

J. AMER. SOC. HORT. SCI. 119(4):727-734. 1994.

Modeling Inflorescence Development of the African Violet (*Saintpaulia ionantha* Wendl.)

James E. Faust¹ and Royal D. Heins²

Department of Horticulture, Michigan State University, East Lansing, MI 48824-1325

Additional index words. leaf expansion rate, photosynthetic photon flux, temperature

Abstract. The effects of temperature and daily-integrated photosynthetic photon flux (PPF_{DI}) on African violet (*Saintpaulia ionantha* Wendl.) flower initiation and development were quantified to provide the basis for an inflorescence development model. The percentage of leaf axils in which an inflorescence initiated and continued development increased as the PPF_{DI} increased from 1 to 4 mol·m⁻²·day⁻¹, while the rate of inflorescence development was a function of the average daily temperature (ADT). The appearance of a visible flower bud (VB) in a leaf axil was related to the growth of the subtending leaf blade. A polynomial model based on ADT and PPF_{DI} was used to describe leaf blade length at visible bud (LBL_{VB}). A nonlinear model was used to describe the influence of ADT on leaf expansion rate (LER). Inflorescence appearance in the leaf axil was predicted by measuring LBL and estimating the time for the leaf blade to develop to the length required for VB. A phasic-development scale was developed to quantify inflorescence development. Days required for an inflorescence to develop from VB to first open flower was described as a function of ADT and either inflorescence height or inflorescence development stage (IDS). Days from leaf emergence to first open flower for the inflorescence initiated in that leaf axil decreased from 86 to 55 as ADT increased from 18 to 26C.

Container-grown flowering plants are produced for specific market dates; therefore, the ability to predict the time of flowering is essential. Prediction requires determining the current crop's developmental status and the rate of development required for the crop to reach anthesis before the market date. The greenhouse environment can be adjusted so that the determined rate of development is achieved.

Scheduling African violet production for specific market dates can be difficult for three reasons. First, the African violet is a day-neutral species with respect to flower initiation and development (Stromme, 1985); therefore, a mechanism to induce flower initiation on a specific date is not known. Second, the apical meristem grows indeterminately and inflorescences develop in leaf axils; however, not all leaf axils produce an inflorescence and there are no *a priori* methods to determine which leaf axils will produce an inflorescence. Third, once flower initiation has occurred, quantitative data relating inflorescence development rate to the greenhouse environment are unavailable.

The average daily temperature (ADT) is the primary factor influencing rate of leaf and flower development (Friend et al., 1962; Hodges, 1991; Rawson and Hindmarsh, 1982; Tollenaar et al., 1979), not the relationship between day and night temperature (Berghage, 1989; Karlsson et al., 1988). However, there is a conflict in the literature as to whether African violet flower development is strictly a function of ADT or if the relationship between day and night temperature also influences the development rate. The African violet has been classified as a species flowering faster when grown with a cooler day than night temperature (Kimmins, 1980; Leopold and Kriedemann, 1975; Mastalerz, 1977) based on data presented by Went (1957). Went showed that African violets flowered more quickly when grown at 14C days and 20C nights than when grown at constant 20C. However, Hildrum and Kristoffersen (1969) observed time to flower; number of flowers, buds, and inflorescences per plant; and flowers and buds per inflorescence to be influenced by ADT, not the relation-

ship between day and night temperature.

Photosynthetic photon flux (PPF) is the primary factor influencing flower initiation and development of many day-neutral species, including African violet. Hildrum and Kristoffersen (1969) observed that the number of flowers, buds, and inflorescences per plant and flowers and buds per inflorescence increased as PPF increased from 3.1 to 9.3 mol·m⁻²·day⁻¹. Stinson and Laurie (1954) reported that flower initiation and development of African violets were inhibited when greenhouse-grown plants were given <2 mol·m⁻²·day⁻¹. Conover and Poole (1981) placed flowering African violets in three postharvest environments that provided 0.8, 1.6, or 3.2 mol·m⁻²·day⁻¹. After 9 months, 6%, 62%, and 100% of the plants possessed newly developed inflorescences from the respective PPF treatments.

Leaf area influences the number of photons absorbed and therefore the capacity of leaves to export photosynthates. The transition of the leaf from a net importer to a net exporter of carbohydrates is related to leaf expansion (Turgeon, 1989). Consequently, flower initiation and development of some species can be influenced by leaf area (Ramina et al., 1979). Research relating flowering to leaf area has not been conducted for African violets.

Phasic-development scales have been used to describe and quantify leaf and inflorescence development (Cockshull and Hodges, 1972; Haun, 1973). Also, scales are valuable tools for describing crop developmental status and making greenhouse climate-control decisions. The Easter lily bud meter is an example of a scale used to predict anthesis based on flower-bud length and air temperature (Healy and Wilkins, 1984).

The objective of our research was to develop a model to predict flowering of African violets. The first step was to predict on which nodes an inflorescence would develop in the leaf axil. The second step was to relate visible bud (VB) appearance to the length of the subtending leaf blade. The third step was to develop quantitative relationships describing inflorescence development rate from VB to first open flower as a function of ADT and either inflorescence height or inflorescence development stage (IDS).

Materials and Methods

General experimental procedures. In all of the experiments, plants were subirrigated with either water or a nutrient solution consisting of (per liter) 3.6 mmol N, 4.0 mmol P, and 1.3 mmol K

Received for publication 12 Apr. 1993. Accepted for publication 21 Sept. 1993. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

¹Graduate research assistant.

²Professor.

from calcium nitrate, phosphoric acid, and potassium nitrate. The high P concentration was associated with the use of phosphoric acid to neutralize the high bicarbonate concentration in the water supply. Electrical conductivity of the medium in the root zone was maintained between 0.5 and 1.0 mS using the 2 water : 1 soil (v/v) method (Warncke and Krauskopf, 1983). Medium pH was maintained between 5.5 and 6.5.

