Modelling Maintenance Respiration in Wheat

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Abstract: Respiration has a profound influence on crop yield because dry matter accumulation by a crop is closely related to assimilation of CO_2 and respiratory activity. This paper describes the development of a simulation model for respiration in wheat. While the growth respiration can be assumed to be proportional to the assimilation of CO_2, the model concentrated on the effects of biotic and environmental factors on maintenance respiration. The model was based on the effect of temperature, water stress and dry matter accumulation on maintenance respiration. It also includes the changes in the rate of maintenance respiration during ontogeny. Since the most important maintenance process in plants is protein turnover an alternative approach was to model the maintenance respiration based on nitrogen content. Diurnal temperature variation was considered to simulate the temperature effect on biomass-based rate of respiration using daily maximum and minimum temperatures as inputs, while the Q_{10} concept for the N-content based model was used. The models were used to estimate seasonal maintenance respiration. The model simulation highlighted the practical difficulties in application of a constant value of maintenance respiration to a crop simulation model. It was concluded that the dry weight based model gave a simulation in closer agreement to field observation than the N-content based model because maintenance respiration is not solely related to protein turnover.

Keywords: Respiration model; Temperature effect; Water stress; Wheat, Q_{10}; Thermal time; Ontogeny

1. INTRODUCTION

McCree [1974] demonstrated that the respiration, R (g CH_2O m^{-2} d^{-1}), of crops can be separated theoretically into two components, growth respiration (R_g) and maintenance respiration (R_m). Growth respiration is proportional to the total assimilation (P) and maintenance respiration is proportional to dry mass (W). This gives:

$$R = R_g + R_m = kP + cW \qquad (1)$$

where k is the coefficient for growth respiration and c is the coefficient for maintenance respiration. The growth respiration is the cost of converting the immediate products of photosynthesis into plant material. It is found that the coefficient k varies considerably between 0.12 and 0.45 with plant species and plant tissues [reviewed by Amthor, 1989]. The value of k=0.20 was reported for wheat [Nilovskaya and Smirnov, 1983; cited by Amthor, 1989] and white clover (*Trifolium repens* L.) [McCree and Silsbury, 1978]. The maintenance respiration refers to the CO_2 that results from protein breakdown, plus the CO_2 produced in respiratory processes that provide energy for maintenance processes.

The maintenance processes include cellular structure and gradients of ions and metabolites, and also the processes of physiological adaptation that maintain cells and active units in changing environment [Penning de Vries, 1975]. The coefficient c varied with many biotic and environmental factors including temperatures, nitrogen status and water stress [Amthor, 1989]. The factors which affect the rate of maintenance respiration also determinate crop growth. In order to improve the accuracy of simulation of the respiration component and hence crop growth, these important factors affecting respiration must be considered. The aims of this paper are: (i) to derive equations to model the effects of some of these factors on respiration at crop level using published experimental data to simulate respiration, and (ii) to compare two models that use different approaches to simulate maintenance respiration in wheat.

2. DESCRIPTION OF THE MODEL

2.1. Modelling Maintenance Respiration Based on Biomass Accumulation

Many studies were conducted to determine the rate of maintenance respiration (c) on dry weight basis in wheat [McCullough and Hunt, 1989 & 1993]. Factors affecting the rate of maintenance respiration include temperature, water stress and crop age. Thus, we can write

$$R_m = s(\varphi)g(\theta)\sum_{i=1}^{k} R_i W_i \qquad (2)$$

where R_m is maintenance respiration (g CH_2O m^{-2} d^{-1}), W_i (g m^{-2}) is the plant dry in ith component, R_i (g CH_2O g^{-1} d^{-1}) is the daily maintenance respiration which is effected by temperature, $s(\varphi)$ and $g(\theta)$ are dimensionless and respectively describe the effect of water stress and crop age on the maintenance respiration in wheat.

