Temperature is one of the most important factors that determine plant growth, development, and yield. Accurate summarization of plant temperature response is thus a prerequisite to successful crop systems modelling and application of such models to management. This paper reports on a general equation that can be used to simulate the temperature response of plants. The equation reads as
\[ r = \frac{R_{\text{max}} (T_{\text{opt}} - T)}{T_{\text{max}} - T_{\text{opt}}}, \]
where \( r \) is the daily rate of growth (or development) at any temperature, \( T_{\text{opt}} \) is the optimum temperature, \( T_{\text{max}} \) is the maximum temperature, and \( R_{\text{max}} \) is the maximum rate of growth or development at \( T_{\text{opt}} \). It has the smallest number of parameters possible to simulate the plant response to the full range of temperatures relevant to plant growth and development. The equation was shown to successfully simulate the growth and development of maize, bean, wheat, barley, sorghum, and lambsquarters. The adjusted \( R^2 \) of fit ranged from 0.747 to 0.988, mostly greater than 0.9. For one maize dataset that contains independent data, the equation was shown to be highly predictive. The equation could find application in crop germplasm classification, crop modelling and environmental control of artificial crop production systems.

**Key words:** Plant, growth, development, temperature response, modelling, maize (Zea mays L.), sorghum (Sorghum bicolor (L.) Moench), bean (Phaseolus vulgaris L.), wheat (Triticum aestivum L.), barley (Hordeum vulgare L.), lambsquarters (Chenopodium album L.).

**INTRODUCTION**

Temperature is among the most important environmental factors that control plant development, growth and yield. All biological processes respond to temperature, and all responses can be summarized in terms of three cardinal temperatures, namely the base or minimum \( T_{\text{min}} \), the optimum \( T_{\text{opt}} \), and the maximum \( T_{\text{max}} \) temperatures. The nature of the response to temperature between these cardinal points, which is important for calculating the phenology, adaptation and yield of various crops (Cross and Zuber, 1972; Shaykewich, 1995), is not however as easy to summarize. Various models have been used, each with strengths and weaknesses.

**Linear model**

Within a limited range of temperature it has been found that the rate of development \( r \) is a linear function of the temperature. In this range, the time required to develop to a certain stage is related to the temperatures above a specified base or minimum temperature. Hence the commonly accepted concepts of thermal time, growing-degree-days (GDD), and leaf unit or phyllochron requirements. The linear model is convenient and effective when the temperature does not approach or exceed the optimum, \( T_{\text{opt}} \).

**Bilinear model**

The GDD approach fails to account for the fact that temperatures greater than \( T_{\text{opt}} \) delay growth or development. Many researchers have thus adopted a bilinear approach (e.g. Olsen, McMahon, and Hammer, 1993) in which two different linear equations [eqn (1)] are used to describe the responses to sub-optimum and supra-optimum temperatures. This approach has been successfully applied to several crops (Omanga, Summerfield, and Qi, 1995, 1996 for pigeonpea; Craufurd et al., 1998 for sorghum, among others).

\[
\begin{align*}
    r &= a_1 + b_1 T \\ & \quad \text{for } T < T_{\text{opt}} \\
    r &= a_2 + b_2 T \\ & \quad \text{for } T > T_{\text{opt}}
\end{align*}
\]

There are four parameters in the bilinear approach, \( a_1, b_1, a_2 \) and \( b_2 \), from which the three cardinal temperatures can be derived. However, the derivations may not be always meaningful. As Craufurd et al. (1998) point out, ‘The estimation of \( T_{\text{min}} \) usually requires considerable extrapolation and the standard error (s.e.) of this \( T_{\text{min}} \) is large in comparison with the s.e. of \( T_{\text{opt}} \)’. The same can be said for
the estimation of $T_{\text{max}}$. In the work of Crauford et al. (1998) estimates of $T_{\text{max}}$ ranged from 36.8 to 58.9°C for leaf appearance rate; and the estimate of $T_{\text{max}}$ for leaf tip appearance rate for one genotype was 198°C, obviously an over-estimation! Furthermore, the maximum rate of any process at $T_{\text{opt}}$ is also likely to be over-estimated since it is obtained from two linear equations, while the real response curve is generally somewhat smooth.

