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A temperature response function for development of the chrysanthemum (*Chrysanthemum x morifolium* Ramat.)

Uma função de resposta do desenvolvimento à temperatura em crisântemo (*Chrysanthemum x morifolium* Ramat.)

Nereu Augusto Streck[1]

ABSTRACT

Developmental models can help growers to decide management practices, and to predict flowering and harvest time. Currently, a double exponential function is proposed as a generalized temperature response function for chrysanthemum. This function is not the most appropriate because its parameters lack biological meaning. The objective of this study was to develop a nonlinear temperature response function of chrysanthemum development that has parameters with biological meaning. The proposed function is a beta function with three parameters, the cardinal temperatures (minimum, optimum, and maximum temperatures for development), which were defined as 0, 22, and 35°C. Published data of temperature response of development of three cultivars, which are independent data sets, were used to test the performance of the double exponential function and the beta function. Results showed that the beta function is better than the double exponential function to describe the temperature response of chrysanthemum development.

Key words: *phenology, flowering, model.*

RESUMO

Modelos de desenvolvimento podem ajudar os produtores no manejo e no planejamento da época de florescimento e colheita. Atualmente, a resposta térmica do desenvolvimento do crisântemo é modelada por uma função exponencial dupla, a qual não é completamente adequada porque os seus parâmetros não têm interpretação biológica. O objetivo deste estudo foi desenvolver uma função de resposta do desenvolvimento à temperatura em crisântemo que tenha parâmetros com interpretação biológica. A função proposta é uma função beta com três parâmetros, que são as temperaturas cardinais (temperaturas mínima, ótima e máxima de desenvolvimento), definidas como 0, 22 e 35°C. Dados independentes da resposta do desenvolvimento à temperatura em três cultivares de crisântemo publicados na literatura foram usados para testar as duas funções de resposta. Os resultados mostraram que a função beta é melhor do que a função exponencial dupla para descrever a resposta do desenvolvimento à temperatura do crisântemo.

Palavras-chave: *fenologia, florescimento, modelo.*

INTRODUCTION

Chrysanthemum (***Chrysanthemum x morifolium*** Ramat.) is a species native of China, and was brought to Europe at the early 19th century and to the USA at the end of the 19th century (KOFRANEK, 1980). Chrysanthemum plants are herbaceous perennials and their flowers (capitula) develop from branched stems. Plants perennate naturally by means of stolons and are propagated asexually by means of stem cuttings taken from basal shoots (COCKSHULL, 1985). Inflorescences are classified based on their shape and form as suitable for garden and greenhouse culture in singles, anemones, pompons, decoratives, and large-flowered (ACKERSON, 1957; KOFRANEK, 1980). As a cut flower, chrysanthemum is market as either "standard" or "spray" form. The standard form consists of a stem from which all but the terminal flower was removed whereas in the spray form, the lateral flowers are kept and the terminal flower is removed (COCKSHULL, 1985).

Chrysanthemum is one of the most popular cut flowers grown in the Americas, Western Europe, and Japan (COCKSHULL, 1985; VAN DER HOEVEN, 1987). During the period 1991-1999, about 146 million standard chrysanthemum flowers and 126 million

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[1] Engenheiro Agrônomo, PhD., Professor Adjunto, Departamento de Fitotecnia, Centro de Ciências Rurais, Universidade Federal de Santa Maria, 97105-900, Santa Maria, RS, Brasil. E-mail: nstreck1@smail.ufsm.br

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bunches of pompom chrysanthemum were sold only in the USA at a wholesale of about US$ 68 million and US$ 155 million, respectively (USDA, 2002). Chrysanthemum is photoperiod-sensitive and classified as a short-day plant (KOFRANEK, 1980; COCKSHULL, 1985). In commercial production systems, a short-day treatment is applied to stimulate floral initiation, while temperature is used to control the time of flowering, thus making possible to produce chrysanthemum flowers all year round (MACHIN & SCOPES, 1978; KOFRANEK, 1980; VAN RUITEN & JONG, 1984).

