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考虑土壤水分限制的春小麦生长简化模型

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摘要: 建立了以日长(L)和日总辐射(TDR)为自变量的春小麦(*Triticum aestivum* L.)碳同化和干物质累积(DMA)的简化模型;考虑了水分限制下光能利用效率(α)、碳传输导度(g_c)均被降低的设定,将反映春小麦水分状况的叶水势(Ψ)作为参数纳入本模型;Ψ则通过多元回归由 80 cm 土层相对含水量($\theta_{R,80}$)、气温(T_a)、水汽压差(VPD)、低于 -1.5 MPa 叶水势之和($\Psi_{c,1.5}$)给出。讨论了模型在"黑河地区地气相互作用研究"中的应用实例。模型分析和模拟结果表明,该简化生长模型能较好地描述春小麦在水分限制和无水分限制条件下的干物质累积过程。

关键词: 春小麦;生长;简化模型;水分限制
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A Simplified Model with Soil Water Limitation on Spring Wheat Growth

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Abstract: The authors constructed a simplified model of spring wheat (*Triticum aestivum* L.) carbon assimilation and dry matter accumulation (DMA) process which consisted of two independent variables, day length (L) and total daily radiation (TDR). Leaf water potential (Ψ) was incorporated into the simplified growth model based on the assumption that both light use efficiency (α) and CO_2 conductance of assimilation (g_c) were depressed by water limitation. Finally, Ψ was estimated from a regression equation in which the independent variables were relative soil water content in the upper 80 cm ($\theta_{R,80}$), ambient temperature (T_a), vapor pressure deficit (VPD), the cumulative leaf water potential below thresholds of -1.5 MPa ($\Psi_{c,1.5}$). Some applications in research program of field experiment of atmosphere-land surface processes in Heihe River region were tested. The simulated data agreed well with the data observed at Linze oasis in 1989 for various levels of water supply and at Zhangye oasis in 1992 in the field. The analysis and simulation using the model demonstrated that the simplified growth model could describe very well the DMA process of spring wheat with and without water limitation in the region of HEIFE (Heihe field experiment).

Key words: spring wheat; growth; simplified model; water limitation

Much attention has been paid to the analysis of wheat plant growth affected by various environmental factors[1-5]. Although there are limitations in using statistical methods, Baier and Robertson[6] studied the relationship between environmental variables and productivity by using regression method. In the 1970s, some researches on complex mechanistic models describing plant growth were undertaken[1,7]. It seems, however, difficult to assess clearly the contribution of a specified variable to growth and productivity from a huge mechanistic model because of the too many arbitrary parameters and the ambiguous variables. An intermediate approach between the regression method and the complex models is the use of simplified mechanistic models which define crop behavior with a few conservative relationships. By using such an approach, Monteith and Scott[8] constructed a much simplified mechanistic model to simulate the effects of temperature on leaf area and canopy structure and of solar radiation on growth. The simulation results were quite satisfactory. Since then some other researchers[9,10] also reported the use of a simplified mechanistic growth model involving environmental variables such as temperature and

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radiation for *Zea mays* and *Triticum aestivum*, respectively.

HEIFE (Heihe field experiment) is a Sino-Japanese cooperational program on the atmosphere-land surface processes in the Heihe River basin, Gansu, China from 1989 to 1993[11]. After the approval of the HEIFE program, both Chinese and Japanese National Committees for World Climate Research Programme (WCRP) accepted as an important program of WCRP because the HEIFE region covers deserts, including Gobi desert, mountain and oasis. In this special arid region, water shortage is one of the most important factors which limit crop growth and yield formation. Therefore, water budget and water resource are the two most important subprograms.

To validate the understanding of the quantitative relationship between environmental factors, water shortage in particular, and spring wheat dry matter accumulation (*DMA*) or/and yield formation in this arid region, a much simplified growth model considering soil water status, radiation and day length is proposed in this research.

1 Materials and Methods

1.1 Field experiments

1.1.1 Experiment in 1989 Field experiments in 1989 were conducted during the growth season at Linze Cooperative Research Station, Lanzhou Institute of Desert Research, the Chinese Academy of Sciences, China (100°29′E, 39°04′N, 1 200 m above M.S.L.). In the north of the experimental field is the Badajilin Desert, and in south of the experimental site are Linze oasis and Qilian Mountain. The mean annual rainfall is 119 mm and the other climatological data have been given by Huang and Pu[12].

