Plant respiration in relation to growth, maintenance, ion uptake and nitrogen assimilation

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Abstract. Respiration in plants is generally observed to comprise two components: one proportional to the growth rate and the other to the plant dry mass. These components are usually interpreted as being related to the growth of new plant material and maintenance of existing plant material, respectively. By analysing data in this way, the respiratory costs of both structural synthesis and maintenance are observed to be greater in the root than the shoot. This contradicts current understanding of the biochemistry of the processes involved. The basic model is developed to incorporate three additional processes. The first is the cost of ion uptake for plant growth. The second allows for the fact that the site of nitrogen assimilation into amino acids may differ from the site of utilization for protein synthesis: when ammonium is supplied, this is incorporated immediately into amino acids owing to its toxicity to the plants; when nitrate is supplied it may be reduced either in the shoot or root, or both, and subsequently transported around the plant for utilization. The third process to be included is an energy cost for the uptake of ions to balance efflux from the root system. The theory is consistent with experimental observation and provides a means of understanding and interpreting respiration and nitrogen metabolism in plants.

Key-words: model; respiration; nitrogen; ion uptake.

Introduction

Respiration in plants is directly related to the energetics of plant growth and yield. The experimental work of McCree (1970) and theoretical treatment by Thornley (1970) served to identify two major components of respiration as those related to the growth of new plant structure and the maintenance of existing plant material. According to this work, the rate of respiration, $R$ (kg carbon d$^{-1}$), of a plant or crop with dry mass $W$ (kg carbon equivalents), is

$$ R = \left(1 - \frac{Y}{Y} \right) \frac{dW}{dt} + mW, \quad (1a) $$

where $Y$ (dimensionless, $0 < Y < 1$), the growth efficiency, is the efficiency of converting substrate carbon into structural carbon, and $m$ (d$^{-1}$) is the maintenance coefficient. Maintenance is usually interpreted as being associated principally with providing energy for the re-synthesis of degraded protein and the transport of ions across cell membranes against electrochemical gradients. By using eqn 1a to analyse experimental data, the respiration parameters $Y$ and $m$ may be calculated. An alternative approach for studying respiration is to consider the energetics of the biochemical pathways of structural synthesis, an approach which was pioneered by Penning de Vries (1975a, b) and has been discussed in detail by Thornley & Johnson (1990, Chapter 12). Of the main plant components, proteins are the most energetically expensive to synthesize, while the synthesis of structural carbohydrate has the highest efficiency. For a known plant composition, the growth efficiency $Y$ may be calculated from the individual efficiencies, and is typically in the range 0.75–0.85.

When shoot and root respiration data are analysed using eqn 1a, the root is seen to have a lower growth efficiency and higher maintenance coefficient than the shoot (Hansen & Jensen, 1977; Szaniawski & Kielkiewicz, 1982; Amthor, 1984), implying a greater respiratory cost for both root structural synthesis and maintenance. Although variation in protein content could be the cause of these differences, Szaniawski & Kielkiewicz (1982) observed no difference in shoot and root protein content. Alternative explanations for the larger root maintenance coefficient could be differences in protein turnover rates or energy driven ionic fluxes within the plant, although these are unlikely to explain the large disparity between the observed maintenance coefficients. For a further discussion of the underlying biochemical and physiological features of plant respiration, see Farrar (1985).

Therefore, it follows that while the general form of eqn 1a provides an accurate description of respiration, in that there is a component which is proportional to the growth rate and another proportional to dry mass, the specific form of this equation is incomplete. Workers who have measured respiration and analysed it using equations of the form of 1a have highlighted various limitations in the model: in this
The first is the cost of ion uptake. The transport of \( \text{NO}_3^- \), \( \text{K}^+ \), \( \text{H}_2\text{PO}_4^- \), \( \text{SO}_4^{2-} \) and \( \text{Cl}^- \) into root cells is understood to be facilitated by carrier proteins, and this transport is driven by energy in the form of ATP, which is generated through respiration (Leonard, 1984). For divalent cations, it is generally assumed that uptake is passive, down an electrochemical gradient. In the case of \( \text{NH}_4^+ \), it appears that uptake is partly active and partly passive, in that uptake can be halved when the source of respiration is removed (Lewis, 1986).