Crop simulation models offer a conceptual framework for the organization of research, have the potential of integrating knowledge of different areas, and are valuable application tools for yield forecast, policy analysis, decision support systems, crop management, planning harvest time and transportation of the products to the marketplace, and selection of appropriate cultivars in breeding programs. A developmental model is also an important part of any crop simulation model, because plant growth is largely related to photosynthesis whereas the partitioning of assimilates to different organs is dependent upon plant developmental stage (PENNING de VRIES et al., 1989; GOUDRIAN & VAN LAAR, 1994). Developmental models can also help growers to predict flowering time. Horticulture is characterized by a high diversity of cultivation systems, and fruit, vegetable, flower and ornamental species, but so far only a few of them have been modeled (GARY et al., 1998).

Virtually all the metabolic processes in living organisms are temperature-dependent. As a consequence, temperature affects almost all aspects of plant growth and development. The first quantitative study of plant-temperature relationship is attributed to René A. F. de Réaumur around 1730 (RÉAUMUR, 1735). Since then, the concept of thermal time has been widely used to describe the temperature response of development in plants and insects (see WANG, 1960; ARNOLD, 1960; PRUESS, 1983 for detailed reviews). The thermal time approach, however, has been criticized because of the assumption of a linear response of plant development to temperature (WANG, 1960; McMASTER & WILHELM, 1997). The response of plant development to temperature is better summarized in terms of three cardinal temperatures, namely the minimum (T_{min}), optimum (T_{opt}), and maximum (T_{max}) temperatures, in a nonlinear fashion, with the response being linear in only a portion of the temperature range that affects development (JONES, 1992; SHAYKEWICH, 1995). Consequently, nonlinear temperature response functions have been introduced in models of several field crops (e.g. HORIE, 1994; WANG & ENGEL, 1998; JAME et al., 1999). In this new approach, the temperature response function [f(T)] varies from 0 to 1 and is multiplied by the maximum rate of development (R_{max}), which is attained under optimum temperature (T_{opt}). When the temperature departs from T_{opt}, the calculated actual rate of development decreases as a function of f(T).

Following this new approach for modeling plant development, LARSEN & PERSSON (1999) proposed a developmental model for chrysanthemum. The development towards flowering in the LARSEN & PERSSON (1999) model is described by a temperature response function and a light response function that multiply R_{max}. For the temperature response function, the following double exponential function was used by LARSEN & PERSSON (1999):

$$f(T) = A[1-e^{-ß\,(T-Tmin)}][1-e^{Tmax-T)}] \quad \text{for } T_{min} \leq T \leq T_{max}$$

$$f(T) = 0 \quad \text{for } T < T_{min} \text{ or } T > T_{max} \qquad (1)$$

where A=2.214, ß=0.058, =0.168, Tmin=6.8°C, T_{max}=30.2°C, and T is the actual air temperature.

Equation 1 is suggested as a generalized temperature response function because the parameters were derived from a data set that included 30 cultivars. However, there are several disadvantages of adopting equation 1 as a generalized temperature response function. First, the parameters A, ß, and γ have no biological meaning. Second, at T_{opt} the response is not unity (or maximum), which causes concerns because it is expected that at optimum temperature, the development rate is maximum, i.e. $R_{Topt} = R_{max}$. Third, it has a large number of parameters (five); the more parameters the more difficult is their estimation by a statistical procedure, as the convergence of the residue squares to a minimum value becomes more difficult and, in this case, at least six data points are needed to fit the curve.

The objective of this study was to develop a nonlinear temperature response function for development in chrysanthemum that is more realistic from a biological point of view than the temperature response function currently available.

MATERIAL AND METHODS

A typical biological response to temperature from T_{min} to T_{opt} follows a logistic curve. The response increases slowly as temperature increases from T_{min}, it then increases in a linear fashion in an intermediate range of temperature, and then the rate of increase in the response decreases as temperature approaches T_{opt}, at which the response is maximal. At temperatures above T_{opt}, the response decreases in a nonlinear fashion and eventually ceases at T_{max} (SHAYKEWICH, 1995). The beta function used by WANG & ENGEL (1998) to describe the response of wheat development to temperature was used in this study to describe the temperature response of development in chrysanthemum. The temperature function [f(T)] varies from 0 to 1 and is defined as:

