



A Model of the Coupling between Respiration, Active Processes and Passive Transport

RODERICK C. DEWAR*

Unité de Bioclimatologie, INRA Centre de Bordeaux, BP81, 33883 Villenave d'Ornon, France

Received: 17 January 2000 Returned for revision: 10 March 2000 Accepted: 8 April 2000

A biochemically-aggregated model is introduced which captures the essential features of the coupling between respiration and active (energy-requiring) plant processes. Each active process is characterized as the conversion of ATP and NADPH (represented by X^*) and a substrate (S) to ADP and NADP (represented by X) and a product (P) (e.g. for protein synthesis, S = amino-acids, P = protein). For each process, respiration generates X^* and CO_2 from glucose (C) and X. Respiration and active processes are thus coupled through the turnover of ATP and NADPH, with C and S representing, respectively, the main energetic and material substrates of the overall reaction $C + S \rightarrow \text{CO}_2 + P$. The model assumes mass action kinetics for the reaction rates, and incorporates passive transport of C and S to the reaction sites from an external region (e.g. phloem) with substrate concentrations C_e and S_e . The behaviour of this coupled respiration—active process—passive transport model is explored analytically. The main results are as follows: (1) In general, the respiration rate coupled to a given active process $S \rightarrow P$ has a non-rectangular hyperbolic dependence on C_e and S_e . (2) Because glucose provides both the energetic and material substrates for structural growth (cellulose synthesis), the associated respiration rate is proportional to C_e . (3) When the passive transport of C and/or S for the process $S \rightarrow P$ becomes limiting, the associated respiration rate reduces to a 'Blackmann response' which is either entirely C-limited or entirely S-limited, depending on the relative availability of C_e and S_e . (4) These predictions are used to interpret empirically-derived growth and maintenance respiration coefficients, as well as widely-reported observations concerning the respiration/photosynthesis ratio and the response of respiration to carbohydrate concentration. (5) It is concluded that the model provides a simple, realistic, physiologically-based representation of the components of respiration, which can be used in plant growth models that separate substrates from structure.

© 2000 Annals of Botany Company

Key words: Coupling, growth, maintenance, model, process, respiration, transport.

INTRODUCTION

Through the oxidation of glucose (C) to CO_2 , respiration generates energy (ATP) and reducing power (NADPH) from ADP and NADP, which are then used to drive active plant processes. In general, we may characterize a given active process as the energy-requiring conversion of a material substrate (S) to a product (P) (Table 1 gives some examples). During the reaction $S \rightarrow P$, ADP and NADP are regenerated from ATP and NADPH. In this way, respiration and active processes are coupled through the turnover of ATP and NADPH (Fig. 1). C and S represent, respectively, the main energetic and material substrates of the overall reaction $C + S \rightarrow \text{CO}_2 + P$.

Over the last 30 years, modelling of respiration has been dominated by the growth-maintenance paradigm, according to which the active processes supported by respiration can be divided into two functionally distinct components called 'growth' and 'maintenance' (McCree, 1970; Thornley, 1970; Amthor, 1994, 2000). Biochemical pathway analysis, pioneered by Penning de Vries (1972, 1974, 1975a,b) and Penning de Vries *et al.* (1974), led to significant advances in the quantitative understanding of the link between respiration, growth and maintenance. However, a feature of that analysis is that it determines only the stoichiometry of the coupling between respiration and

active processes, and not their absolute rates. This situation is understandable, given the complexity of the underlying biochemistry and corresponding uncertainties about the metabolic control of respiration. As a result, however, most plant growth models are unbalanced in that respiration is

TABLE 1. Some examples of active processes, their material substrates and products [in the notation of eqn (1) and Fig. 1]

Process (subscript label i)	Material substrate (S)	Product (P)
Protein synthesis (pr)	Amino-acids	Protein
Amino-acid synthesis (aa)	Ammonia, glucose*	Amino-acids
Structural dry matter synthesis (x)	Glucose	Cellulose
Nitrate reduction (nr)	Nitrate	Ammonia
Nitrogen fixation (nf)	Dinitrogen	Ammonia
Nitrogen uptake (nu)	Root surface NH_3 or HNO_3	Plant NH_3 or HNO_3
Ion membrane transport (it)	External ion	Internal ion
Phloem loading (pl)	Non-vascular sucrose	Phloem sucrose

* The present formulation of the model deals with a single material substrate for each process (S), but in principle this could be generalized to two or more material substrates. For amino-acid synthesis, the single-substrate formulation (with S = ammonia) may be adequate if glucose limitation occurs mainly through ATP and NADPH production [eqn (1A)] rather than through the supply of C skeletons [eqn (1B)].

* Fax +33(0)5 56 84 31 35, e-mail dewar@bordeaux.inra.fr

represented much more empirically than photosynthesis (Cannell and Thornley, 2000; Thornley and Cannell, 2000).

In order to restore some balance, what would be useful, but is currently lacking, is a physiologically-based model for the dependence of the rates of respiration and active processes on the main limiting substrates C and S of each process, as well as on other regulatory factors such as transport of substrates to the reaction sites. In order to be of practical use in plant growth models, such a model should capture the essential features of the coupling between respiration and active processes, without attempting to represent the underlying biochemistry in great detail. The separation of substrates from structure provides an appropriate level of detail for modelling the components of respiration (Cannell and Thornley, 2000; Thornley and Cannell, 2000).

The specific aims of this study were: (1) to develop a physiologically-based model of the coupling between respiration and active processes for use in plant growth models; and (2) to compare the analytical predictions of the model with various empirical results for respiration that have been widely reported in the literature. The aim here was not to fit the model to particular data sets, but rather to evaluate semi-quantitatively the ability of the model to explain a number of general observations concerning respiration.

