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Temperature driven leaf unfolding rate in *Hibiscus rosa-sinensis*

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ABSTRACT

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Leaf unfolding rate of *Hibiscus rosa-sinensis* cultivars 'Brilliant Red' and 'Pink Versicolor' was determined in the 5–35°C temperature range at intervals of 6°C. Plants of neither cultivar survived at 5°C, and growth was very slow at 11°C. The rate of leaf unfolding was similar for the two cultivars in the studied temperature range. Daily leaf unfolding rate for hibiscus was described by a cubic polynomial function of temperature (T) where leaves day^{-1}=0.06289−0.02026$\cdot T$+0.001750$\cdot T^2$−0.00002983$\cdot T^3$. Based on this function, predicted leaf unfolding varied from 0.012 leaves day^{-1} at 11°C to a maximum of 0.229 leaves day^{-1} at 32°C. A linear function (leaves day^{-1}=−0.1130+0.01148$\cdot T$) approximated the curvilinear relationship in the range from 10–30°C. A degree-day relationship was calculated to 0.0115 leaves per degree day using the linear function with a base temperature of 9.8°C. To unfold one leaf, 87 degree-days were required as determined by the developed linear model. A linear model was developed from the linear function where leaf unfolding was 0 at temperatures $<$10°C and leaf unfolding was calculated at 30°C at temperatures $\geq$30°C. The cubic function and the linear model predicted a similar leaf unfolding rate based on hourly average temperatures recorded in a Florida commercial greenhouse during two times of the year. During a 78-day period from 25 February to 14 May, 9.95 and 9.98 leaves were predicted to unfold by the linear and cubic models respectively. During a 65-day period from 21 July to 24 September, 12.28 and 12.04 leaves were predicted to unfold by the linear and cubic models respectively. The predicted leaf unfolding rate was compared with actual leaf unfolding for the nine cultivars 'Aloha Pink', 'Brilliant Red', 'Euterpe', 'Florida Sunset', 'Painted Lady', 'Pink Versicolor', 'Sundance', 'Tawny', and 'Vista'. Predicted leaf unfolding was within 0.9 leaves of observed leaf unfolding for all cultivars over a 7-week period after pinching. After about 7 weeks, the models progressively overpredicted leaf unfolding. Over-prediction was correlated with the appearance of flower buds.

Keywords: average temperature; degree-days; *Hibiscus rosa-sinensis*; leaf unfolding; leaves day^{-1}, vegetative growth.

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INTRODUCTION

Scheduling and timing of crops are important procedures in the floriculture industry. Developmental progress of plants producing a known number of leaves prior to flower initiation can be tracked by the rate of leaf appearance. A leaf unfolding function relating the appearance of leaves to temperature gives the opportunity to track growth rate and maintain plant production on a desired schedule during the vegetative phase.

Plant response studied over a wide range of temperatures are curvilinear. The curvilinear plant responses can often be approximated by linear relationships in the temperature range from zero growth to near the temperature of maximum growth rate. Linearization facilitates the use of thermal unit systems, such as degree-days, to time the crop. Degree-days are calculated by accumulating daily temperatures above a base temperature in the linear region of the temperature response curve (Arnold, 1959).

Leaf unfolding rate in many plants is determined by average daily temperature in the linear temperature range. In the range of 22–29°C day temperatures and 12–22°C night temperatures, leaf appearance in sunflowers was linearly related to mean temperature (Rawson and Hindmarch, 1982). Leaf emergence in maize was 'nearly linear' in the range 12–26°C (Tollenaar et al., 1979) and Easter lily leaf unfolding was linear in the range 14–30°C (Karlsson et al., 1988). A positive linear relationship was also found for wheat as the temperature increased to 25°C. Further temperature increases beyond 25°C resulted in decreased leaf unfolding rate for wheat (Friend et al., 1962).

A decrease in leaf unfolding rate is expected in all plants as temperature increases above the optimum temperature for maximum leaf unfolding. Significant errors in predicting leaf unfolding are expected if temperatures which fall below the base temperature of no growth or above the optimum temperature of maximum growth are averaged with temperatures in the linear temperature range (LeDuc and Holt, 1987).

Hibiscus is produced in heated greenhouses in temperate climates and in unheated greenhouses in subtropical climates. Low or high temperatures may slow plant development and seriously affect crop scheduling and timing. A model allowing prediction of the accumulated vegetative crop development under a wide range of temperature conditions would improve production planning.

