

Simulation of Maintenance Respiration in Wheat (*Triticum aestivum* L.)

^{1,2}D.L. Liu, ^{1,2,3}Y. Yang, ⁴J. Mo and ²B.J. Scott

¹NSW Department of Industry and Investment NSW, Primary Industries,
Wagga Wagga Agricultural Institute, PMB, Wagga Wagga, NSW 2650, Australia

²EH Graham Centre for Agricultural Innovation (An alliance between NSW Department of Primary
Industries and Charles Sturt University), Wagga Wagga, NSW 2650, Australia

³Key Laboratory of Agricultural Water Resources, Center for Agricultural Resources Research,
Institute of Genetics and Developmental Biology, CAS, Shijiazhuang, Hebei 050020, China

⁴Department of Primary Industries, Yanco Agricultural Institute,
PMB, Yanco, NSW 2703, Australia

Abstract: Respiration has a profound influence on crop yield because dry matter accumulation by a crop is closely related to assimilation of CO₂ 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 CO₂, 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 Q₁₀ concept for the N-content based model was used. The models were used to estimate seasonal maintenance respiration. The simulation results highlighted the practical difficulties in application of a constant value of maintenance respiration to a crop simulation model. It is concluded that the dry weight based model simulates maintenance respiration better than the N-content based model because maintenance respiration is not solely related to protein turnover.

Key words: Respiration model % Temperature effect % Water stress % Wheat % Q₁₀ % Thermal time % Ontogeny

INTRODUCTION

Explicitly modeling respiration costs is a key feature of mechanistic models of plant growth as respiration is an essential metabolic process in the growth and maintenance of all plant tissues and an important component for whole-plant and ecosystem carbon balances as well the global carbon cycle. Concern over global warming as a result of rising atmospheric concentration of carbon dioxide (CO₂) stimulated interest in the development of ecosystem models that have a detailed respiration component [1].

In a changing climate, rising atmospheric (CO₂) and increasing temperature may be considered as the two main factors affecting plant respiration [2-4]. However, the

response of plant respiration to elevated [CO₂] is subject to disputes. Many investigators believe plant respiration is reduced at high [CO₂] [5-7]. However, Gonzalez-Meler *et al.* [3] reviewed studies of plant respiration on elevated atmospheric [CO₂] and concluded that specific respiration rates are generally not reduced when plants are grown at elevated [CO₂]. Bunce [8] also testified that elevated [CO₂] had no effect on night-time respiration through an experiment of soybeans grown in field plots at the current ambient and elevated [CO₂] in open top chambers. In contrast, studies on the effects of temperature on plant respiration are more conclusive. Bunce [9] showed that low temperature reduced rates of respiration, while increased temperature increased rates of respiration. Bunce [10] concluded that short-term increases in

temperature early in the dark period led to exponential increases in rates of respiration. For rapidly growing plants, Frantz *et al.* [2] found that the whole-plant respiration was slightly sensitive to temperature and that the sensitivity does not change among the species tested, even after 20 days of treatment. This can be explained by the classical respiration theory, that is, the whole plant respiration R ($\text{g CH}_2\text{O mG}^2 \text{dG}^1$) can be separated into growth (R_g) and maintenance respirations (R_m) [11]. Growth respiration is proportional to the total assimilation (P) and maintenance respiration is proportional to dry mass (W). This gives:

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

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 materials. The rate of the metabolic process of conversion will obey the rule of temperature dependence. However, since it may be similar or close to that of photosynthesis rate, the k coefficient (the ratio of both rates) will be independent on changing temperature. The maintenance respiration rate is temperature dependent [11]. Because the maintenance respiration is proportional to accumulated dry matter, for a young and rapidly growing plant, the whole plant response to temperature is only slightly sensitive as found by Frantz *et al.* [2], who's results further support the theory outlined by Eq. (1).