The following section describes the model, which is based on a biochemically-aggregated reaction scheme for the turnover of ATP and NADPH at the reaction sites. The model also incorporates passive transport of C and S to the reaction sites from an external region. Simple analytical expressions are derived for the components of respiration as functions of the external substrate C and S concentrations. The predictions are compared with empirical results concerning growth and maintenance respiration, the respiration/photosynthesis ratio, and the response of respiration rate to carbohydrate concentration. The overall approach and future development of the model are discussed.

MODEL ASSUMPTIONS AND ANALYTIC PREDICTIONS

General reaction scheme for the coupling between respiration and an active process

Consider the following general reaction scheme for the coupling between respiration and an active process $S \rightarrow P$ at the reaction sites of the process:



where C denotes glucose, X denotes ADP and NADP, and X^* denotes ATP and NADPH (Fig. 1). Equation (1A) represents respiration (oxidative phosphorylation) with co-substrates C and X, and eqn (1B) represents the active process with co-substrates S and X^* . C and S represent, respectively, the energetic and material substrates of the overall reaction $C + S \rightarrow CO_2 + P$. In the case of protein synthesis, for example, S denotes amino-acids and P

denotes protein. The model is presented here in general form, and is considered to be applicable to each of the processes listed in Table 1, with S and P denoting the appropriate material substrate and product.

Mass action kinetics are assumed. Denoting the rate constants for the two reactions by k_c and k_s , respectively, the rate of formation of X^* is (see Appendix for symbol definitions and units):

$$\frac{dX^*}{dt} = k_c CX - k_s SX^* \quad (2)$$

where C and S are the concentrations of C and S at the reaction site. Here it is assumed that the pools of X and X^* are specific to each process, being localized at the appropriate reaction sites. This assumption is re-examined in the Discussion.

It is assumed that $X_0 = X + X^*$ (the total concentration of species X at the reaction sites) is a constant, and that X^* is in a dynamic steady state (i.e. $dX^*/dt = 0$). The steady-state value of X^* is then [from eqn (2)]

$$X^* = \frac{k_c CX_0}{k_c C + k_s S} \quad (3)$$

and the steady-state turnover rate of X is

$$v = k_s SX^* = \frac{k_c C k_s S X_0}{k_c C + k_s S} = \frac{\alpha_c C \alpha_s S}{\alpha_c C + \alpha_s S} \quad (4)$$

where in the final expression the rescaled reaction rate constants $\alpha_c = k_c X_0$ and $\alpha_s = k_s X_0$ are introduced. Equation (4) predicts that the steady-state value of v is co-limited by the substrate C and S concentrations at the reaction sites, the dependence being described by a rectangular hyperbola. The corresponding respiration rate (R), utilization rate of substrate S (U), and production rate of product P (G) in the steady state of X^* are:

$$R = \lambda_c v \quad (5A)$$

$$U = \lambda_s v \quad (5B)$$

$$G = \lambda_p v \quad (5C)$$

where λ_c , λ_s and λ_p are coefficients describing the stoichiometry of these fluxes relative to the turnover of X (see Appendix).

C and S substrate transport

It is assumed that the substrates C and S for process $S \rightarrow P$ are passively transported to the reaction sites from an external region with substrate concentrations C_e and S_e , respectively (Fig. 1). Let the transport rates of C and S be

$$T_c = g_c (C_e - C) \quad (6A)$$

$$T_s = g_s (S_e - S) \quad (6B)$$

where g_c and g_s are conductances. In the case of protein synthesis, C_e and S_e might be identified with the glucose and amino-acid concentrations in the phloem, with g_c and g_s representing conductances for the transport of glucose

