

# A VERNALIZATION MODEL IN ONION (*Allium cepa* L.)

## MODELO DE VERNALIZAÇÃO EM CEBOLA (*Allium cepa* L.)

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- REVIEW -

### ABSTRACT

Vernalization is a process required for certain plant species, among them onion (*Allium cepa* L.), to enter the reproductive stage, through an exposure to low, non-freezing temperatures. Currently, there is a lack of a realistic vernalization model in onion, which provides a rationale for this effort. The objective of this study was to develop a vernalization model that describes the response of development to vernalizing temperatures and to the duration of the vernalization period in onion. The temperature response of vernalization was described by a nonlinear beta function that has three coefficients (the cardinal temperatures), which were defined as 0, 10, and 16°C. The response to the duration of the vernalization period was described by a nonlinear MMF function with four coefficients (the response of unvernallized plants, the response of fully vernalized plants, the duration of the vernalization treatment when plants are half fully vernalized and a shape coefficient), which were defined as 0, 1, 30 vernalization days, and 5, respectively. The vernalization model successfully described the response of development to vernalizing temperatures and to the duration of the vernalization period of several American, European, Japanese, and Brazilian onion cultivars published in the literature, which were independent data sets.

Key words: low temperatures, bolting, flowering.

### INTRODUCTION

The onion (*Allium cepa* L.) is the species of greatest economic importance of the *Allium* genus (RABINOWITZ, 1985). The main cultivation objects are the bulbs, which are widely used mostly for seasoning, although leaves are also of economic interest. In 2001, about 3 million metric tons of onion bulbs were produced only in the USA at a wholesale of about US\$ 700 million (USDA, 2002).

Onion is a biennial herbaceous plant, and temperature and photoperiod are the major environmental factors that control its development (BREWSTER, 1983, 1987; RABINOWITZ, 1985). Therefore, onion developmental models have a temperature [ $f(T)$ ], and a photoperiod [ $f(P)$ ] functions (BREWSTER, 1987). Bulbs, consisting of leaf bases, young leaves, and leaf primordia, are formed during the first growing season in response to long days. Therefore, for bulb production, seedlings are transplanted in the spring in Southern Brazil. The first growing season ends when the green leaves and the roots senesce, with the bulbs entering a dormant phase. At the end of the dormant phase of the bulbs, roots and leaves restart growth, characterizing the second growing season. The exposure of vegetative plants (after a juvenile phase that corresponds to a minimum 7-10 initiated leaves) or bulbs to low temperatures induces flowering, which terminates the growth of the main axis (RABINOWITZ,

1985). The exposure to low temperatures either in natural winter or in artificial cold treatment that causes induction of flowering in several plant species, among them onion, is called vernalization (PINTHUS, 1985; FLOOD & HALLORAN, 1986).

Vernalization in onion has been of research interest because of the need to understand and prevent bolting (flowering in the first growing season) in seed-sown overwintered crops, and also because of the need to induce flowering for seed production in breeding programs in the shortest period possible (BREWSTER, 1987). Lack of cold temperatures to induce flowering is the main constrain to onion seed production in many tropical countries (KIMANI et al., 1994). In Brazil, natural vernalization in the field and consequently onion seed production are restricted to the Rio Grande do Sul and Santa Catarina States (MULLER & CASALI, 1982).

The response of plants to vernalization is given by the combination of two factors, the temperature during the vernalization period, and the duration of the vernalization period (HODGES & RITCHIE, 1991; RITCHIE, 1991). With respect to the temperature response, vernalization has three cardinal (minimum, optimum, and maximum) temperatures (WANG & ENGEL, 1998; YAN & HUNT, 1999b). On the other hand, 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). Therefore, a vernalization model shall have a temperature response function [ $f(T_v)$ ], and a VD response function [ $f(VD)$ ].

