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

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Abstract. Leaf unfolding rate (LUR) was determined for 'Utah' African violet plants grown in growth chambers under 20 combinations of temperature and photosynthetic photon flux (PPF). A nonlinear model was used to predict LUR as a function of shoot temperature and daily integrated PPF. The maximum predicted LUR was 0.27 leaves/day, which occurred at 25°C and a daily integrated PPF of 10 mol/m² per day. The optimum temperature for leaf unfolding decreased to 23°C, and the maximum rate decreased to 0.18 leaves/day as the daily integrated PPF decreased from 10 to 1 mol/m² per day. A greenhouse experiment using 12 combinations of air temperature and daily integrated PPF was conducted to validate the LUR model. Plant temperatures used in the model predicted leaf development more accurately than did air temperatures, but using average hourly temperature data was no more accurate than using average daily temperature data.

The African violet is an important greenhouse crop in the United States. In 1990, 23 million pots were sold at a wholesale value of $27.6 million (Agricultural Statistics Board, 1990). Production in the United States peaks at holidays—Valentine's Day is the largest marketing date. Most commercial producers of African violets begin production by purchasing small plants, or "plugs," which usually have 8 to 12 unfolded leaves. The plugs are transplanted into 0.5-liter (10-cm-diameter) pots, grown, and then sold when the plants have 20 to 25 unfolded leaves and five or more open flowers. Production from transplant to anthesis requires 8 to 12 weeks (Fischer, 1991).

Phenology development scales have been used to identify the status of plant development (Hanks and Ritchie, 1991). Vegetative development can be described by leaf number and the rate at which leaves appear, or unfold. Phenological scales are useful to the grower for identifying the current developmental status of a crop and the development required over a future period for a crop to be at the proper stage of development at the market date.

Temperature is the primary variable used in models to predict rates of plant development (Hodges, 1991). Average hourly temperatures (Karlsson et al., 1991), average daily temperatures (Karlsson et al., 1988), and minimum and maximum daily temperature (Hodges and French, 1985) data have been used in plant-development models for different species. Air temperature is most commonly used in leaf-development models.

Photosynthetic photon flux (PPF) is not usually included as a variable in leaf-development models; however, low daily integrated PPF can influence development by limiting the supply of photosynthates. Hanchey (1955) observed that leaf count on African violets decreased below 10 mol/m² per day. The African violet is a shade crop, so both temperature and PPF need to be considered in the development of a phenology model for African violet.

The objectives of our research were twofold: first, to describe the influence of temperature and PPF on the rate of leaf development of the African violet; and second, to develop a model that would predict leaf development in a greenhouse environment.

Materials and Methods

Model description. Leaf unfolding rate (LUR), expressed as the number of leaves unfolded per day, describes the rate at which leaves unfold, or appear, at the apical meristem. A leaf was considered unfolded when the leaf blade reached 7 mm in length. The slope of a linear regression line fit to the number of unfolded leaves as a function of time represented the LUR for a given plant.

The following nonlinear functions (Landsberg, 1977; Reed et al., 1976) were used to describe LUR as a function of both temperature and daily integrated PPF:

\[ LUR = A(T - T_{\text{Min}})(T_{\text{Max}} - T)^B \]  
\[ A = \frac{LUR_{\text{Max}}}{(T_{\text{Opt}} - T_{\text{Min}})(T_{\text{Max}} - T_{\text{Opt}})^B} \]  
\[ B = \frac{(T_{\text{Max}} - T_{\text{Min}})}{(T_{\text{Opt}} - T_{\text{Min}})} \]

where \( T \) is temperature and \( T_{\text{Min}} \) and \( T_{\text{Max}} \) refer to the minimum temperature and the maximum temperature at which LUR is zero. \( T_{\text{Opt}} \) is the temperature at which the maximum LUR occurs for a given daily integrated PPF (PPF_D). \( LUR_{\text{Max}} \) is the value for LUR at \( T_{\text{Opt}} \). The following nonlinear functions were used to describe \( T_{\text{Opt}} \) and \( LUR_{\text{Max}} \):

\[ T_{\text{Opt}} = a_0 + a_1 \exp(b_1 \text{PPF}_D) \]  
\[ LUR_{\text{Max}} = b_0 + b_1 \exp(b_2 \text{PPF}_D) \]

Abbreviations: LUR, leaf unfolding rate; PPF, photosynthetic photon flux.

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where $a_0$ and $b_0$ indicate the asymptotic values of the functions, and $a_1$, $a_2$, $b_1$, and $b_2$ represent parameter estimates.