Although the growth respiration is not temperature dependent, the growth respiration coefficient may vary. Amthor [5] reviewed a large body of literature and found that the coefficient k in Eq. (1) varied considerably between 0.12 and 0.45 with plant species. The value of $k = 0.20$ was reported for wheat [12] and white clover (*Trifolium repens* L.) [13].

This simplest framework often involves a combination of empiricism and mechanism [14]. The disadvantage of the growth-maintenance respiration paradigm is that it does not separate substrates from structure, implicitly assuming that maintenance respiration is a fixed cost, uncoupled to assimilation supply and consequently the use of fixed rate coefficients chosen from a range of measured values [15]. Hurley Pasture Model (HPM) [16] and Edinburgh Forest Model (EFM) [17, 18] are the first two models which separated C and N substrates from structure [15]. However it is less easy to estimate respiration associated with protein turnover, maintenance of cell ion concentrations and gradients and all forms of respiration involving the alternative pathway

and futile cycles [19]. Therefore, in this study we use the simplest framework to simulate maintenance respiration as the basis for incorporating detailed functions to model the response of maintenance respiration to various environmental factors. It is also reasoned that the simple model is highly flexible to be incorporated into system models that simulate crop production at the crop level, regional level or in relation to global warming.

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, which 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 [20]. The coefficient c varied with many biotic and environmental factors including temperatures, nitrogen status, water stress [21], salt stress [22] and different plant organs [23]. 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 including temperature, water stress, nitrogen content and plant ontogeny, 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.

Description of the Model

Modelling Maintenance Respiration Based on Biomass Accumulation:

A few studies were conducted to determine the rate of maintenance respiration (c) on dry weight basis in wheat [24, 25]. Factors affecting the rate of maintenance respiration include temperature, water stress and crop age. Thus, considering that a whole plant consists of k components organs, we can write

$$R_m = s(j)g(q) \sum_{i=1}^k R_i W_i \quad (2)$$

where R_m is the rate of maintenance respiration expressed in terms of carbohydrate units (CH_2O) per unit ground area ($\text{g mG}^2 \text{dG}^1$), W_i (g mG^2) is the plant dry matter in i th component, R_i ($\text{g gG}^1 \text{dG}^1$) is the daily maintenance respiration which is affected by temperature, $s(n)$ and $g(2)$ are dimensionless and respectively describe the effect of water stress and crop age on the maintenance respiration in wheat.

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, r_i , decreases. The r_i for the i th organ at temperature T is described by

$$r_i = I_i e^{g_i T} \quad T \leq T_o \quad (3a)$$

$$r_i = \frac{I_i e^{g_i T_o}}{1 + (T - T_o)/T_u} \quad T > T_o \quad (3b)$$

in units of $g \text{ CO}_2 \text{ gG}^{-1} \text{ sG}^{-1}$, where g is a constant with a unit of $g \text{ CO}_2 \text{ gG}^{-1} \text{ sG}^{-1}$ and $($ is a constant with a unit of per degree temperature. Figure 1 shows the maintenance respiration rate in wheat using the data of Stoy [26] and Mitchell *et al.* [27] to fit Eq. (3), from which $g = 5.9780 \text{ g CO}_2 \text{ gG}^{-1} \text{ sG}^{-1}$ and $(= 0.0848$ per $^\circ\text{C}$ for shoot and $g = 3.4300 \text{ g CO}_2 \text{ gG}^{-1} \text{ sG}^{-1}$ and $(= 0.0706$ per $^\circ\text{C}$ for ears were determined. It was assumed that for an optimum temperature $T_o = 28.0^\circ\text{C}$. T_u is a unit of temperature, i.e. 1°C . From now on, we omit the T_u from the equation by writing T and T_o as a dimensionless.