Because the exposure to low temperatures affects plant development in many species, vernalization models have been developed for several crops such as winter wheat (*Triticum aestivum* L.) (RITCHIE, 1991; WANG & ENGEL, 1998), carrot (*Daucus carota* L.) (YAN & HUNT, 1999b), calabrese (*Brassica oleracea* var. *italica*) (WURR et al., 1995), and lily (*Lilium* spp.) (STRECK, 2002b). A literature search, however, revealed a lack of a vernalization model in onion. BREWSTER (1987) fitted data of daily vernalization rate to temperature with a step-wise linear function but did not test the temperature function against independent data. A step-wise function is not the most appropriate response function as a temperature response function because biological systems are more likely to respond to environmental factors, including temperature, in a smooth and continuous fashion rather than in a combination of linear functions that introduce abrupt changes in the response (SHAYKEWICH, 1995; STRECK, 2002a). Moreover, in the

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BREWSTER (1987) model, no response to VD is proposed. Both the onion models of WEISSER (1994) and TEI et al. (1996) do not have a vernalization function as they simulate onion growth and development only for the first growing phase, i.e., until falling over of the tops, when onion crops in the field are usually not exposed to vernalizing temperatures. However, for seed production, a vernalization model is of interest. This provides a rationale for developing a vernalization model in onion.

The objective of this study was to develop a vernalization model that describes the response of development to vernalizing temperatures and to the duration of the vernalization period in onion.

## MATERIAL AND METHODS

Vernalization, as any other biological process, has a response to temperature with a minimum ( $T_{min}$ ), an optimum ( $T_{opt}$ ), and a maximum ( $T_{max}$ ) temperature (WANG & ENGEL, 1998; YAN & HUNT, 1999b). A typical biological response to temperature from  $T_{min}$  to  $T_{opt}$  follows a logistic curve (SHAYKEWICH, 1995). The response increases slowly as temperature increases from  $T_{min}$ , it increases in a linear fashion at intermediate temperatures, and the rate of increase decreases as temperature approaches  $T_{opt}$ , where the response is at a maximal. At temperatures above  $T_{opt}$ , the response decreases and eventually ceases at  $T_{max}$ . There are several functions that can describe the temperature response of biological processes (LANDSBERG, 1977). Among them is the beta function, which has been used to describe the response of growth and development to temperature in different crops such as winter wheat (WANG & ENGEL, 1998), muskmelon (*Cucumis melo* L.) (STRECK, 2002a), and kiwifruit (*Actinidia deliciosa* (A. Chev.) C. F. Liang & A. R. Ferguson) (STRECK, 2003). The beta function as the temperature function  $[f(T)]$  varies from 0 to 1 and is defined as:

$$f(T) = \frac{[2(T - T_{min})^\alpha (T_{opt} - T_{min})^\alpha - (T - T_{min})^{2\alpha}]}{(T_{opt} - T_{min})^{2\alpha}} \quad (1)$$

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

$$\alpha = \ln 2 / \ln [(T_{max} - T_{min}) / (T_{opt} - T_{min})] \quad (2)$$

where  $T_{min}$ ,  $T_{opt}$ , and  $T_{max}$  are the cardinal temperatures (minimum, optimum, and maximum).

Equation (1) is a flexible curve and, by changing the cardinal temperatures, it can attain several shapes (Figure 1). In defining the cardinal temperatures for vernalization in onion, it was assumed that  $T_{min}$  is 0°C,  $T_{opt}$  is 10°C, and  $T_{max}$  is 16°C. The assumption of a minimum temperature of 0°C was based on the results by BOSWELL (1923), who showed that inflorescence initiation in onion was suppressed by temperatures of about 0°C. A value of 10°C for  $T_{opt}$  was selected based on AGUIAR (1984) and RABINOWITCH (1985). The assumption of a maximum temperature of 16°C was based on BREWSTER (1987) who used this value as the maximum temperature for vernalization in onion. Therefore, the function to describe the temperature response of vernalization  $[f(T_v)]$  in onion was:

$$f(T_v) = \frac{[2(T)^\alpha (10)^\alpha - (T)^{2\alpha}]}{(10)^{2\alpha}} \quad \text{for } T_{min} \leq T \leq T_{max} \quad (3)$$

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

with  $\alpha = 1.47477$ .