Estimating parameters. Parameter estimates and asymptotic 95% confidence limits for the nonlinear functions used to model leaf development [Eqs. 1–5] were estimated with SAS procedure NLIN (SAS Institute, 1989). In previous experiments, the minimum temperature for leaf growth of the African violet was $=8^\circ$C (our unpublished data); therefore, the value of $T_{min}$ was fixed at 8$^\circ$C.

Design of experiment. ‘Utah’ African violet plants with $8 \times 10$ unfolded leaves were transplanted from 3-cm-diameter (22 cm$^2$) cells into 10-cm-diameter pots (450 cm$^3$) containing a commercial peat-based medium (Bacco Professional Plant Mix, Michigan Peat Co., Houston, Texas). Immediately after transplanting, plants were placed into one of five (15.1-m$^3$) walk-in growth chambers (Hotpack, Model UWP 3009-2, Philadelphia). Air temperatures were adjusted to maintain plant temperatures at 14, 18, 22, 26, and 30 ± 1$^\circ$C. Four PPF treatments were located in each of five temperature treatments. Five plants were grown in each of the 20 treatments. Orthogonal polynomial contrasts were used to determine the trend analyses. SAS procedure GLM (SAS Institute, 1989) was used for the methods of average hourly temperature data were compared when the LUR model was validated. The methods were based on: 1) average hourly plant temperature; 2) average hourly air temperature; 3) average daily plant temperature; and 4) average daily air temperature. The calculated average temperatures were used along with the daily integrated PPF to predict LUR on either an hourly or daily basis.

Two techniques were used to compare the predictive usefulness of the four methods of using temperature data in the LUR model. First, the absolute deviation between actual and predicted leaf count was calculated for each recorded leaf count. Second, the slope of the observed leaf count plotted against the predicted leaf count was calculated by linear regression. Accurate prediction of LUR would result in a slope equal to one; therefore, the absolute deviation between the slope of the predicted leaf count and the slope of the observed leaf count provided another comparison of the methods for entering temperature data into the LUR model.

Results

The leaves of each plant unfolded as a linear function of time for the $22C/7$-mol/m$^2$ per day treatment (Fig. 1); all other treatments produced similar results. Temperature, daily integrated PPF, and the interaction between temperature and daily integrated PPF influenced LUR significantly. LUR increased as temperature increased from 14$^\circ$C to an optimum temperature, and then decreased sharply as temperature increased above the optimum temperature. LUR also increased at all temperatures as daily integrated PPF increased from 1 to 7 mol/m$^2$ per day, but did not increase further at 10 mol/m$^2$ per day (Fig. 2).

The model [Eqs. 1–5] predicted LUR based on temperature and daily integrated PPF data (Fig. 2). The interaction between temper-
Fig. 2. Nonlinear model [Eqs. 1–5] describing LUR as a function of temperature and daily integrated PPF ($R^2 = 0.99$). Symbols represent treatment means.

Table 1. Parameter estimates and 95% confidence intervals calculated for use in the LUR model for African violets [Eqs. 1–5].

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Asymptotic 95% confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_{\text{Max}}$</td>
<td>30.83 30.36 31.31</td>
</tr>
<tr>
<td>$T_{\text{opt}}$</td>
<td>25.44 23.22 27.66</td>
</tr>
<tr>
<td>$a_1$</td>
<td>-3.127 -4.861 -1.392</td>
</tr>
<tr>
<td>$a_2$</td>
<td>-0.193 -0.559 0.173</td>
</tr>
<tr>
<td>$b_0$</td>
<td>0.266 0.252 0.280</td>
</tr>
<tr>
<td>$b_1$</td>
<td>-0.137 -0.182 -0.112</td>
</tr>
<tr>
<td>$b_2$</td>
<td>-0.418 -0.621 -0.215</td>
</tr>
</tbody>
</table>

Fig. 3. The influence of daily integrated PPF on (A) $T_{\text{opt}}$ [Eq. 4] and (B) LUR$_{\text{Max}}$ [Eq. 5]. Vertical bars indicate asymptotic 95% confidence intervals for $T_{\text{opt}}$ and LUR$_{\text{Max}}$ values estimated at each daily integrated PPF treatment.

Fig. 4. A comparison between air and plant temperature (A) over the course of a cloudy day (30 Dec. 1990), (B) a sunny day (3 Jan. 1991), and (C) a cloudy day in which the plants were growing under high-pressure sodium lamps from 0600 to 1800 hr (30 Dec. 1990).
Table 2. Comparison of four methods of using temperature data to predict leaf count in African violets.