2.1.1. Temperature Effect

Like many metabolic processes, maintenance respiration rate is highly dependent on temperature and increases exponentially with increasing temperature up to an optimum temperature (T_o). If temperature is higher than T_o the respiration rate decreases. r_i for the ith organ at T is described by

$$r_i = \lambda_i e^{\gamma_i T} \qquad T \le T_o \qquad (3a)$$

$$r_i = \frac{\lambda_i e^{r_i T_o}}{1 + T - T_o} \qquad T > T_o \qquad (3b)$$

in units of g CO_2 g^{-1} min^{-1}, where λ and γ are constants. Figure 1 shows the maintenance respiration rate in wheat using the data of Stoy [1965] and Mitchell et al. [1991] to fit Eq. (3), from which λ=5.978 and γ=0.0848 for shoot and λ=3.430 and γ=0.0706 for ears were determined. It is assumed that for an optimum temperature T_o=28.0 °C.

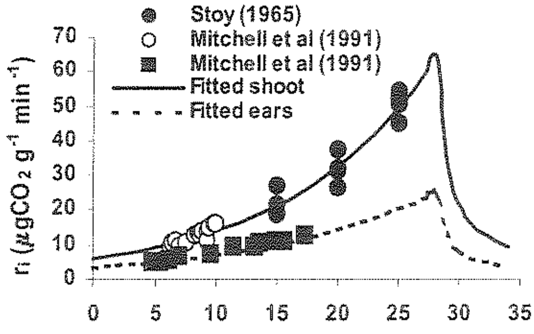

Figure 1. Compared the observed and fitted relationships between maintenance respiration rate and temperature for shoot and ears of wheat.

The daily maintenance respiration can be defined by

$$R_i = \sigma \int_0^{1440} r_i dt \qquad (4)$$

in units of $gCH_2Og^{-1}d^{-1}$, 1440 is the time for a day in minutes. σ=0.68, which is the relative molecular masses of CH_2O to CO_2.

The temperature collected for the purpose of running a simulation model is rarely in minute intervals. Daily maximum temperature (T_{max}) and minimum temperature (T_{min}) are commonly used to run crop growth simulation models. To calculate R_i in Eq (4) the temperature in minutes can be extrapolated assuming a linear change between T_{max} and T_{min}. Solution of Eq (4) gives the daily maintenance respiration as:

$$R_i = \Theta\,(e^{\gamma_i T_{max}} - e^{\gamma_i T_{min}})$$

$$T_{min} < T_{max} \le T_o \qquad (5a)$$

$$R_i = \Theta\left[e^{\gamma_i T_o} - e^{\gamma_i T_{min}} + \lambda_i \gamma_i e^{\gamma_i T_i} \ln(1 + T_{max} - T_o)\right]$$

$$T_{min} < T_o \le T_{max} \qquad (5b)$$

$$R_i = \Theta \gamma_i\, e^{\gamma_i T_o} \ln\left[\frac{1 + T_{max} - T_o}{1 + T_{min} - T_o}\right]$$

$$T_o < T_{min} \le T_{max} \qquad (5c)$$

in units of g CH_2O $g^{-1}d^{-1}$, where

$$\Theta = \frac{1440\lambda_i \sigma}{\gamma_i (T_{max} - T_{min})}$$

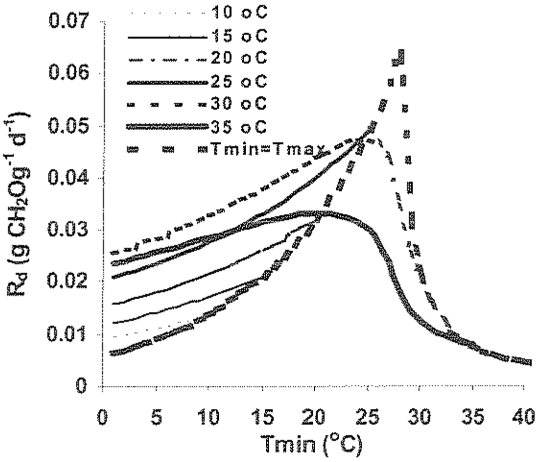

Figure 2. Daily rate of maintenance respiration (R_d) calculated for shoots by Eq (5a,b,c) as a function of minimum temperature (x axis) and maximum temperatures (see legend).