The second factor which is incorporated relates to nitrogen assimilation. If nitrate is supplied, it may be reduced and incorporated into amino acids either in the root or shoot. (While organic nitrogen in the form of amides and ureides is also found in plants, these involve reduced nitrogen and are quite similar energetically: for simplicity, they are all referred to as amino acids here.) The amino acids may then be translocated around the plant, so that the site of nitrate reduction need not be the same as the site of protein synthesis. Depending on the plant species and growing conditions, nitrate reduction may be predominantly in the shoot or the root, or there may be some intermediate strategy (Pate, 1973; Andrews, 1986). Of the energy required to synthesize protein with nitrate as the source of nitrogen, approximately 81% is used in reducing nitrate and synthesizing amino acids (see below). The advantage of synthesizing amino acids in the shoot and translocating them to the root is that energy from photo-phosphorylation may be used directly for nitrate reduction (and possibly other metabolic processes). Therefore, it is important to account for the site of nitrate reduction in modelling and interpreting respiration data. On the other hand, if nitrogen is supplied as ammonium, only around 2% of the energy involved in protein synthesis is required to synthesize the constituent amino acids (see below). Furthermore, owing to its toxicity to the plant, the ammonium will be immediately assimilated into amino acids in the root.

The third process which is included in the model relates to ionic leakage. Jackson, Volk & Israel (1980) have demonstrated that there may be significant efflux of nitrate from plant roots (presumably due to the electrochemical gradient between the root interior and the external medium), and it follows that there will be a respiratory cost in order to replenish this efflux. Similarly, other ions which require active uptake are likely to be leaked from the root system.

Equation 1a is developed to include these processes. Two equations, one for the whole plant and one for the root, of the form

\[
\frac{dW}{dt} = R = g \left( \frac{1}{W} \right) + m,
\]

for the specific respiration rate, \( r \left( \text{d}^{-1} \right) \), are derived, where \( g \) (dimensionless) and \( m \) (d\(^{-1}\)) are the respiration coefficients. The \( g \) coefficients involve parameters relating to ion uptake, nitrate reduction (for the case where nitrate is the form of nitrogen supply), plant structural composition, as well as the growth efficiencies for structural synthesis. The usual approach when analysing respiration data with equations of the form 1a or 1b is to obtain estimates of the growth efficiencies and compare these with theoretical values obtained from knowledge of the biochemical reactions involved. In the present model, the methods are combined: values for the efficiencies are taken from biochemical calculations, measured values for plant structural composition are used, and the parameters regarding ion uptake and nitrate reduction are estimated. The \( m \) (d\(^{-1}\)) coefficients involve the respiratory costs of maintaining plant protein and energy-driven ionic fluxes within the plant as well as, in the root, the costs associated with the re-uptake of leaked ions. The present theory is an extension of that presented by Johnson (1983, 1987), where eqn 1a was modified to include a term for nitrate uptake.

This approach to modelling respiration is phenomenological as opposed to mechanistic, in that related events are described rather than defining physiological processes in response to driving forces. For example, it will be seen that nitrate uptake is taken to be proportional to plant growth rate (eqn 4a), which is not a mechanistic response: in a mechanistic model, uptake will depend on root mass and activity and perhaps other factors such as plant carbon and nitrogen substrate levels. The present analysis may be used to evaluate the physiological parameters for use in mechanistic crop growth models (e.g. Johnson & Thornley, 1985).