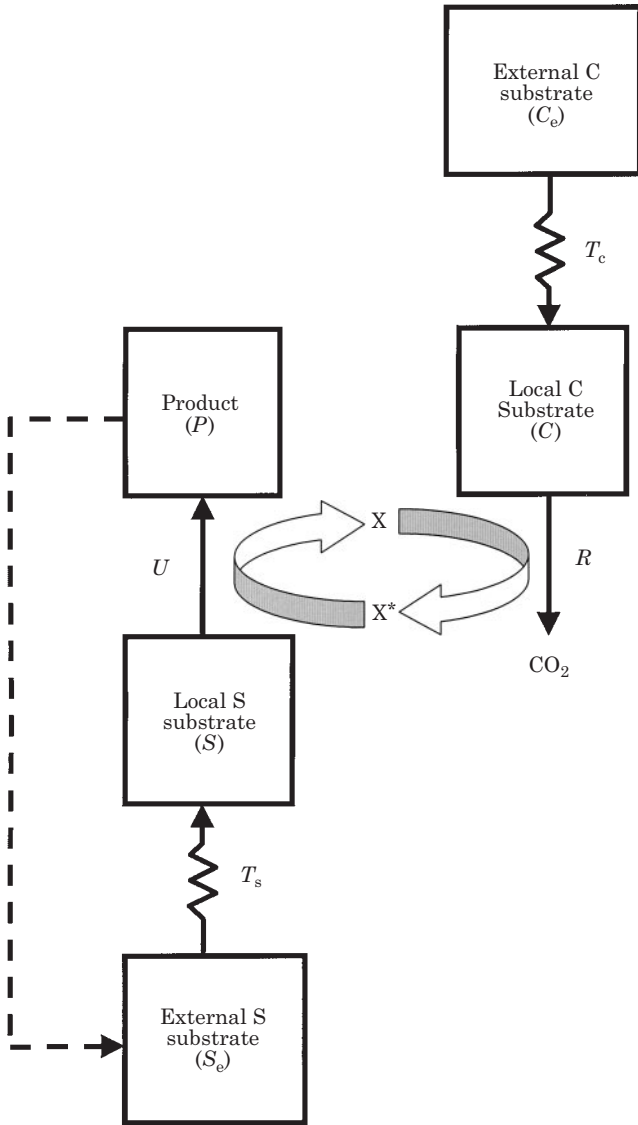


FIG. 1. Schematic representation of the coupling between respiration ($C + X \rightarrow X^* + CO_2$), an active process ($S + X^* \rightarrow X + P$), and passive transport (external site \rightarrow reaction site). 'Local' indicates the reaction site. C (glucose) and S denote, respectively, the energetic and material substrates for the overall reaction $C + S \rightarrow CO_2 + P$. X denotes ADP and NADP, X^* denotes ATP and NADPH. R , U , T_c and T_s denote, respectively, the rates of respiration, S utilization, C transport and S transport. Some examples to which the scheme is applicable are listed in Table 1. The broken line indicates the possibility of conversion of P back to S (e.g. protein turnover to amino-acids).

and amino-acids between the phloem and the sites of protein synthesis. In the case of plant N uptake, the external region supplying C (phloem) is different from that supplying S (bulk soil), and g_c and g_s are the corresponding transport conductances for glucose (phloem \rightarrow root surface) and soil mineral N (bulk soil \rightarrow root surface).

When the substrates C and S at the reaction sites are in a steady state, C transport balances C utilization ($T_c = R$),

and S transport balances S utilization ($T_s = U$). It is then useful to re-express the turnover rate of X [eqn (4)] in terms of C_e and S_e rather than C and S . Using the steady-state substrate flux balance and eqns (4), (5) and (6) to eliminate C and S , it is straightforward to show that the turnover rate of X (v) has the following non-rectangular hyperbolic dependence on C_e and S_e :

$$(\theta_c + \theta_s - \theta_c \theta_s) v^2 - (\beta_c C_e + \beta_s S_e) v + \beta_c C_e \beta_s S_e = 0 \quad (7A)$$

where the constants

$$\theta_c = \frac{\alpha_c \lambda_c}{g_c + \alpha_c \lambda_c} \quad \theta_s = \frac{\alpha_s \lambda_s}{g_s + \alpha_s \lambda_s} \quad (7B)$$

and

$$\beta_c = \frac{\alpha_c g_c}{g_c + \alpha_c \lambda_c} \quad \beta_s = \frac{\alpha_s g_s}{g_s + \alpha_s \lambda_s} \quad (7C)$$

depend on the transport conductances (g_c and g_s) and reaction rate constants (α_c and α_s). The fluxes R , U and G are then given by eqn (5A–C), in which v is the appropriate (quadratic) solution to eqn (7A). Note that in the limit where both conductances are large (specifically, $g_c \gg \alpha_c \lambda_c$ and $g_s \gg \alpha_s \lambda_s$, so that both θ_c and $\theta_s \rightarrow 0$, $\beta_c \rightarrow \alpha_c$, $\beta_s \rightarrow \alpha_s$), transport becomes non-limiting and eqn (7A) reduces to the rectangular hyperbola [eqn (4)] as the external and reaction site concentrations equalize.

Structural dry matter synthesis is C-limited

Equation (7A) implies that, in general, the steady-state turnover rate of X for a given active process is co-limited by the external substrate concentrations C_e and S_e , and hence so is the rate of that process [eqn (5C)]. In the case of structural dry matter (cellulose) synthesis, the situation simplifies because glucose provides both the energetic and material substrates ($C_e = S_e$). Equation (7A) then implies that the corresponding turnover rate of X is directly proportional to C_e . Introducing the subscript x for structural dry matter synthesis (see Table 1), we have

$$v_x = a_x C_e \quad (8A)$$

where the constant a_x is given by the appropriate solution of the quadratic equation

$$(\theta_{c,x} + \theta_{s,x} - \theta_{c,x} \theta_{s,x}) a_x^2 - (\beta_{c,x} + \beta_{s,x}) a_x + \beta_{c,x} \beta_{s,x} = 0 \quad (8B)$$

The rate of structural dry matter synthesis (G_x) is then also proportional to C_e [from eqns (5C) and (8A)]:

$$G_x = \lambda_{p,x} v_x = \lambda_{p,x} a_x C_e \quad (8C)$$

In the slow transport limit, respiration is either C-limited or S-limited

The non-rectangular hyperbola [eqn (7A)] describing co-limitation by C_e and S_e also simplifies in the limit where the transport of C or S substrate is a slow process. For example, if the conductance, g_c , for C substrate transport is much smaller than the reaction rate constant for respiration (specifically, $g_c \ll \alpha_c \lambda_c$, so that $\theta_c \rightarrow 1$ and $\beta_c \rightarrow g_c/\lambda_c$), then eqn (7A) reduces to:

$$v = \min\left(\frac{g_c}{\lambda_c} C_e, \beta_s S_e\right) \quad (9A)$$

where min denotes the minimum value. In this case, respiration is limited either entirely by C substrate (through transport) or entirely by S substrate (through a combination of transport and conversion of S to P, as quantified by parameter β_s). Likewise, if the conductance g_s for S substrate transport is much smaller than the reaction rate constant for conversion of S to P (specifically, $g_s \ll \alpha_s \lambda_s$, so that $\theta_s \rightarrow 1$ and $\beta_s \rightarrow g_s/\lambda_s$), then eqn (7A) reduces to:

$$v = \min\left(\beta_c C_e, \frac{g_s}{\lambda_s} S_e\right) \quad (9B)$$

Again, respiration is limited either entirely by C substrate (this time though transport and glucose oxidation, as quantified by parameter β_c) or entirely by S substrate (through transport alone). Finally, if C and S substrate transport are both limiting (as might be the case, for example, if C and S share the same transport pathway), then:

$$v = \min\left(\frac{g_c}{\lambda_c} C_e, \frac{g_s}{\lambda_s} S_e\right) \quad (9C)$$