The next step in the vernalization model is a function that describes the response to the duration of the vernalization period, i.e.,  $f(VD)$ . 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, with plants exposed to a short period not differing from unvernallized plants and, after a maximum period of vernalization, plants are fully vernalized and they do not respond to further exposure to vernalizing temperatures (CHUJO, 1966; WANG et al., 1995; BROOKING, 1996; RAWSON et al., 1998; MAHFOOZI et al., 2001). It was assumed that the VD response in onion also follows a sigmoidal shape. There are several functions with a sigmoidal shape. Among them, a flexible sigmoidal response function is the Morgan-Mercer-Flodin (MMF) function (MORGAN et al., 1975):

$$Y = (ab + cX^n) / (b + X^n) \quad (4)$$

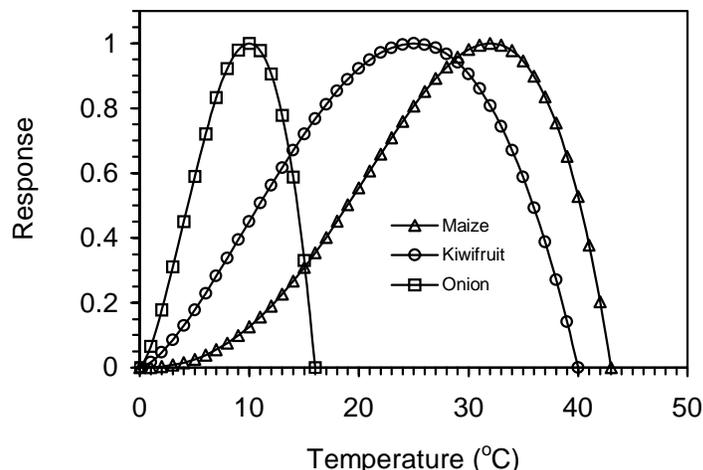


Figure 1 - The beta function (eq. 1) describing the temperature response of three plant processes: the response of seedling growth rate in maize (*Zea mays* L.) with  $T_{min}=0^{\circ}\text{C}$ ,  $T_{opt}=32^{\circ}\text{C}$ , and  $T_{max}=43^{\circ}\text{C}$  (YAN & HUNT, 1999a); the temperature response of growth and development in kiwifruit (*Actinidia deliciosa* (A. Chev.) C. F. Liang & A. R. Ferguson) with  $T_{min}=0^{\circ}\text{C}$ ,  $T_{opt}=25^{\circ}\text{C}$ , and  $T_{max}=40^{\circ}\text{C}$  (STRECK, 2003); the temperature response of vernalization in onion (*Allium cepa* L.) with  $T_{min}=0^{\circ}\text{C}$ ,  $T_{opt}=10^{\circ}\text{C}$ , and  $T_{max}=16^{\circ}\text{C}$  (eq. 3).

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 (4) 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 VD response function  $[f(VD)]$  in onion,  $X$  is VD and  $Y$  varies from 0 to 1, with 0 corresponding to unvernallized plants and 1 corresponding to fully vernalized plants. Consequently, the coefficients  $a$  and  $c$  in eq. (4) 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  $f(VD)$  is 0.5. A value of  $VD_{0.5} = 30$  VD for onion was assumed in this study based on the results reported by AGUIAR (1984), who reported that the number of umbels/plant at 30 VD was about half of the number of umbels/plant when onion plants of several cultivars were fully vernalized (90 and

120 VD). By varying the coefficient  $n$ , the MMF function can assume a variety of shapes (Figure 2). 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  $n$  approaches infinity. A value of  $n=5$  was selected based on the study by STRECK (2002b,c) who used this value in the vernalization response function for lily and winter wheat, respectively. When  $n=5$ , the response is close to zero at values less than 15 VD (at 15 VD the response is 0.03) and greater than 0.97 at values higher than 60 VD. With these assumptions, the function to describe the response to VD [ $f(\text{VD})$ ] in onion was:

