Simulating leaf appearance in some Brazilian spring wheat genotypes

Simulação do aparecimento de folhas em alguns genótipos de trigo de primavera brasileiros

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Abstract: The calculation of leaf appearance rate (LAR) is an important part of many wheat simulation models. The strength of a crop simulation model is how well it works under a wide range of different environments and with different genotypes. This study evaluates the performance of an existing model recently developed for winter wheat (the Streek LAR model) in simulating the main stem LAR and Haun Stage of some Brazilian spring wheat cultivars. The Streek LAR model is composed of three non-linear response functions combined in a multiplicative fashion, and model coefficients have biological meaning and operational definitions. The original and a modified version of the Streek LAR model were used in this study. The modified version of the Streek LAR model consisted of adapting two coefficients for local cultivars. A field experiment was carried out at Santa Maria, RS, Brazil, which provided independent data for evaluating the two versions of the Streek LAR model. Thirteen Brazilian wheat cultivars were sown on 05 July 2003, and the number of main stem leaves, represented by the Haun Stage, was measured weekly. The original version of the model overpredicted most of the Haun Stage data, with an overall (including data for all cultivars) root mean square error (RMSE) of 1.5 leaves. Simulations were greatly improved with the modified version of the model, decreasing the overall RMSE to 0.8 leaves. RMSE lower than one leaf was obtained with the Modified Streek LAR model for ten out of the thirteen spring wheat cultivars evaluated.

Key words: Triticum aestivum, leaf number, air temperature, model.

Resumo: O cálculo da taxa de aparecimento de folhas (TAF) é um importante componente de vários modelos de simulação de trigo. Um modelo deve ter boa performance em uma ampla faixa de condições ambientais e com diferentes genótipos. Este trabalho avalia a performance de um modelo de simulação recentemente desenvolvido para trigo de inverno (o modelo de TAF de Streek) em simular a TAF e o Estágio de Haun no colmo principal de algumas cultivares brasileiras de trigo de primavera. O modelo de TAF de Streek é composto por três funções de resposta não lineares combinadas de modo multiplicativo e os coeficientes têm significado biológico e definição operacional. A versão original e uma versão modificada do modelo de TAF de Streek foram usadas neste trabalho. A versão modificada consistiu em adaptar dois coeficientes para cultívar locais. Um experimento a campo em Santa Maria, RS, Brasil, com treze cultivares brasileiras de trigo semeadas em 05 de julho de 2003, forneceu dados independentes para avaliar as duas versões do modelo. O número de folhas no colmo principal, representado pelo Estágio de Haun, foi medido semanalmente. A versão original do modelo superestimou a maioria dos dados de Estágio de Haun, com uma raiz quadrada do quadrado do erro médio (RMSE) geral (incluindo dados das treze cultivares) de 1,5 folhas. As simulações foram melhoradas com a versão modificada do modelo, diminuindo o RMSE geral para 0,8 folhas, sendo o RMSE menor que uma folha em dez das treze cultivares de trigo de primavera.

Palavras-chave: Triticum aestivum, número de folhas, temperatura do ar, modelo.

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Introduction

Wheat (*Triticum aestivum* L.) is the leading cereal in terms of area and the second in volume of grains (USDA, 2005), with approximately one sixth of the arable area of the world being cultivated with wheat (Slafer & Satorre, 2000). Wheat is the main winter cereal in Brazil both in terms of area and production (USDA, 2005). The annual consumption of wheat in Brazil is about 10 million metric tons (Cunha, 2005). During the last 10 years, about 40% of the Brazilian demand for wheat has been produced in Brazil in an area of around 2 million hectares (Scheeren, 2005). Therefore, research on this crop has the potential to affect the well being of a considerable number of people both worldwide and in Brazil.