Temperatures reported in this paper refer to air temperatures unless plant temperature is specifically mentioned. Plant temperatures were used in data analysis when plant temperature deviated from air temperature by $>1^{\circ}\text{C}$. Plant temperature was measured by inserting a hypodermic-needle thermocouple probe (Hyp1-30-1/2-T-G-60-SAP-M; Omega International, Stamford, Conn.) into stem, petiole, and leaf tissue and calculated as the mean temperature of the plant tissues.

Inflorescence development in a leaf axil (Expt. 1). One hundred twenty 'Utah' African violet plants with 8 to 10 leaves were transplanted into 10-cm-diameter (450-cm³) pots and placed into four 10-m² glass greenhouses maintained at air temperatures of 15, 20, 25, and $30 \pm 1^{\circ}\text{C}$ from Dec. 1990 through Feb. 1991. Each greenhouse was divided to provide three irradiance treatments. Neutral-density shade cloth was placed above plants in the low-irradiance treatment to reduce ambient irradiance by 50%. Plants in the intermediate-irradiance treatment received ambient irradiance. The high-irradiance treatment received ambient irradiance plus $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from 0600 to 1800 hr each day ($4.3 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) provided by 400-W high-pressure sodium lamps. One layer of neutral-density shade cloth (50% reduction) was pulled over plants in all irradiance treatments when ambient PPF was $>300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Average daily-integrated PPF (PPF_{DI}) was 2.6, 4.5, and $8.8 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ at canopy level for the three PPF treatments over the course of the experiment as determined at canopy level with quantum sensors (LI-190SB; LI-COR, Lincoln, Neb.) and a datalogger (Easy Logger 800; Omnidata International, Logan, Utah).

On every plant, each leaf's axil was examined three times per week for the presence of an inflorescence $>2 \text{ mm}$. The length of each leaf blade on the plant was measured after 10 flowers had opened on the plant. Leaves were numbered so that the most recently unfolded leaf at the time of transplanting was designated as leaf 0, and successive leaves were designated 1, 2, 3, etc. Leaves that unfolded before the start of the experiment were numbered -1, -2, -3, etc., from the second most recently unfolded to the oldest leaf.

Influence of PPF on inflorescence initiation and development (Expt. 2). One hundred 'Utah' African violet plants with 8 to 10 unfolded leaves were transplanted into 10-cm-diameter (450-cm³) pots. Plants were placed into four PPF treatments in each of two walk-in growth chambers (model UWP 3009-2; HotPack, Philadelphia). Air temperature was set to maintain plant temperatures at $26 \pm 1^{\circ}\text{C}$ during the day and $23 \pm 1^{\circ}\text{C}$ during the night. Cool-white fluorescent lamps delivered a PPF of 25, 45, 90, or $180 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at canopy level for 12 h per day, resulting in a PPF_{DI} of 1, 2, 4, or $8 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. Neutral-density shade cloth was used to produce the PPF levels.

After 10 flowers opened on a plant, the leaf axils were examined for the presence of an inflorescence $>1 \text{ cm}$. The percentage of leaf axils with an inflorescence $>1 \text{ cm}$ long was calculated for each leaf number. Analysis of variance was performed to determine the influence of PPF on inflorescence development for each leaf number.

Relationship between day and night temperature on time to flower (Expt. 3). Eighty 'Utah' African violet plants with 8 to 10

unfolded leaves were transplanted into 10-cm-diameter (450-cm³) pots and placed into four walk-in growth chambers (HotPack) with air temperatures maintained at 15, 20, 25, and $30 \pm 1^{\circ}\text{C}$. Five plants per treatment were moved among chambers at 0800 and 2000 hr each day for a total of 16 day and night temperature combinations. Cool-white fluorescent lamps (VHO F96T12; Philips, Bloomfield, N.J.) delivered a PPF of $170 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for 12 h per day, resulting in a PPF_{DI} of $7 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$.

The dates of flower opening were recorded for the first five flowers of each plant. A flower was considered opened when the five petals formed a planar surface. Plant temperature was 1 to 2°C higher than air temperature during the photoperiod and 1 to 2°C lower than air temperature during the dark period. Plant temperatures were used in regression analysis.

Influence of ADT and PPF on the time from transplant to VB (Expt. 4). Twenty-seven 'Sparkle' African violet plants with 8 to 10 unfolded leaves were transplanted into 10-cm-diameter (450-cm³) pots and placed in three growth chambers (model E-15; Conviron, Asheville, N.C.) set to maintain plant temperature at 18, 22, or $26 \pm 1^{\circ}\text{C}$. Each growth chamber was divided into three PPF treatments. Cool-white fluorescent lamps (VHO F72T12; Philips) delivered a PPF of 50, 100, or $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for 12 h per day, resulting in a PPF_{DI} of 2.2, 4.3, and $8.7 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. The actual temperature of the plants in the $2.2 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ treatment in the 18°C growth chamber was $\approx 16^{\circ}\text{C}$.

Leaf blade length (LBL) was measured and all leaf axils were examined for VB every 2 to 3 days for 64 days. Data were analyzed as a split-plot design with temperature as the main plots. SAS's general linear model (GLM) procedure was used for analysis of variance (ANOVA) (SAS Institute, 1989).

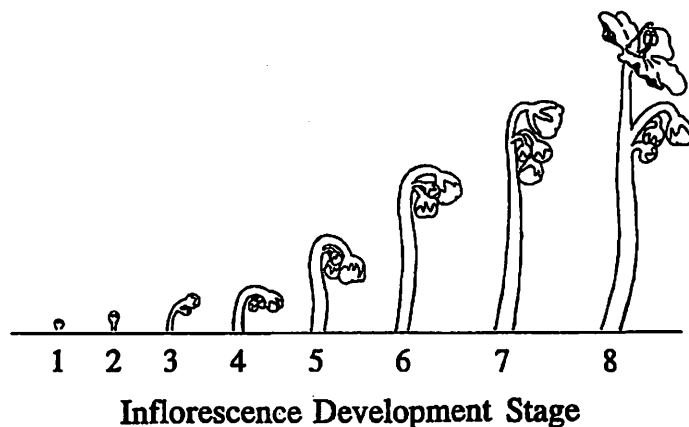


Fig. 1. Phenological description for each stage of inflorescence development of *Saintpaulia ionantha*.