Spring wheat (*Triticum aestivum* L.) cv. "3131" seeds were sown on March 20, 1989, at a density of 49 g/m^2, resulting in about 460 plants/m^2 in a lysimeter system which consisted of 12 tanks containing loamy sand, each with an area of 2.4 m^2 and a depth of 1 m. The rates of fertilizer application were N 83.79 kg/hm^2 and P 34.12 kg/hm^2. There was enough potassium for spring wheat growth in the soil[12].

Before sowing, the average soil moisture in the upper 20 cm depth was around 25 % which was about 65 % of the field capacity for this type of soil. After emergence, three irrigation levels were set, sufficient, moderate and insufficient water supply. Each irrigation level was replicated three times each with three tanks. The control of irrigation for the three water treatments was done as described by Zheng and Huang[13]. The actual total water supply (including irrigation and rainfall) was 483 mm, 250 mm, and 183 mm for sufficient, moderate and insufficient water supplies, respectively, for the whole growth season.

Due to the importance of flag leaf in light interception, gas exchange, *DMA* and growth for spring wheat, Ψ of flag leaf was used as a parameter to indicate the status of whole plant, and was estimated by the following multiple regression equation[14]:

$$\Psi = a_1 + a_2/\theta_{R,80} + a_3 T_a + a_4 \Psi_{c,1.5} + a_5 VPD \quad (1)$$

where a_1 to a_5 are constants, T_a is the ambient temperature, $\Psi_{c,1.5}$ is the cumulative leaf water potential below thresholds of -1.5 MPa, *VPD* is the vapor pressure deficit, and $\theta_{R,80}$ is the relative soil water content in the upper 80 cm expressed as the ratio between actual water content and field capacity of the soil. In the day between soil water measurement, $\theta_{R,80}$ was interpolated from the value of measured $\theta_{R,80}$ by using Lagrange interpolation method. The actual soil water content was measured using samples taken with an auger[15] on the day of biomass determination. Dry and wet bulb temperatures were measured concurrently with the measurement of leaf water potential by using an aspirated psychrometer at a height of 1.5 m above the soil. *VPD* was calculated from the observed data. Actual Ψ was measured by the pressure chamber method[16] using model ZLZ-4 plant water potential chamber (Research Laboratory of Plant Physiology, Lanzhou University). Five samples were taken for each measurement. The measurements of biomass were taken at interval of two hours from 6:00 am to 22:00 pm in the day of harvesting. Biomass was determined randomly by the dispersed individual plant method[17] in the sampling interval of 10 days. Radiation was measured by Model 75F-Ⅱ portable radiometer. The data of day length (*L*) was from Linze Meteorological Observatory that is 40 km away from the experimental site.

1.1.2 Experiment in 1992 Field experiment in 1992 was carried out at Zhangye oasis station of HEIFE (100°22′E, 38°50′N, 1 565 m above M.S.L.). The seeds of spring wheat were sown on March 25, 1992, at a density of 54.5 g/m^2 resulting in about 500 plants/m^2. Before sowing, the average soil moisture in the upper 20 cm depth was around 24 %. The actual total water supply including rainfall and irrigation was 350 mm in the whole growth season. 98.45 kg of N, 40.76 kg of P per hectare were applied. The climatic factors such as total solar radiation, T_a and relative humidity were measured by CM11 radiometer, DTS12 temperature sensor and HMP30u humidity sensor at MILOS 200 Automatic Weather Station

(Vaisala, Finland), respectively. *VPD* was calculated from temperature and relative humidity. The data of L came from the HEIFE Meteorological Observatory that is only 100 m from the sampling site. Other investigations and conditions were the same as done in 1989 at Linze oasis[13].

1.2 Model descriptions

1.2.1 No water limitation Supposing that the growth of wheat could be simply represented as dry matter accumulation, it can be expressed as:

$$W_{(i)} = W_{(i-1)} + \Delta W \qquad (2)$$

where, $W_{(i)}$ and $W_{(i-1)}$ are the total dry matter of spring wheat at the time of i and $i-1$, ΔW is the increment of dry matter from time of $i-1$ to i. The rate of increase is

$$\frac{\Delta W}{\Delta t} = (A - R) \qquad (3)$$

Δt is the interval of time, A is the rate of carbon assimilation, R is the rate of respiration. A lot of research on respiration demonstrated that R was always at a much lower level than A[1,18-20]. Therefore, R was taken as a constant in our model for simplification.

