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A generalized vernalization response function for lily (*Lilium* spp.)

Uma função geral de resposta à vernalização em lírio (***Lilium*** *spp.*)

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Abstract - *Vernalization is a process required by certain plant species, including lily (**Lilium** spp.), to enter the reproductive stage, through an exposure to low, non-freezing temperatures. A literature search yielded no previous attempt to model the vernalization response in lily. The objective of this study was to develop a generalized nonlinear vernalization response function for lily. The nonlinear vernalization function has coefficients with biological meaning derived from another species (**Triticum aestivum** L.). Data of time from bulb planting to flowering at different effective vernalization days (VD) treatments in 10 lily genotypes, which are from published research, were used as independent data for evaluating the nonlinear vernalization function. These data sets represent a wide range of lily genotypes with different vernalization responses. The generalized nonlinear vernalization function described well the lily developmental response to VD, with a root mean square error of 0.089. It is concluded that the vernalization response in lily can be described by a vernalization function that is independent of genotype. The implication of this conclusion is that most of the genetic variation of the vernalization response encountered among genotypes can be accounted for by using a single function, thus, reducing the input data set necessary in crop simulation models.*

Key words: *vernalization, response function, model, plant development, **Lilium**.*

Resumo - *Vernalização é um processo que certas espécies de plantas, incluindo lírio (**Lilium** spp.), necessitam para entrar no período reprodutivo, através da exposição a baixas temperatures. Uma revisão de literatura revelou nenhum estudo anterior objetivando modelar a resposta de desenvolvimento à vernalização em lírio. O objetivo deste estudo foi desenvolver uma função geral não linear de resposta a vernalização em lírio. A função não linear tem coeficientes com interpretação biológica e foi derivada de outra espécie (**Triticum aestivum** L.). Dados independentes da duração do período compreendido do plantio dos bulbos até o florescimento das plantas em diferentes tratamentos de dias de vernalização em 10 genótipos de lírio publicados na literatura foram usados como dados independentes para testar a função não linear de vernalização. Neste conjunto de dados estão representados genótipos com diferentes respostas à vernalização. A função geral não linear de vernalização descreveu bem a resposta de desenvolvimento à vernalização dos diferentes genótipos com uma raiz quadrada média do erro de 0,089. Concluiu-se que a resposta à vernalização em diferentes genótipos de lírio pode ser descrita por uma função geral não linear de vernalização. A implicação desta conclusão é que uma grande parte da variação genética na resposta à vernalização pode ser descrita pela mesma função de resposta, o que diminui o número de dados necessários em modelos de simulação de culturas.*

Palavras-chave*: vernalização, função de resposta, modelo, desenvolvimento vegetal, **Lilium**.*

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Introduction

Lily (*Lilium* spp.) is one of the six more important genera of flower bulbs produced worldwide (DE HERTOGH & LE NARD, 1993). Major markets for lily include fresh cut flowers, potted flowering plants, and gardens and landscapes (DE HERTOGH, 1996; GRASSOTTI, 1996; MYNETT, 1996). The importance of this genus in the world flower market is in large part due to the diversity of the species and the large number of hybrids and cultivars commercially available (DE HERTOGH, 1996).

Most of lily species require an exposure to low, non-freezing, temperatures to accelerate shoot emergence and flowering (ROH & WILKINS, 1977a; ROH, 1985). The exposure to low temperatures either in natural or in artificial cold treatment is called vernalization. Vernalization is a natural survival mechanism common to certain fall planted species to tolerate low temperatures during the winter. The first description of a cold requirement was by G. GASSNER in 1918 for winter cereals (see review by PURVIS, 1961). Research on the effect of vernalizing temperatures on lily species started in the 1930's (WEILER & LANGHANS, 1968). The works by PURVIS (1939, 1947, 1948) and PURVIS & GREGORY (1937, 1952) provided the hypotheses and the basis for what is currently known about the vernalization process in plants. Since then, the effect of vernalizing temperatures on plants has been widely studied and the factors that influence vernalization response have been identified, i.e., temperature range over which the vernalization process takes place, duration of the vernalization period, genotype responses, and plant age (CHUJO, 1966; JEDEL et al., 1986; WANG et al., 1995; RAWSON et al., 1998).