$$f(\text{VD}) = (\text{VD})^5 / [(30)^5 + (\text{VD})^5] \quad (5)$$

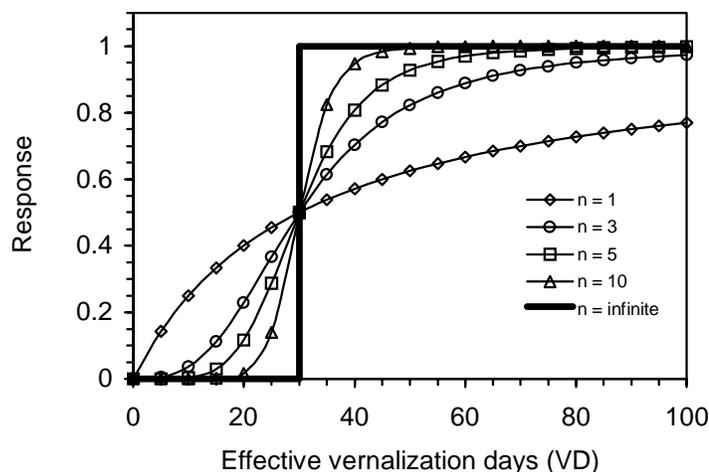


Figure 2 - Responses of the MMF function (eq. 4) for differing values of the shape coefficient ( $n$ ) with  $a=0$  (intercept),  $b=1$  (asymptote), and  $X_{0.5}=30$  (half of the maximum response).

The performance of eq. (3) and (5) was evaluated with independent data published in the literature. Data to evaluate

eq. (3) are from European and Japanese onion cultivars from eight trials. The sources of these trials are presented in Table 1. In these trials, bulbs (AURA, 1963) or seedlings (SHISHIDO & SAITO, 1975; BREWSTER, 1983) were exposed to different vernalizing temperatures in controlled environment rooms. After the exposure to vernalizing temperatures, bulbs or plants were transferred to rooms at nonvernalizing temperatures (20-25°C) and days to flowering (AURA, 1963; SHISHIDO & SAITO, 1975) or days to inflorescence initiation were measured. Data of days to flowering and days to inflorescence initiation were transformed in rate of development by taking the reciprocal of time, i.e.,  $1 \text{ days}^{-1}$ . Data were then normalized to vary from 0 to 1 by dividing each value by the maximum development rate.

Data to evaluate eq. (5) are from Japanese, American, and Brazilian onion cultivars from six trials. The sources of these trials are presented in Table 2. In these trials, seedlings (SHISHIDO & SAITO, 1975) or bulbs (AGUIAR et al., 1983) were exposed to vernalizing temperatures for different periods (calendar days) and transferred to temperatures above the maximum temperature for vernalization in controlled rooms at 20°C (SHISHIDO & SAITO, 1975) or in the field (AGUIAR et al., 1983). The developmental parameters measured after the exposure to several days under vernalizing temperatures were percentage of onion plants flowering (SHISHIDO & SAITO, 1975) and number of umbels/plot (AGUIAR et al., 1983). These data were normalized in order to obtain a 0 to 1 response, representing unvernallized and fully vernalized plants, respectively. The percentage of flowering data from SHISHIDO & SAITO (1975) were normalized by dividing each value by 100. The number of umbels/plot data from AGUIAR et al. (1983) were normalized by:

$$\text{Response} = (\text{NU} - \text{NU}_{\text{OV}}) / (\text{NU}_{\text{LV}} - \text{NU}_{\text{OV}}) \quad (6)$$

where  $\text{NU}_{\text{OV}}$  is the number of umbels/plot of unvernallized plants (0 calendar days),  $\text{NU}$  is the number of umbels/plot for a given vernalization treatment, and  $\text{NU}_{\text{LV}}$  is the number of umbels/plot at the longest vernalization treatment (75 calendar days). Plants at the longest vernalization treatment were assumed to be fully vernalized.

Table 1 - Source of the trials used to evaluate eq. (3).

Trial #	Cultivar	Treatments (temperature, °C)	Source
1	Hytti	4, 11	AURA (1963)
2	Imai-wase	5, 9, 14.7	SHISHIDO & SAITO (1975)
3	Sapporoki	5, 9, 13	SHISHIDO & SAITO (1975)
4	Senshuki	5, 9, 14.7	SHISHIDO & SAITO (1975)
5	Senshyu (Normal N)	6, 9, 12	BREWSTER (1983)
6	Senshyu (Low N)	6, 9, 12	BREWSTER (1983)
7	Rijnsburger (Normal N)	6, 9, 12	BREWSTER (1983)
8	Rijnsburger (Low N)	6, 9, 12	BREWSTER (1983)

Table 2 - Source of the trials used to evaluate eq. (5).