### Theory

Throughout the analysis, all plant and respiration components are expressed in carbon units. Let the plant dry mass, \( W_{pl} \) (kg carbon), be divided into substrate, degradable and non-degradable components, comprising mainly sugars, protein and large molecule carbohydrate (e.g. cellulose), respectively. Denote these fractional components of \( W_{pl} \) by \( f_S \), \( f_D \), \( f_N \) respectively, so that the absolute amounts are

\[
f_S W_{pl}, \quad f_D W_{pl}, \quad f_N W_{pl},
\]

kg carbon. It is assumed that the synthesis of the degradable component (protein) comprises two separate stages: nitrate or ammonium to amino acids, and amino acids to protein. When nitrate is supplied, the first stage need not occur at the same location as the second so that, for example, amino acids may be produced in the shoot and then utilized for protein synthesis in the root. Structural carbohydrate synthesis occurs in a single step.
Growth efficiencies for structural synthesis

The growth efficiencies for structural synthesis may be evaluated from the energetics of the biochemical reactions involved. This approach was pioneered by Penning de Vries (1975a, b). In the present analysis, the values are derived from Thornley & Johnson (1990) since the presentation of the theory is more extensive. In defining these growth efficiencies, glucose, amino acids, protein and cellulose are all expressed as carbon equivalents. Likewise, the energy associated with structural synthesis is defined in terms of the carbon respired in providing that energy. It is assumed that the source of carbon for structural synthesis is glucose, which provides both the carbon skeletons and energy. In general, if the carbon in the substrate which provides the carbon skeletons is \( C_{\text{substrate}} \), the structural carbon in the product is \( C_{\text{product}} \), and the respiratory carbon which provides the energy required to synthesise that product is \( E \), then the growth efficiency is

\[
Y = \frac{C_{\text{product}}}{C_{\text{substrate}} + E} \tag{3a}
\]

and the associated respiration is

\[
C_{\text{substrate}} + E - C_{\text{product}} \tag{3b}
\]

\( C_{\text{substrate}} \) is not necessarily the same as \( C_{\text{product}} \) since some carbon (in the form of \( \text{CO}_2 \)) may be evolved, or required, in the reaction synthesizing the product, and this is separate from the \( \text{CO}_2 \) respired in generating the required energy. The definition given in eqn 3a means that 1 kg substrate (carbon), providing both the carbon skeletons and energy, produces \( Y \) kg product (carbon) with \((1-Y)\) kg carbon respired. It is often convenient to evaluate the respiration per unit of product synthesized (rather than per unit substrate utilized), which is (divide 3b by \( C_{\text{product}} \) and use 3a)

\[
\frac{1-Y}{Y} \tag{3c}
\]

First consider the synthesis of protein. Let \( Y_{ga} \) be the growth efficiency of amino acid synthesis with glucose as the source of carbon, and let \( Y_{ap} \) be the growth efficiency of protein synthesis from these amino acids. The overall growth efficiency of protein synthesis is \( Y_{gp} \). The associated energy terms involved are denoted by \( E_{\text{ga}}, E_{\text{ap}} \) and \( E_{\text{gp}} \). Let the structural carbon in the glucose which provides the carbon skeletons for amino acid synthesis be \( C_g \). In synthesizing protein from amino acids, all the carbon skeletons are provided by the amino acids, so that the structural carbon content of the amino acids and protein are the same: define this structural carbon content as \( C_p \). The growth efficiencies are, therefore,

\[
Y_{ga} = \frac{C_p}{C_g + E_{\text{ga}}}, \quad Y_{ap} = \frac{C_p}{C_p + E_{\text{ap}}}, \quad Y_{gp} = \frac{C_p}{C_g + E_{\text{gp}}} \tag{3d}
\]

where the energy terms are related by

\[
E_{\text{gp}} = E_{\text{ga}} + E_{\text{ap}} \tag{3e}
\]