**Multi-linear model**

A multi-linear model is constructed from three or more linear components (e.g. Coelho and Dale, 1980). Because of this, it is less rigid than the bilinear model. Some of the most recent crop system simulation packages, CROPSIM (Hunt and Pararajasingham, 1995, and later versions) for instance, have adopted this approach, even though it requires five or more parameters to describe the temperature response of a process. Although closer to reality than linear or bilinear models, once well calibrated, the greater number of parameters renders the approach subject to calibration errors. Moreover, the parameters are usually highly empirical.

**Exponential and polynomial models**

There is reason to believe that the temperature response of a given process should be a smooth curve (Cross and Zuber, 1972), rather than rigid combinations of linear equations, which introduce abrupt changes. Exponential and polynomial equations give smooth curves. The exponential equation is usually effective in simulating the responses at low to intermediate temperatures. It does not simulate the response to high temperatures, however, because it does not allow for a reduced rate of development at high temperatures. A quadratic equation in the form of eqn (2) (Yan and Hunt—Temperature Response Model handbook) is characterized by a unimodal response to an independent variable $x$ in the range of [0, 1]. The function has a density of zero when $x \leq 0$ or $x \geq 1$ and a maximum density at an optimum $x$ between 0 and 1. Replacing the dependent variable $x$ with temperature ($T$) between a base temperature ($T_{\text{min}}$) and a maximum temperature ($T_{\text{max}}$) leads to an expression that can be used to describe a temperature response (Yin et al., 1995):

$$ r = R_{\text{max}} \left( \frac{T - T_{\text{min}}}{T_{\text{opt}} - T_{\text{min}}} \right) \left( \frac{T_{\text{max}} - T}{T_{\text{opt}} - T_{\text{min}}} \right)^{c - T_{\text{opt}}/T_{\text{min}}} $$

(3)

Equation (3) fits experimental data to five parameters, the three cardinal temperatures, the maximum rate $R_{\text{max}}$ at $T_{\text{opt}}$, and $c$, a parameter that determines the shape of curve. Yin and colleagues (Yin and Kropl, 1996; Yin, Kropl and Goudriaan, 1996) reported successful simulation of rice development using this equation.

Compared with previous models, the expression by Yin and colleagues has the advantage of producing smooth and realistic curves. All parameters except $c$ are biologically meaningful. We have simplified the equation by eliminating $c$ and placing $T_{\text{min}}$ equal to zero. Here, we report on the effectiveness of this simplified equation in summarizing published temperature response data for the growth and development of maize, sorghum, wheat, barley, beans and lambsquarters.

**MATERIALS AND METHODS**

**Model**

As discussed by Shaykewich (1995), the typical first leg of a biological temperature response curve is of a generalized logistic type. Activity increases slowly with temperature at values just above a base at which activity is zero, then increases linearly with temperatures in an intermediate range, and finally increases slowly as temperatures approach an optimum. At temperatures above the optimum, activity is reduced as temperatures increase, and eventually ceases when a maximum temperature is reached. All the currently used temperature models except eqn (3) describe only part of the whole picture. However, eqn (3) used by Yin and colleagues, and a simplified expression in which the shape parameter $c$ is omitted, can effectively describe the whole picture. The simplified expression has the following form:

$$ r = R_{\text{max}} \left( \frac{T_{\text{max}} - T}{T_{\text{opt}} - T_{\text{min}}} \right) \left( \frac{T - T_{\text{min}}}{T_{\text{opt}} - T_{\text{min}}} \right)^{T_{\text{opt}}/T_{\text{min}}} $$

(4)

This equation has four parameters: the three cardinal temperatures plus $R_{\text{max}}$, the maximum rate of growth or development at $T_{\text{opt}}$. The rate of growth or development will be zero (i.e. $r = 0$) if $T = T_{\text{min}}$ or if $T = T_{\text{max}}$; it will be maximum (i.e. $r = R_{\text{max}}$) if $T = T_{\text{opt}}$. It is a special form of eqn (3) with $c = T_{\text{opt}}/T_{\text{min}}$, and is similar to one previously used by Reed et al. (1976) to describe the temperature response of photosynthesis. In this latter case, the parameter $c$ was set equal to 1.
When the rate of development or growth is presented relative to the maximum rate, eqn (4) becomes eqn (4A):

$$\frac{r}{R_{\text{max}}} = \left(\frac{T_{\text{max}} - T}{T_{\text{max}} - T_{\text{opt}}}\right) \left(\frac{T - T_{\text{min}}}{T_{\text{max}} - T_{\text{min}}}\right)^{\frac{T_{\text{max}} - T_{\text{opt}}}{T_{\text{max}} - T_{\text{min}}}}$$  \hspace{1cm} (4A)