2.1.2. Water Stress Effect

Many studies showed that slight water deficits are accompanied by increases in maintenance respiration rate, but that more severe water stress decreases respiration [Upchurch et al., 1955; Brix, 1962; Kaul, 1966]. Water stress commonly reduces crop growth and photosynthesis, which in turn should decrease growth respiration. However, water stress often accumulates a large amount of organic solutes and maintenance of these may require increased maintenance respiratory activity [Amthor, 1989]. The effect of water stress can be described by

$$s(\varphi) = \zeta_{\min} + \frac{a\varphi}{(1+b\varphi)^c} \qquad (6)$$

where φ is soil extractable water (φ=0 for wilting soil water content and φ=1 for field capacity), ζ_{min} is the value of $s(\varphi)$ when φ=0, a, b and c are constant. ζ_{min}=0.49, a=7.48, b=1.63 and c=2.78 were determined by using the data of Kaul [1966] (Figure 3).

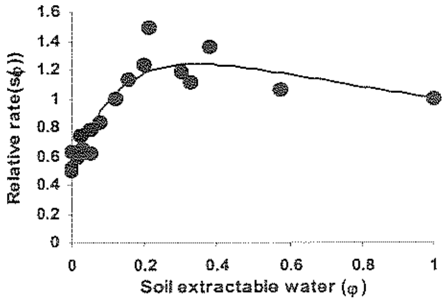

Figure 3. The observed respiration rate expressed as ratio to that at field capacity related to soil extractable water and fitted relationship of Eq (6).

2.1.3 Changes during Ontogeny

Stoy [1965] found the maintenance respiration in wheat decreased with plant age. There are many reports in other crops. For example, McCree [1983] reported that maintenance coefficient of grain sorghum during the vegetative growth decreased from about 1.6 mg CO_2 $g^{-1}h^{-1}$ for young plants to about 1.2 mg CO_2 $g^{-1}h^{-1}$ in the older plants. The decrease in maintenance respiration rate with ontogeny may have been due to a decrease in protein content as the maintenance respiration rate was linearly related to plant protein content irrespective of crop age [McCree, 1983]. Gent and Kiyomoto [1985] showed canopy maintenance respiration per unit of dry weight declined with ontogeny, while Gent and Kiyomoto [1992] reported that averaged respiration rate in six winter wheat cultivars decreased to 71% at heading-anthesis and 33% at grain fill stage from stem elongation. The changes in maintenance respiration during ontogeny can be described by

$$g(\theta) = \begin{cases} 1 & \theta \le \theta_s \\ \dfrac{1}{1 + \dfrac{(\theta - \theta_s)}{(\theta_{0.5} - \theta_s)}} & \theta > \theta_s \end{cases} \qquad (7)$$

where θ is the thermal time (°Cd) above a base temperature of 5°C accumulated from emergence, θ_s is the thermal time at which maintenance respiration starts to decrease, $\theta_{0.5}$ is thermal time when the maintenance respiration rate is half of its maximum, $g(\theta)$=0.5. It is assumed that the maintenance respiration is not effected by crop aging until $\theta > \theta_s$. By analysis of the data of Puckridge and Ratkowsky [1971] the values for parameters $\theta_{0.5}$ and θ_s were determined to be 460 °Cd and 219 °Cd, respectively (Figure 4).

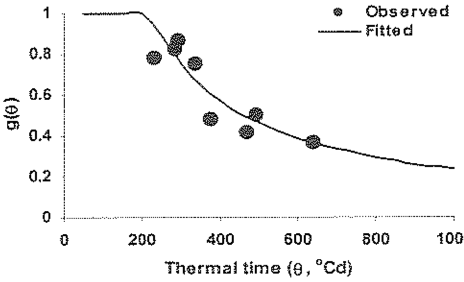

Figure 4. Relationship between relative maintenance respiration $g(\theta)$ and thermal time, θ in wheat. The observed data is extracted from Puckridge and Ratkowsky [1971].