The purpose of this study was to quantify the temperature-controlled leaf unfolding rate in *Hibiscus rosa-sinensis*. Linear and polynomial functional relationships were developed to describe and summarize the effects of temperature on leaf appearance rate in two hibiscus cultivars. The selected polynomial function and model developed from the linear function were validated under commercial conditions for the two cultivars used to develop the functions and for seven additional cultivars.

MATERIALS AND METHODS

Leaf unfolding rate was determined in the two hibiscus cultivars 'Brilliant Red' and 'Pink Versicolor'. Hibiscus plants growing in 15-cm pots were received from Yoder Brothers, Inc. (Alva, FL) and were placed in a 50% shaded greenhouse at Michigan State University for 3 weeks to acclimatize. After the 3 week period, 42 plants of each cultivar with comparable development and at least six developing shoots on each plant were selected and distributed among six growth rooms. The air temperatures in the growth rooms were maintained such that the apical leaf and stem tissue had temperatures of 5, 11, 17, 23, 29 or 35°C during the light and dark span. Constant tissue temperatures were maintained by lowering chamber air temperature during the light period to account for tissue heating from lamp radiant energy. Irradiance at canopy level was 200 μmol m^{-2} s^{-1} from cool-white fluorescent lamps for 10 h day^{-1} (7.2 mol m^{-2} day^{-1}). Plants were subirrigated as necessary with a nutrient solution consisting of 7.1 mol m^{-3} (7.1 mM) N and 2.5 mol m^{-3} (2.5 mM) K.

The most recently unfolded leaf (>1 cm in length) on six shoots of each plant was marked by a hanging paper tag. The number of unfolded leaves above the marked leaf was recorded daily for each individual shoot. The time of data collection during the day was also noted as data were not always collected at the same time every day. Linear regression functions were developed for each individual shoot relating leaf number to time. The first derivative of these functions gave the rate of leaf unfolding (leaves h^{-1}). The resulting leaf unfolding rates were converted from an hourly to a daily basis and then pooled for further regression analyses to determine the daily temperature driven leaf unfolding rate.

Separate regression functions were developed for the two cultivars. These multiple linear regressions were performed to describe the rate of leaf unfolding (leaves day^{-1} vs. temperature) using first, second, third, and fourth order terms of temperature as independent variables. Selection of final regression functions was based on significance of included independent variables, F and R^2 values of the equations, and the adequacy of prediction. All independent variables included in the selected functions were significant at the 0.1% level. The selected functions for the two cultivars were compared using the Williams and Kloot method (Williams, 1959). The Williams and Kloot test is a symmetric test where two selected functions are compared for their ability to predict the independent variable. An unsymmetrical test is a test where one function is the accepted one and the question of its replacement by an alternative is considered. The test conducted here is equivalent to a test of the significance of the difference between the residual sum of squares left by each function.

No significant differences could be established between the two developed functions in predicting rate of leaf unfolding in 'Brilliant Red' and 'Pink Versicolor'. The complete database from both cultivars was then pooled and used to determine the hibiscus leaf unfolding function. Data from all temperatures were used to develop a higher order prediction. A linear model was also developed for the 11–29°C temperature range, as inspection of the plotted data means suggested such a model to be adequate for prediction of leaf unfolding at temperatures from 11 to 29°C.

Both the linear and cubic models were validated by comparing actual leaf unfolding for nine hibiscus cultivars ('Aloha Pink', 'Brilliant Red', 'Euterpe', 'Florida Sunset', 'Painted Lady', 'Pink Versicolor', 'Sundance', 'Tawny', and 'Vista') with predicted leaf unfolding. Unfolded leaf number was recorded weekly on 20 plants of each cultivar. Temperatures were recorded hourly in unheated Florida greenhouse structures (Yoder Brothers Inc., Alva, FL) and used for the calculations. Average hourly temperatures were used instead of average daily temperatures because daytime temperatures frequently exceeded 30°C. When temperatures were less than 10°C or exceeded 30°C, calculations using the linear model were made at 10°C and 30°C, respectively. Actual temperatures were used for calculations using the cubic model. Hourly rates were summed to provide predicted daily and weekly leaf unfolding rates.

RESULTS

Hibiscus plants grown at experimental temperatures of 5 and 11°C experienced chilling injury. The 5°C plants were severely damaged and did not survive, while the 11°C plants grew slowly.