Trial#	Cultivar	Treatments (days of vernalization) <sup>1</sup>	Temperature during vernalization (°C)	Source
1	Sapporoki	20, 30, 40, 50, 60	5	SHISHIDO & SAITO (1975)
2	Sapporoki	20, 30, 40, 50, 60	9	SHISHIDO & SAITO (1975)
3	Pera IPA-1	0, 15, 30, 45, 60, 75	7-8	AGUIAR et al. (1983)
4	Baia Triunfo	0, 15, 30, 45, 60, 75	7-8	AGUIAR et al. (1983)
5	Rôxa do Barreiro	0, 15, 30, 45, 60, 75	7-8	AGUIAR et al. (1983)
6	Texas Grano-502	0, 15, 30, 45, 60, 75	7-8	AGUIAR et al. (1983)

<sup>1</sup>Calendar days

Because the temperature during the vernalization treatments in the trials used to evaluate eq. (5) (SHISHIDO & SAITO, 1975; AGUIAR et al., 1983) was not at the optimum

temperature for vernalization assumed in the model presented here (10°C), the daily vernalization rate [ $f_{\text{vn}}(T)$ , units of  $\text{day}^{-1}$ ]

was calculated with eq. (3). The VD treatments for these trials were calculated by:

$$VD = \sum f_vn(T) \quad (7)$$

Published research data used to evaluate eqs. (3) and (5) were in tables and figures in the original papers. Data from figures were extracted by enlarging the diagram at least 150% to minimize random errors of interpolation and estimating the values of the developmental parameters.

The observed response to temperature and VD data were compared to the  $f(T_v)$  predicted by eq. (3) and  $f(VD)$  predicted by eq. (5), respectively. The root mean square error (RMSE) was calculated and used as a measure of the performance of eqs. (3) and (5) (JANSSEN & HEUBERGER, 1995):

$$RMSE = [\sum (P_i - O_i)^2 / N]^{0.5} \quad (8)$$

where  $P_i$  = predicted data,  $O_i$  = observed data,  $N$  = number of observations, and  $i = 1 \dots N$ . 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 temperature response of some biological processes using eq. (1) is represented in Figure 1. The response of seedling growth rate in maize (*Zea mays* L.) has cardinal temperatures of 0°C, 32°C, and 43°C (YAN & HUNT, 1999a). The temperature response of growth and development in kiwifruit has cardinal temperatures of 0°C, 25°C, and 40°C (STRECK, 2003). The temperature response of vernalization in onion (*Allium cepa* L.) was defined in this study as having cardinal temperatures of 0°C, 10°C, and 16°C.

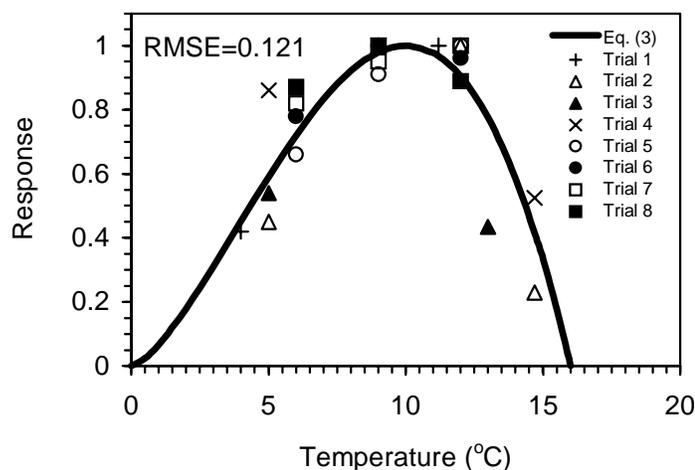


Figure 3 - The performance of the beta function (eq. 3) in describing the temperature response of vernalization in onion (*Allium cepa* L.). Observed data are from published data of European and Japanese onion cultivars.

The observed vernalization response to temperature of different onion cultivars and the temperature response curve predicted with the beta function (eq. 3) are presented in Figure 3. The observed data show a maximum response in the range of 9-12°C and a decrease when temperature departs from  $T_{opt}$ . This trend was captured by the beta function (eq. 3), which had a good performance over the entire range of observed data

(RMSE = 0.121). Also, the observed data, as they were normalized with respect to their maximum, all fall into a similar pattern of response to temperature, suggesting a general type of response for different cultivars and nitrogen treatments, and also for bulbs and seedlings.