The daily maintenance respiration can be defined by

$$R_i = s \int_0^D r_i dt \quad (4)$$

in carbohydrate units (CH_2O) per unit ground area ($g \text{ mG}^{-2} \text{ dG}^{-1}$), $D = 86400 \text{ s}$ and is the length of a day in seconds. $F = 0.68$, 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 second 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 seconds can be extrapolated assuming a linear approximation between T_{max} and T_{min} [28]. Solution of Eq (4) gives the daily maintenance respiration as:

$$R_i = \Theta (e^{g_i T_{max}} - e^{g_i T_{min}}) \quad T_{min} < T_{max} \leq T_o \quad (5a)$$

$$R_i = \Theta \left[e^{g_i T_o} - e^{g_i T_{min}} + I_i g_i e^{g_i T_o} \ln(1 + T_{max} - T_o) \right] \quad T_{min} < T_o \leq T_{max} \quad (5b)$$

$$R_i = \Theta g_i e^{g_i T_o} \ln \left[\frac{1 + T_{max} - T_o}{1 + T_{min} - T_o} \right] \quad T_o < T_{min} \leq T_{max} \quad (5c)$$

in carbohydrate units (CH_2O) per unit ground area ($g \text{ mG}^{-2} \text{ dG}^{-1}$), where

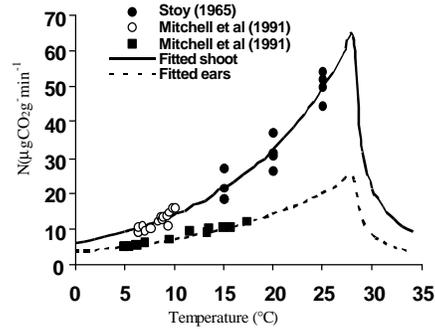


Fig. 1: Compared the observed and fitted relationships between maintenance respiration rate and temperature for shoot and ears of wheat.

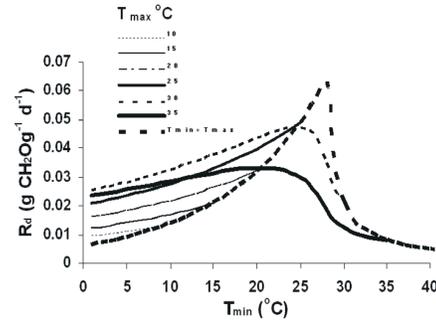


Fig. 2: Daily rate of maintenance respiration (R_d) calculated for shoots by Eq (5a, b, c) as a function of minimum temperature (x axis) and maximum temperatures (see legend).

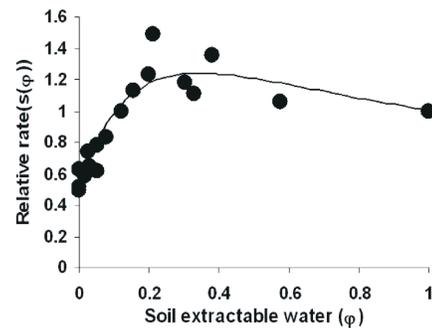


Fig. 3: The relationship between normalized respiration rate and soil extractable water, as fitted by the relationship of Eq (6).

$$\Theta = \frac{D I_i s}{g_i (T_{max} - T_{min})}$$

Figure 2 illustrates the daily rate of maintenance respiration as functions of temperature.

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 [29, 30, 31]. 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 [21]. The effect of water stress can be described by

$$s(j) = z_{\min} + \frac{aj}{(1 + bj)^c} \quad (6)$$

where n is a relative factor of soil extractable water ($n = 0$ for wilting soil water content and $n = 1$ for field capacity), z_{\min} is the value of $s(n)$ when $n = 0$, a , b and c are constants. $z_{\min} = 0.49$, $a = 7.48$, $b = 1.63$ and $c = 2.78$ were determined by using the data of Kaul [31] (Fig. 3).