The rate of leaf unfolding increased to a maximum and then leveled off for both cultivars (Fig. 1). The selected functions describing the leaf unfolding response included the first, second, and third order temperature terms. Based on the test by Williams and Kloot (Williams, 1959), the two selected cultivar functions were considered equal in predicting the rate of 'Brilliant Red' and 'Pink Versicolor' leaf unfolding. The Williams and Kloot test demonstrated the difference between the residual sum of squares for the two functions was nonsignificant (F-value$=0.5\times10^{-6}$). The following function, based on pooled data from both cultivars, was calculated to describe the temperature (T) controlled leaf unfolding rate in hibiscus

$$\text{Leaves day}^{-1}=0.06289-0.02026\cdot T+0.001750\cdot T^2-0.00002983\cdot T^3 \quad (R^2=0.96) \qquad (1)$$

The rate of leaf unfolding based on the 11–29°C temperature data was described by the linear function

$$\text{Leaves day}^{-1}=-0.113+0.01148\cdot T \quad (R^2=0.93) \qquad (2)$$

The largest difference in prediction between the cubic and the linear equa-

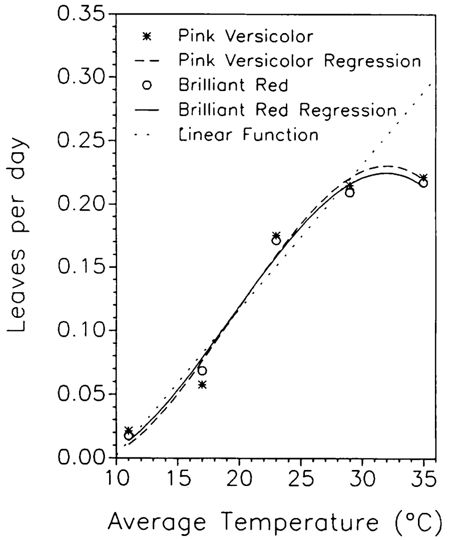

Fig. 1. Leaf unfolding rate of *Hibiscus rosa-sinensis* in response to average daily temperature. The 'Pink Versicolor' function was leaves $day^{-1}=0.2148-0.04317\cdot T+0.002792\cdot T^2-0.00004442\cdot T^3$ ($R^2=0.96$), the 'Brilliant Red' function was leaves $day^{-1}=0.08986-0.02373\cdot T+0.001892\cdot T^2-0.00003177\cdot T^3$ ($R^2=0.96$), and the linear function (11–29°C data) was leaves $day^{-1}=-0.113+0.01148\cdot T$ ($R^2=0.93$). T is the temperature in °C.

tions (eqns. (1) and (2), respectively) in the 11–29°C range was 0.01 leaves day^{-1} at 25°C which represented a 5.5% deviation. The base temperature below which no leaf unfolding is expected was estimated at 9.8°C using the linear leaf unfolding function (eqn. (2)). Maximum rate of leaf unfolding calculated by the cubic function (eqn. (1)) was 0.23 leaves day^{-1} at 32°C.

A linear model was developed from the linear function by setting leaf unfolding to 0 when the temperature was < 10°C and by calculating leaf unfolding at 30°C when the temperature was ≥ 30°C. The linear model and the cubic model predicted essentially equal leaf unfolding rates over time even though hourly rates varied significantly at high temperatures (Figs. 1 and 2). When temperatures were < 30°C, both models predicted similar hourly leaf unfolding rates (e.g. 11 March data, Fig. 2). However, when temperatures exceeded 30°C, the cubic model predicted a slower leaf unfolding rate than the linear model (e.g. 26 August data, Fig. 2). Higher predicted leaf unfolding rates by the cubic model than the linear model in the 20–25°C temperature range partially offset the slower predicted leaf unfolding rates at temperatures above 30°C and resulted in similar total predicted leaf numbers over time. During a 78-day period from 25 February to 14 March, 9.95 and 9.98 leaves were predicted to unfold by the linear and cubic models respectively. During

