\*@EXP(AJ8-AK8\*(AE8-1)))^(-1/AJ\$4)) AH8: (A18\*(1+AJ8\*@EXP(AJ8-AK8\*(AE8)))^(-1/AJ\$4)) 8 (-270.8+13.16\*\$18+0.253\*\$18\*2-17.57\*\$15\*AH\$3+50.73\*\$J8-1.115\*\$J8\*2)\*@EXP(-0.3738\*(AH\$3+AH\$3)-0.5722\*(AH\$3+AH \$3)^2)\*\$B\$2 AJ8: ((-4.69+3.742\*AJ\$4+0.126\*AH\$4+0.065\*\$I8+0.146\*\$J8)) AK8: (-0.0408+0.0311\*AJ8-0.00024\*AJ8\*AH\$4-0.00213\*AH\$4+0.00549\*\$J8+0.04775\*AH\$3) AM8: (AM7+((AQ8-AP8)/AR8)) AN8: ((@LN((((AM7)^(1/(-1/AS\$4)))-1)/AS8)-AS8)/-AT8)+1 A08: (A07+(A08-AP8)) AP8: (AR8\*(1+AS8\*@EXP(AS8-AT8\*(AN8-1)))^(-1/AS\$4)) AQ8: (AR8\*(1+AS8\*@EXP(AS8-AT8\*(AN8)))^(-1/AS\$4)) R 8

(-270.8+13.16\*\$18+0.253\*\$18^2-17.57\*\$15\*AQ\$3+50.73\*\$J8-1.115\*\$J8^2)\*@EXP(-0.3738\*(AQ\$3+AQ\$3)-0.5722\*(AQ\$3+AQ \$3)^2)\*\$8\$2

AS8: ((-4.69+3.742\*AS\$4+0.126\*AQ\$4+0.065\*\$18+0.146\*\$J8)) AT8: (-0.0408+0.0311\*AS8-0.00024\*AS8\*AQ\$4-0.00213\*AQ\$4+0.00549\*\$J8+0.04775\*AQ\$3) AV8: (AV7+((AZ8-AY8)/BA8)) AW8: ((@LN((((AV7)^(1/(-1/BB\$4)))-1)/BB8)-BB8)/-BC8)+1 AX8: (AX7+(AZ8-AY8)) AY8: (BA8\*(1+BB8\*@EXP(BB8-BC8\*(AW8-1)))^(-1/BB\$4)) AZ8: (BA8\*(1+BB8\*@EXP(BB8-BC8\*(AW8)))^(-1/BB\$4)) 8 (-270.8+13.16\*\$18+0.253\*\$18^2-17.57\*\$15\*AZ\$3+50.73\*\$J8-1.115\*\$J8^2)\*@EXP(-0.3738\*(AZ\$3+AZ\$3)-0.5722\*(AZ\$3+AZ \$3)^2)\*\$R\$2 BB8: ((-4.69+3.742\*BB\$4+0.126\*AZ\$4+0.065\*\$18+0.146\*\$J8)) BC8: (-0.0408+0.0311\*BB8-0.00024\*BB8\*AZ\$4-0.00213\*AZ\$4+0.00549\*\$J8+0.04775\*AZ\$3) BE8: (BE7+((BI8-BH8)/BJ8)) BF8: ((@LN((((BE7)^(1/(-1/BK\$4)))-1)/BK8)-BK8)/-BL8)+1 BG8: (BG7+(B18-BH8)) BH8: (BJ8\*(1+BK8\*@EXP(BK8-BL8\*(BF8-1)))^(-1/BK\$4)) BI8: (BJ8\*(1+BK8\*@EXP(BK8-BL8\*(BF8)))^(-1/BK\$4)) 8 D (-270.8+13.16\*\$I8+0.253\*\$I8^2-17.57\*\$I5\*BI\$3+50.73\*\$J8-1.115\*\$J8^2)\*@EXP(-0.3738\*(BI\$3+BI\$3)-0.5722\*(BI\$3+BI \$3)^2)\*\$B\$2 BK8: ((-4.69+3.742\*BK\$4+0.126\*BI\$4+0.065\*\$I8+0.146\*\$J8)) BL8: (-0.0408+0.0311\*BK8-0.00024\*BK8\*B1\$4-0.00213\*B1\$4+0.00549\*\$J8+0.04775\*B1\$3) BN8: (BN7+((BR8-BQ8)/BS8)) BO8: ((@LN((((BN7)^(1/(-1/BT\$4)))-1)/BT8)-BT8)/-BU8)+1 BP8: (BP7+(BR8-BQ8)) BQ8: (BS8\*(1+BT8\*@EXP(BT8-BU8\*(BO8-1)))^(-1/BT\$4)) BR8: (BS8\*(1+BT8\*@EXP(BT8-BU8\*(B08)))^(-1/BT\$4)) 8 (-270,8+13,16\*\$I8+0,253\*\$I8^2-17.57\*\$I5\*BR\$3+50.73\*\$J8-1.115\*\$J8^2)\*aEXP(-0.3738\*(BR\$3+BR\$3)-0.5722\*(BR\$3+BR \$3)^2)\*\$8\$2 BT8: ((-4.69+3.742\*BT\$4+0.126\*BR\$4+0.065\*\$18+0.146\*\$J8)) BU8: (-0.0408+0.0311\*BT8-0.00024\*BT8\*BR\$4-0.00213\*BR\$4+0.00549\*\$J8+0.04775\*BR\$3) BW8: (BW7+((CA8-BZ8)/CB8)) BX8: ((@LN((((BW7)^(1/(-1/CC\$4)))-1)/CC8)-CC8)/-CD8)+1 BY8: (BY7+(CA8-BZ8)) BZ8: (CB8\*(1+CC8\*@EXP(CC8-CD8\*(BX8-1)))^(-1/CC\$4)) CA8: (CB8\*(1+CC8\*@EXP(CC8-CD8\*(BX8)))^(-1/CC\$4)) C в 8 (-270.8+13.16\*\$18+0.253\*\$18^2-17.57\*\$15\*CA\$3+50.73\*\$J8-1.115\*\$J8^2)\*@EXP(-0.3738\*(CA\$3+CA\$3)-0.5722\*(CA\$3+CA \$3)^2)\*\$8\$2 CC8: ((-4.69+3.742\*CC\$4+0.126\*CA\$4+0.065\*\$18+0.146\*\$J8)) CD8: (-0.0408+0.0311\*CC8-0.00024\*CC8\*CA\$4-0.00213\*CA\$4+0.00549\*\$J8+0.04775\*CA\$3) CF8: (CF7+((CJ8-CI8)/CK8)) CG8: ((@LN((((CF7)^(1/(-1/CL\$4)))-1)/CL8)-CL8)/-CM8)+1 CH8: (CH7+(CJ8-CI8)) CI8: (CK8\*(1+CL8\*@EXP(CL8-CM8\*(CG8-1)))^(-1/CL\$4)) CJ8: (CK8\*(1+CL8\*@EXP(CL8-CM8\*(CG8)))^(-1/CL\$4)) c 8 (-270.8+13.16\*\$18+0.253\*\$18^2-17.57\*\$15\*CJ\$3+50.73\*\$J8-1.115\*\$J8^2)\*aEXP(-0.3738\*(CJ\$3+CJ\$3)-0.5722\*(CJ\$3+CJ \$3)^2)\*\$8\$2 CL8: ((-4.69+3.742\*CL\$4+0.126\*CJ\$4+0.065\*\$18+0.146\*\$J8)) CM8: (-0.0408+0.0311\*CL8-0.00024\*CL8\*CJ\$4-0.00213\*CJ\$4+0.00549\*\$J8+0.04775\*CJ\$3) CO8: (CO7+((CS8-CR8)/CT8)) CP8: ((aLN((((CO7)^(1/(-1/CU\$4)))-1)/CU8)-CU8)/-CV8)+1 CQ8: (CQ7+(CS8-CR8)) CR8: (CT8\*(1+CU8\*@EXP(CU8-CV8\*(CP8-1)))^(-1/CU\$4)) CS8: (CT8\*(1+CU8\*@EXP(CU8-CV8\*(CP8)))^(-1/CU\$4)) (-270.8+13.16\*\$18+0.253\*\$18^2-17.57\*\$15\*C\$\$3+50.73\*\$J8-1.115\*\$J8^2)\*@EXP(-0.3738\*(C\$\$3+C\$\$3)-0.5722\*(C\$\$3+C\$ \$3)^2)\*\$B\$2 CU8: ((-4.69+3.742\*CU\$4+0.126\*CS\$4+0.065\*\$18+0.146\*\$J8)) CV8: (-0.0408+0.0311\*CU8-0.00024\*CU8\*CS\$4-0.00213\*CS\$4+0.00549\*\$J8+0.04775\*CS\$3) CX8: (CX7+((DB8-DA8)/DC8)) CY8: ((@LN((((CX7)^(1/(-1/DD\$4)))-1)/DD8)-DD8)/-DE8)+1 CZ8: (CZ7+(DB8-DA8)) DA8: (DC8\*(1+DD8\*@EXP(DD8-DE8\*(CY8-1)))^(-1/DD\$4)) DB8: (DC8\*(1+DD8\*@EXP(DD8-DE8\*(CY8)))^(-1/DD\$4))

n r 8 (-270,8+13,16\*\$18+0,253\*\$18^2-17,57\*\$15\*DB\$3+50,73\*\$J8-1,115\*\$J8^2)\*aEXP(-0.3738\*(DB\$3+DB\$3)-0.5722\*(DB\$3+DB \$3)^2)\*\$8\$2 DD8: ((-4.69+3.742\*DD\$4+0.126\*DB\$4+0.065\*\$18+0.146\*\$J8)) DE8: (-0.0408+0.0311\*DD8-0.00024\*DD8\*DB\$4-0.00213\*DB\$4+0.00549\*\$J8+0.04775\*DB\$3) DG8: (DG7+((DK8-DJ8)/DL8)) DH8: ((@LN((((DG7)^(1/(-1/DM\$4)))-1)/DM8)-DM8)/-DN8)+1 D18: (D17+(DK8-DJ8)) DJ8: (DL8\*(1+DM8\*@EXP(DM8-DN8\*(DH8-1)))^(-1/DM\$4)) DK8: (DL8\*(1+DM8\*@EXP(DM8-DN8\*(DH8)))^(-1/DM\$4)) n 8 (-270.8+13.16\*\$18+0.253\*\$18^2-17.57\*\$15\*DK\$3+50.73\*\$J8-1.115\*\$J8^2)\*@EXP(-0.3738\*(DK\$3+DK\$3)-0.5722\*(DK\$3+DK \$3)^2)\*\$8\$2 DM8: ((-4.69+3.742\*DM\$4+0.126\*DK\$4+0.065\*\$18+0.146\*\$J8)) DN8: (-0.0408+0.0311\*DM8-0.00024\*DM8\*DK\$4-0.00213\*DK\$4+0.00549\*\$J8+0.04775\*DK\$3) A9: 3 B9: (B8+(-0.099+0.0123\*\$J9-0.000085\*\$G9^2-0.000118\*\$H9^2)) C9: (@IF(B9<1,3\*B9,C8+(-0.3472+0.046\*J9-0.000373\*G9^2-0.000564\*H9^2))) D9: @IF(E9<\$A\$2.0.(C9-\$F\$2)/(\$E\$2-\$F\$2-1)) E9: (A9) F9: (C9+5) G9: 21.9 H9: 20.3 19: (G9-H9) J9: ((G9\*10)+(H9\*14))/24 K9: (N9+W9+AF9+A09+AX9+BG9+BP9+BY9+CH9+CQ9+CZ9+D19) L9: (L8+((P9-09)/09)) M9: ((@LN((((L8)^(1/(-1/\$R\$3)))-1)/R9)-R9)/-S9)+1 N9: (N8+(P9-09)) 09: (Q9\*(1+R9\*@EXP(R9-S9\*(M9-1)))^(-1/\$R\$3)) P9: (99\*(1+R9\*@EXP(R9-S9\*(M9)))^(-1/\$R\$3)) Q9: (464.7+11.099\*19+0.348\*19^2)\*\$B\$2 R9: ((-1.311+3.875\*\$R\$3+0.115\*\$N\$3+0.052\*19)) s9: (-0.506257+0.106433\*R9+0.0241836\*J9) U9: (U8+((Y9-X9)/Z9)) V9: ((@LN((((U8)^(1/(-1/AA\$4)))-1)/AA9)-AA9)/-AB9)+1 W9: (W8+(Y9-X9)) X9: (Z9\*(1+AA9\*@EXP(AA9-AB9\*(V9-1)))^(-1/AA\$4)) Y9: (Z9\*(1+AA9\*@EXP(AA9-AB9\*(V9)))^(-1/AA\$4)) 0 7 1\*\$R\$2 AA9: ((-4.69+3.742\*AA\$4+0.126\*Y\$4+0.065\*\$I9+0.146\*\$J9)) AB9: (-0.0408+0.0311\*AA9-0.00024\*AA9\*Y\$4-0.00213\*Y\$4+0.00549\*\$J9+0.04775\*Y\$3) AD9: (AD8+((AH9-AG9)/A19)) AE9: ((@LN((((AD8)^(1/(-1/AJ\$4)))-1)/AJ9)-AJ9)/-AK9)+1 AF9: (AF8+(AH9-AG9)) AG9: (AI9\*(1+AJ9\*@EXP(AJ9-AK9\*(AE9-1)))^(-1/AJ\$4)) AH9: (AI9\*(1+AJ9\*@EXP(AJ9-AK9\*(AE9)))^(-1/AJ\$4)) 0 (-270.8+13.16\*\$19+0.253\*\$19^2-17.57\*\$16\*AH\$3+50.73\*\$J9-1.115\*\$J9^2)\*@EXP(-0.3738\*(AH\$3+AH\$3)-0.5722\*(AH\$3+AH \$3)^2)\*\$8\$2 AJ9: ((-4.69+3.742\*AJ\$4+0.126\*AH\$4+0.065\*\$19+0.146\*\$J9)) AK9: (-0.0408+0.0311\*AJ9-0.00024\*AJ9\*AH\$4-0.00213\*AH\$4+0.00549\*\$J9+0.04775\*AH\$3) AM9: (AM8+((AQ9-AP9)/AR9)) AN9: ((@LN((((AM8)^(1/(-1/AS\$4)))-1)/AS9)-AS9)/-AT9)+1 409 · (408+(409-4P9)) AP9: (AR9\*(1+AS9\*@EXP(AS9-AT9\*(AN9-1)))^(-1/AS\$4)) AQ9: (AR9\*(1+AS9\*@EXP(AS9-AT9\*(AN9)))^(-1/AS\$4)) (-270.8+13.16\*\$19+0.253\*\$19^2-17.57\*\$16\*AQ\$3+50.73\*\$J9-1.115\*\$J9^2)\*@EXP(-0.3738\*(AQ\$3+AQ\$3)-0.5722\*(AQ\$3+AQ \$3)^2)\*\$B\$2 AS9: ((-4.69+3.742\*AS\$4+0.126\*AQ\$4+0.065\*\$19+0.146\*\$J9)) AT9: (-0.0408+0.0311\*AS9-0.00024\*AS9\*AQ\$4-0.00213\*AQ\$4+0.00549\*\$J9+0.04775\*AQ\$3) AV9: (AV8+((AZ9-AY9)/BA9)) AW9: ((@LN((((AV8)^(1/(-1/BB\$4)))-1)/BB9)-BB9)/-BC9)+1 AX9: (AX8+(AZ9-AY9))