The seemingly complex equation actually contains only three parameters: the minimum, optimum and maximum temperatures. $R_{\text{max}}$ is a theoretical value or experimentally established value for the process in question, rather than the maximum value measured in a specific experiment. Thus eqn (4A) can not be used in curve fitting unless the $R_{\text{max}}$ is well established.

One further simplification can be made by assuming that the minimum temperature is 0 °C, i.e. $T_{\text{min}} = 0$, for growth and development. Equations (4) and (4A) thereby become eqns (5) and (5A), respectively.

$$r = R_{\text{max}} \left(\frac{T_{\text{max}} - T}{T_{\text{max}} - T_{\text{opt}}}\right) \left(\frac{T - T_{\text{min}}}{T_{\text{max}} - T_{\text{min}}}\right)^{\frac{T_{\text{max}} - T_{\text{opt}}}{T_{\text{max}} - T_{\text{min}}}}$$  \hspace{1cm} (5)

$$\frac{r}{R_{\text{max}}} = \left(\frac{T_{\text{max}} - T}{T_{\text{max}} - T_{\text{opt}}}\right) \left(\frac{T - T_{\text{min}}}{T_{\text{max}} - T_{\text{min}}}\right)^{\frac{T_{\text{max}} - T_{\text{opt}}}{T_{\text{max}} - T_{\text{min}}}}$$  \hspace{1cm} (5A)

The assumption of a base on 0 °C may seem unreasonable since it is well accepted that the minimum temperatures for summer crops like maize and bean are well above 0 °C, usually around 10 °C or higher (e.g. Cross and Zuber, 1972). However, examination of the response curves of the equation (Fig. 1) shows that the assumption could be useful in most cases.

Figure 1 presents a group of hypothesized response curves based on eqn (5A), all assuming a $T_{\text{opt}}$ of 0 °C and a $T_{\text{max}}$ of 40 °C but with varying $T_{\text{min}}$ from 5 to 35 °C. The linear part of the response with $T_{\text{opt}} = 35$ °C would intersect the x-axis at around 15 °C, and for the curve with $T_{\text{min}} = 30$ °C it would be around 5 °C. Regardless of the assumption of $T_{\text{min}} = 0$, the x-axis intercept (the apparent base temperature) is always lowered with a lower $T_{\text{min}}$ and increased with a higher $T_{\text{opt}}$. It is therefore evident that the difference in minimum temperature between genotypes or species is reflected in their difference in $T_{\text{opt}}$, a unique property of this beta distribution equation.

The beta distribution equation is conveniently fitted to experimental data using the non-linear regression procedure of SigmaStat 2.0 (Jandel Scientific Inc.). As there are only three model parameters in eqn (5) and two in eqn (5A), theoretically as few as four or three measurements would be sufficient for the curve fitting, provided that the treatment temperatures span $T_{\text{opt}}$. However, for all practical purposes, more than four measurements would be required to provide reliable parameter estimates.