$$f(T) = [2(T-T_{min})^{\alpha}(T_{opt}-T_{min})^{\alpha} - (T-T_{min})^{2\alpha}]/(T_{opt}-T_{min})^{2\alpha}$$
$$\text{for } T_{min} \leq T \leq T_{max}$$
$$f(T) = 0 \quad \text{for } T < T_{min} \text{ or } T > T_{max} \qquad (2)$$
$$\alpha = \ln 2/\ln[(T_{max}-T_{min})/(T_{opt}-T_{min})] \qquad (3)$$

where T_{min}, T_{opt}, and T_{max} are the cardinal temperatures for development (minimum, optimum, and maximum). Equation 2 is a flexible curve and, by changing the cardinal temperatures, it can attain several shapes (WANG & ENGEL, 1998). The cardinal temperatures for development in chrysanthemum were assumed to be $T_{min} = 0^{o}C$, $T_{opt} = 22^{o}C$, and $T_{max} = 35^{o}C$, which are the same as for wheat (***Triticum aestivum*** L.) (WANG & ENGEL, 1998). The reason why these cardinal temperatures were chosen is because of the similar range of optimum temperature for development in the two species. The T_{opt} for chrysanthemum development varies from 19-23°C(KARLSSON et al., 1989; LARSEN & PERSSON, 1999), whereas the T_{opt} for wheat development varies from 19-24 °C (PORTER & GAWITH, 1999). Thus, it was assumed in this study that the two species also have in common T_{min} and T_{max}. Therefore, the function to describe the temperature response of development in chrysanthemum with the above cardinal temperatures is:

$$f(T) = 0.019814\,(T)^{\alpha} - 9.8147 \times 10^{-5}\,(T)^{2\alpha}$$
$$\text{for } T_{min} \leq T \leq T_{max}$$
$$f(T) = 0 \text{ for } T < T_{min} \text{ or } T > T_{max} \qquad (4)$$
$$\text{with } \alpha = 1.492868.$$

The following independent data sets of temperature response of developmental parameters of three chrysanthemum cultivars reported in the literature were used to test and compare the performance of equations 1 and 4: data of time to visible buds (days) of cv. "Bright Golden Anne" at six temperatures (10, 15, 18.5, 20, 25, and 30ºC) from KARLSSON et al. (1989) (their Table 2), data of leaf appearance rate (leaves day^{-1}) of cv. "Pert" at six temperatures (12, 15, 18, 21, 24, and 27ºC) from LARSEN & HIDÉN (1995) (their Figure 5), and data of time to flowering (days) of cv. "Snowdon" at six temperatures (9.6, 10.9, 17.1, 20.4, 22.9, and 26.1ºC) from ADAMS et al. (1998) (their Figure 1). Data from figures were extracted by enlarging the diagram and estimating the values by interpolation. Data of time to flowering and time to visible buds were transformed in rate of development by taking the reciprocal of time, i.e., 1 days^{-1}. Data were then normalized to vary from 0 to 1 by dividing each value by the maximum development or leaf appearance rate.

The response to temperature predicted by equation 1 and by equation 4 was compared with the observed values. Model performance was evaluated considering how well predicted values of a given model matched observed values, how well a model performs compared to other (or existing) models, and how general was the model (SADLER & SCHROLL, 1997). The prediction capability was addressed by calculating two statistics, the root mean square error (RMSE) and the index of agreement (d). The RMSE expresses the average error produced by a model (the lower the RMSE the better the model) and has the same dimensions as the model output or the observed data (in this study it is dimensionless). RMSE was calculated as (JANSSEN & HEUBERGER, 1995):

$$RMSE = [\Sigma(P_i - O_i)^2/N]^{0.5} \qquad (5)$$

where P_i = predicted data, O_i = observed data, N = number of observations, and i = 1…N.

The index of agreement (d) measures the degree to which the predictions of a model are error free, and is dimensionless (WILLMOTT, 1981). The values of d range from 0, for complete disagreement, to 1, for perfect agreement between the observed and predicted values. The index d was calculated as (WILLMOTT, 1981):

$$d = 1 - [\Sigma(P_i-O_i)^2]/\ \Sigma[(|P_i-\bar{O}|)+(|Oi-\bar{O}|)]2 \qquad (6)$$

where $\bar{O}$ is the average of the observed values.