Changes During Ontogeny: Stoy [26] found that the maintenance respiration in wheat decreased with plant age. There are many reports in other crops. For example, McCree [32] reported that maintenance coefficient of grain sorghum during the vegetative growth decreased from about 1.6 mg CO₂ g⁻¹h⁻¹ for young plants to about 1.2 mg CO₂ g⁻¹h⁻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 [32]. Gent and Kiyomoto [33] showed canopy maintenance respiration per unit of dry weight declined with ontogeny, while Gent and Kiyomoto [34] 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

$$g(q) = \begin{cases} 1 & q \leq q_s \\ \frac{1}{1 + \frac{(q - q_s)}{(q_{0.5} - q_s)}} & q > q_s \end{cases} \quad (7)$$

where 2 is the thermal time (°Cd) above a base temperature of 5°C accumulated from emergence, 2_s is the thermal time at which maintenance respiration starts to decrease, $2_{0.5}$ is thermal time when the maintenance respiration rate is half of its maximum, $g(2) = 0.5$. It is assumed that the maintenance respiration is not affected by crop aging until $2 > 2_s$. By analysis of the data of Puckridge and Ratkowsky [35] the values for parameters $2_{0.5}$ and 2_s were determined to be 460°Cd and 219°Cd, respectively (Fig. 4).

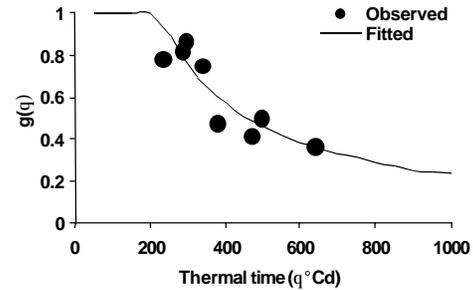


Fig. 4: Relationship between relative maintenance respiration $g(2)$ and thermal time, q in wheat. The observed data is extracted from Puckridge and Ratkowsky [35].

Maintenance Respiration Based on Nitrogen Accumulation: It was observed that maintenance respiration was correlated with plant protein content [32, 36, 37]. Since maintenance expenditure is largely attributable to protein turnover [20], an alternative approach to modelling maintenance respiration may be based on nitrogen content of the crop. Thus, the maintenance respiration may be calculated by

$$R_m = s(j) \sum_{i=1}^k r_i N_i v_i(T) \quad (8)$$

where k is number of plant organs, $s(n)$ is effect of water stress as defined in Eq (6), D_i is the coefficient (gCO₂ (g N)G⁻¹), N is nitrogen content in unit of ground area (g N m²), $v_i(T)$ is the temperature effect. According to Choudhury [38], the value of D_i at $T = 20$ °C for above ground green components and roots of wheat was 0.5343 and 1.0686 g CO₂ (gN)G⁻¹, respectively. $v_i(T)$ is calculated by Q₁₀ approach as:

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

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.* [39]. The weather data was obtained from the Metaccess database [40]. Daily data were used for the simulation. The emergence of the crop was estimated to occur 7 day after sowing.

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) (Fig. 5B). In the early stage, the N-model simulates values of main maintenance cost of about 40 % higher than the DW-model. However, the difference in total R_d is small (Fig. 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.

When plants are small, tissue is largely meristematic and respiratory losses are mainly due to growth respiration [41], 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 Fig. 5 which 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 [42] (Fig. 6), the respiration rates were higher (Fig. 7), but with a similar pattern to that without water stress (Fig. 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 [20]. Kaul [31] suggested that mild water deficits may increase stomatal opening thus lowering the diffusive resistance of stomata and may also stimulate metabolic activity.

The simulation based on crops older than 70 DAS gave estimates of R_d of about 0.7 to 1.3% of dry weight (Fig. 5B; Fig. 7B). This agreed well with the field measurements [43, 44, 45] and theoretical derivation. Penning de Vries [20] derived theoretically maintenance respiration of 0.007-0.01 g g⁻¹ dry weight. McCullough and Hunt [25] used a constant value of 1% of dry weight for calculation of maintenance respiration for wheat. This value was used as it was obtained from field gas exchange studies on barley [43, 44] and the measurements of the post-anthesis growth of wheat plants [45].