Thornley *et al*[20] expressed the response of carbon assimilation by leaf to light intensity and carbon dioxide concentration as the following:

$$A = \frac{\alpha I\,(g_c C - \beta)}{\alpha I + g_c C} \qquad (4)$$

where, α is the light use efficiency; I is the light intensity intercepted by leaf surface; C is carbon dioxide concentration; g_c is the overall conductance of CO_2; β is the photorespiration. Considering the relationship between intercepted light within the canopy (I) and light intensity over the canopy (I_O) for a "closed canopy", we define

$$I = I_o\, e^{-KLAI} \qquad (5)$$

LAI is the leaf area index; K is the light extinction coefficient for the canopy. For a day with length L, we can write the total assimilation in a day for entire canopy as follows:

$$A_D = \int^{L} \int^{LAI} A \, dh \, dt \qquad (6)$$

If the step of integration is a day, the dry matter (*DM*) accumulated in a day could be calculated from equation (3). Leaf area expanded gradually with *DM* accumulating. In this simplified model, a simple linear function was used to describe the relation between *LAI* and *DM*[19], i.e.

$$LAI = aW + b \qquad (7)$$

where, a and b are constants.

1.2.2 Water limitation Lawlor[21] pointed out that photosynthesis was limited by water stress through increase in both stomatal resistance and mesophyll resistance together as the total resistance. In another word, g_c in equation (4) is given by the value of stomatal conductance (g_s) plus mesophyll conductance (g_m) for CO_2. The relationship between g_m, g_s and leaf water potential (ψ) could be written as the following:

$$g_m = c\psi + d \qquad (8)$$

$$g_s = q\, e^{j\psi} \qquad (9)$$

where c, d, q and j are constants.

Boyer *et al*[22] observed that α was depressed as ψ was reduced in a way described by the equation

$$\alpha = \alpha_m \frac{\psi^h - \psi^p}{(\psi - \psi^p) + (\psi^h - \psi^p)} \qquad (10)$$

where α_m is the maximal light use efficiency; ψ^p and ψ^h are the values of ψ where α is approximately α_m and the half of α_m, respectively.

Substituting g_c using equations (8), (9) and (10) into equation (4), we can calculate the daily assimilation of spring wheat canopy under water limitation from equation (3).

1.3 Parameters and constants used in the model

Tables 1 and 2 give the values of some parameters and constants used in this simplified model for spring wheat growth.

Table 1 The values of several parameters and constants used in the simplified model *

Parameters	Values
α_m (mg CO_2/J)	0.011
β (μg CO_2/m^2/s)	0.17
ψ^p (MPa)	-0.1
ψ^h (MPa)	-1.5
a (m^2/g)	0.010 2
b (m^2/m^2)	0.071
c (cm/s/MPa)	-0.156 5
d (cm/s)	0.36
j (MPa^{-1})	-1.624
q (cm/s)	0.186 8
R (g/d/m^2)	8.5

* Part of the data are from Charles-Edwards[19].

Table 2 The values of constants in regression equation of ψ and its R^2

Experimental site	a_1	a_2	a_3	a_4	a_5	R^2	s.e. *
	MPa	%MPa	MPa·°C^{-1}	MPa	KPa^{-1}		
Linze oasis, 1989	1.36	-0.70	-0.021	0.016	-0.030	0.90	0.13
Zhangye oasis, 1992	1.35	-0.72	-0.018	0.016	-0.028	0.94	0.10

s.e., the data are based on 216 observations in 1989 in Linze oasis and 144 observations in 1992 in Zhangye oasis.

2 Results and Discussion

2.1 Influence of initial weight of DM on DMA

A computer experiment was firstly carried out about the effect of initial weight of *DM* on growth using the simplified growth model. In the experiments, some variables were assumed to be constants, i.e., daily total radiation (*DTR*), *L* and *ψ* were given as 15 MJ/m^2, 12 h and -1.5 MPa, respectively. The independent variable was the initial weight of *DM* that varied from 0.5 g/m^2 to 500 g/m^2. The simulation days used in the simplified model were relative days and the total period of experiment was 80 d. The results showed that *DMA* was influenced remarkably by the value of initial weight of *DM* (Fig. 1). The accumulating rate of *DM* was very small at the beginning of simulation at an initial weight of *DM* in 0.5 g/m^2. On the contrary, the accumulation rate of *DM* appeared almost linear at the beginning of simulation for initial weight of *DM* in 500 g/m^2. One can say that the results of computer experiment shown in Fig. 1 gave a very good agreement with the real growth processes of spring wheat, especially under the condition of low initial weight of *DM*.