**Datasets**

1. **Maize (Zea mays L.) seedling growth rate** (Lehenhauer 1914, from Shaykewich 1995). Seedling elongation rates of maize were measured at temperatures from 5 to 43 °C and presented as relative to the measured maximum rate.
2. **Maize seventh leaf elongation rate** (Barlow 1977, from Coelho and Dale, 1980). Leaf elongation was measured at temperatures from 10 to 40 °C. The rate was presented relative to the recorded maximum.
3. **Maize dry matter production rate** (Allmaras 1964, from Coelho and Dale, 1980). Dry matter production of maize plants was measured at temperatures from 13 to 37 °C and presented as relative to the measured maximum.
4. **Maize days to tassel initiation** (Warrington and Kanemasu, 1983a). Days to tassel initiation at mean temperatures from 11 to 36 °C were presented for two cultivars.
5. **Maize leaf appearance rate** (Tollemaar et al., 1999). This dataset includes two independent experiments. In expt 1, the leaf appearance rate (number of leaves per day) of maize at six constant temperatures from 10 to 35 °C was measured. In expt 2, 16 day/night temperature regimes were used. This experiment allows evaluation of the model using independent data.
6. **Maize leaf appearance rate** (Warrington and Kanemasu, 1983b). Rate of leaf appearance measured at temperatures from 5 to 37 °C was presented for two cultivars.
7. **Wheat (Triticum aestivum L.) rate of development towards terminal spikelet initiation** (Slatyer and Rawson, 1994). After being treated for 50 d at 4 °C, four wheat cultivars were grown at constant temperatures of 10, 13, 16, 19, 22, and 25 °C under an 18 h photoperiod. Days to terminal spikelet initiation were presented.
8. **Wheat leaf expansion rate** (Kemp and Blacklow, 1982). The extension rates of the fourth and fifth leaves at temperatures ranging from 5 to 38 °C were presented relative to the measured maximum.
9. **Wheat and barley (Hordeum vulgare L.) leaf appearance rate** (Cao and Moss, 1989). Four wheat cultivars and four barley cultivars were grown at constant temperatures of 1-5, 10, 12-5, 17-5, 20, 22-5, and 25 °C under a 14 h photoperiod. Rate of leaf appearance was reported.
10. **Sorghum (Sorghum bicolor (L.) Moench) time to panicle initiation** (Craufurd et al., 1998). Nine sorghum genotypes were compared at mean daily temperatures from 17 to 33 °C under short days. Data on rate of development towards panicle initiation for two cultivars were presented.
(11) *Bean* (*Phaseolus vulgaris* L.) *rate of development towards flowering* (Wallace and Enríquez, 1980). Days to first flowering of four photoperiod-insensitive bean lines grown at mean temperatures of 19 to 30 °C were presented. 

(12) *Lambsquarters* (*Chenopodium album* L.) *shoot elongation rate* (Roman, 1998). Seedlings of lambsquarters were grown under daily mean temperatures of 8 to 43 °C, and the rate of shoot elongation (mm h⁻¹) was measured.

**RESULTS**

**Temperature response of maize**

The model parameters for the six datasets of maize are summarized in Table 1. The adjusted $R^2$ ranged from 0.854 to 0.983. When model parameters estimated from six constant temperatures in the dataset of Tollenaar et al. (1979; Table 1) were used to predict the leaf appearance rate for 16 varying day/night temperature regimes, the model was found to be highly predictive (Fig. 2).

Despite the large differences among the six datasets in terms of investigators, cultivars, as well as attributes, the estimated $T_{opt}$ and $T_{max}$ are close (Table 1). Thus it is tempting to suggest that different aspects of growth and development for most maize cultivars share a common temperature response curve, with an optimum temperature around 31 °C and a maximum temperature around 41 °C. Figure 5 compares the measured relative rates from all six maize datasets with predicted relative rates based on a single curve with $T_{opt} = 41$ and $T_{max} = 31$ °C, with a general goodness of fit $R^2 = 0.920$ ($n = 101$).

**Temperature response of rate of development to flowering in common beans**

Results from fitting the model to data dealing with rate of development towards flowering for four photoperiod-insensitive common bean genotypes are listed in Table 2. The $R^2$ values of the fits, though not high compared with the maize datasets, are higher than those obtained for the same dataset by the linear or quadratic models. The $R^2$ values for the four genotypes obtained by a quadratic model were 0.685, 0.741, 0.806 and 0.801, respectively (Yan and Wallace, 1998). This comparison is interesting since both models have three parameters, the minimum number of parameters required to describe a response curve with an optimum. The average $T_{opt}$ over the genotypes was 28.7 °C, lower than that obtained by the quadratic model, and the estimates among the lines were less variable.