The conclusion here is that whenever the passive transport of C and/or S is a slow process relative to the corresponding reaction rate (respectively, respiration or S \rightarrow P conversion), the respiration rate reduces to a 'Blackmann response' which is either entirely C-limited or entirely S-limited, depending on the relative availability of external C and S substrates.

MODEL COMPARISON WITH EMPIRICAL OBSERVATIONS

In this section, the analytical predictions of the model derived above are compared with various empirical results for respiration that have been widely reported in the literature. The aim here is not to fit the model to particular data sets, but rather to evaluate the ability of the model to explain a number of general observations concerning respiration.

Response of respiration to carbohydrate concentration

Experimental studies have shown that for many species, plant respiration rate is positively correlated with carbohydrate concentration, the relationship frequently being

asymptotic (Cunningham and Syvertsen, 1997; Moser *et al.*, 1982; Farrar, 1985). This observation is qualitatively consistent with the non-rectangular hyperbolic response of the components of respiration to C_e predicted here by eqns (5A) and (7A). The correlation between respiration and carbohydrate concentration is found to be particularly strong in growing tissue (Ryle *et al.*, 1976; Penning de Vries *et al.*, 1979). This observation is consistent with the model prediction that structural growth is directly proportional to C_e [eqn (8C)]. Moreover, if C_e were depleted by structural growth then other processes would become more C-limited, thus enhancing the correlation between total respiration and carbohydrate concentration in growing tissue, a mechanism that would also explain the lack of such a correlation found in mature tissues or organs (Coggeshall and Hodges, 1980; Farrar, 1985).

The physiological interpretation of apparent growth and maintenance respiration

An approximately linear relationship is often found between whole-system respiration (R_{sys}) and structural growth rate (G_x) (see the many references cited by Amthor, 1994) which may be written

$$R_{sys} = g_R G_x + m_R \quad (10)$$

The empirical coefficients g_R and m_R are often interpreted as being associated with the underlying processes of plant growth and maintenance (McCree, 1970; Thornley, 1970; Amthor, 1994). This empirical relationship may be interpreted in terms of the present model as follows.

In a given tissue or organ, C_e , the external (e.g. phloem) glucose pool, may be the common energy source for several active processes, including structural dry matter (cellulose) synthesis. In the previous section it was shown that G_x , the rate of cellulose synthesis, is directly proportional to C_e [eqn (8C)]. For other processes, it was shown that the dependence of respiration rate on C_e and S_e reduces to a Blackmann response (i.e. either entirely C-limited or S-limited) in the slow transport limit [eqn (9A–C)]. It follows that for those processes that are entirely C-limited, the associated respiration rate will be linearly correlated with G_x .

For example, if a certain process (labelled by subscript i) is C-limited as in eqn (9A) or (9C), then the associated respiration rate is [from eqns (5A), (8C), and either (9A) or (9C)]:

$$R_i = \lambda_c v_i = g_{c,i} C_e = \frac{g_{c,i}}{\lambda_{p,x} a_x} G_x \quad (11A)$$

and if process i is C-limited as in eqn (9B), then the respiration rate is

$$R_i = \frac{\lambda_c \beta_{c,i}}{\lambda_{p,x} a_x} G_x \quad (11B)$$

Respiration associated with structural dry matter synthesis itself can be written [from eqns (5A) and (5C)] as:

$$R_x = \frac{\lambda_c}{\lambda_{p,x}} G_x \quad (11C)$$

The sum of these C-limited processes will, therefore, give rise to the apparent growth respiration term $g_R G_x$ in eqn (10).

In contrast, for a process i that is entirely limited by material substrate ($S_{e,i}$), as in the S-limited branches of eqn (9A–C), the associated respiration rate is given [from eqns (5A) and (9A)] by:

$$R_i = \lambda_c \beta_{s,i} S_{e,i} \quad (12A)$$

or [from eqns (5A) and either (9B) or (9C)]:

$$R_i = \frac{\lambda_c g_{s,i}}{\lambda_{s,i}} S_{e,i} \quad (12B)$$

For each such process, the associated respiration rate is directly proportional to the external substrate S concentration ($S_{e,i}$). The sum of these S-limited processes will give rise to the apparent maintenance coefficient m_R in eqn (10), in which the contribution from each process is proportional to the concentration of the corresponding material substrate.

If the slow transport approximation applies to the principal active processes contributing to whole-system respiration (and this, of course, remains to be established), then the model suggests a simple physiological interpretation of the apparent growth and maintenance components of respiration estimated by fitting eqn (10) to experimental data. According to this interpretation, apparent growth respiration is associated with C-limited processes (i.e. processes limited mainly by energy), and apparent maintenance respiration is associated with S-limited processes (i.e. processes limited mainly by material substrate).