Lily plants respond to vernalization by decreasing their time to flowering (i.e., there is an increase in the development rate towards flowering as vernalization progresses). The decrease in the time to flowering is caused by a decrease in the number of primordia that become leaves, i.e., a decrease in final leaf number (ROH & WILKINS, 1977a,b; ROH, 1985). The plant response to vernalization is given by the combination of two factors, the temperature during the vernalization period, and the duration of the vernalization period. Vernalization has three cardinal (minimum, optimum, and maximum) temperatures (YAN & HUNT, 1999). Cardinal temperatures for vernalization have been identified for different species. For instance, the cardinal temperatures for vernalization in wheat (*Triticum aestivum* L.) are -1.3, 4.9, and 15.7ºC (PORTER & GAWITH, 1999), in carrot (*Daucus carota* L.) are -1, 6.5, and 16ºC (ATHERTHON et al., 1990), in calabrese (*Brassica oleracea* var. *italica*) are -2.8, 15.8, and 23.6ºC (WURR et al., 1995), and in lily are 0, 5, and 21ºC (ROH & WILKINS, 1977a, ROH, 1985; HOLCOMB & BERGHAGE, 2001). The duration of the exposure to vernalizing temperatures is measured as effective vernalization days (VD). One VD is attained when the plant is exposed to the optimum temperature for vernalization for a period of one day (24 h). As temperature departs from the optimum, only a fraction of one VD is accumulated by the plant at a given calendar day (HODGES & RITCHIE, 1991; RITCHIE, 1991).

Because of its direct and indirect (through vernalization) effects on flowering time, temperature is one of the major environmental factors that affect the development rate in lily, along with photoperiod (WILKINS et al., 1968; ROH & WILKINS, 1977b,c,d). In order to account for the effect of VD on the development rate, many crop simulation models use a response function for VD [vernalization function, f(V)], which varies from 0 to 1, as a modifier of the development rate (e.g. WEIR et al., 1984; RITCHIE, 1991; WANG & ENGEL, 1998). A literature search showed that existing lily developmental models assume that bulbs are already vernalized at the time they are planted in commercial greenhouses, and therefore no f(V) is part of the algorithm to predict flowering in such lily models (e.g. FISHER et al., 1997a,b; FISHER & LIETH, 2000). While there is no doubt that lily models without a vernalization function have a practical application as the producer knows that bulbs should be vernalized at about 5ºC for a six-week period (FISHER et al., 1997a), such lily models fail as a tool to understand the process of development in lily plants grown in natural (field) ecosystems. This provides a rationale for developing a vernalization function for lily.

In simulation models of field crops, f(V) is typically modeled by a three-stage linear function (e.g. WEIR et al., 1984; REININK et al., 1986; RITCHIE, 1991; CAO & MOSS, 1997, WANG & ENGEL 1998). The three-stage linear function has two coefficients: The minimum or base vernalization days (VD_b), defined as the VD below which no development occurs, and the maximum or full vernalization days (VD_{full}), defined as the VD above which the development rate is maximum. The response function [f(V)] is 0 when VD is equal to or less than (VD_b), then increases linearly to 1 when (VD_{full}) is achieved, and for any VD equal to or greater then VD_{full}, f(V) =1. The three-stage linear approach lacks generality because the end points of the response function are genotype dependent (WEIR et al., 1984; HODGES & RITCHIE, 1991; CAO & MOSS, 1997; WANG & ENGEL, 1998). From a modeling perspective, this is a disadvantage because the values of the two coefficients (VD_b and (VD_{full}) are unknown for many genotypes, thus necessitating controlled experiments in order to quantify them, which are expensive, and time and labor demanding. Another disadvantage of the three-stage linear approach is its little biological meaning as it is composed of a combination of linear equations that introduce abrupt changes at the transition points of the response function. Plant developmental response to VD is smooth and continuous, which causes a significant departure from linearity (CHUJO, 1966; WANG et al., 1995; BROOKING, 1996; RAWSON et al., 1998). Therefore, although attractive because it is simple to implement, the three-stage linear approach may not be the most appropriate response function for f(V), and was not pursued in this study. To overcome the disadvantages of the three-stage linear f(V), STRECK (2002) suggested the use of a nonlinear response function for f(V) in wheat. The nonlinear f(V) was superior to the three-stage linear f(V), and successfully described the vernalization response of winter wheat cultivars developed in different parts of world and with different vernalization responses.