However, both models presented in this paper predicted 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 (Fig. 5B) and between 0.9% and 5.5% for the N-model and 0.9% and 3.8% for DW-model with water stress (Fig. 7B).

The simulation models provide an insight into the dynamics in R_d with crop growth stages and the effect of environmental factors. McCree [46] pointed out that the use of a constant rate for maintenance respiration in the daily C balance equation was incorrect, with considerable variations observed in both growth and maintenance

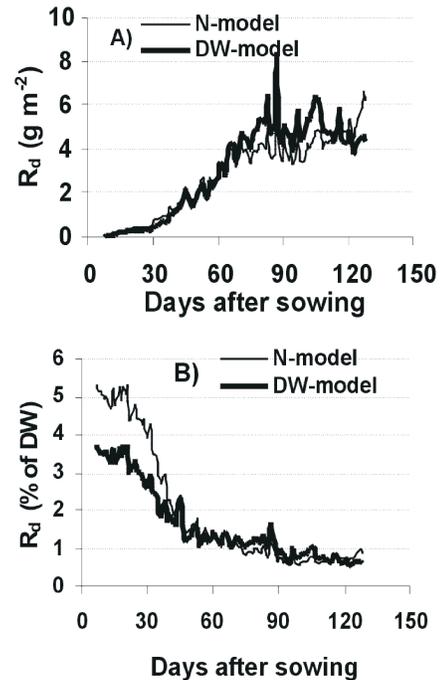


Fig. 5: The simulated rate of maintenance respiration by both the N-model and DW-model in g CH₂O m⁻² (A) and % of dry weight (B) under the conditions of no water stress.

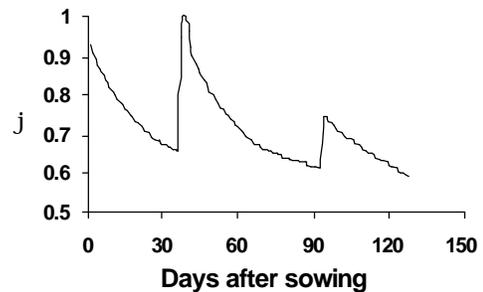


Fig. 6: Simulated water stress based on CRES -Wheat model [42].

respiration during the ontogeny [32]. Maintenance respiration was decreased by about a factor of four between panicle initiation and mature in sorghum plant [37] and a factor of five between young and mature wheat [35]. 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.

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

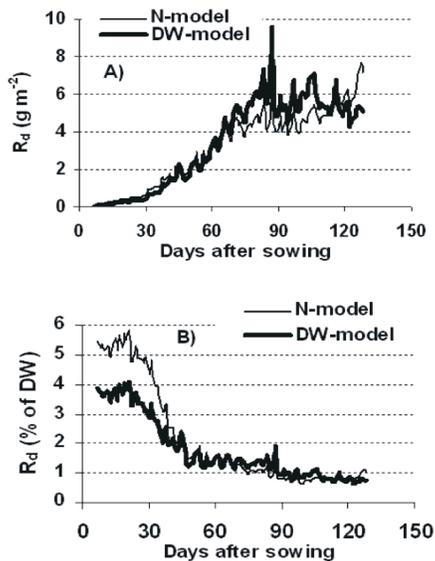


Fig. 7: Simulated the rate of maintenance respiration by both the N-model and DW-model in $\text{g CH}_2\text{O mG}^2$ (A) and % of dry weight (A) with the effect of water stress.

environmental factors such as water and nutrients. Simulation studies have demonstrated that crop yield can be very sensitive to the values used for the maintenance respiration [46, 47]. We conclude that incorporating biotic and environmental factors to a maintenance respiration module are essential in developing crop growth models and can improve the accuracy of crop simulation models.

CONCLUSIONS

Maintenance respiration has great influence on wheat yield as dry matter accumulation and ultimate 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 simulates field observations better than the N-model. This is because maintenance respiration is not solely determined by protein turnover.

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