Stage	Phenological description of inflorescence development
1	Reproductive bud becomes visible (2 mm long) in the leaf axil.
2	The peduncle subtending the primary bud becomes visible.
3	The peduncle begins to curve.
4	The pedicel has curved at a 90° angle with respect to the peduncle.
5	The pedicel has curved at an angle $<90^{\circ}$ with respect to the peduncle, and the secondary buds are located at the highest point of the inflorescence.
6	The primary bud and pedicel have begun to increase the angle with respect to the peduncle, the pedicel is located at the highest point of the inflorescence, and the primary bud begins to push through the leaf canopy.
7	The upper half of the pedicel and the primary bud are at a 90° angle with respect to the lower half of the pedicel.
8	All five petals are reflexed to a 90° angle with respect to the pedicel.

Influence of ADT and PPF on the rate of inflorescence development from VB to first open flower (Expt. 5). Thirty-six 'Sparkle' African violet plants with four or more developing inflorescences were placed into three growth chambers (Conviron) set to maintain plant temperature at 18, 22, and 26 ± 1°C. Each growth chamber was divided into three PPF treatments. Cool-white fluorescent lamps (VHO F72T12; Philips) and 60-W incandescent bulbs delivered a PPF of 50, 100, or 200 μmol·m⁻²·s⁻¹ for 12 h per day, resulting in a PPF_{DT} of 2.2, 4.3, and 8.7 mol·m⁻²·day⁻¹.

Inflorescence height and IDS were determined every 2 to 3 days for 40 days. Inflorescence height was measured from the point of stem attachment to the uppermost point of the inflorescence. A split-plot design was used with temperature as the main plots. SAS's GLM procedure was used for ANOVA (SAS Institute, 1989).

A phasic-development scale was developed to quantify inflorescence development (Fig. 1), which was divided into eight stages based on the curvature of the inflorescence. As the inflorescence of an African violet grows through the leaf canopy, the pedicel and peduncle curve to protect the primary flower bud. The degree of curvature of the peduncle and pedicel was used to identify the stages of the phasic-development scale.

Model development—time to VB. The time of flower initiation in African violet is uncertain; therefore, some physical measure other than time is necessary to predict macroscopic visibility (2

mm long) of an inflorescence. We chose to relate the time to VB to the LBL of a subtending leaf on a pre-VB plant; therefore, leaf-blade measurements could be used to predict VB. The number of days to VB (D_{VB}) would be

$$D_{VB} = \frac{LBL_{VB} - LBL}{LER} \quad [1]$$

where LER is the leaf expansion rate (mm·day⁻¹).

The following nonlinear function (Brondum and Heins, 1993; Landsberg, 1977; Reed et al., 1976) was used to describe LER as a function of ADT:

$$LER = a (ADT - T_{Min}) (T_{Max} - ADT)^b \quad [2]$$

$$a = \frac{LER_{Max}}{(T_{Opt} - T_{Min}) (T_{Max} - ADT)^b} \quad [3]$$

$$b = \frac{T_{Max} - T_{Opt}}{T_{Opt} - T_{Min}} \quad [4]$$

where T_{Min} and T_{Max} are the minimum and maximum temperatures at which LER = 0, T_{Opt} is the temperature at which the maximum LER occurs, and LER_{Max} is the maximum value for LER at T_{Opt} (Table 1).

Table 1. Parameter estimates for the nonlinear model describing leaf expansion rate (LER) (Eqs. [2–4]) and the polynomial model describing leaf blade length at visible bud (LBL_{VB}) (Eq. [5]).

Model	Parameter	Estimate	Asymptotic 95% confidence interval	
			Lower	Upper
LER	T _{Min}	13.8	11.6	15.9
	T _{Max}	29.0	17.0	41.0
	T _{Opt}	24.0	22.8	25.1
	LER _{Max}	1.26	1.10	1.42
			SE of estimate	
LBL _{VB}	c ₀	-18.5		20.4
	c ₁	6.38		1.83
	c ₂	-0.155		0.04
	c ₃	-0.564		0.12

Table 2. Parameter estimates for three models describing the time from visible bud to first open flower as a function of average daily temperature and either inflorescence height (Eq. [6]) or inflorescence developmental stage (IDS) (Eq. [7]).

Model	Parameter	Coefficient	Estimate	Asymptotic 95% confidence interval	
				Lower	Upper
Inflorescence height	d	d ₀	0.0352	0.0192	0.0512
		d ₁	0.0000501	0.000374	0.000784
	e	e ₀	65.6	61.0	70.2
		e ₁	-1.36	-1.57	-1.16
	f	f ₀	-2.42	-7.77	2.92
		f ₁	-0.0173	-0.256	0.222
			SE of estimate		
IDS		g ₀	73.3		1.805
		g ₁	-1.68		0.079
		g ₂	-9.39		0.356
		g ₃	0.219		0.016

A polynomial function was used to describe LBL_{VB} as a function of ADT and PPF_{DI} :

$$LBL_{VB} = c_0 + c_1 \times ADT + c_2 \times ADT^2 + c_3 \times PPF_{DI} \quad [5]$$

where the coefficients are represented by c_0 , c_1 , and c_2 (Table 1).

Model development—time from VB to first open flower. Once VB has occurred, the time to first open flower is determined by the rate of inflorescence development. Two methods were used to quantify inflorescence development: inflorescence height measurements and the phasic-development scale. A model was developed to determine the number of days from VB to first open flower (D_F) based on ADT and either inflorescence height or IDS. The following nonlinear function was used:

$$D_F = \exp(-d \times \text{Inflorescence height}) \times e + f \quad [6]$$

where inflorescence height was measured in mm and parameters d , e , and f were each described as linear functions of ADT from 18 to 26°C (e.g., $d = d_0 + d_1 \times ADT$; $e = e_0 + e_1 \times ADT$; $f = f_0 + f_1 \times ADT$) (Table 2).