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AY9: (BA9\*(1+BB9\*@EXP(BB9-BC9\*(AW9-1)))^(-1/BB\$4)) AZ9: (BA9\*(1+BB9\*@EXP(BB9-BC9\*(AW9)))^(-1/BB\$4)) В 9 A (-270.8+13.16\*\$I9+0.253\*\$I9^2-17.57\*\$I6\*AZ\$3+50.73\*\$J9-1.115\*\$J9^2)\*@EXP(-0.3738\*(AZ\$3+AZ\$3)-0.5722\*(AZ\$3+AZ \$3)^2)\*\$B\$2 BB9: ((-4.69+3.742\*BB\$4+0.126\*AZ\$4+0.065\*\$19+0.146\*\$J9)) BC9: (-0.0408+0.0311\*BB9-0.00024\*BB9\*AZ\$4-0.00213\*AZ\$4+0.00549\*\$J9+0.04775\*AZ\$3) BE9: (BE8+((BI9-BH9)/BJ9)) BF9: ((@LN((((BE8)^(1/(-1/BK\$4)))-1)/BK9)-BK9)/-BL9)+1 BG9: (BG8+(B19-BH9)) BH9: (BJ9\*(1+BK9\*@EXP(BK9-BL9\*(BF9-1)))^(-1/BK\$4)) BI9: (BJ9\*(1+BK9\*@EXP(BK9-BL9\*(BF9)))^(-1/BK\$4)) R 0 (-270.8+13.16\*\$I9+0.253\*\$I9^2-17.57\*\$I6\*BI\$3+50.73\*\$J9-1.115\*\$J9^2)\*@EXP(-0.3738\*(BI\$3+BI\$3)-0.5722\*(BI\$3+BI \$3)^2)\*\$8\$2 BK9: ((-4.69+3.742\*BK\$4+0.126\*BI\$4+0.065\*\$I9+0.146\*\$J9)) BL9: (-0.0408+0.0311\*BK9-0.00024\*BK9\*BI\$4-0.00213\*BI\$4+0.00549\*\$J9+0.04775\*BI\$3) BN9: (BN8+((BR9-BQ9)/BS9)) BO9: ((@LN((((BN8)^(1/(-1/BT\$4)))-1)/BT9)-BT9)/-BU9)+1 BP9: (BP8+(BR9-BQ9)) BQ9: (BS9\*(1+BT9\*@EXP(BT9-BU9\*(B09-1)))^(-1/BT\$4)) BR9: (BS9\*(1+BT9\*@EXP(BT9-BU9\*(B09)))^(-1/BT\$4)) 0 R S (-270.8+13.16\*\$I9+0.253\*\$I9^2-17.57\*\$I6\*BR\$3+50.73\*\$J9-1.115\*\$J9^2)\*@EXP(-0.3738\*(BR\$3+BR\$3)-0.5722\*(BR\$3+BR \$3)^2)\*\$B\$2 BT9: ((-4.69+3.742\*BT\$4+0.126\*BR\$4+0.065\*\$19+0.146\*\$J9)) BU9: (-0.0408+0.0311\*BT9-0.00024\*BT9\*BR\$4-0.00213\*BR\$4+0.00549\*\$J9+0.04775\*BR\$3) BW9: (BW8+((CA9-BZ9)/CB9)) BX9: ((@LN((((BW8)^(1/(-1/CC\$4)))-1)/CC9)-CC9)/-CD9)+1 BY9: (BY8+(CA9-BZ9)) BZ9: (CB9\*(1+CC9\*@EXP(CC9-CD9\*(BX9-1)))^(-1/CC\$4)) CA9: (CB9\*(1+CC9\*@EXP(CC9-CD9\*(BX9)))^(-1/CC\$4)) С 9 B (-270.8+13.16\*\$19+0.253\*\$19^2-17.57\*\$16\*CA\$3+50.73\*\$J9-1.115\*\$J9^2)\*@EXP(-0.3738\*(CA\$3+CA\$3)-0.5722\*(CA\$3+CA \$3)^2)\*\$B\$2 CC9: ((-4.69+3.742\*CC\$4+0.126\*CA\$4+0.065\*\$I9+0.146\*\$J9)) CD9: (-0.0408+0.0311\*CC9-0.00024\*CC9\*CA\$4-0.00213\*CA\$4+0.00549\*\$J9+0.04775\*CA\$3) CF9: (CF8+((CJ9-CI9)/CK9)) CG9: ((@LN((((CF8)^(1/(-1/CL\$4)))-1)/CL9)-CL9)/-CM9)+1 CH9: (CH8+(CJ9-CI9)) CI9: (CK9\*(1+CL9\*@EXP(CL9-CM9\*(CG9-1)))^(-1/CL\$4)) CJ9: (CK9\*(1+CL9\*@EXP(CL9-CM9\*(CG9)))^(-1/CL\$4)) 0 C K (-270.8+13.16\*\$I9+0.253\*\$I9^2-17.57\*\$I6\*CJ\$3+50.73\*\$J9-1.115\*\$J9^2)\*@EXP(-0.3738\*(CJ\$3+CJ\$3)-0.5722\*(CJ\$3+CJ \$3)^2)\*\$B\$2 CL9: ((-4.69+3.742\*CL\$4+0.126\*CJ\$4+0.065\*\$19+0.146\*\$J9)) CM9: (-0.0408+0.0311\*CL9-0.00024\*CL9\*CJ\$4-0.00213\*CJ\$4+0.00549\*\$J9+0.04775\*CJ\$3) CO9: (CO8+((CS9-CR9)/CT9)) CP9: ((@LN((((CO8)^(1/(-1/CU\$4)))-1)/CU9)-CU9)/-CV9)+1 CQ9: (CQ8+(CS9-CR9)) CR9: (CT9\*(1+CU9\*@EXP(CU9-CV9\*(CP9-1)))^(-1/CU\$4)) CS9: (CT9\*(1+CU9\*@EXP(CU9-CV9\*(CP9)))^(-1/CU\$4)) С Т 9 (-270.8+13.16\*\$I9+0.253\*\$I9^2-17.57\*\$I6\*C\$\$3+50.73\*\$J9-1.115\*\$J9^2)\*0EXP(-0.3738\*(C\$\$3+C\$\$3)-0.5722\*(C\$\$3+C\$ \$3)^2)\*\$B\$2 CU9: ((-4.69+3.742\*CU\$4+0.126\*CS\$4+0.065\*\$19+0.146\*\$J9)) CV9: (-0.0408+0.0311\*CU9-0.00024\*CU9\*CS\$4-0.00213\*CS\$4+0.00549\*\$J9+0.04775\*CS\$3) CX9: (CX8+((DB9-DA9)/DC9)) CY9: ((@LN((((CX8)^(1/(-1/DD\$4)))-1)/DD9)-DD9)/-DE9)+1 CZ9: (CZ8+(DB9-DA9)) DA9: (DC9\*(1+DD9\*@EXP(DD9-DE9\*(CY9-1)))^(-1/DD\$4)) DB9: (DC9\*(1+DD9\*@EXP(DD9-DE9\*(CY9)))^(-1/DD\$4)) D С 9 (-270.8+13.16\*\$I9+0.253\*\$I9^2-17.57\*\$I6\*DB\$3+50.73\*\$J9-1.115\*\$J9^2)\*@EXP(-0.3738\*(DB\$3+DB\$3)-0.5722\*(DB\$3+DB \$3)^2)\*\$B\$2 DD9: ((-4.69+3.742\*DD\$4+0.126\*DB\$4+0.065\*\$I9+0.146\*\$J9)) DE9: (-0.0408+0.0311\*DD9-0.00024\*DD9\*DB\$4-0.00213\*DB\$4+0.00549\*\$J9+0.04775\*DB\$3)

DG9: (DG8+((DK9-DJ9)/DL9)) DH9: ((@LN((((DG8)^(1/(-1/DM\$4)))-1)/DM9)-DM9)/-DN9)+1 D19: (D18+(DK9-DJ9)) DJ9: (DL9\*(1+DM9\*@EXP(DM9-DN9\*(DH9-1)))^(-1/DM\$4)) DK9: (DL9\*(1+DM9\*@EXP(DM9-DN9\*(DH9)))^(-1/DM\$4)) ٥ n (-270.8+13.16\*\$19+0.253\*\$19^2-17.57\*\$16\*DK\$3+50.73\*\$J9-1.115\*\$J9^2)\*@EXP(-0.3738\*(DK\$3+DK\$3)-0.5722\*(DK\$3+DK \$3)^2)\*\$B\$2 DM9: ((-4.69+3.742\*DM\$4+0.126\*DK\$4+0.065\*\$I9+0.146\*\$J9)) DN9: (-0.0408+0.0311\*DM9-0.00024\*DM9\*DK\$4-0.00213\*DK\$4+0.00549\*\$J9+0.04775\*DK\$3) A10: 4 B10: (B9+(-0.099+0.0123\*\$J10-0.000085\*\$G10^2-0.000118\*\$H10^2)) C10: (@IF(B10<1,3\*B10,C9+(-0.3472+0.046\*J10-0.000373\*G10^2-0.000564\*H10^2))) D10: @IF(E10<\$A\$2,0,(C10-\$F\$2)/(\$E\$2-\$F\$2-1)) E10: (A10) F10: (C10+5) G10: 22.6 H10: 21.7 I10: (G10-H10) J10: ((G10\*10)+(H10\*14))/24 K10: (N10+W10+AF10+AO10+AX10+BG10+BP10+BY10+CH10+CQ10+CZ10+DI10) L10: (L9+((P10-010)/Q10)) M10: ((@LN((((L9)^(1/(-1/\$R\$3)))-1)/R10)-R10)/-S10)+1 N10: (N9+(P10-010)) 010: (Q10\*(1+R10\*@EXP(R10-S10\*(M10-1)))^(-1/\$R\$3)) P10: (Q10\*(1+R10\*@EXP(R10-S10\*(M10)))^(-1/\$R\$3)) Q10: (464.7+11.099\*I10+0.348\*I10^2)\*\$B\$2 R10: ((-1.311+3.875\*\$R\$3+0.115\*\$N\$3+0.052\*110)) \$10: (-0.506257+0.106433\*R10+0.0241836\*J10) U10: (U9+((Y10-X10)/Z10)) V10: ((@LN((((U9)^(1/(-1/AA\$4)))-1)/AA10)-AA10)/-AB10)+1 W10: (W9+(Y10-X10)) X10: (Z10\*(1+AA10\*@EXP(AA10-AB10\*(V10-1)))^(-1/AA\$4)) Y10: (Z10\*(1+AA10\*@EXP(AA10-AB10\*(V10)))^(-1/AA\$4)) Ω 7 1 (-270.8+13.16\*\$I10+0.253\*\$I10^2-17.57\*\$I7\*Y\$3+50.73\*\$J10-1.115\*\$J10^2)\*@EXP(-0.3738\*(Y\$3+Y\$3)-0.5722\*(Y\$3+Y\$ 3)^2)\*\$B\$2 AA10: ((-4.69+3.742\*AA\$4+0.126\*Y\$4+0.065\*\$110+0.146\*\$J10)) AB10: (-0.0408+0.0311\*AA10-0.00024\*AA10\*Y\$4-0.00213\*Y\$4+0.00549\*\$J10+0.04775\*Y\$3) AD10: (AD9+((AH10-AG10)/AI10)) AE10: ((@LN((((AD9)^(1/(-1/AJ\$4)))-1)/AJ10)-AJ10)/-AK10)+1 AF10: (AF9+(AH10-AG10)) AG10: (AI10\*(1+AJ10\*@EXP(AJ10-AK10\*(AE10-1)))^(-1/AJ\$4)) AH10: (AI10\*(1+AJ10\*@EXP(AJ10-AK10\*(AE10)))^(-1/AJ\$4)) n (-270.8+13.16\*\$I10+0.253\*\$I10^2-17.57\*\$I7\*AH\$3+50.73\*\$J10-1.115\*\$J10^2)\*@EXP(-0.3738\*(AH\$3+AH\$3)-0.5722\*(AH\$ 3+AH\$3)^2)\*\$B\$2 AJ10: ((-4.69+3.742\*AJ\$4+0.126\*AH\$4+0.065\*\$I10+0.146\*\$J10)) AK10: (-0.0408+0.0311\*AJ10-0.00024\*AJ10\*AH\$4-0.00213\*AH\$4+0.00549\*\$J10+0.04775\*AH\$3) AM10: (AM9+((AQ10-AP10)/AR10)) AN10: ((@LN((((AM9)^(1/(-1/AS\$4)))-1)/AS10)-AS10)/-AT10)+1 A010: (A09+(A010-AP10)) AP10: (AR10\*(1+AS10\*@EXP(AS10-AT10\*(AN10-1)))^(-1/AS\$4)) AQ10: (AR10\*(1+AS10\*@EXP(AS10-AT10\*(AN10)))^(-1/AS\$4)) Þ (-270.8+13.16\*\$I10+0.253\*\$I10^2-17.57\*\$I7\*AQ\$3+50.73\*\$J10-1.115\*\$J10^2)\*@EXP(-0.3738\*(AQ\$3+AQ\$3)-0.5722\*(AQ\$ 3+AQ\$3)^2)\*\$B\$2 AS10: ((-4.69+3.742\*AS\$4+0.126\*AQ\$4+0.065\*\$110+0.146\*\$J10)) AT10: (-0.0408+0.0311\*AS10-0.00024\*AS10\*AQ\$4-0.00213\*AQ\$4+0.00549\*\$J10+0.04775\*AQ\$3) AV10: (AV9+((AZ10-AY10)/BA10)) AW10: ((@LN((((AV9)^(1/(-1/BB\$4)))-1)/BB10)-BB10)/-BC10)+1 AX10: (AX9+(AZ10-AY10)) AY10: (BA10\*(1+BB10\*@EXP(BB10-BC10\*(AW10-1)))^(-1/BB\$4)) AZ10: (BA10\*(1+BB10\*@EXP(BB10-BC10\*(AW10)))^(-1/BB\$4)) 1 n R (-270.8+13.16\*\$110+0.253\*\$110^2-17.57\*\$17\*AZ\$3+50.73\*\$J10-1.115\*\$J10^2)\*@EXP(-0.3738\*(AZ\$3+AZ\$3)-0.5722\*(AZ\$