A comparison of the cardinal temperatures for vernalization in onion (0, 10, and 16°C) with other species shows some differences and similarities. The cardinal temperatures for vernalization in winter wheat are -1.3, 4.9, and 15.7°C (PORTER & GAWITH, 1999), in carrot are -1, 6.5, and 16°C (ATHERTHON et al., 1990), in calabrese are -2.8, 15.8, and 23.6°C (WURR et al., 1995), and in lily are 0, 5, and 21°C (ROH & WILKINS, 1977, ROH, 1985; HOLCOMB & BERGHAGE, 2001). The  $T_{max}$  for vernalization in onion is similar to the  $T_{max}$  for vernalization in carrot and winter wheat. The  $T_{min}$  and  $T_{opt}$ , however, are higher in onion than in carrot and winter wheat, which is probably a reflect of an adaptation to different natural habitats, as onion is native to middle or southern Asia, with secondary centers of development in western Asia and the Mediterranean area (RABINOWITCH, 1985), whereas most of carrot and winter wheat cultivars are from regions with colder temperatures (HILLER & KELLY, 1985; PINTHUS, 1985).

The observed response to VD of different onion cultivars and the VD response predicted with the MMF function (eq. 5) are illustrated in Figure 4. Even though there are a few outliers in the data (cultivars Sapporoki, Baia Triunfo, and Texas Grano - 502 at about 50 VD and cultivar Pera IPA-1 at 40 VD), the general trend of the observed data was described well by the MMF function, with a RMSE = 0.134, and, more importantly, observed data spread around the predicted curve. Observed data show that onion plants are not vernalized (i.e., the response is zero) at values less than 17 VD and onion plants are fully vernalized (i.e., the response is one) at values greater than 60 VD, and so does the MMF function (the predicted response is 0.05 and 0.97 at 17 VD and 60 VD, respectively).

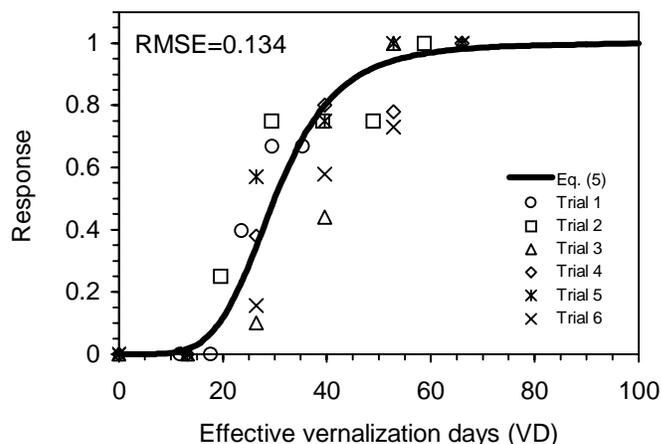


Figure 4 - The performance of the MMF function (eq. 5) in describing the VD response of in onion (*Allium cepa* L.). Observed data are from published data of American, Brazilian, and Japanese onion cultivars. Each point represents the fraction of full vernalization: 0 = unvernallized plants and 1 = fully vernalized plants.

Comparing the response to VD in onion and other species, onion has a need for a longer period than winter wheat and lily. Winter wheat and lily plants start to respond to a VD higher

than 7-10 VD, are half vernalized at about 22 VD, and fully vernalized at 40-50 VD (STRECK, 2002b,c) whereas the data shown here (Figure 4) indicate that onion plants start to respond only after 17 VD, are half vernalized at about 30 VD and fully vernalized at 60 VD.

Several response functions used in crop simulation models are dependent on genotype. This is often a constrain 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 assumes that the similarities among genotypes are more important than the differences (MAJOR & KINIRY, 1991). The results of this study (Figure 3) indicate that the vernalization response to temperature in onion can be described by a generalized nonlinear function. These results agree with previous studies that successfully modeled the response of growth and development to temperature with generalized functions in several crops such as maize (YAN & HUNT, 1999a), chrysanthemum (LARSEN & PERSSON, 1999), wheat (STRECK, 2002c), muskmelon (STRECK, 2002a), and kiwifruit (STRECK, 2003).