A polynomial model was also used to predict D_F based on ADT and IDS (Table 2).

$$D_F = g_0 + g_1 \times ADT + g_2 \times IDS + g_3 \times ADT \times IDS \quad [7]$$

Comprehensive flowering model. The number of days to the first open flower (D) was predicted with Eq. [8], which combines the models predicting time to VB and time from VB to first open flower.

$$D = \begin{cases} D_{VB} + D_F & \text{VB not present} \\ D_F & \text{VB present} \end{cases} \quad [8]$$

Both Eqs. [6 and 7] were used to predict D_F .

Parameter estimates. Parameters for the nonlinear function (Eqs. [2–4]) were estimated using SAS's NLIN procedure (SAS Institute, 1989). Parameters for the multiple linear regression (Eqs. [5 and 8]) and parameters for the linear regression (Eqs. [6 and 7]) were estimated using SAS's GLM procedure (SAS Institute, 1989).

Model validation (Expt. 6). Twelve 'Sparkle' African violet plugs were placed in each of two greenhouses, which were set to maintain air temperatures of 20 and 25°C from March to May 1991. Each greenhouse was divided to provide two irradiance treatments. The plants in the high-irradiance treatment received natural PPF, while those in the low-irradiance treatment were covered by two layers of neutral-density shade cloth, reducing the ambient irradiance by 75%. One layer of neutral-density shade cloth (50% reduction) was pulled over the plants in both treatments when the natural PPF exceeded $\approx 300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The average PPF_{DI} for the low- and high-irradiance treatments over the time of the experiment was 3.2 and $8.2 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, respectively, and the average daily plant temperature in the two greenhouses was 21.5 and 25.0°C. LBL, inflorescence height, and IDS were determined three times per week. Data collected during the validation were used to test the model's prediction of the time of VB and first open flower for individual inflorescences.

Results

LBL at the time of flowering and the percentage of leaf axils in which an inflorescence developed were related to leaf number

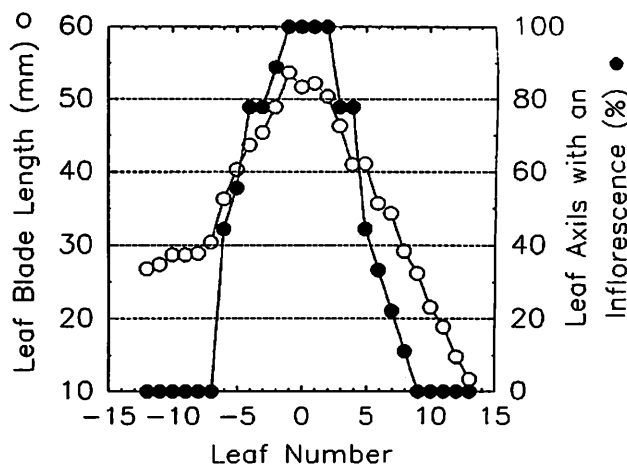


Fig. 2. The relationship between leaf-blade length measured at the time of flowering (○) and the percentage of leaf axils that formed an inflorescence (●) with respect to leaf number for *Saintpaulia ionantha*.

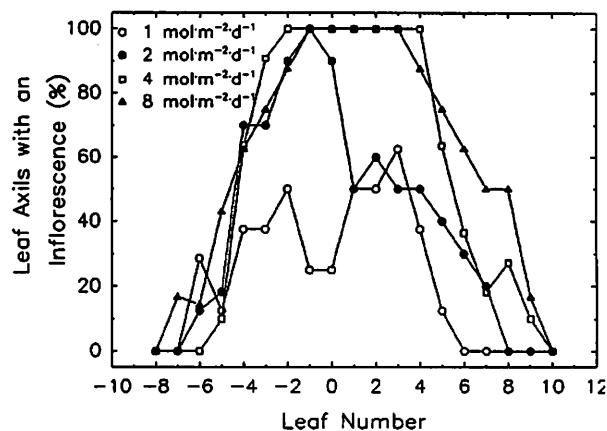


Fig. 3. The influence of PPF_{DI} on the percentage of leaf axils that formed an inflorescence with respect to leaf number for *Saintpaulia ionantha*.

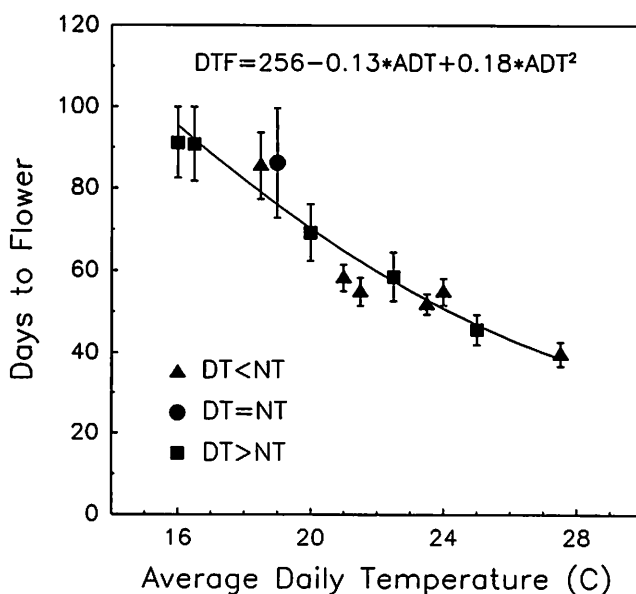


Fig. 4. The number of days to flower (DTF) for *Saintpaulia ionantha* shown as a function of average daily temperature (ADT), using the measured plant temperatures ($r^2=0.81$). Data points and error bars represent treatment means and 95% confidence intervals. DT and NT represent day temperature and night temperature, respectively.