2.2 Modelling Maintenance Respiration Based on Nitrogen Accumulation

It was observed that plant protein content was correlated with the maintenance coefficient [McCree, 1983; Jones et al., 1978; Stahl and McCree, 1988]. Since maintenance expenditure is largely attributable to protein turnover [Penning de Vries, 1975], an alternative approach to modelling maintenance respiration may be based on nitrogen content of the crop. Thus, the maintenance respiration may be calculated by

$$R_m = s(\varphi)\sum_{i=1}^{k} \rho_i N_i v_i(T) \qquad (8)$$

where $s(\varphi)$ is effect of water stress as defined in Eq (6), ρ_i is the coefficient (gCO_2 (g N)$^{-1}$), N is nitrogen content (g N m^{-2}), $v_i(T)$ is the temperature effect. According to Choudhury [2000], the value of ρ_i at T=20 °C for above ground green components and roots of wheat was 0.5343 and 1.0686 g CO_2 $(gN)^{-1}$, respectively. $v_i(T)$ is calculated by Q_{10} approach as:

$$v_i(T) = 2^{0.1(T-20)} \qquad (9)$$

3. DATA

In order to simulate the daily maintenance respiration, biomass and nitrogen accumulation data are needed. The data of dry matter and nitrogen accumulation were obtained from Angus et al. [1980]. The weather data was obtained from the Metaccess database [Donnelly et al., 1997]. Daily data were interpolated. The emergence of the crop was estimated to occur 7 day after sowing.

4. RESULTS AND DISCUSSIONS

Figure 5 showed the simulated maintenance respiration by both the N-model and DW-model without water stress. The simulated percentage of maintenance respiration to accumulated dry matter in wheat by both the N-model and DW-model were close after 45 DAS (days after sowing) (Figure 5B). In the early stage, the N-model simulates values of maintenance cost of about 1.5 % higher than the DW-model. However, the difference in total R_d is small (Figure 5A). In the late growth stage, the percentage of R_d to DW by both models was close, but the N-model simulates lower values of R_d than the DW-model between 75 and 105 DAS and higher value after 120 DAS.

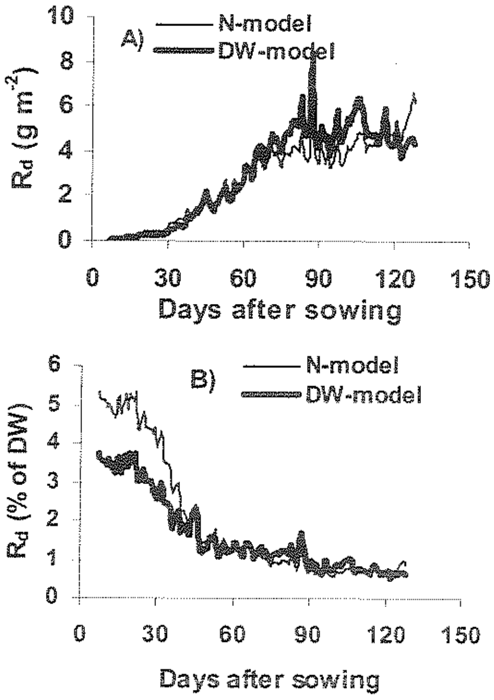

Figure 5. The simulated rate of maintenance respiration by both the N-model and DW-model in g CH_2O m^{-2} (A) and % of dry weight (B) under the conditions of no water stress.

When plants are small, tissue is largely meristematic and respiratory losses are mainly due to growth respiration [Robson, 1982], so that even large differences in the maintenance respiration rate will have little effect on dry matter accumulation. As plant dry weight increases, maintenance respiration will become increasingly important. This can be seen from Figure 5 that showed R_d increased as plant dry matter increase although the respiration rate declined from 3.8 to 5.2% to less than 1%.

When the models incorporated water stress (Figure 6), the respiration rates were higher (Figure 7), but with a similar pattern to that without water stress (Figure 5). Water stress was considered to cause an increased ion concentration in cells and changes in metabolic activity of plants and turnover rate of some enzyme [Penning de Veries, 1975]. Kaul [1966] suggested that mild water deficits may increase stomatal opening thus lowering the diffusive resistance of stomata and may also stimulate metabolic activity.

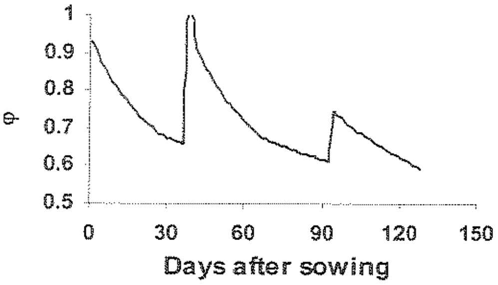

Figure 6. Simulated water stress based on CRES – Wheat model [Ritchie, 1985].