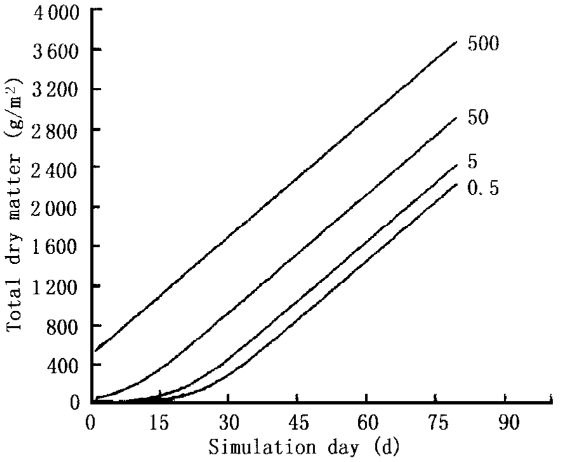

Fig. 1. Effects of initial weight of dry matter on simulated total dry matter accumulation by the simplified model.
Supposed leaf water potential = -1.5 MPa, day length = 12 h, total daily radiation = 15 MJ/m^2.

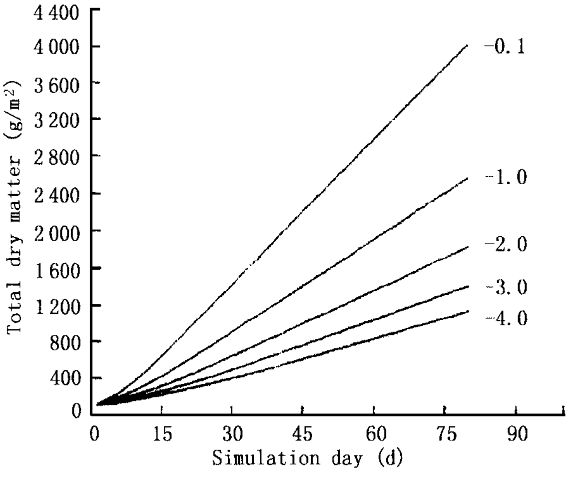

Fig. 2. Effects of leaf water potential on simulated total dry matter accumulation by the simplified model.
Supposed initial weight of dry matter = 100 g/m^2, day length = 10 h, total daily radiation = 10 MJ/m^2.

2.2 Influence of Ψ on DMA

Another computer experiment was run to evaluate the effect of Ψ on *DMA* (Fig. 2). In this case, *TDR*, *L* and initial weight of *DM* were given as 10 MJ/m^2, 10 h and 100 g/m^2, respectively. The independent variable was only Ψ that varied from -0.1 MPa to -4.0 MPa. At high water status (Ψ = -0.1 MPa), simulated total *DM* could reach more than 4 000 g/m^2 at the end of simulation. Much lower values of total *DM* were obtained for the other four leaf water status levels. Less than 1 000 g/m^2 of the total *DM* was obtained under the driest condition used, i.e., a Ψ of -4.0 MPa.

2.3 Estimation of ψ

The simulation of Ψ has been developed in several large-scale models involving plant transpiration or water balance[23,24]. Unfortunately, some parameters in most of the models were not readily available.

Richter[25] once gave a review on the relationships between Ψ and biotic, nonbiotic factors. Saranga *et al*[14] developed a very simple equation for calculating Ψ of cotton plant under field conditions. The aim of our study was to establish a simplified calculation of wheat Ψ based on multiple regression method using few affecting factors and then incorporated the calculated Ψ, the most important intermediate variable, into the final simplified growth model.

The high variability of Ψ was explained as the relative soil water content in the upper layer[14]. Only a small variability of Ψ was due to the variations of *VPD*, T_a and the history of stress of the crop represented by $\Psi_{c,1.5}$. The simplified equation for predicting Ψ was found to be:

$$\Psi = a_1 + a_2/\theta_{R,80} + a_3 T_a + a_4 \Psi_{c,1.5} + a_5 VPD$$

Table 2 gives the values of constants in the multiple regression equation used for prediction at the two experimental sites in different years. The differences in values of constants between the two experimental sites were very small. In Linze oasis, the R^2 was 0.90 and s.e. of the predicted Ψ was 0.13. And the R^2 and s.e. in Zhangye oasis was 0.94 and 0.10 respectively.

The applicability of the multiple regression equation to the prediction of Ψ was validated by using data from the three soil water regimes in the Linze oasis experiment (Fig. 3). A comparison between the calculated and the measured Ψ revealed a good correspondence. This indicated that the simplified predicting equation for Ψ based on the data of climatic, plant and soil variables could be used in the subsequent construction of the growth model involving Ψ.