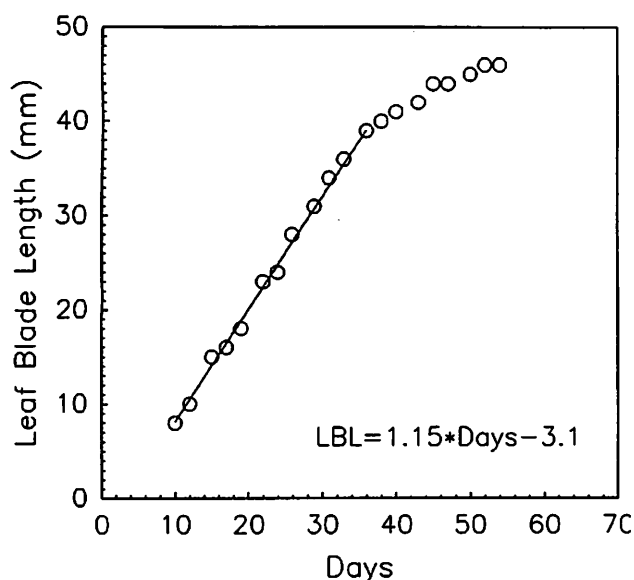


Fig. 5. Relationship between time and leaf blade length (LBL) until visible bud (VB) appearance in the leaf axil for *Saintpaulia ionantha* ($r^2 = 0.99$). The slope of the linear regression ($1.15 \text{ mm}\cdot\text{day}^{-1}$) represents the rate of leaf expansion during the first 40 mm of leaf expansion for an individual leaf grown at 22C.

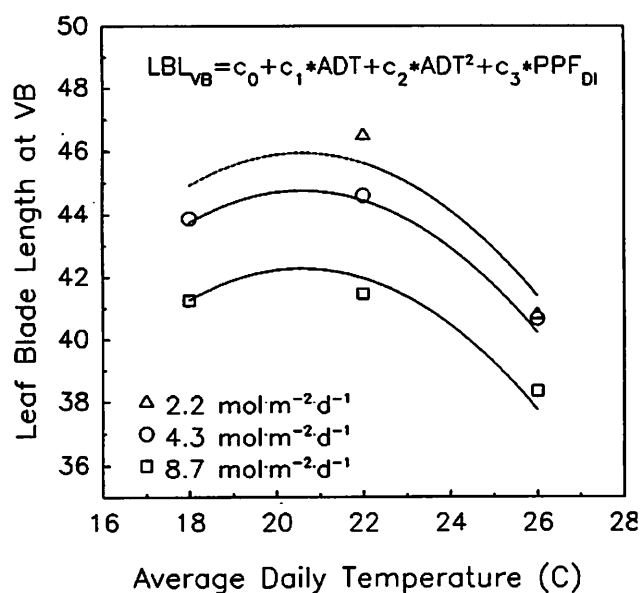


Fig. 7. A model describing the influence of daily-integrated photosynthetic photon flux (PPF_{Di}) and average daily temperature (ADT) on leaf blade length at visible bud (LBL_{VB}) for *Saintpaulia ionantha* based on Eq. [5] and parameter estimates from Table 1 ($r^2 = 0.36$). Plants in the 18C, $2.2\text{-mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ treatment did not reach VB during the experiment. Dashed lines represent predictions outside the observed data range.

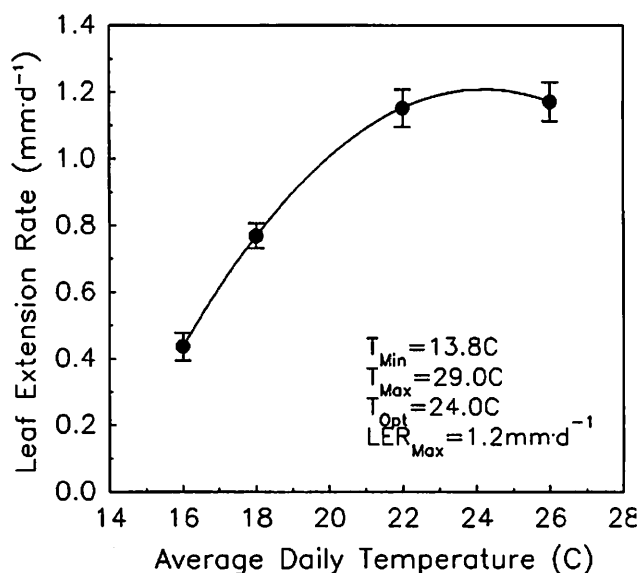


Fig. 6. Leaf expansion rate (LER) for *Saintpaulia ionantha* shown as a function of average daily temperature (ADT) ($r^2 = 0.87$) based on Eqs. [2-4] and parameter estimates from Table 1. Data points represent the treatment means after the data from the PPF treatments were pooled, and error bars display the 95% confidence intervals.

(Fig. 2). Leaves that expanded before transplanting, leaf numbers -12 to -7, were <40 mm long at maturity and did not have inflorescences develop in the leaf axils. As leaf number increased from -6 to -1, LBL increased from 37 to 54 mm and the percentage of leaf axils developing an inflorescence increased from 0% to 100%. An inflorescence developed in the axil of leaf numbers -1 to 2 on every plant in the experiment. LBL and the percentage of leaf axils with an inflorescence decreased as leaf number increased from 3 to 13 as a result of the leaves being increasingly smaller and younger at the time of data collection. In general, leaf number -1 was the first leaf to develop an inflorescence in 100% of the leaf axils, and leaves that grew to ≥ 40 mm in length had an inflorescence develop in 60% or more of the leaf axils.

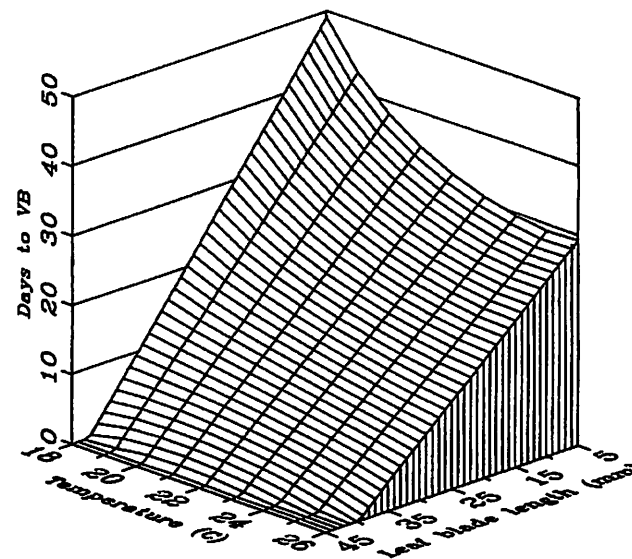


Fig. 8. Surface response of the predicted number of days to visible bud (VB) for *Saintpaulia ionantha* as influenced by average daily temperature and measured leaf blade length (Eq. [1]).