The simulation based on crops older than 70 DAS gave estimates of R_d of about 0.7 to 1.3% of dry weight (Figure 5 B; Figure 7B). This agreed well with the field measurements [Biscoe et al., 1975; Morgensen, 1977; Vos, 1981] and theoretical derivation. Penning de Vries [1975] derived theoretically maintenance respiration of 0.007-0.01 g g^{-1} dry weight. McCullough and Hunt [1989] used a constant value of 1% of dry weight for calculation of maintenance respiration for wheat. This value is considered as it was obtained from field gas exchange studies on barley [Biscoe et al., 1975; Morgensen, 1977] and the measurements of the post-anthesis growth of wheat plants [Vos, 1981].

However, both models presented in this paper showed that maintenance respiration rate was not constant. It varied between 0.6% and 5.4% for the N-model and 0.6% and 3.8% for the DW-model without water stress (Figure 5B) and between 0.9% and 5.5% for the N-model and 0.9% and 3.8% for DW-model with water stress (Figure 7B).

The additional value of the modelling is that the simulations provide an insight into the dynamics in

R_d with crop growth stages and the effect of environmental factors.

McCree [1988] pointed out that the use of a constant rate for maintenance respiration in the daily C balance equation was incorrect; considerable changes are often observed in both growth and maintenance respiration during the ontogeny [McCree, 1983]. Maintenance respiration was decreased by about a factor of four between panicle initiation and mature in sorghum plant [Stahl and McCree, 1988] and a factor of five between young and mature wheat [Puckridge and Ratkowsky, 1971]. The DW-model including temperature, water and crop age showed a similar range to these observations, while the N-model indicated a greater decrease in percentage R_d of DW with plant age.

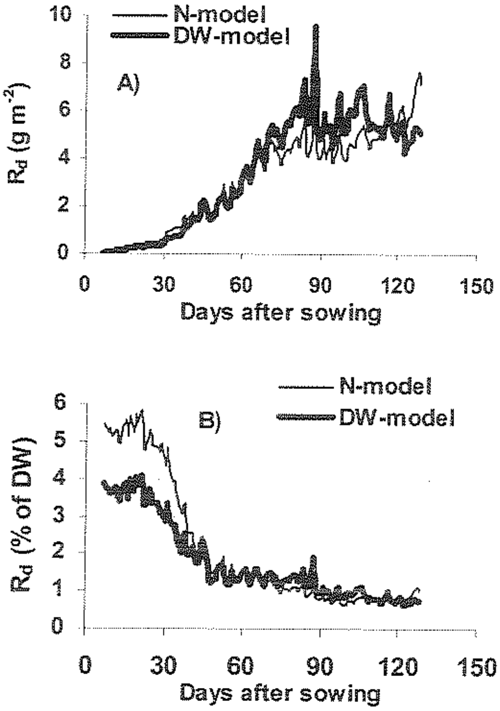

Figure 7. Simulated the rate of maintenance respiration by both the N-model and DW-model in g CH_2O m^{-2} (A) and % of dry weight (A) with the effect of water stress.

The work here highlights the practical difficulties in application of the McCree equation or a constant value of maintenance respiration rate in a crop simulation model. In particular, the model includes modules that deal with the effect of temperature and crop development and other environmental factors such as water and nutrients. Simulation studies [Hunt and Loomis, 1979; McCree, 1988] have demonstrated that crop yield can be very sensitivity to the values used for the maintenance respiration. We concluded that incorporating biotic and environmental factors to a maintenance respiration module are essential in developing crop growth models and can increase the accuracy of crop simulation models.

5. CONCLUSIONS

Maintenance respiration has great influence on wheat yield as dry matter accumulation and partitioning into the grain yield by the crop are closely related to assimilation of CO_2 and respiratory activity. To successfully simulate the biomass and crop yield in wheat, it was essential to include the effects of biotic and environmental factors in the maintenance respiration module. The DW-model showed a simulation is closer agreement with field observation than the N-model. This is because maintenance respiration is not solely contributed by protein turnover.

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