The calculation of leaf appearance rate (LAR) on the main stem is an important part of many wheat simulation models (Weir et al., 1984; Amir & Sinclair, 1991; McMaster et al., 1991; Hodges & Ritchie, 1991; CAO & MOSS, 1997). The integration of LAR over time gives the number of accumulated or emerged leaves on the main stem (NL), which is an excellent measure of plant development. In wheat, NL is often represented by the Haun Stage (HS), which is the number of fully expanded leaves plus the ratio of the length of the expanding leaf to the penultimate leaf (Haun, 1973). The main stem HS is related to the timing of several wheat developmental stages such as tillering, double ridge, terminal spikelet, booting, and anthesis (Klepper et al., 1982; Brooking et al., 1995; Streck et al., 2003a). Leaf area expansion that intercepts solar radiation for canopy photosynthesis, which affects dry matter accumulation and crop yield, is also related to main stem HS (Amir & Sinclair, 1991; McMaster et al., 1991).

The LAR model of Wang & Engel (1998) is one of several wheat LAR models described in the literature (Miglietta, 1991; Bindi et al., 1995; Jamieson et al., 1995). The Wang and Engel model was superior to the phyllochron model in simulating the LAR and HS of several winter wheat genotypes sown at different dates in two growing seasons at Lincoln, NE, USA (Xue et al., 2004). The better performance of the Wang and Engel model compared to the phyllochron model derived from temperature effects on LAR being more realistically taken into account in the former compared to the latter model (Xue et al., 2004). The Wang and Engel model uses a non-linear response function to describe the response of LAR to temperature whereas in the phyllochron model the response of LAR to temperature is described by a linear response function (Xue et al., 2004). Non-linear response functions are more realistic for representing the effect of environmental factors on plant development than linear response functions such as the thermal time approach (Yin et al., 1995; Granier & Tardieu, 1998; Bonhomme, 2000; Streck., 2002). Another advantage of the Wang and Engel model is that the effects of environmental factors on LAR in the Wang and Engel model are combined in a multiplicative fashion. The multiplicative approach is biologically more realistic for representing the interactions between plant development and environmental factors than other approaches such as the additive or the limiting factor approaches (Wang & Engel, 1998; Streck et al., 2003a). The Wang and Engel LAR model was further modified by Streck et al. (2003b), hereafter referred to as the Streck LAR model, by incorporating a chronology response function that takes into account the effect of seed reserves on the rate of appearance of the first two leaves and a decrease in LAR with increase in leaf number, as a consequence of higher order leaves take more time to appear because of an increase in the distance that each primordium has to traverse to appear at the whorl for each subsequent leaf. These modifications improved the predictions of main stem HS with the Streck LAR model in several winter wheat genotypes compared to the predictions with the Wang and Engel model (Streck et al., 2003b).

The strength of a crop simulation model is how well it works under a wide range of different environmental conditions. Therefore, it is important to evaluate simulation models in different environments and also with different genotypes. The fact that the Streck LAR model was evaluated for winter wheat but not for spring wheat provided a rationale for this study. The objective of this study was to evaluate the Streck LAR model for simulating the main stem LAR and HS of some Brazilian spring wheat cultivars.

Material and Methods

The Streck LAR model has the general form (Streck et al., 2003b):

\[
\text{LAR} = \text{LAR}_{\text{max}} f(T) f(P) f(C) \quad (1)
\]
where LAR is the daily leaf appearance rate (leaves day$^{-1}$), LAR$_{max}$ is the maximum daily leaf appearance rate (leaves day$^{-1}$) of the first two leaves under optimum temperature, and $f(T)$, $f(P)$, and $f(C)$ are dimensionless temperature, photoperiod, and chronology response functions (varying from 0 to 1) for LAR, respectively.

The temperature function $f(T)$ (Figure 1a) is:

$$f(T) = \frac{2(T - T_{min})^2(T_{opt} - T_{min})^2(T - T_{max})^2}{(T_{opt} - T_{min})^2}$$  

for $T_{min} \leq T \leq T_{max}$  

for $T < T_{min}$ or $T > T_{max}$, then $f(T) = 0$

$$a = \frac{ln2}{ln[(T_{max} - T_{min})/(T_{opt} - T_{min})]}$$  

where $T_{min}$, $T_{opt}$, and $T_{max}$ are the cardinal temperatures (minimum, optimum, and maximum) for LAR, and $T$ is the daily mean air temperature.