The percentage of leaf axils with inflorescences increased as the PPF_{Di} increased from 1 to 4 $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Fig. 3). Increasing PPF_{Di} from 4 to 8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ did not further promote flower initiation. Leaf number -1 was the first leaf to produce an inflorescence in 100% of the leaf axils when PPF_{Di} was at least 4 $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$.

When comparing the distribution of data points around the regression line, no relationship was detected between the way ADT was delivered and time to flower. The number of days from transplant to flower was closely correlated to ADT (Fig. 4); therefore, ADT was used to develop the flowering model. Leaves of plants grown at 30C days were chlorotic, and no inflorescences developed regardless of night temperature.

LBL was a linear function of time from 7 to ≈ 40 mm for all

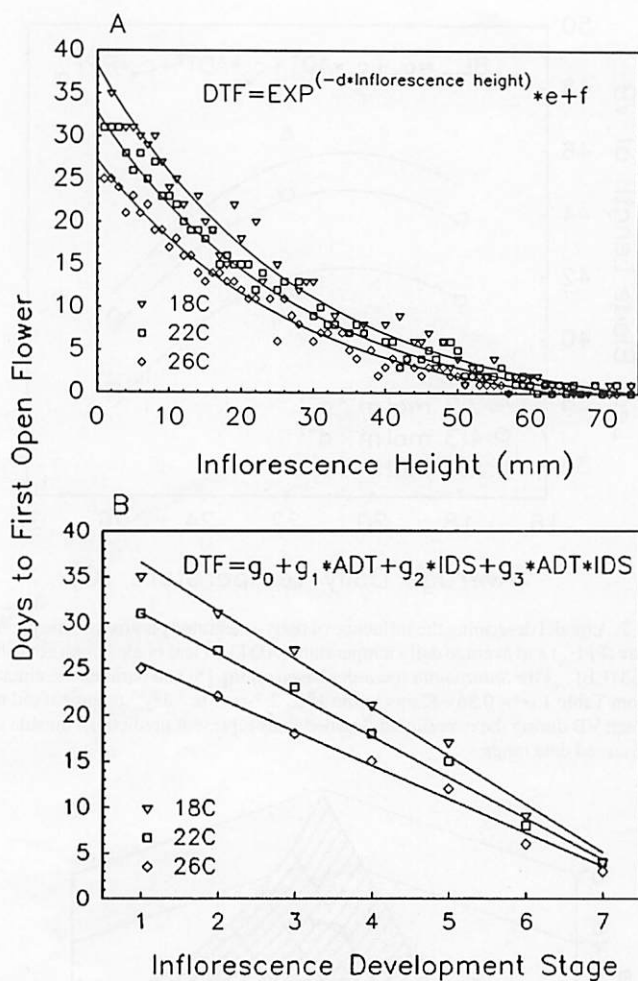


Fig. 9. The influence of average daily temperature (ADT) and (A) inflorescence height and (B) inflorescence development stage on the number of days from visible bud to first open flower for *Saintpaulia ionantha* ($r^2 = 0.94$ and 0.93 , respectively). The parameters d , e , and f are described by linear functions of ADT (e.g., $d = d_0 + d_1 \times ADT$; $e = e_0 + e_1 \times ADT$; $f = f_0 + f_1 \times ADT$). Symbols represent the means while the lines represent the predicted number of days to first open flower based on Eqs. [6 and 7] and parameter estimates from Table 2.

treatments (Fig. 5). The slope of the linear regression line represented the LER for a given leaf. The time of VB appearance in the leaf axil was not influenced by PPF_{DI} , so PPF data were pooled. The maximum LER was estimated to be $1.2 \text{ mm} \cdot \text{day}^{-1}$ at 24C (Fig. 6, Table 1). T_{Min} and T_{Max} for LER were estimated at 13.8 and 29.0C, respectively (Table 1).

LBL_{VB} was influenced by ADT and PPF_{DI} (Fig. 7), and a polynomial function was used to describe the response (Table 1). LBL_{VB} increased as ADT increased from 18 to 22C, then decreased as ADT increased to 26C. LBL_{VB} decreased as PPF_{DI} increased from 2.2 to $8.7 \text{ mol} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. Plants grown at $2.2 \text{ mol} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ and 18C did not flower during the experiment. A VB appeared in the leaf axil when the subtending leaf blade was 69% to 74% of the fully expanded LBL.

Eq. [1] was used to predict the time required for a VB to appear in the leaf axil based on measured LBL and predicted LER. The predicted number of days for a VB to appear in the axil of a 6-mm-long leaf blade decreased from 49 to 29 as ADT increased from 18 to 26C (Fig. 8).

D_f decreased from 37 to 26 as ADT increased from 18 to 26C. Inflorescence height and IDS were separately used to model the time from VB to first open flower (Fig. 9, Table 2). The rate of