Comparison between the two models was addressed by calculating the statistic E_{12}, i.e., the accuracy of model 1 relative to model 2 (ALLEN & RAKTOE, 1981):

$$E_{12} = MSE_1/MSE_2 \qquad (7)$$

where MSE_1 and MSE_2 are the mean square error of the predictions with model 1 and 2, respectively:

$$MSE_1 = \Sigma(P_{1i} - O_i)^2 \qquad (8)$$
$$MSE_2 = \Sigma(P_{2i} - O_i)^2 \qquad (9)$$

The statistic E_{12} is dimensionless and varies from 0 to infinity. A value of E_{12} between 0 and 1 implies that model 1 is superior to model 2. If E_{12} is greater than 1 then model 2 is better. In this study, for the purpose of calculating the statistic E_{12}, the beta function (equation 4) is considered model 1 and the double exponential function (equation 1) is model 2.

Model generality was addressed by comparing statistics (RMSE, d and E_{12}) using independent data sets.

RESULTS AND DISCUSSION

The observed data of temperature response of developmental parameters of the three chrysanthemum cultivars at different temperatures, and the temperature response curve predicted with the double exponential function (equation 1) and with the beta function (equation 4) are presented in Figure 1. The observed data, as they were normalized with respect to their maximum, all fell into a similar pattern of response to temperature, suggesting a general type of temperature response of developmental parameters for different cultivars. The observed data clearly show a maximum response in the range of 20 - 24°C, and a decrease when temperature departs from T_{opt}. The trend of the observed data is well captured by the beta function (equation 4) and not so well by the double exponential function (equation 1). The breadth of the curve predicted with equation 1 is narrower that the one predicted with equation 4, resulting in under prediction of most of the observed data when the double exponential function was used. The only region of the temperature response that was well predicted by equation 1 is close to T_{opt}, which is about 21ºC and similar to the T_{opt} in equation 4.

The statistics of the performance of both models are presented in table 1. All statistics suggest that the beta function (equation 4) is better than the double exponential function (equation 1). The RMSE was reduced about 75%, the index d was closer to 1, and the relative accuracy was well below 1 when the beta function was used compared to the double exponential function.

The double exponential function (equation 1) has T_{min}=6.8ºC and T_{max}=30.2ºC whereas the beta function (equation 4) has T_{min}=0ºC and T_{max} =35ºC. Note that the observed data of temperature response of developmental parameters in the three cultivars (Figure 1) offer little support to believe that minimum and maximum temperatures for chrysanthemum development are 6.8ºC and 30.2ºC, respectively, as assumed in equation 1. On the other hand, the observed data show that the assumption of a minimum temperature of 0ºC and a maximum temperature of 35ºC for chrysanthemum in equation 4 seems to be reasonable. At the lowest temperature (9.6ºC) that has observed data, the response of time to flowering of cv. Snowdon is 0.467 whereas the response predicted by equation 1 is 0.321 and by equation 4 is 0.496. At the highest temperature (30ºC) that has observed data, the response of time to visible buds in the cultivar Bright Golden Anne was 0.687 whereas equation 1 predicted a response of 0.054 and equation 4 predicted a response of 0.653.

One may argue that the response curve of equation 1 could be wider by simply changing T_{min} and T_{max}. This is not the case because if T_{min} and T_{max} in equation 1 are changed, then the value of the other three parameters also needs to be changed in order to maintain a 0-1 response, as the values of the parameters in equation 1 are dependent on each other. This fact exemplifies the empirical nature of equation 1 and is a constraint from a modeling perspective. Another problem with equation 1 is that at T_{opt} the response is 0.977, and not unity, which is unrealistic from a biological point of view. These facts and the bad performance in describing the data presented here (Figure 1 and Table 1) confirm that the double exponential function proposed by LARSEN & PERSSON (1999) is not appropriate as a generalized temperature response function for development in chrysanthemum.

On the other hand, several reasons contribute to adopt the beta function (equation 4) as a generalized temperature response function for development in chrysanthemum. First, its performance was good over a wide range of temperature response and superior to the function currently used (Figure 1 and Table 1). Second, it has less number of parameters (three) compared to the double exponential function (five). The use of Occam's Razor in crop modeling is encouraged (SINCLAIR & MUCHOW, 1999), i.e., the simplest theory is preferred to more complex ones.

Table 1 - Statistics of the performance of the two models in predicting the temperature response of development in chrysanthemum.