Several reasons contribute to adopt eq. (3) as a generalized temperature response function for vernalization in onion. Firstly, the coefficients (the cardinal temperatures) have biological meaning. Secondly, eq. (3) is a robust function, as the cardinal temperatures ( $T_{min}$ ,  $T_{opt}$ , and  $T_{max}$ ) were derived from independent studies and different cultivars. Thirdly, the function (eq. 3) describes what is currently accepted in terms of temperature response of biological systems, including vernalization, i.e., temperatures close to  $T_{min}$ , the response is close to 0, the response increases in a linear fashion at intermediate temperatures, the response reaches a maximum when temperature approaches  $T_{opt}$ , and the response decreases down to 0 at  $T_{max}$  (SHAYKEWICH, 1995).

The VD response function developed in this study (eq. 5) also has the potential of working as a generalized function for several reasons. First, the values of the coefficients in eq. (5) have biological meaning. Second, the coefficients  $a$ ,  $c$  and  $n$  of eq. (5) were derived from two other species (*Triticum aestivum* L. and *Lilium* spp.), and the coefficient  $VD_{0.5}$  was derived from different cultivars and worked well for the onion cultivars used in the evaluation (Figure 4), indicating its robust and general nature. Third, this function (eq. 5) 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 leads to plants behaving as if they never were exposed to vernalizing temperatures. An exposure to more than a minimum VD causes the plant to respond and behave differently than unvernallized plants. After a maximum VD, the plant is fully vernalized, i.e. there is no further response to VD. Fourth, the response of eq. (5) is realistic. Biological systems are likely to respond to environmental factors in a smooth and continuous fashion (SHAYKEWICH, 1995). However, as indicated by the outliners in Figure 4, some onion cultivars may have a different response to VD, and there might be a need to adjust the coefficient  $VD_{0.5}$  for some cultivars.

Current onion models (e.g. WEISSER, 1994; TEI et al., 1996) fail to describe the response of onion development to vernalization, which is a constraint when the goal of the enterprise is seed production. This study provides a vernalization model, which represents a contribution to the

existing approaches for modeling onion development. The  $f(VD)$  can be used to calculate development rate by multiplying a temperature and photoperiod function, such as in models of other crops that need to be vernalized to enter the reproductive phase such as winter wheat (e.g. WANG & ENGEL, 1998).

## CONCLUSION

The vernalization model developed and evaluated in this study describes the effects of temperature and VD on the vernalization rate in onion. The temperature and VD response functions have general nature. The implication of these results is that most of the genetic variation of the vernalization response encountered among cultivars can be accounted for by using a single function, thus, reducing the number of input data necessary for onion simulation models.

## RESUMO

Vernalização é um processo que certas espécies de plantas, incluindo cebola (*Allium cepa* L.), necessitam para entrar no período reprodutivo, através da exposição a baixas temperaturas. Uma revisão de literatura revelou que não existe um modelo de vernalização adequado em cebola. O objetivo deste estudo foi desenvolver um modelo de vernalização em cebola que descreva a resposta do desenvolvimento à temperaturas vernalizantes e à duração do período de vernalização. A resposta da vernalização à temperatura foi descrita com uma função não linear (função beta) que tem três coeficientes (as temperaturas cardiais), os quais foram definidos como 0, 10 e 16°C. A resposta do desenvolvimento à duração do período de vernalização foi descrita por uma função não linear (função MMF) que tem quatro coeficientes (a resposta de plantas não vernalizadas, a resposta de plantas completamente vernalizadas, a duração do período de vernalização em que as plantas estão metade vernalizadas e um coeficiente que governa a curvatura da função de resposta), os quais foram definidos como 0, 1, 30 dias de vernalização e 5, respectivamente. O modelo de vernalização desenvolvido e avaliado neste estudo descreveu adequadamente a resposta do desenvolvimento à temperaturas vernalizantes e à duração do período de vernalização de várias cultivares de cebola de origem americana, européia, japonesa e brasileira publicados na literatura.

*Palavras-chave:* temperaturas baixas, pendoamento, florescimento.

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