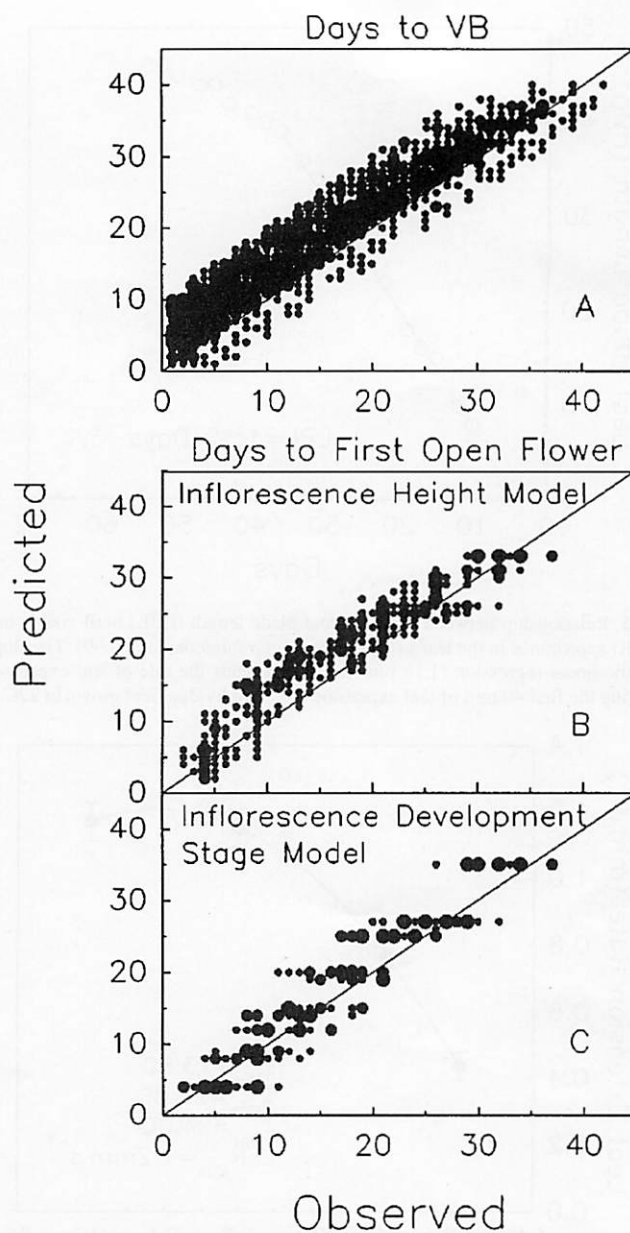


Fig. 10. Comparison between the observed (●) and the predicted (—) number of days to (A) the appearance of visible bud (VB) in the leaf axil (Eq. [1]) and to the first open flower using (B) the inflorescence height model (Eq. [6]) and (C) the inflorescence development stage model (Eq. [7]) for *Saintpaulia ionantha* based on parameter estimates from Tables 1 and 2. Symbol size represents the number of observations for each point; ●, ●, ● indicate one to two, three to four, and more than five observations, respectively.

increase in inflorescence height increased as ADT increased from 18 to 26C. Final inflorescence height was not influenced by ADT or PPF_{DI} . The rate of progress of an inflorescence through each IDS increased as ADT increase from 18 to 26C. The phasic-development scale accurately described the progression of inflorescence development under all ADT and PPF_{DI} experimental conditions.

Considerable variation in inflorescence development was observed during the experiment; however, the models accurately described VB appearance in the leaf axil and the development of the inflorescence to time of first open flower (Fig. 10). The predicted time to VB appearance was consistently longer than the observed time. Inflorescence height and IDS models accurately described the development of an inflorescence from VB to first

open flower. The greenhouse-validation experiment showed that the comprehensive flowering model could predict the time to VB and time from VB to first open flower for an African violet crop.

Discussion

Previously published information (Hildrum and Kristoffersen, 1969; Johansson, 1978; Stinson and Laurie, 1954; Went, 1957) and results from experiments described in this paper indicate that the African violet is a day-neutral species for which absorbed PPF is the primary factor influencing flower initiation and that ADT is the primary factor influencing rate of inflorescence development.

Leaf area and PPF influence absorbed PPF and, therefore, the ability of a leaf to become a strong source of photosynthates for flower initiation. Transplanting a plant from a high-density environment in which there is strong competition with surrounding plants for photons to a low-density environment that is free from competition with other plants influences leaf expansion and the capacity of leaves to intercept photons. Likewise, increasing root substrate volume when transplanting increases water and nutrient availability and leaf expansion (Ruff et al., 1987). The experiments described in this paper showed that leaves that developed on plants growing in high-density environments before transplanting did not fully expand after transplanting, while the youngest leaves at the time of transplanting and the leaves that enlarged after transplanting expanded to a much larger size (Fig. 2). As a result, compared to older leaves, the youngest leaves at the time of transplanting have a greater potential of intercepting visible radiation to produce sufficient photosynthates for flower initiation and subsequent development. Even with significant leaf expansion, flower initiation and development is limited when the PPF is $<4 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Fig. 3). Leaf area and PPF are important factors influencing flower initiation and development.

The observed relationship between leaf expansion and inflorescence development suggests that moving a plant from a high- to a low-density environment when there are fewer leaves on the plant could result in inflorescence development occurring on a lower leaf number; i.e., transplanting a younger plant will result in earlier flowering. However, our observations (data not presented) suggest that the first six to eight leaves to develop from a vegetative cutting will develop a vegetative shoot in the leaf axil, rather than an inflorescence, if the subtending leaf fully expands. Vegetative-shoot development is commercially undesirable because it results in delayed flowering and a poorer-quality plant. It is recommended that plants be maintained at a high density until eight or more leaves unfold before transplanting to a low-density environment; therefore, the first leaves to fully expand will produce an inflorescence in the leaf axil, not a vegetative shoot.

We attribute the overprediction of the time to VB during the greenhouse validation experiment to the different morphological characteristics associated with the growth-chamber-grown plants vs. the greenhouse-grown plants. Plants grown in the growth chamber had stiffer and more brittle petioles and leaves, which created more difficulty in examining the leaf axils for a VB. We believe that VB appearance was recorded sooner in the greenhouse-validation experiment because the leaf axils were examined more easily.

Once an inflorescence was visible in the leaf axil, the rate at which the inflorescence developed was a function of ADT and was not related to day and night temperature (Fig. 4). These results conflict with those of Went (1957), who suggested that African violets performed better when the day temperature is cooler than the night temperature, but agree with those of Hildrum and

Kristoffersen (1969), who found that the rate of development was a function of ADT. The possibility exists that Went's conclusions were a result of poor daytime temperature control; i.e., plant temperatures were warmer than expected. Results from Went's experiment continue to be reported in horticulture texts (Kimmins, 1980; Leopold and Kriedemann, 1975; Mastalerz, 1977) as an exception to the general flowering response to temperature. Based on the results presented in this paper and the observations of Hildrum and Kristoffersen (1969), the African violet should be classified as a species in which the inflorescence development rate is a function of ADT.