The photoperiod function $f(P)$ (Figure 1b) is:

$$f(P) = 1 - \exp[(-\omega(P-P_c))]$$  

for $P \geq P_c$

if $P < P_c$, then $f(P) = 0$

where $P$ is the actual photoperiod (h), $P_c$ is the critical photoperiod (h) below which LAR is zero, and $\omega$ is a photoperiod sensitivity coefficient (h$^{-1}$).

The chronology function $f(C)$ (Figure 1c) is:

$$f(C) = 1 \text{ for } HS < 2$$  

$$f(C) = (HS/2)^b \text{ for } HS \geq 2$$

where HS is the Haun Stage and $b$ is a dimensionless sensitivity coefficient.

The main stem number of emerged leaves, represented by the Haun Stage (HS), is calculated by accumulating daily LAR values (i.e. at a one day time step) starting at emergence.

In our study, we evaluated two versions of the Streck model: the Streck LAR model with the original coefficients, hereafter referred as the Original Streck LAR model, and we modified two coefficients and named this form of the model as the Modified Streck LAR model. One modification was $T_{min}$ in the temperature response function (eq. 2 and 3), which was originally 0°C (STRECK et al., 2003b), and was changed to 5°C. A $T_{min}$=5°C is a

Figure 1. The temperature response function [$f(T)$, eq. (2)] (a), and photoperiod response function [$f(P)$, eq. (4)] (b), and the chronology response function [$f(C)$, eq. (5) and eq. (6)] (c) used in the Modified Streck LAR model for spring wheat.
better assumption than $T_{\text{min}} = 0^\circ C$ for Brazilian spring wheats (MOTA, 1989; RODRIGUES et al., 2001).

The other modification was the LAR$_{\text{max}}$ value. STRECK et al. (2003b) used LAR$_{\text{max}} = 0.320$ leaves day$^{-1}$. We estimated LAR$_{\text{max}}$ from an independent experiment carried out at Santa Maria, RS, Brazil (latitude: 29°43'S, longitude: 53°43'W, and altitude: 95 m). The region has a sub-tropical climate Cfa formula according to Köppen’s climate classification, with warm summer and rain well distributed throughout the year (MORENO, 1961). Soil type at the experimental site was a Rhodic Paleudalf (USDA Taxonomy). In this experiment, cultivar BRS 179 was sown in a 5 m row on 22 April 2003 at the field area of the Plant Science Department, Federal University of Santa Maria (UFSM). Plants were fertilized following local recommendation. Five plants were tagged with colored wires one week after emergence. These plants were used to measure the main stem HS (HAUN, 1973) once a week throughout the experiment. The LAR$_{\text{max}}$ was estimated by changing (increasing and decreasing) the original LAR$_{\text{max}}$ value by a 5% step until minimizing the root mean square error (RMSE, eq. 7) between observed and estimated HS values (MEDEIROS et al., 2000). The estimated LAR$_{\text{max}}$ that rendered the lowest RMSE was 0.288 leaves day$^{-1}$ and was assumed to be cultivar independent.

Other model coefficients in the Modified Streck LAR model were as published previously (STRECK et al., 2003b), i.e., $T_{\text{opt}} = 22^\circ C$, $T_{\text{max}} = 35^\circ C$, $\omega = 0.2$ hr$^{-1}$, $P_c = 0$, and $b = -0.3$. The photoperiod ($P$) including civil twilight (when the sun is from 0 to 6° below the horizon) in eq. (4) was calculated with the algorithm of KIESLING (1982).