More generally, eqn (7A) predicts that processes may be co-limited by C_e and S_e , in which case their associated respiration rate would be a hyperbolic function of G_x and S_e . In principle, therefore, the non-rectangular hyperbola allows for a continuous spectrum of possible relationships between R , G_x and S_e for each process, of which eqns (11) and (12) are limiting cases. This point is illustrated in Fig. 2. Nonetheless, the experimental fact remains that the linear relationship of eqn (10) appears to apply reasonably well to a large body of data on growth and respiration (Amthor, 1994). This suggests that the simple interpretation given above, based on the slow transport approximation of the model, is worthy of further consideration.

Note that respiration can also be entirely C-limited or S-limited, independent of the slow transport approximation, if the external availability of either C or S itself becomes limiting, as follows directly from eqn (7A) in the limit $C_e \rightarrow 0$ with S_e fixed ($v \rightarrow \beta_c C_e$) or $S_e \rightarrow 0$ with C_e fixed ($v \rightarrow \beta_s S_e$).

Correlation between m_R and tissue nitrogen concentration

It is often found experimentally that m_R is linearly correlated with tissue nitrogen (N) concentration (e.g. Ryan, 1991, 1995; Wullschlegel *et al.*, 1992; Maier *et al.*, 1998). This observation can be explained by the model if protein synthesis is mainly S-limited (i.e. amino-acid limited), so that the associated respiration rate (R_{pr}) contributes to m_R rather than to g_R . Specifically, we have $R_{pr} \propto A_e$, where A_e is the external (e.g. phloem) amino-acid concentration. Also, if protein synthesis is in dynamic equilibrium with protein turnover (Fig. 1), then we have $R_{pr} \propto$ protein synthesis = protein turnover $\propto P$, where P is protein concentration (assuming first-order turnover kinetics). It follows that $P \propto A_e$ in dynamic equilibrium, and hence that $R_{pr} \propto A_e + P$. Therefore, R_{pr} is linearly correlated with total (free + protein) amino-acid concentration. If R_{pr} is a significant contribution to m_R , then it follows that m_R will be strongly correlated with tissue N concentration.

Approximate constancy of the respiration/photosynthesis ratio

In the limiting case where all principal active processes are C-limited, m_R would be zero. This limiting case has been modelled previously (Dewar *et al.*, 1998, 1999) and leads to a possible interpretation of experiments (Heilman *et al.*, 1977; Ruget *et al.*, 1981; André *et al.*, 1982; Gifford, 1994, 1995) in which the ratio of whole-plant respiration to gross photosynthesis was found to be relatively constant, independent of plant mass (equivalent to $m_R \approx 0$).

Simulations of the respiration/photosynthesis ratio using the Hurley Pasture and Edinburgh Forest models (Thornley and Cannell, 2000) show that, even when active processes are not entirely C-limited, partial dependence on C maintains the respiration/photosynthesis ratio within the narrow range 0.35–0.45, depending on time of season, growth stage and other factors. Therefore, all major active processes need not be entirely C-limited in order to explain the observed range of the respiration/photosynthesis ratio.

The non-rectangular hyperbolic response of respiration to C and S predicted by the present model ensures that all active processes eventually depend on C substrate concentration as the available energy is reduced. Therefore, the respiration/photosynthesis ratio will remain relatively stable, as observed.

DISCUSSION

Modelling respiration—the need for a substrate-level approach

The main motivation for developing the present model has been the need for a simple, physiologically-based representation of the components of respiration for use in plant and ecosystem models. Recently, Cannell and Thornley reviewed various approaches to modelling plant respiration (Cannell and Thornley, 2000; Thornley and Cannell, 2000). One of their recommendations was to separate C substrate from structure so that the C substrate dependence of the components of respiration can be represented. In particular,

Thornley and Cannell (2000) highlighted the problem of treating maintenance respiration as a fixed cost unrelated to C substrate supply, and advocated the use of empirical C-dependent maintenance rate coefficients, as in the Hurley Pasture Model (HPM: Thornley and Verberne, 1989) and the Edinburgh Forest Model (EFM: Thornley, 1991; Thornley and Cannell, 1996).

The present model follows the above recommendation by linking respiration to the availability of energetic and material substrates, but goes one mechanistic step further by deriving this link from a simplified description of the coupling between respiration and active processes through ATP and NADPH turnover (Fig. 1). This approach avoids the use of maintenance respiration altogether. The model encapsulates the view that respiration is co-limited by the supply of C substrates ('push' limited) and by the supply of ADP and NADP [eqn (1A)], the latter being determined by the demand for ATP and NADPH from active processes ('pull' limited; Amthor, 1994). In the model, the demand for ATP and NADPH is regulated by the supply of material substrate S [eqn (1B)]. The model could be implemented within the HPM, the EFM or any other model that separates substrates from structure (e.g. Dewar *et al.*, 1998, 1999).

Another motivation for developing the present model was to restore some balance between the representation of respiration and photosynthesis in plant growth models. Thornley and Johnson (1990, Chapter 9) derived a non-rectangular hyperbola for the response of gross photosynthesis of leaves to irradiance and ambient CO₂ concentration. They based their derivation on a similarly simplified picture of ATP and NADPH turnover during the light and dark reactions of photosynthesis (respectively, photons + X → X* and CO₂ + X* → X + C). The derivation here of a non-rectangular hyperbola for the response of respiration to the external substrate C and S concentrations is analogous to their approach, and is based on the same level of biochemical aggregation. The non-rectangular hyperbola, therefore, provides a simple, versatile model of both photosynthesis and respiration whose parameters may be interpreted physiologically.