In this study, the idea of generality and biological meaning for the vernalization response function was pursued for lily. A literature search yielded no previous attempt to model the vernalization response in lily, which provides a rationale for this effort. The objective of this study was to develop a generalized nonlinear vernalization response function for lily.

Material and methods

Results on the effect of VD on time to flowering in other species (e.g. wheat) suggest a sigmoidal shaped curve for describing the plant developmental response to VD (e.g. CHUJO, 1966; WANG et al., 1995; BROOKING, 1996; RAWSON et al., 1998; MAHFOOZI et al., 2001). There are several functions with a sigmoidal shape. Among them, a flexible sigmoidal response function is the MMF function (MORGAN et al., 1975):

$$Y = (ab + cX^n)/(b + X^n) \qquad (1)$$

where Y is the dependent (or response) variable, X is the independent (or explanatory) variable, a is the intercept when X=0, c is the asymptote as X approaches infinity, n is a shape coefficient, and b is interpreted as $b=(X_{0.5})^n$, with $X_{0.5}$ being the value of X when Y is half of the maximum response. Equation (1) is a general function that can take the form of a rectangular hyperbola when n=1, the Hill equation (HILL, 1913) when a=0, and the Michaelis-Menten equation (MICHAELIS & MENTEN, 1913) when a=0 and n=1.

For the vernalization response function [f(V)], X is VD and Y varies from 0 to 1, with 0 corresponding to unvernalized plants and 1 corresponding to fully vernalized plants. Consequently, the coefficients a and c in eq. (1) have values of 0 and 1, respectively. The coefficient $VD_{0.5}$ is defined analogously to the coefficient $X_{0.5}$ as the VD when the response is one half of the response of fully vernalized plants, i.e., when f(V) is 0.5. A value of $VD_{0.5}$ = 22.5 VD was used by STRECK (2002) for winter wheat and the same value was used in this study for lily. By varying the coefficient n, the MMF function can assume a variety of shapes (Figure 1). If n=1, the response curve is hyperbolic. As the coefficient n increases, the response becomes increasingly sigmoidal, increasing in steepness until it becomes a step function when n

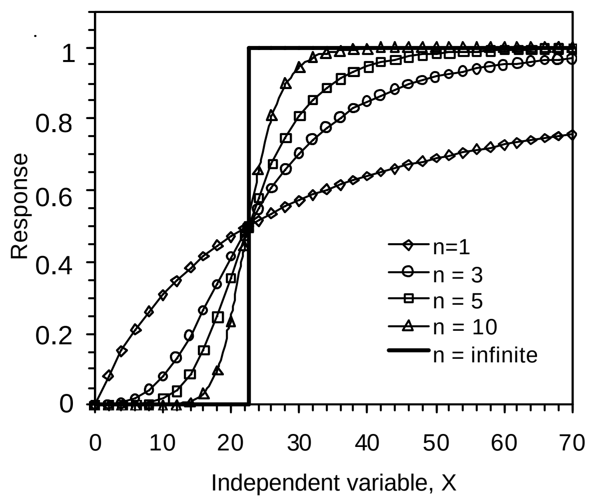

Figure 1. Responses of the MMF function (eq. 1) for differing values of the shape coefficient (n) with a=0 (intercept), b=1(asymptote), and $X_{0.5}$=22.5 (half of the maximum response).

approaches infinity. A value of n=5 was selected based on the study by STRECK (2002) who used this value in the vernalization response function for winter wheat. When n=5, the response is close to zero at values less than 8-10 VD (at 10 VD the response is 0.02) and greater than 0.98 at values higher than 50 VD. With these assumptions, the vernalization response function, f(V), becomes:

$$f(V) = (VD)^5/[(22.5)^5 + (VD)^5] \quad (2)$$

Equation (2) is suggested as a general function to describe the vernalization response in lily.