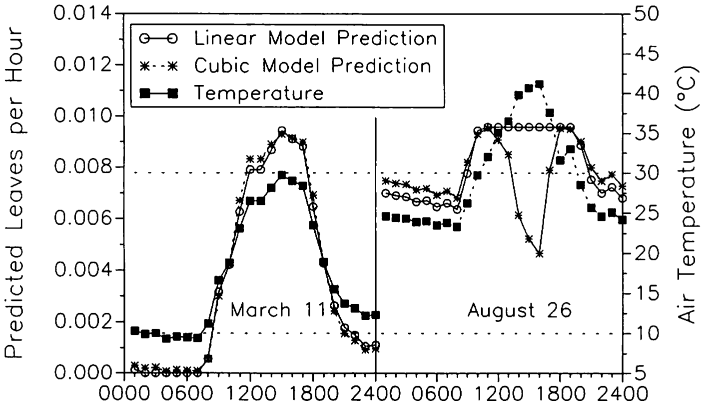

Fig. 2. Predicted hourly leaf unfolding rate based on hourly average temperature. The linear model was leaves $day^{-1} = -0.1140 + 0.01154 \cdot T$ and the cubic model was leaves $day^{-1} = 0.06289 - 0.02026 \cdot T + 0.001750 \cdot T^2 - 0.00002983 \cdot T^3$. T is the temperature in °C. Leaf unfolding for the linear model was set at 0 when temperature was less than 10°C and calculated at 30°C when temperature exceeded 30°C.

TABLE 1

Comparison of actual and predicted number of unfolded leaves 7 weeks after pinch in several cultivars of *Hibiscus rosa-sinensis*

Cultivar	Week of pinch[1]	Leaf No.		Deviation
		Predicted[2]	Actual	
'Aloha Pink'	30	8.23	8.0	−0.23
'Brilliant Red'	9	5.92	5.7	−0.22
	30	8.61	8.4	−0.21
'Euterpe'	8	5.67	5.2	−0.47
	29	8.20	8.2	0.00
'Florida Sunset'	9	6.08	5.8	−0.28
	30	8.23	7.5	−0.73
'Painted Lady'	8	5.67	6.0	0.33
	29	8.20	9.1	0.90
'Pink Versicolor'	8	5.67	5.5	−0.17
	29	8.20	7.9	−0.30
'Sundance'	31	8.89	9.0	0.11
'Tawny'	29	8.20	8.4	0.20
'Vista'	30	8.23	7.0	−0.33

[1]The week of the year starting with 1 January.
[2]Predicted leaf number is based on the linear model of leaves $day^{-1} = -0.113 + 0.01148 \cdot T$.

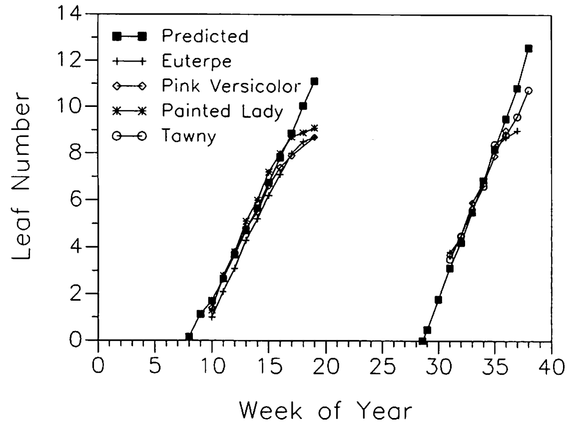

Fig. 3. Comparison of actual vs. predicted leaf unfolding for *Hibiscus rosa-sinensis* 'Euterpe', 'Pink Versicolor', 'Painted Lady', and 'Tawny' grown in unheated greenhouses in Florida. Plants were pinched on 11 March and 16 August 1989.

a 65-day period from 21 July to 24 September, 12.28 and 12.04 leaves were predicted to unfold by the linear and cubic models respectively. Temperatures during these two periods averaged 22.7 °C and 28.1 °C, respectively, and ranged from a low of 7.7 °C to a high of 44.1 °C.

The linear and the cubic models accurately predicted leaf unfolding for at least 7 weeks during the validation process in Florida (Table 1, Fig. 3). Predicted leaf unfolding was within 0.9 leaves of observed leaf unfolding for all cultivars over a 7 week period after pinching. The deviation after about 7 weeks between actual unfolded leaves and the predicted leaf unfolding coincided with the appearance of flower buds (Fig. 3).

DISCUSSION

The rate of leaf unfolding was found to be similar in the two studied cultivars (Fig. 1). The ability of the selected models to predict leaf unfolding for nine cultivars in the validation process also suggested leaf unfolding rate to be similar among hibiscus cultivars.