Ambiguity in the interpretation of growth and maintenance respiration

In the slow transport limit, the non-rectangular hyperbolic model of respiration produces the Blackmann response of respiration to C and S [eqn (9)]. This result leads to a possible physiological interpretation of empirically-derived growth and maintenance respiration, according to which apparent growth respiration is associated with C-limited processes [i.e. processes limited mainly by energy, eqn (11)] and apparent maintenance respiration with S-limited processes [i.e. processes limited mainly by material substrate, eqn (12)].

Although the present model may thus provide some physiological insights into apparent growth and maintenance respiration, at the same time it suggests that the interpretation of eqn (10) remains potentially problematic. For example, a given process will switch its apparent

contribution to respiration from maintenance to growth if it changes dynamically from being S-limited to C-limited as a result of dynamic changes in the external availability of C and S (Fig. 2). Thus, even if the slow transport approximation applies, leading to a simple Blackmann response for respiration in relation to C and S, the interpretation of g_R and m_R in eqn (10) in terms of individual active processes may be ambiguous.

In particular, the model questions the notion that processes whose function is plant maintenance always contribute to m_R . For example, the model predicts that protein synthesis eventually becomes C-limited as the availability of energy is reduced relative to that of amino-acids. In that case, the associated respiration rate R_{pr} would contribute to g_R rather than to m_R . Thus, while the re-synthesis of

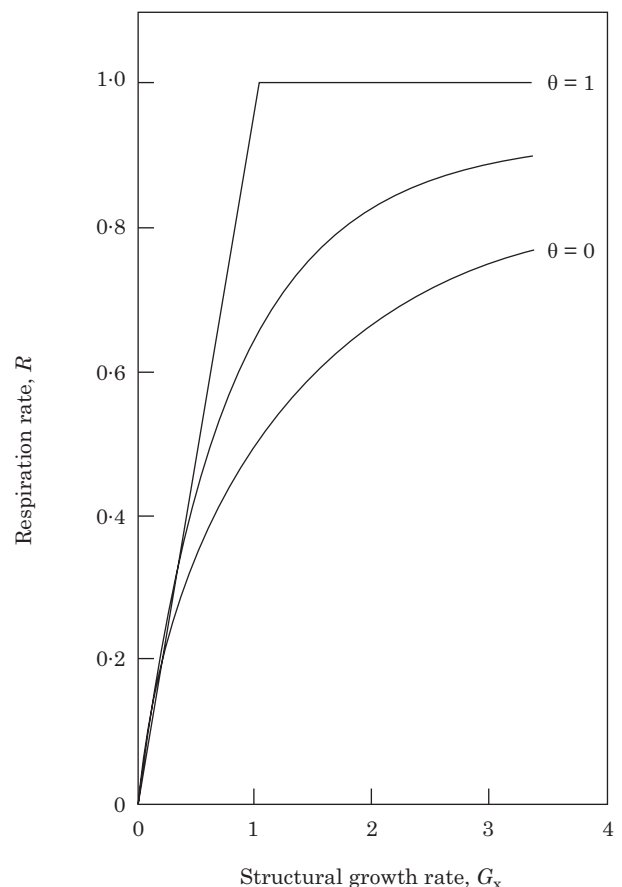


FIG. 2. The relationship between R , the rate of respiration coupled to active process $S \rightarrow P$, and G_x , the rate of structural growth (cellulose synthesis), predicted by eqns (5A), (7A) and (8C) for different values of the parameter $\theta = \theta_c + \theta_s - \theta_c \theta_s$ in eqn (7A). The values $\theta = 0$ (rectangular hyperbola) and $\theta = 1$ (Blackmann response) are indicated, and the intermediate curve is for $\theta = 0.7$. Other parameter values (illustrative only): $\beta_c = \beta_s S_e = \lambda_c = \lambda_{p,x} a_x = 1$. With this parameter choice, the value of G_x is numerically equal to C_e , the external C substrate concentration, and the asymptotic value of R corresponding to C-saturated (S-limited) respiration is equal to 1. The Blackmann response shows that as C_e increases, the process $S \rightarrow P$ switches its apparent contribution to respiration from growth to maintenance. The lower curves show the switch occurring more gradually. The figure illustrates potential ambiguities in the interpretation of apparent growth and maintenance respiration in terms of the underlying active processes.

previously-degraded proteins is traditionally viewed in functional terms as a process contributing to plant maintenance, this functional view may not necessarily be manifested empirically in eqn (10). The same point applies to other processes traditionally classed as maintenance, such as ion membrane transport.

As a basis for modelling respiration, therefore, eqn (10) poses certain problems of interpretation. However, eqn (10) may still be useful as an empirical model for certain components of respiration, provided m_R is not treated as a fixed cost independent of C substrate (Thornley and Cannell, 2000). By taking a more mechanistic approach, the present model avoids the use of maintenance respiration altogether.

Future model development

Here it has been assumed that the pool of ATP and NADPH which couples respiration and each active process, is specific to that process, being localized at the appropriate reaction sites. In the present model, therefore, different processes may be coupled only through sharing a common external C substrate pool. However, the model could be developed to include the case in which different processes share (or compete for) a common pool of ATP and NADPH, by extending the reaction scheme of eqn (1) to include more than one active process (e.g. $S_1 + X^* \rightarrow X + P_1$ and $S_2 + X^* \rightarrow X + P_2$), then setting $dX^*/dt = 0$ as before.