A widely accepted approach to quantify the vernalization response in plants is to measure the time (calendar time or thermal time) from planting to flowering (CHUJO, 1966; RAWSON et al., 1998; STRECK, 2002). This approach was used in the remainder of this paper.

In order to evaluate the performance of eq. (2), independent data of bulb planting to flowering (TF) at different VD treatments of 10 lily genotypes from different trials were used. The sources of these trials are presented in Table 1. These are data from published research, representing commercial genotypes developed in different regions of the world and with different vernalization responses. In all these trials, bulbs were exposed to vernalizing temperatures for different number of days and planted afterwards in controlled environments where they grew under constant temperatures above the maximum temperature for vernalization. Only experiments where the vernalization treatments were conducted near optimum vernalizing temperature (5ºC, ROH, 1985) were used, so that one calendar day was assumed to be equal to one VD. In some of the trials other treatments besides vernalization days were also tested such as bulbs planted at different depths (e.g. CHOI et al., 1996), providing a rich dada set for model evaluation. Published research data of TF were in tables in the original papers. A total of 87 individual measurements were used.

Data on TF of the data sets presented in Table 1 were normalized in order to obtain a 0 to 1 response, representing unvernalized and fully vernalized plants, respectively, by:

$$NTF = (TF_{0VD} - TF)/(TF_{0VD} - TF_L) \quad (3)$$

where NTF is the normalized time to flowering, TF_{0VD} is the time to flowering of unvernalized plants, i.e. at 0 VD, TF is the time to flowering for a given VD treatment, and TF_L is the time to flowering at the longest VD treatment. Plants at the longest VD treatment were assumed to be fully vernalized because the TF at this treatment had values similar to the TF at immediately one or two shorter VD treatments.

The NTF data were compared to the f(V) predicted by eq. (2). The root mean square error (RMSE) was calculated and used as a measure of the performance of eq. (2) (JANSSEN & HEUBERGER, 1995):

$$RMSE = [\Sigma(P_i - O_i)^2/N]^{0.5} \quad (4)$$

where P_i = predicted data, O_i = observed data, N = number of observations, and i = 1…N. The RMSE expresses the spread in P_i-O_i and has the same dimensions as the predicted and the observed data (in this study it is unitless). The lower the RMSE the better the prediction.

Results and discussion

The observed vernalization response of the 10 lily genotypes and the response predicted with the MMF function [eq. (2)] are illustrated in Figure 2. The general trend of the observed data was described

Table 1. Lily species, genotypes, and source of the trials used to evaluate eq. (2).

Species	Genotype	Source of data
Lilium longiflorum Thunb.	Cultivar Ace	WEILER & LANGHANS (1968), Table2
Lilium longiflorum Thunb.	Cultivar Nellie White	DOLE & WILKINS (1994), Table 2
Lilium speciosum Thunb.	Cultivar Superstar	WEILER (1973), Table 2
Lilium x elegans Thunb.	Hybrid Line A	LEE et al. (1996), Table 1
Lilium x elegans Thunb.	Hybrid Line B	LEE et al. (1996), Table 2
Lilium x elegans Thunb.	Hybrid Line C	LEE et al. (1996), Table 3
Lilium x elegans Thunb.	Cultivar Connecticut King	CHOI et al. (1996), Table 2
Lilium x elegans Thunb.	Cultivar Enchantment	CHOI et al. (1996), Table 2
Lilium x elegans Thunb.	Cultivar Pojitano	CHOI et al. (1996), Table 2
Lilium x elegans Thunb.	Cultivar Himonoto	CHOI et al. (1996), Table 2