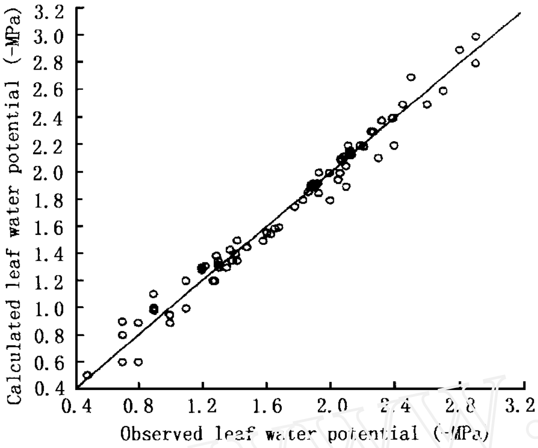

Fig. 3. Comparison of measured and calculated leaf water potential by Scholander method and multiple regression method, respectively. Data were based on 75 observations in Linze oasis experiment.

2.4 Applications

In practice, the simplified growth model is used first to calculate the value of ψ. Such calculation is based on the regression equation of ψ on T_a, VPD, $\theta_{R,80}$ and the plant stress index $\Psi_{c,1.5}$. Then DMA was estimated by using the values of Ψ, L and TDR. The simplified growth model was used in the research program of HEIFE. The measured initial DM was firstly inputted when the model was run. The outputs of the model were rather close to the measured data (Fig. 4). The deviation of simulated data from measured data after day 60 may due not only to the error of measurement for biomass itself but also to the values of some parameters used in the model. And furthermore, this can be explained by the use of the linear relation in the simplified model between LAI and the weight of DM. In 1989 at Linze oasis, the measured data gave a maximal biomass production as 4 kg/m^2 for sufficient water supply, and only 0.9 kg/m^2 for insufficient water supply. Ψ varied from -1.5 MPa to -2.5 MPa for these two water regimes on most days of simulation. The simplified model could describe satisfactorily the growth of spring wheat at various levels of water supply. It could be seen from the results of simulation that even the much simplified model could simulate the real process of DMA for spring wheat.

In conclusion, the simplifications used in the model are reasonable and acceptable. It can be used to simulate spring wheat growth with and without water limitation. Further modification of the model should be aimed at the recalculation of respiration and LAI.

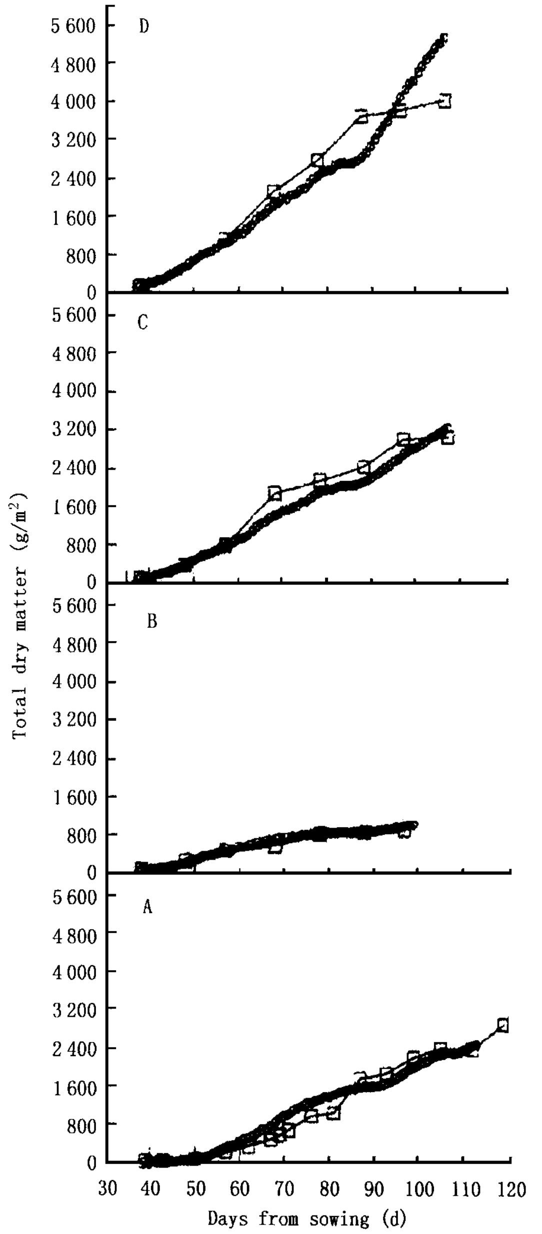

Fig. 4. Comparison of measured data (□) and simulated data (○) from the simplified model.
A, Zhangye oasis in 1992, field; B, Linze oasis in 1989, insufficient water supply; C, Linze oasis in 1989, moderate water supply; D, Linze oasis in 1989, sufficient water supply.

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