**Temperature response of wheat and barley**

The adjusted $R^2$ fit for the relative expansion rate of the fourth and fifth leaf of a wheat cultivar in temperatures from 5 to 38 °C (Kemp and Blacktow, 1982) was 0.951, with a $T_{opt}$ of $30 ± 0.35$ °C and a $T_{max}$ of $41.6 ± 0.71$ °C, a magnitude similar to that of maize (Table 1). The adjusted $R^2$ fit to measured leaf appearance rate data for four wheat and four barley cultivars (Lao and Moss, 1989) was from 0.998 to 0.949, and averaged 0.986 (Table 3). The estimated $T_{opt}$ for the four wheat cultivars was from 21.2 to 24.6 °C, and the $T_{max}$ was from 43.3 to 50.0 °C. Note that the standard error for the $T_{max}$ estimates was much higher.

**Table 1. Parameters of a beta distribution equation fitted to temperature response data for various growth and development aspects of maize (Zea mays L.)**

<table>
<thead>
<tr>
<th>Traits</th>
<th>$R_{max}$</th>
<th>$T_{opt}$ (°C)</th>
<th>$T_{max}$ (°C)</th>
<th>Adjusted $R^2$</th>
<th>$n$</th>
<th>Data source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf appearance rate (leaves d⁻¹)</td>
<td>0.581 ± 0.024</td>
<td>41.2 ± 1.42</td>
<td>31.3 ± 0.60</td>
<td>0.983</td>
<td>6</td>
<td>Tollenaar et al., 1979</td>
</tr>
<tr>
<td>Leaf appearance rate (leaves d⁻¹)</td>
<td>0.433 ± 0.016</td>
<td>41.1 ± 0.69</td>
<td>31.7 ± 0.36</td>
<td>0.945</td>
<td>26</td>
<td>Warrington and Kanematsu, 1983</td>
</tr>
<tr>
<td>Rate of development to tassel initiation (d⁻¹)</td>
<td>0.081 ± 0.002</td>
<td>40.8 ± 0.94</td>
<td>29.7 ± 0.43</td>
<td>0.902</td>
<td>36</td>
<td>Warrington and Kanematsu, 1983a</td>
</tr>
<tr>
<td>Relative leaf elongation rate</td>
<td>—</td>
<td>40.1 ± 0.19</td>
<td>32.6 ± 0.31</td>
<td>0.979</td>
<td>8</td>
<td>Barlow, 1977</td>
</tr>
<tr>
<td>Relative seedling growth rate</td>
<td>—</td>
<td>42.7 ± 0.28</td>
<td>32.0 ± 0.56</td>
<td>0.949</td>
<td>14</td>
<td>Lehenhauer, 1914</td>
</tr>
<tr>
<td>Relative dry matter production rate</td>
<td>—</td>
<td>39.8 ± 0.66</td>
<td>31.0 ± 0.50</td>
<td>0.854</td>
<td>10</td>
<td>Allmaras, 1964</td>
</tr>
<tr>
<td>Average</td>
<td>41.0</td>
<td>31.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$R_{max}$: Maximum rate of growth or development; $T_{max}$: maximum temperature for growth or development; $T_{opt}$: optimum temperature for growth or development.
**Fig. 3.** Measured relative rates of all development or growth of maize, together with predicted relative rates based on a single curve with $T_{\text{max}} = 41$ °C and $T_{\text{opt}} = 31$ °C.

**Table 2.** Parameters of a beta distribution equation fitted to temperature response data for rate of development towards first flowering in common beans (*Phaseolus vulgaris* L.).

<table>
<thead>
<tr>
<th>Genotype</th>
<th>$R_{\text{max}}$ (l/day)</th>
<th>$T_{\text{max}}$ (°C)</th>
<th>$T_{\text{opt}}$ (°C)</th>
<th>Adjusted $R^2$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Line 38</td>
<td>0.039 ± 0.0007</td>
<td>41.5 ± 2.79</td>
<td>29.8 ± 1.09</td>
<td>0.866</td>
<td>32</td>
</tr>
<tr>
<td>Line 39</td>
<td>0.0368 ± 0.0006</td>
<td>37.3 ± 1.29</td>
<td>27.9 ± 0.42</td>
<td>0.798</td>
<td>32</td>
</tr>
<tr>
<td>Line 40</td>
<td>0.0379 ± 0.0006</td>
<td>39.5 ± 2.03</td>
<td>28.8 ± 0.73</td>
<td>0.837</td>
<td>32</td>
</tr>
<tr>
<td>Line 41</td>
<td>0.0364 ± 0.0006</td>
<td>38.8 ± 2.04</td>
<td>28.2 ± 0.66</td>
<td>0.747</td>
<td>32</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>39.3</td>
<td>28.7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Data from Wallace and Enriquez, 1980. $R_{\text{max}}$, Maximum rate of development; $T_{\text{max}}$, maximum temperature for development; $T_{\text{opt}}$, optimum temperature for development.