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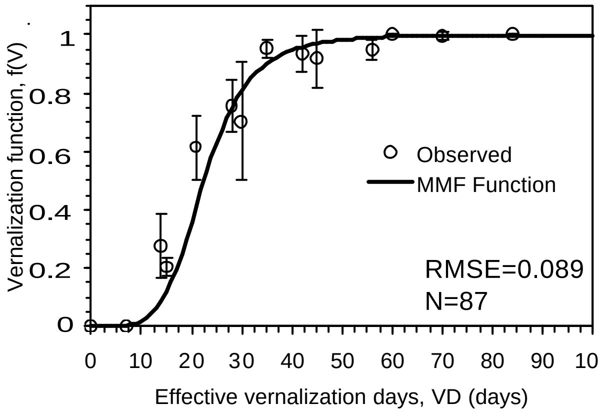

Figure 2. The observed vernalization response of 10 lily genotypes and the f(V) predicted with the MMF function [(eq. 2)]. Each point is the average of observed data from the literature (Table 1) and represents the fraction of full vernalization: 0 = unvernalized plants and 1 = fully vernalized plants. Error bars represent one standard deviation of the mean.

well by the MMF function, with observed data spread around the curve. Observed data show that lily plants are not vernalized (i.e., the response is zero) at values less than 7 VD and lily plants are fully vernalized (i.e., the response is close to one) at values greater than 50 VD, and so does the MMF function. The RMSE of the estimate is 0.089, which is similar to the RMSE of 0.083 reported by STRECK (2002) when the same f(V) was used to describe the vernalization response of 12 winter wheat cultivars with a wide range of vernalization response.

Several response functions used in crop simulation models are dependent on genotype. This creates a problem when a model needs to be used with genotypes that have unknown coefficients. Also, 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 or explanations of phenomena should be in terms of known quantities. Therefore, the search for generalized response functions is a major goal in crop modeling. This type of philosophy in crop modeling has been encouraged as it assumes that the similarities among genotypes are more important than the differences (MAJOR & KINIRY, 1991). As shown in this paper, most of the variation in the response of lily development to vernalization in a wide range of genotypes can be accounted for by a general vernalization function (eq. 2). Several reasons contribute to the adoption of eq. (2) as a generalized vernalization function in lily.

First, the values of the coefficients in eq. (2) have biological meaning. Coefficients a and c represent the developmental response of unvernalized and fully vernalized plants, respectively. The coefficient $VD_{0.5}$ represents the effective vernalization days when plants show half of the response of fully vernalized plants. The coefficient n gives the expected sigmoidal shape of the response to VD.

Second, the coefficients of eq. (2) are from another species (*Triticum aestivum* L.) and worked well for *Lilium* spp., indicating its robust and general nature.

Third, this function (eq. 2) describes what is currently accepted in terms of vernalization response in plants (SLAFER & RAWSON, 1994; CAO & MOSS, 1997). A short period of exposure to vernalizing temperatures (less than 8-10 VD) leads to lily plants behaving as if they never were exposed to vernalizing temperatures. An exposure to more than 10 VD causes the lily plant to respond and behave differently than unvernalized plants. After 50 VD, the lily plant is fully vernalized, i.e. there is no further response to VD.

Fourth, the response of eq. (2) is realistic. Biological systems are likely to respond to environmental factors in a smooth and continuous fashion (SHAYKEWICH, 1995).

Conclusion

The developmental response of lily to VD can be modeled by a generalized nonlinear function that has coefficients with biological meaning. The implication of this conclusion is that most of the genetic variation of the vernalization response encountered among genotypes can be accounted for by using a single function, thus, reducing the input data set necessary in lily simulation models. The MMF function as expressed as eq. (2) can be used as a generalized vernalization function for lily.

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