It has also been assumed that respiration is the only source of ATP and NADPH. Cannell and Thornley (2000) recommend that when modelling foliage respiration, account should be taken of the fact that some of the energy for active processes in leaves may be supplied by the light reactions of photosynthesis. They suggest adjusting foliage growth and maintenance coefficients according to current photosynthetic activity. This could also be done in the context of the present model, by extending eqn (1) to include the light and dark reactions of photosynthesis as represented in Thornley and Johnson's (1990) model (respectively, $\text{photons} + X \rightarrow X^*$ and $\text{CO}_2 + X^* \rightarrow X + \text{C}$). The active process $S \rightarrow P$ [eqn (1B)] might then represent Rubisco synthesis (others could be added as outlined above). One implication here is that increases in leaf irradiance and ambient $[\text{CO}_2]$ would, respectively, increase and decrease leaf ATP and NADPH (X^*), leading, respectively, to an increase and decrease in the synthesis of Rubisco. Such an approach offers the possibility of representing photosynthetic acclimation to light and $[\text{CO}_2]$ in a semi-mechanistic way (J.H.M. Thornley, pers. comm. 1998).

CONCLUSION

The model presented here provides a simple, physiologically-based representation of the components of respiration in terms of the supply of energetic and material substrates, which can be used in plant growth models that separate substrate from structure. The non-rectangular hyperbola and its simplification to a Blackmann response can explain

a number of general observations reported in the literature. The model is open to further development and testing. More quantitative tests of the model will require further data on the relationship between respiration rates and the concentrations of C and material substrates.

ACKNOWLEDGEMENTS

I thank John Thornley for comments on a draft of this paper, and for sending copies of his papers with Melvin Cannell (Cannell and Thornley, 2000; Thornley and Cannell, 2000) prior to publication.

LITERATURE CITED

- Author JS. 1994. Plant respiratory responses to the environment and their effects on the carbon balance. In: Wilkinson RE, ed. *Plant-environment interactions*. New York: Decker, 501–554.
- Author JS. 2000. The McCree–de Wit–Penning de Vries–Thornley Respiration Paradigm: Thirty years later. *Annals of Botany* 86: (in press).
- André M, Massimino J, Daguene A, Massimino D, Thierry J. 1982. The effect of a day at low irradiance of a maize crop. II. Photosynthesis, transpiration and respiration. *Physiologia Plantarum* 54: 283–288.
- Cannell MGR, Thornley JHM. 2000. Modelling the components of plant respiration: some guiding principles. *Annals of Botany* 85: 45–54.
- Coggeshall BM, Hodges HF. 1980. The effect of carbohydrate concentration on the respiration rate of soybean. *Crop Science* 20: 86–90.
- Cunningham GL, Syvertsen JP. 1977. The effect of nonstructural carbohydrate levels on dark CO_2 release in creosotebush. *Photosynthetica* 11: 291–295.
- Dewar RC, Medlyn BE, McMurtrie RE. 1998. A mechanistic analysis of light and carbon use efficiencies. *Plant, Cell and Environment* 21: 573–588.
- Dewar RC, Medlyn BE, McMurtrie RE. 1999. Acclimation of the respiration/photosynthesis ratio to temperature: insights from a model. *Global Change Biology* 5: 615–622.
- Farrar JF. 1985. The respiratory source of CO_2 . *Plant, Cell and Environment* 8: 427–438.
- Gifford RM. 1994. The global carbon cycle: a viewpoint on the missing sink. *Australian Journal of Plant Physiology* 21: 1–5.
- Gifford RM. 1995. Whole plant respiration and photosynthesis of wheat under increased CO_2 concentration and temperature: long-term vs. short-term distinctions for modelling. *Global Change Biology* 1: 385–396.
- Heilman JL, Kanemasu ET, Paulsen GM. 1977. Estimating dry-matter accumulation in soybean. *Canadian Journal of Botany* 55: 2196–2201.
- McCree KJ. 1970. An equation for the rate of respiration of white clover plants grown under controlled conditions. In: Setlik I, ed. *Prediction and measurement of photosynthetic productivity*. Wageningen: Pudoc, 221–229.
- Maier CA, Zarnoch SJ, Dougherty PM. 1998. Effects of temperature and tissue nitrogen on dormant season stem and branch respiration in a young loblolly pine (*Pinus taeda*) plantation. *Tree Physiology* 18: 11–20.
- Moser LE, Volenc JJ, Nelson CJ. 1982. Respiration, carbohydrate content, and leaf growth of tall fescue. *Crop Science* 22: 781–786.
- Penning de Vries FWT. 1972. Respiration and growth. In: Rees AR, Cockshull KE, Hand DW, Hurd RJ, eds. *Crop processes in controlled environments*. London: Academic Press, 327–347.
- Penning de Vries FWT. 1974. Substrate utilization and respiration in relation to growth and maintenance in higher plants. *Netherlands Journal of Agricultural Science* 22: 40–44.