LBL followed a sigmoidal curve from the time of leaf initiation to a fully expanded leaf. LER, as defined in this paper, was determined during the linear portion of the sigmoid curve. LER was estimated with a nonlinear equation, which uses minimum and maximum temperatures for leaf expansion as model parameters. The minimum and maximum temperatures were estimated at 13.8 and 29.0C. We have observed that chilling injury of African violet occurs between 10 and 12.5C, while death due to high-temperature stress occurs when plant temperatures are maintained at constant 30C. Consequently, we believe that the nonlinear LER model presented describes plant growth better than a polynomial model.

Inflorescence height and IDS were used to predict flowering. Our observations of different African violet cultivars suggest that inflorescence development follows the basic pattern described by the phasic-development scale, regardless of cultivar, whereas morphological measurements such as inflorescence height can vary widely from cultivar to cultivar. Consequently, the phasic-development scale may be the most useful means to predict flowering date of multiple cultivars by commercial growers. The phasic-development scale will allow commercial growers to identify the current status of an African violet crop and will be a tool for making production decisions. Initially, the grower can determine the VB date that must be achieved for the crop to be on schedule for the market date. Once VB has occurred, progress toward flowering can be monitored with frequent crop inspection, and the greenhouse temperature can be manipulated to achieve the market date.

In summary, African violet flowering was divided into two parts: 1) time from transplant to VB and 2) time from VB to first open flower. Assuming that flower initiation has not occurred before transplanting, an inflorescence developed in the second most recently unfolded leaf present at the time of transplanting when the plant was provided a PPF_{DI} of $\geq 2 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. An inflorescence was macroscopically visible in the leaf axil when the subtending leaf blade extended to ≈ 38 to 46 mm, depending on the temperature and PPF; therefore, the time to VB appearance in the leaf axil depended on the rate at which the leaf extended, which was a function of ADT. D_p was a function of ADT and could be tracked by following inflorescence height or IDS.

Literature Cited

- Berghage, R.D. 1989. Modeling stem elongation in the poinsettia. PhD diss. Michigan State Univ., East Lansing.
- Brondum, J.J. and R.D. Heins. 1993. Modeling temperature and photoperiod effects on growth and development of dahlia. *J. Amer. Soc. Hort. Sci.* 118:36-42.
- Cockshull, K.E. and A.P. Hughes. 1972. Flower initiation in *Chrysanthemum morifolium*: The influence of light level. *J. Hort. Sci.* 47:113-127.
- Conover, C.A. and R.T. Poole. 1981. Light acclimatization of African violet. *HortScience* 16:92-93.
- Friend, D.J.C., V.A. Helson, and J.E. Fisher. 1962. Leaf growth in Marquis wheat, as regulated by temperature, light intensity, and day-length. *Can. J. Bot.* 40:1299-1311.

- Haun, J.R. 1973. Visual quantification of wheat development. *Agron. J.* 65:116-119.
- Healy, W.E. and H.F. Wilkins. 1984. Temperature effects on 'Nellie White' flower bud development. *HortScience* 19:843-844.
- Hildrum, H. and T. Kristoffersen. 1969. The effect of temperature and light intensity on flowering in *Saintpaulia ionantha* Wendl. *Acta Hort.* 14:249-255.
- Hodges, T. 1991. Temperature and water stress effects on phenology, p. 7-13. In: T. Hodges (ed.). *Predicting crop phenology*. CRC Press, Boca Raton, Fla.
- Johansson, D.R. 1978. Saintpaulias in their natural environment with notes on their present status in Tanzania and Kenya. *Biol. Conservation* 14:45-62.
- Karlsson, M.G., R.D. Heins, and J.E. Erwin. 1988. Quantifying temperature-controlled leaf unfolding rates in 'Nellie White' Easter lily. *J. Amer. Soc. Hort. Sci.* 113:70-74.
- Kimmins, R.K. 1980. Gloxinias, African violets, and other gesneriads, p. 287-300. In: R.A. Larson (ed.). *Introduction to floriculture*. Academic Press, New York.
- Landsberg, J.J. 1977. Some useful equations for biological studies. *Expt. Agr.* 13:273-286.
- Leopold, A.C. and P.E. Kriedemann. 1975. *Plant growth and development*. 2nd ed. McGraw-Hill, New York.
- Mastalerz, J.W. 1977. *The greenhouse environment*. Wiley, New York.
- Ramina, A., W.P. Hackett, and R.M. Sachs. 1979. Flowering in *Bougainvillea*. *Plant Physiol.* 64:810-813.
- Rawson, H.M. and J.H. Hindmarsh. 1982. Effects of temperature on leaf expansion in sunflower. *Austral. J. Plant Physiol.* 9:209-219.
- Reed, K.L., E.R. Hamerly, R.F. Dinger, and P.G. Jarvis. 1976. An analytical model for field measurement of photosynthesis. *J. Applied Ecol.* 13:925-942.
- Ruff, M.S., D.T. Krizek, R.M. Mirecki, and D.W. Inouye. 1987. Restricted root zone volume: Influence on the growth and development of tomato. *J. Amer. Soc. Hort. Sci.* 112:763-769.
- SAS Institute. 1989. *SAS/STAT user's guide*. version 6. 4th ed. vol. 2. SAS Inst., Cary, N.C.
- Stinson, R.F. and A. Laurie. 1954. The effect of light intensity on the initiation and development of flower buds in *Saintpaulia ionantha*. *Proc. Amer. Soc. Hort. Sci.* 64:459-467.
- Stromme, E. 1985. *Saintpaulia ionantha*, p. 48-49. In: A. Halevy (ed.). *CRC handbook of flowering*. vol. 3. CRC Press, Boca Raton, Fla.
- Tollenaar, M., T.B. Daynard, and R.B. Hunter. 1979. Effect of temperature on rate of leaf appearance and flowering date in maize. *Crop Sci.* 19:363-366.
- Turgeon, R. 1989. The sink-source transition in leaves. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 40:119-138.
- Warncke, D. and D. Krauskopf. 1983. *Greenhouse growth media: testing and nutrition guidelines*. Michigan State Univ. Ext. Bul. E-1736.
- Went, F.W. 1957. *The experimental control of plant growth*. Chronica Botanica, New York.