Although many hibiscus cultivars may have similar rates of leaf appearance, time to flower will vary depending on the number of leaves formed prior to the initiation of the first flower. In this study, the average number of leaves below the first flower was 7.4 ± 1.1 leaves for 'Brilliant Red' and 6.1 ± 0.8 leaves for 'Pink Versicolor' (data not presented). The leaf number did not vary among plants grown at the different experimental temperatures. 'Pink Versicolor' having fewer leaves than 'Brilliant Red' has been observed to flower earlier than 'Brilliant Red' under the same environmental conditions (M.

Hackmann, personal observation, 1989). Flowering will be delayed more significantly at low temperatures than high temperatures in cultivars forming many leaves compared with cultivars with a low leaf number. For example, the differentiation of one additional leaf prior to the formation of a flower bud is expected to delay flowering 35 days at 12°C but only 5 days at 30°C.

The hibiscus leaf unfolding response was curvilinear (Fig. 1). The temperature range included in this study was sufficiently wide to reveal the curvilinear shape and maximum rate of hibiscus leaf unfolding. A cubic regression function (eqn. (1)) had the ability to describe hibiscus leaf appearance from 11 to 35°C. At 29°C, the rapid linear rate increase discontinued (Fig. 1) and only small variations in leaf unfolding rates were observed from 29 to 35°C. The highest rate of leaf unfolding was estimated at 0.23 leaves day^{-1} at 32°C from eqn. (1). Tollenaar et al. (1979) also used a cubic function to describe the rate of maize leaf unfolding.The maximum rate in the maize study occurred at 31–32°C and was 0.57 leaves day^{-1}.

Many leaf unfolding responses have previously been described as linear functions of average daily temperatures (Friend et al., 1962; Tollenaar et al., 1979; Rawson and Hindmarch, 1982; Kiniry et al., 1983; Wang and Roberts, 1983; Karlsson et al., 1988, 1989). A linear function (eqn. (2)) approximated the leaf unfolding response in the 10–30°C temperature range (Fig. 1). A linear model was developed from the linear function by setting leaf unfolding to 0 when the temperature was <10°C and by calculating leaf unfolding at 30°C when the temperature was ≥ 30°C. The close prediction between the linear model and cubic function in the validation process (Fig. 2) indicated the adequacy of using either model to predict leaf unfolding in the hibiscus when using hourly temperature values. When temperatures consistently exceed 30°C, use of hourly temperature values in a computer program is most efficient to track leaf unfolding rate over time. If a computer program is already in use, the linear model holds no advantage over the more biologically accurate polynomial model.

If temperatures do not fall below the base temperature or exceed the linear range temperature, a linear function allows the use of degree days to schedule a crop (Arnold, 1959). The slope of a linear leaf unfolding function is leaves per degree day and the inverse of the slope is degree days per leaf. The number of hibiscus leaves per degree day was predicted to be 0.0115 and the number of degree days per leaf to be 87 with a base temperature of 9.8°C. Total number of degree days required from pinch to visible flower bud in hibiscus can be determined by the number of leaves initiated below the first flower.

Hibiscus leaf unfolding rate increased 0.011 leaves day^{-1} for each 1°C temperature increase in the linear portion of the temperature response curve. Similar rate increases for 1°C temperature increase have been observed in chrysanthemum at 0.018 additional leaves day^{-1} (Karlsson et al., 1989), in peas at 0.020 additional leaves day^{-1} (Balvoll and Bremer, 1965), in sunflowers at 0.022 additional leaves day^{-1} (Rawson and Hindmarch, 1982), and in maize at 0.031 leaves day^{-1} (Tollenaar et al., 1979). The reported leaf unfolding rate for Easter lily was considerably higher than the observed rate for hibiscus. For 1 °C temperature increase, Easter lily unfolded 0.094 additional leaves day^{-1} (Karlsson et al., 1988).

Leaf unfolding rate for nine hibiscus cultivars was predicted within 0.9 leaves over a 7-week period. After the appearance of flower buds, the leaf unfolding rate was overpredicted. The developed leaf unfolding models were based on data collected from developing shoots prior to visible flower buds. The results indicated a second model was required to adequately describe hibiscus leaf unfolding rate after flower bud appearance. Instead of developing an additional leaf unfolding model, a flower development model may be more appropriate.

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