- Penning de Vries FWT. 1975a.** The cost of maintenance processes in plant cells. *Annals of Botany* **39**: 77–92.
- Penning de Vries FWT. 1975b.** The use of assimilates in higher plants. In: Cooper JP, ed. *Photosynthesis and productivity in different environments*. New York: Cambridge University Press, 459–480.
- Penning de Vries FWT, Brunsting AHM, van Laar HH. 1974.** Products, requirements and efficiency of biosynthesis: a quantitative approach. *Journal of Theoretical Biology* **45**: 339–377.
- Penning de Vries FWT, Witlage JM, Kremer D. 1979.** Rates of respiration and of increase in structural dry matter in young wheat, ryegrass and maize plants in relation to temperature, to water stress and to their sugar content. *Annals of Botany* **44**: 595–609.
- Rugé F, André M, Massimino J. 1981.** Evolution de la respiration et croissance, au cours d'un cycle de végétation, de Maïs cultivé en chambre de mesure. *Physiologie Végétale* **19**: 277–299.
- Ryan MG. 1991.** Effects of climate change on plant respiration. *Ecological Applications* **1**: 157–167.
- Ryan MG. 1995.** Foliar maintenance respiration of subalpine and boreal trees and shrubs in relation to nitrogen content. *Plant, Cell and Environment* **18**: 765–772.
- Ryle GJA, Cobby JM, Powell CE. 1976.** Synthetic and maintenance respiration losses of $^{14}\text{CO}_2$ in unicultum barley and maize. *Annals of Botany* **40**: 721–728.
- Thornley JHM. 1970.** Respiration, growth and maintenance in plants. *Nature* **227**: 304–305.
- Thornley JHM. 1991.** A transport-resistance model of forest growth and partitioning. *Annals of Botany* **68**: 211–226.
- Thornley JHM, Cannell MGR. 1996.** Temperate forest responses to carbon dioxide, temperature and nitrogen: a model analysis. *Plant, Cell and Environment* **19**: 1331–1348.
- Thornley JHM, Cannell MGR. 2000.** Modelling the components of respiration: representation and realism. *Annals of Botany* **85**: 55–67.
- Thornley JHM, Johnson IR. 1990.** *Plant and crop modelling*. Oxford: Oxford University Press.
- Thornley JHM, Verberne ELJ. 1989.** A model of nitrogen flows in grassland. *Plant, Cell and Environment* **12**: 863–886.
- Wullschlegel SD, Norby RJ, Gunderson CA. 1992.** Growth and maintenance in leaves of *Liriodendron tulipifera* L. exposed to long-term carbon-dioxide enrichment in the field. *New Phytologist* **121**: 515–523.

APPENDIX

Symbol definitions and units

Abbreviations: C, glucose; S (P), substrate (product) of active process $S \rightarrow P$; X, ADP and NADP; X^* , ATP and NADPH; XDM, structural dry matter (cellulose). See [Table 1](#) for process subscript labels *i*.

Symbol	Definition (relevant equations)	Units
a_x	Coefficient of proportionality (8A)	$\text{mol X (mol C)}^{-1} \text{ s}^{-1}$
C (C_e)	Reaction site (external) C concentration	mol C m^{-3}
g_c ($g_{c,i}$)	C transport conductance (process <i>i</i>) (6)	s^{-1}
g_s ($g_{s,i}$)	S transport conductance (process <i>i</i>) (6)	s^{-1}
g_R	Growth respiration coefficient (10)	$\text{mol C (mol XDM)}^{-1}$
G (G_i)	Production rate (process <i>i</i>) (5C, 8C)	$\text{mol P m}^{-3} \text{ s}^{-1}$
k_c	Reaction rate constant (1A)	$\text{m}^3 (\text{mol C})^{-1} \text{ s}^{-1}$
k_s	Reaction rate constant (1B)	$\text{m}^3 (\text{mol S})^{-1} \text{ s}^{-1}$
m_R	Maintenance respiration coefficient (10)	$\text{mol C m}^{-3} \text{ s}^{-1}$
P	Product concentration	mol P m^{-3}
R (R_i)	Respiration (coupled to process <i>i</i>) (5A, 11, 12)	$\text{mol C m}^{-3} \text{ s}^{-1}$
R_{sys}	Whole-system respiration rate (10)	$\text{mol C m}^{-3} \text{ s}^{-1}$
S	Reaction site S concentration	mol S m^{-3}
S_e ($S_{e,i}$)	External S concentration (process <i>i</i>)	mol S m^{-3}
T_c	C transport rate (6A)	$\text{mol C m}^{-3} \text{ s}^{-1}$
T_s	S transport rate (6B)	$\text{mol S m}^{-3} \text{ s}^{-1}$
U	S utilization rate (5B)	$\text{mol S m}^{-3} \text{ s}^{-1}$
v (v_i)	Turnover rate of X (process <i>i</i>) (4, 7A, 8A, 9)	$\text{mol X m}^{-3} \text{ s}^{-1}$
X	Concentration of X	mol X m^{-3}
X^*	Concentration of X^* (3)	mol X m^{-3}
X_0	Total concentration of $X + X^*$	mol X m^{-3}
α_c	Rescaled reaction rate constant, $k_c X_0$ (4)	$\text{mol X (mol C)}^{-1} \text{ s}^{-1}$
α_s	Rescaled reaction rate constant, $k_s X_0$ (4)	$\text{mol X (mol S)}^{-1} \text{ s}^{-1}$
β_c ($\beta_{c,i}$)	Parameter combination (process <i>i</i>) (7C, 8B)	$\text{mol X (mol C)}^{-1} \text{ s}^{-1}$
β_s ($\beta_{s,i}$)	Parameter combination (process <i>i</i>) (7C, 8B)	$\text{mol X (mol S)}^{-1} \text{ s}^{-1}$
λ_c	Stoichiometric coefficient (5A)	$\text{mol C (mol X)}^{-1}$
λ_p ($\lambda_{p,i}$)	Stoichiometric coefficient (process <i>i</i>) (5C)	$\text{mol P (mol X)}^{-1}$
λ_s ($\lambda_{s,i}$)	Stoichiometric coefficient (process <i>i</i>) (5B)	$\text{mol S (mol X)}^{-1}$
θ_c ($\theta_{c,i}$)	Parameter combination (process <i>i</i>) (7B, 8B)	dimensionless
θ_s ($\theta_{s,i}$)	Parameter combination (process <i>i</i>) (7B, 8B)	dimensionless