**Table 3.** Simulations using a beta distribution equation of the temperature response of rate of leaf appearance of wheat (*Triticum aestivum* L.) and barley (*Hordum vulgare* L.).

<table>
<thead>
<tr>
<th>Genotypes</th>
<th>$R_{\text{max}}$ (leaves d$^{-1}$)</th>
<th>$T_{\text{max}}$ (°C)</th>
<th>$T_{\text{opt}}$ (°C)</th>
<th>Adjusted $R^2$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wheat</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yamhill</td>
<td>0.207 ± 0.001</td>
<td>45.3 ± 0.89</td>
<td>21.2 ± 0.21</td>
<td>0.998</td>
<td>8</td>
</tr>
<tr>
<td>Stephens</td>
<td>0.206 ± 0.001</td>
<td>43.3 ± 1.43</td>
<td>21.3 ± 0.36</td>
<td>0.995</td>
<td>8</td>
</tr>
<tr>
<td>Nugaines</td>
<td>0.221 ± 0.001</td>
<td>46.6 ± 2.23</td>
<td>22.8 ± 0.62</td>
<td>0.995</td>
<td>8</td>
</tr>
<tr>
<td>Tres</td>
<td>0.209 ± 0.002</td>
<td>50.0 ± 3.31</td>
<td>24.6 ± 1.02</td>
<td>0.994</td>
<td>8</td>
</tr>
<tr>
<td>Barley</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Klages</td>
<td>0.220 ± 0.002</td>
<td>42.7 ± 1.72</td>
<td>20.2 ± 0.38</td>
<td>0.989</td>
<td>8</td>
</tr>
<tr>
<td>Steptoe</td>
<td>0.210 ± 0.001</td>
<td>46.4 ± 2.53</td>
<td>20.9 ± 0.55</td>
<td>0.987</td>
<td>8</td>
</tr>
<tr>
<td>63BI</td>
<td>0.252 ± 0.004</td>
<td>45.5 ± 5.68</td>
<td>21.8 ± 1.44</td>
<td>0.949</td>
<td>8</td>
</tr>
<tr>
<td>DL71</td>
<td>0.239 ± 0.003</td>
<td>42.5 ± 3.89</td>
<td>21.5 ± 0.77</td>
<td>0.979</td>
<td>8</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>45.3</td>
<td>21.8</td>
<td>0.986</td>
<td></td>
</tr>
</tbody>
</table>

Data from Cao and Moss, 1989. $R_{\text{max}}$, Maximum rate of leaf appearance; $T_{\text{max}}$, maximum temperature for leaf appearance; $T_{\text{opt}}$, optimum temperature for leaf appearance.
The rate of development to panicle initiation of two sorghum cultivars reported by Craufurd et al. (1998) was also simulated well by eqn (5) (Table 5), although these data were simulated equally well by the bilinear model (Craufurd et al., 1998) (compare Fig. 4A and B). The difference in (from 0.89 to 3.31 °C) than for the $T_{\text{opt}}$ (from 0.21 to 1.02 °C). This is because estimation of the $T_{\text{max}}$ involved much extrapolation due to lack of data in the high temperature range. Cultivar Nugaines had higher maximum rate of leaf appearance than the other three cultivars. For the four barley cultivars, the estimated $T_{\text{opt}}$ values were close, and ranged from 20.2 to 21.5 °C. The estimated $T_{\text{max}}$ values were also close, ranging from 42.5 to 46.4 °C, with cultivars 83BI and DL71 having higher maximum leaf appearance rates than Klages and Stephens. Except for the wheat cultivar Tres, all wheat and barley cultivars had a similar $T_{\text{opt}}$ around 21 °C.