A field experiment was carried out at the same location, to provide an independent data set for evaluating the Original Streck LAR model and the Modified Streck LAR model. Thirteen Brazilian spring wheat cultivars (Granito, Rubi, Fundacep 40, Fundacep 37, Fundacep 36, Fundacep 31, Fundacep 30, Fundacep 29, CEP 27, Embrapa 16, BRS 177, BRS 179, and BRS 194) were sown on 05 July 2003 in 4.0 x 0.6 m plots. Each plot had one cultivar with three rows 0.30 m apart. The plots were located side by side, following an experimental protocol previously used and widely accepted for phenology studies in wheat (PASCALE & MOTA, 1966; MOTA & GOEDERT, 1969). The plant density was about 200 plants m$^{-2}$, the same as used in STRECK et al. (2003b). Plants were also fertilized following local recommendation. Four days after emergence, eight plants in the center row were randomly selected and tagged with colored wires. The main stem HS was measured on these tagged plants once a week.

Daily minimum and maximum air temperature were measured by a standard meteorological station located at about 300 m from the plots. Mean daily temperature ($T$) used in the temperature response function (eq. 2 and 3) was calculated as the average of daily minimum and maximum temperatures.

The values of main stem HS simulated by the Original Streck LAR model and by the Modified Streck LAR model were compared with observed main stem HS values of the thirteen cultivars, which were independent data sets. The statistic used to evaluate model performance was the root mean square error (RMSE), calculated as (JANSSEN & HEUBERGER, 1995):

$$\text{RMSE} = \sqrt{\frac{\Sigma(s-o)^2}{N}}$$

(7)

where $s =$ simulated HS values, $o =$ observed HS values, and $N =$ number of observations. The unit of RMSE is the same as $s$ and $o$, i.e., leaves. The lower the RMSE the better the model prediction.

Results and Discussion

Simulated vs. observed values of main stem HS by both models when data for all thirteen cultivars were pooled are presented in Figure 2. The Original Streck LAR model overpredicted most of the HS data, with a RMSE = 1.5 leaves. Simulations were greatly improved with the Modified Streck LAR model, with a RMSE = 0.8 leaves and more data points near the 1:1 line. The performance of the LAR models varied among cultivars (Table 1). The best and the poorest performance of the Original model were for cultivars Granito (RMSE = 0.6 leaves) and Embrapa 16 (RMSE = 2.2 leaves) and with the Modified model were for cultivars Fundacep 36 (RMSE = 0.2 leaves) and Embrapa 16 (RMSE = 1.3 leaves), respectively. Some of the RMSE values with the Modified Streck LAR model are within the range of RMSE (0.2-0.5 leaves) reported by STRECK et al. (2003b), whereas the RMSE with the Original LAR model was always greater than 0.6 leaves.
Table 1. Root mean square error (RMSE) for the simulation of the main stem Haun Stage of thirteen Brazilian spring wheat cultivars by the Original Streck LAR model (RMSE$_{\text{original}}$) and by the Modified Streck LAR model (RMSE$_{\text{modified}}$). Santa Maria, RS, Brazil, 2003.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>RMSE$_{\text{original}}$ (leaves)</th>
<th>RMSE$_{\text{modified}}$ (leaves)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fundacep 36</td>
<td>0.9</td>
<td>0.2</td>
</tr>
<tr>
<td>Fundacep 30</td>
<td>1.1</td>
<td>0.3</td>
</tr>
<tr>
<td>Fundacep 40</td>
<td>1.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Rubi</td>
<td>0.9</td>
<td>0.3</td>
</tr>
<tr>
<td>Granito</td>
<td>0.6</td>
<td>0.6</td>
</tr>
<tr>
<td>Fundacep 37</td>
<td>1.5</td>
<td>0.7</td>
</tr>
<tr>
<td>BRS 177</td>
<td>1.5</td>
<td>0.7</td>
</tr>
<tr>
<td>BRS 179</td>
<td>1.7</td>
<td>0.7</td>
</tr>
<tr>
<td>BRS 194</td>
<td>1.8</td>
<td>0.9</td>
</tr>
<tr>
<td>Fundacep 31</td>
<td>1.6</td>
<td>0.7</td>
</tr>
<tr>
<td>Cep 27</td>
<td>1.9</td>
<td>1.1</td>
</tr>
<tr>
<td>Fundacep 29</td>
<td>2.0</td>
<td>1.1</td>
</tr>
<tr>
<td>Embrapa 16</td>
<td>2.2</td>
<td>1.3</td>
</tr>
</tbody>
</table>