3+AZ\$3)^2)\*\$B\$2

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BB10: ((-4.69+3.742\*BB\$4+0.126\*AZ\$4+0.065\*\$110+0.146\*\$J10)) BC10: (-0.0408+0.0311\*BB10-0.00024\*BB10\*AZ\$4-0.00213\*AZ\$4+0.00549\*\$J10+0.04775\*AZ\$3) BE10: (BE9+((BI10-BH10)/BJ10)) BF10: ((@LN((((BE9)^(1/(-1/BK\$4)))-1)/BK10)-BK10)/-BL10)+1 PC10+ (PC0+(PT10-PH10)) BH10: (BJ10\*(1+BK10\*@EXP(BK10-BL10\*(BF10-1)))^(-1/BK\$4)) BI10: (BJ10\*(1+BK10\*@EXP(BK10-BL10\*(BF10)))^(-1/BK\$4)) 1 (-270.8+13.16\*\$110+0.253\*\$110^2-17.57\*\$17\*81\$3+50.73\*\$J10-1.115\*\$J10^2)\*@EXP(-0.3738\*(B1\$3+B1\$3)-0.5722\*(B1\$ 3+81\$3)^2)\*\$8\$2 BK10: ((-4.69+3.742\*BK\$4+0.126\*BI\$4+0.065\*\$110+0.146\*\$J10)) BL10: (-0.0408+0.0311\*BK10-0.00024\*BK10\*BI\$4-0.00213\*BI\$4+0.00549\*\$J10+0.04775\*BI\$3) BN10: (BN9+((BR10-B010)/BS10)) B010: ((@LN((((BN9)^(1/(-1/BT\$4)))-1)/BT10)-BT10)/-BU10)+1 BP10: (BP9+(BR10-B010)) BQ10: (BS10\*(1+BT10\*@EXP(BT10-BU10\*(BO10-1)))^(-1/BT\$4)) BR10: (BS10\*(1+BT10\*@EXP(BT10-BU10\*(BO10)))^(-1/BT\$4)) 1 ٥ (-270.8+13.16\*\$110+0.253\*\$110^2-17.57\*\$17\*8R\$3+50.73\*\$J10-1.115\*\$J10^2)\*@EXP(-0.3738\*(BR\$3+BR\$3)-0.5722\*(BR\$ 3+BR\$3)^2)\*\$B\$2 BT10: ((-4.69+3.742\*BT\$4+0.126\*BR\$4+0.065\*\$[10+0.146\*\$J10)) BU10: (-0.0408+0.0311\*BT10-0.00024\*BT10\*BR\$4-0.00213\*BR\$4+0.00549\*\$J10+0.04775\*BR\$3) BW10: (BW9+((CA10-BZ10)/CB10)) BX10: ((@LN((((BW9)^(1/(-1/CC\$4)))-1)/CC10)-CC10)/-CD10)+1 BY10: (BY9+(CA10-BZ10)) BZ10: (CB10\*(1+CC10\*@EXP(CC10-CD10\*(BX10-1)))^(-1/CC\$4)) CA10: (CB10\*(1+CC10\*@EXP(CC10-CD10\*(BX10)))^(-1/CC\$4)) c n (-270.8+13.16\*\$110+0.253\*\$110^2-17.57\*\$17\*CA\$3+50.73\*\$J10-1.115\*\$J10^2)\*@EXP(-0.3738\*(CA\$3+CA\$3)-0.5722\*(CA\$ 3+CA\$3)^2)\*\$B\$2 CC10: ((-4.69+3.742\*CC\$4+0.126\*CA\$4+0.065\*\$110+0.146\*\$J10)) CD10: (-0.0408+0.0311\*CC10-0.00024\*CC10\*CA\$4-0.00213\*CA\$4+0.00549\*\$J10+0.04775\*CA\$3) CF10: (CF9+((CJ10-CI10)/CK10)) CG10: ((@LN((((CF9)^(1/(-1/CL\$4)))-1)/CL10)-CL10)/-CM10)+1 CH10: (CH9+(CJ10-CI10)) CI10: (CK10\*(1+CL10\*@EXP(CL10-CM10\*(CG10-1)))^(-1/CL\$4)) CJ10: (CK10\*(1+CL10\*@EXP(CL10-CM10\*(CG10)))^(-1/CL\$4)) ٥ ĸ (-270.8+13.16\*\$110+0.253\*\$110^2-17.57\*\$17\*CJ\$3+50.73\*\$J10-1.115\*\$J10^2)\*@EXP(-0.3738\*(CJ\$3+CJ\$3)-0.5722\*(CJ\$ 3+CJ\$3)^2)\*\$8\$2 CL10: ((-4.69+3.742\*CL\$4+0.126\*CJ\$4+0.065\*\$I10+0.146\*\$J10)) CM10: (-0.0408+0.0311\*CL10-0.00024\*CL10\*CJ\$4-0.00213\*CJ\$4+0.00549\*\$J10+0.04775\*CJ\$3) CO10: (CO9+((CS10-CR10)/CT10)) CP10: ((aLN((((CO9)^(1/(-1/CU\$4)))-1)/CU10)-CU10)/-CV10)+1 CQ10: (CQ9+(CS10-CR10)) CR10: (CT10\*(1+CU10\*@EXP(CU10-CV10\*(CP10-1)))^(-1/CU\$4)) CS10: (CT10\*(1+CU10\*@EXP(CU10-CV10\*(CP10)))^(-1/CU\$4)) c т ٥ (-270.8+13.16\*\$110+0.253\*\$110^2-17.57\*\$17\*C\$\$3+50.73\*\$J10-1.115\*\$J10^2)\*@EXP(-0.3738\*(C\$\$3+C\$\$3)-0.5722\*(C\$\$ 3+CS\$3)^2)\*\$B\$2 CU10: ((-4.69+3.742\*CU\$4+0.126\*CS\$4+0.065\*\$I10+0.146\*\$J10)) cv10: (-0.0408+0.0311\*cu10-0.00024\*cu10\*cs\$4-0.00213\*cs\$4+0.00549\*\$J10+0.04775\*cs\$3) CX10: (CX9+((DB10-DA10)/DC10)) CY10: ((@LN((((CX9)^(1/(-1/DD\$4)))-1)/DD10)-DD10)/-DE10)+1 CZ10: (CZ9+(DB10-DA10)) DA10: (DC10\*(1+DD10\*@EXP(DD10-DE10\*(CY10-1)))^(-1/DD\$4)) DB10: (DC10\*(1+DD10\*@EXP(DD10-DE10\*(CY10)))^(-1/DD\$4)) D (-270.8+13.16\*\$I10+0.253\*\$I10^2-17.57\*\$I7\*DB\$3+50.73\*\$J10-1.115\*\$J10^2)\*@EXP(-0.3738\*(DB\$3+DB\$3)-0.5722\*(DB\$ 3+DB\$3)^2)\*\$B\$2 DD10: ((-4.69+3.742\*DD\$4+0.126\*DB\$4+0.065\*\$110+0.146\*\$J10)) DE10: (-0.0408+0.0311\*DD10-0.00024\*DD10\*DB\$4-0.00213\*DB\$4+0.00549\*\$J10+0.04775\*DB\$3) DG10: (DG9+((DK10-DJ10)/DL10)) DH10: ((@LN((((DG9)^(1/(-1/DM\$4)))-1)/DM10)-DM10)/-DN10)+1 DI10: (DI9+(DK10-DJ10)) DJ10: (DL10\*(1+DM10\*@EXP(DM10-DN10\*(DH10-1)))^(-1/DM\$4))

DK10: (DL10\*(1+DM10\*@EXP(DM10-DN10\*(DH10)))^(-1/DM\$4))

D L 1 0 (-270.8+13.16\*\$110+0.253\*\$110^2-17.57\*\$17\*DK\$3+50.73\*\$J10-1.115\*\$J10^2)\*@EXP(-0.3738\*(DK\$3+DK\$3)-0.5722\*(DK\$ 3+DK\$3)^2)\*\$B\$2 DM10: ((-4.69+3.742\*DM\$4+0.126\*DK\$4+0.065\*\$[10+0.146\*\$J10)) DN10: (-0.0408+0.0311\*DM10-0.00024\*DM10\*DK\$4-0.00213\*DK\$4+0.00549\*\$J10+0.04775\*DK\$3) 899: 'pot ht C99: 'ph D99: 'lat h A100: @IF(\$I\$2=2,A6+10,A6) B100: +\$G\$2 C100: +\$H\$2+((EU6+EK6+EB6+DS6)/100)+B100 D100: (C100+(K6/100)) A101: @IF(\$I\$2=2,A7+10,A7) B101: +\$G\$2 C101: +\$H\$2+((EU7+EK7+EB7+DS7)/100)+B101 D101: (C101+(K7/100)) A102: @IF(\$1\$2=2,A8+10,A8) B102: +\$G\$2 C102: +\$H\$2+((EU8+EK8+EB8+DS8)/100)+B102 D102: (C102+(K8/100)) A103: @IF(\$1\$2=2.A9+10.A9) B103: +\$G\$2 C103: +\$H\$2+((EU9+EK9+EB9+DS9)/100)+B103 D103: (C103+(K9/100))

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