<table>
<thead>
<tr>
<th>Air temp (°C)</th>
<th>Daily integrated PPF (mol/m² per day)</th>
<th>Deviation between predicted and observed leaf counts (no. leaves)</th>
<th>Deviation between slopes of the predicted and actual leaf counts (no. leaves)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hourly Plant</td>
<td>Air</td>
<td>Daily Plant</td>
</tr>
<tr>
<td>15</td>
<td>2.6</td>
<td>0.53</td>
<td>1.47</td>
</tr>
<tr>
<td>20</td>
<td>4.5</td>
<td>0.94</td>
<td>2.22</td>
</tr>
<tr>
<td>25</td>
<td>2.6</td>
<td>0.70</td>
<td>0.89</td>
</tr>
<tr>
<td>30</td>
<td>4.5</td>
<td>0.92</td>
<td>1.40</td>
</tr>
<tr>
<td>Mean</td>
<td>0.88 a</td>
<td>1.37 b</td>
<td>0.79 a</td>
</tr>
</tbody>
</table>

*Mean separation by l.s.d, P < 0.05.*

Fig. 5. Comparison between the predicted (solid line) and observed (circles) leaf count of plants grown in a greenhouse under 12 temperature/PPF treatments.

over 77 days of the validation experiment (Fig. 5). Predicted leaf count was within one leaf of the observed leaf count 84% of the time (more than 300 measurements on 48 plants) when average daily plant temperatures were used in the model (Fig. 6).

**Discussion**

The influence of temperature on leaf development of African violets was similar to that on other plant species. In African violets, we estimated T_{Min} to be 8°C, T_{Op} to be between 23 and 25.5°C, and T_{Max} to be 30.8°C—temperatures similar to those determined for other tropical species (Kiniry et al., 1991). LUR_{Max} varies considerably from 0.10 leaves/day for banana (*Musa paradisiaca* L.) (Allen et al., 1988) to 2.5 leaves/day for the Easter lily (*Lilium longiflorum* Thunb.) (Karlsson et al., 1988). LUR_{Max} for African violets was 0.27 leaves/day, which occurred on plants grown at 26°C and 10 mol/m² per day.

Leaf development was influenced by daily integrated PPF. PPF is not typically used in plant development models because the daily integrated PPF at which most crops are produced is sufficiently high to saturate the photosynthetic apparatus. However, African violets are susceptible to physiological damage at high PPF, so growers often produce African violets at PPF that limit photosynthesis and leaf development. Therefore, daily integrated PPF was included as a variable in the LUR model.

No significant differences resulted from using average hourly temperatures in the model as compared to average daily temperatures. Similar results have been observed by researchers using degree-day models (Cross and Zuber, 1972; Gilmore and Rogers, 1958). The temperature-response curves used in the LUR model were developed from data collected on plants grown at constant temperatures, but these response curves may not reflect the developmental responses that occur during brief exposures to temperatures outside the linear-response range. Therefore, the model reflects development rates that occur over broader time intervals; thus, average daily temperatures were the most accurate for predicting leaf development.

Plant temperatures gave a more accurate prediction of leaf count with the LUR model than did air temperatures. The actual tissue temperature of the developing plant must be determined to predict specific organ or tissue development accurately. Harris and Scott (1969) independently fluctuated the temperature of carnation (*Dianthus caryophyllus* L.) flower buds and leaves and observed that the temperature of an organ determined the development rate for that organ.

Plant temperature depends on the energy exchange between the plant and its environment. During the night period of the greenhouse experiment, plant temperatures were frequently 2 to 5°C below air temperature. Part of this temperature difference can be attributed to net energy loss to the greenhouse glass via longwave radiation (Hanan et al., 1978). However, we also have observed a 1 to 3°C drop in temperature of African violets during dark periods in growth chambers. Vogelezang (1988) observed that meristem temperature of African violets is correlated more closely with soil temperature than air temperature. African violet has a rosette growth habit, and the meristem is typically <3 cm above the soil surface. Therefore, we hypothesize that the observed difference between air and plant temperature is due in part to evaporative cooling occurring from the wet soil surface.
In summary, a LUR model based on average daily plant temperatures and daily integrated PPF accurately predicted leaf development of African violets grown for 77 days in a greenhouse under a range of air temperatures from 15 to 30°C and PPF from 2.6 to 8.8 mol/m² per day. Plant temperature predicted leaf development more accurately than did air temperature. No benefit was obtained by using average hourly temperatures rather than average daily temperatures.

Literature Cited