Statistic	Equation 1	Equation 4
RMSE	0.192	0.049
d	0.805	0.977
E_{12}		0.065

RMSE=root mean square error; d=index of agreement, E_{12}=accuracy of the beta function relative to the double exponential function.

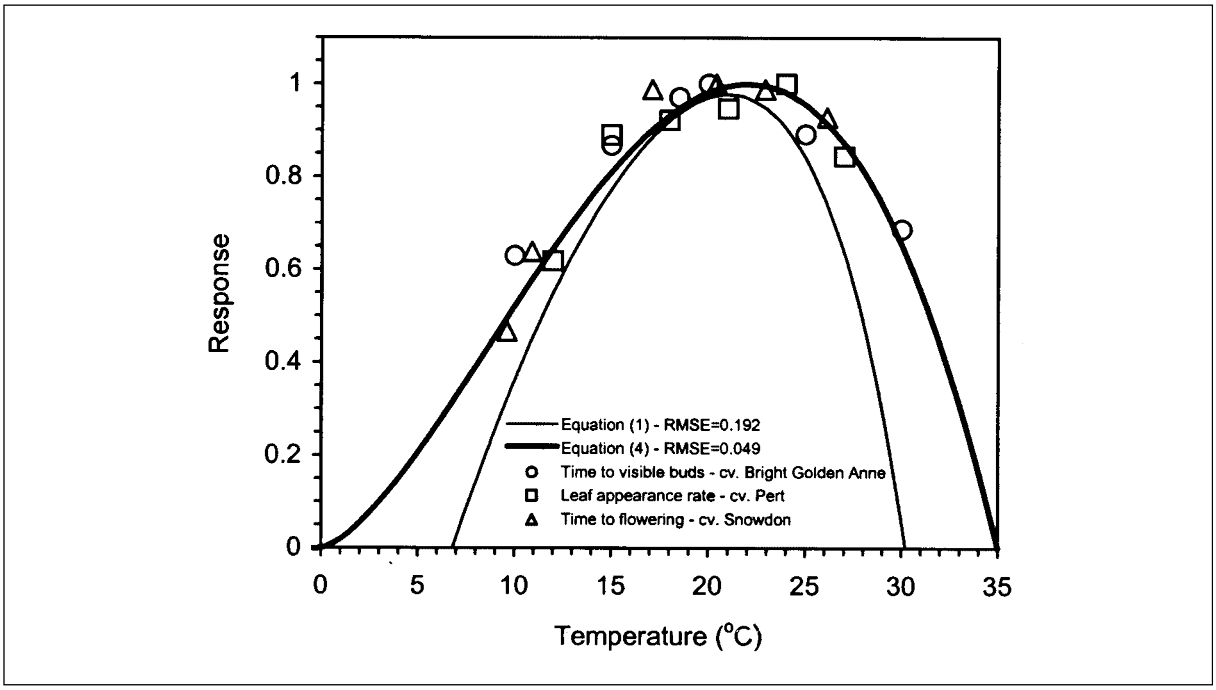

Figure 1 - The performance of the double exponential function [equation (1)] and the beta function [equation (4)] in describing the temperature response of developmental parameters of three chrysanthemum cultivars. Observed data are normalized data of time to visible buds (days) of cv. "Bright Golden Anne" from KARLSSON et al. (1989), leaf appearance rate (leaves day^{-1}) of cv. "Pert" from LARSEN & HIDÉN (1995), and time to flowering (days) of cv. "Snowdon" from ADAMS et al. (1998).

Furthermore, less number of parameters decreases the number of input data necessary in crop simulation models. Third, its parameters (cardinal temperatures) have biological meaning. Cardinal temperatures have operational definitions and are widely accepted in studies of temperature response in plants (PORTER & GAWITH, 1999). Fourth, the cardinal temperatures (0, 22, and 35°C) were derived from another species (***Triticum aestivum*** L.) and worked well for three different cultivars of chrysanthemum (***Chrysanthemum x morifolium*** Ramat.), indicating a robust and general nature.

CONCLUSION

A beta function is better than a double exponential function to describe the temperature response of chrysanthemum development. The cardinal temperatures of 0, 22, and 35°C are reasonable for chrysanthemum development.

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