Figure 2. Simulated vs. observed values for main stem Haun Stage using the two LAR models (Original Streck LAR model and Modified Streck LAR model). Data are pooled for thirteen spring wheat cultivars sown in the field at Santa Maria, RS, Brazil, during the 2003 growing season. The solid line is the 1:1 line.
Simulation of main stem HS from emergence to flag leaf with the Modified Streck model for cultivars Fundacep 36 and Embrapa 16 are presented in Figure 3. These simulations represent the best and the poorest performance of the Modified Streck LAR model. For cultivar Fundacep 36 the simulated HS values almost matched the observed HS values, while the model overpredicted most of the data for cultivar Embrapa 16.

The parameter LAR$_{\text{max}}$ estimated for Brazilian spring wheat cultivars (0.288 leaves day$^{-1}$) is slightly lower than the LAR$_{\text{max}}$ estimated for American winter wheat cultivars (0.320 leaves day$^{-1}$) (STRECK et al., 2003b). These different values of LAR$_{\text{max}}$ reflect expected differences in genetic background among genotypes developed for different purposes and environments in Brazil (spring wheat) and in the United States (winter wheat).

In this application of the Streck LAR model, we adjusted two coefficients in the modified version of this model for spring wheat cultivars. We estimated the coefficient LAR$_{\text{max}}$ from one cultivar (BRS 179) and assumed that this coefficient was genotype independent. This assumption was also previously used and worked well for four winter wheat cultivars (STRECK et al., 2003b). In the f(T), we assumed a Tmin = 5°C based on previous reports for Brazilian wheat (MOTA, 1989; RODRIGUES et al., 2001). We also assumed that the temperature f(T), the photoperiod f(P), and the chronology f(C) response functions were genotype independent as assumed elsewhere (STRECK et al., 2003b). If we accept an error of up to one leaf in the simulation of HS, which is reasonable for most applications (STRECK et al., 2003b), these assumptions worked well for ten out of the thirteen genotypes used in this study that had RMSE smaller than one leaf.

The fact that the RMSE with the Modified Streck LAR model for cultivar BRS 179 was not the smallest (Table 1) is somehow surprising. As
the coefficient $LAR_{\text{max}}$ was estimated from an experiment using this cultivar, it was expected that the simulation of main stem HS for this cultivar would be the best one. While random and unknown factors might have played a role in explaining the errors associated with the simulations for this cultivar, minor factors that affect $LAR$ in wheat (KIRBY, 1995), such as those related to chemical and physical soil properties, sowing date and weather conditions (for instance solar radiation), which are not taken into account in the model, can not be ruled out and may have contributed to a greater RMSE for BRS 179 compared to the cultivars that had smaller RMSE.

Coefficients in crop simulation models are often assumed dependent on genotype. This creates a problem when a model needs to be used for genotypes that have unknown coefficients and for new cultivars that are released every year. 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 and explanations of phenomena should be in terms of known quantities. This type of philosophy has been encouraged in crop modeling and it assumes that the similarities among genotypes are more important than the differences (MAJOR & KINIRY, 1991). Therefore, the search for generalized coefficients and response functions is a major goal in crop modeling. The fact that the $LAR$ in ten spring wheat genotypes used in this study can be predicted with a RMSE less than one leaf using the same set of model coefficients and response functions indicates two important features of the Streck $LAR$ model that are sought for any crop simulation model: generality and robustness while maintaining accurate predictions.

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References