Results of fits to data on rate of development towards terminal spikelet initiation for four wheat cultivars (Slater and Rawson, 1994) are listed in Table 4. The adjusted $R^2$ fits were from 0.01 to 0.847, relatively poor compared with those for other datasets. The small number of measurements ($n = 6$) could have been one reason for these relatively poor fits. Again, the standard errors for the $T_{\text{max}}$ estimation were about twice as large (therefore less reliable) as those for the $T_{\text{opt}}$ estimation. The estimated $T_{\text{opt}}$ values, however, were similar among the cultivars and averaged 20.6 °C, which is also close to the $T_{\text{opt}}$ for leaf appearance (average 21 °C, Table 3). From Table 4, the earliness of the wheat cultivars is reflected in their maximum rate of development ($R_{\text{max}}$).

Temperature response of rate of development to panicle initiation in sorghum

The rate of development to panicle initiation of two sorghum cultivars reported by Craufurd et al. (1998) was also simulated well by eqn (5) (Table 5), although these data were simulated equally well by the bilinear model (Craufurd et al., 1998) (compare Fig. 4A and B). The difference in
maturity between these two cultivars is primarily reflected in their $R_{\text{max}}$.

Temperature response of shoot elongation rate of lambsquarters

Lambsquarters is an important weed in the maize fields (Roman, 1998). Applying a beta distribution equation to the data of Roman (1998) reveals that the shoot elongation rate of lambsquarters has a $T_{\text{opt}}$ of 27.8 ± 1.32 and a $T_{\text{max}}$ of 42.2 ± 0.89 °C. Thus the growth of this weed seems to have a lower optimum temperature and a higher maximum temperature, i.e. a wider temperature adaptation, than maize (compare with Table 1). If this relation is supported in more extensive work, it will be significant in understanding lambsquarters-maize interactions.

DISCUSSION AND CONCLUSIONS

This work shows that a beta distribution equation, as expressed in eqn (5), describes well the temperature response of a number of plant processes. It is attractive for several reasons. First, it has only three parameters, namely the optimum temperature, the maximum temperature and the maximum rate of growth or development that can be measured only at the optimum temperature. Second, all three parameters are self-explanatory and have clear biological definitions. Third, it gives a smooth curve as opposed to a series of lines with abrupt changes between them, which is inevitable with a bilinear or multi-linear model. Depicting the response to temperature as a smooth curve is more realistic than some other depictions. Fourth, it deals with the plant response to the whole range of temperatures, rather than just a fraction of them. It also combines the advantages of several equations: the exponential response at low temperatures, the positive linear response at intermediate temperatures, the parabola response around optimum temperatures, and the negative linear response at high temperatures (Fig. 1). Finally, it gives high to modest fits for a range of datasets taken from the literature (Tables 1–3), and for one dataset (Olennaar et al., 1979) that allowed evaluation using independent data, it showed high predictive ability (Fig. 2).

Because temperature is among the most important single factor determining plant growth and development, and hence agricultural production, a good model that allows for summarization and hence simulation of the temperature response of plant growth and development would be valuable in several applications. Knowledge of the optimum and maximum temperatures of the growth and development of a genotype is of vital importance to the successful prediction of its maturity, adaptation and yield in a particular environment. Knowledge of the differences among different genotypes or species in their optimum and maximum temperature for growth and development is also an important aspect when understanding differential plant adaptation and genotype (or species) × environment interactions. For example, examination of the curves in Fig. 1 shows that for a $T_{\text{max}}$ of 40 °C, a response curve with $T_{\text{opt}} = 20$ °C would give a wider range of adaptation, as indicated by the area under the curve, than lower or higher $T_{\text{opt}}$ values. We thus foresee that the beta distribution equation as defined here will find application in plant germplasm research and screening, in crop system modelling, as well as in temperature control of artificial agricultural production systems. We do not argue that the model will be useful for all plant processes, especially for those that appear to have a wide range of optimum temperature (e.g. photosynthesis), but do foresee that the model will have application for many processes, including those currently handled by using a degree-day or heat unit approach. Further tests will be necessary, however, to confirm the value of the approach outlined.

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