The value of \( Y_{ap} \) depends on whether or not the supplied nitrogen is reduced—that is nitrate or ammonium—since a considerable amount of energy is required to reduce nitrate. \( Y_{ap} \) is independent of the form of supplied nitrogen. The following values may be derived from Thornley & Johnson (1990, Table 12.6):

nitrate supplied:

\[
Y_{ga} = 0.62, \quad Y_{gp} = 0.58, \tag{3f}
\]

ammonium supplied:

\[
Y_{ga} = 0.94, \quad Y_{gp} = 0.84; \tag{3g}
\]

\[
Y_{ap} = 0.89. \tag{3h}
\]

Some of these values differ slightly from those derived by Penning de Vries (1975b); for example, Penning de Vries (1975b) gives \( Y_{ga} = 0.54 \) with nitrate supplied and \( Y_{gp} = 0.84 \) with ammonium supplied. (Note that Penning de Vries defines the efficiencies as kg product per kg glucose utilized and does not convert to carbon equivalents: his values quoted here have been converted to carbon equivalents [Johnson, 1987].)

It is worth noting from eqns 3d and 3e that the total respiratory cost of synthesizing one unit of protein is

\[
\frac{1}{Y_{gp}} = \frac{1 - Y_{ga}}{Y_{ga}} + \frac{1 - Y_{ap}}{Y_{ap}}. \tag{3i}
\]

where the terms on the right hand side define the respiration associated with the synthesis of the constituent amino acids and the subsequent synthesis of the protein respectively. Equation 3i may be written

\[
Y_{gp} = \frac{1}{1 + \left( \frac{1 - Y_{ga}}{Y_{ga}} \right) + \left( \frac{1 - Y_{ap}}{Y_{ap}} \right)}, \tag{3j}
\]

which provides a useful check of the biochemical calculations.

The relative energetic costs for each stage of protein synthesis may be derived from Thornley & Johnson (1990, Table 12.6) as

nitrate supplied:

\[
E_{\text{ga}} = 0.81, \tag{3k}
\]

ammonium supplied:

\[
E_{\text{ga}} = 0.02, \tag{3l}
\]

indicating that the cost of amino acid synthesis dominates the cost of protein synthesis when nitrate is supplied, whereas it is negligible when ammonium is supplied.

All plant non-degradable structure is taken to be cellulose with growth efficiency

\[
Y_{cc} = 0.95, \tag{3m}
\]

(Thornley & Johnson, 1990, Table 12.2). Although significant quantities of other structural compounds...
such as hemicellulose are likely to be present, they all have similar growth efficiencies (Thornley & Johnson, 1990, Table 12.2).

**Ion uptake**

The rate of nitrogen uptake required to support the plant growth rate is

\[ F_N \frac{dW_{pl}}{dt} \]

kg nitrogen d\(^{-1}\), expressed either on a per plant or ground area basis, where \(F_C\) and \(F_N\), kg carbon or nitrogen (kg protein)\(^{-1}\), are the carbon and nitrogen fractions of degradable structure (protein). (Note that \(F_N/F_C\) is the ratio of nitrogen to carbon in degradable structure [protein].) Equation 4a implies that the rate of nitrogen uptake balances the rate of incorporation of nitrogen into plant structure. The nitrogen uptake will be totally active if nitrate is supplied, and partially active if ammonium is supplied. Let \(\xi\) denote the active fraction of nitrogen uptake, so that \(\xi = 1\) for nitrate and \(0 < \xi < 1\) for ammonium (or a combination of nitrate and ammonium). The respiration associated with the uptake of nitrogen in eqn 4a is, therefore,

\[ \frac{\xi F_N}{F_C} \frac{dW_{pl}}{dt} \]

kg carbon d\(^{-1}\), where \(\alpha\), kg carbon (kg nitrogen)\(^{-1}\), is the respiratory cost for ion uptake expressed on a nitrogen basis. If \(\lambda\) is the molar fraction of nitrogen containing ions which are taken up actively, it follows that the respiratory cost for active ion uptake is

\[ \frac{\lambda F_N}{F_C} \frac{dW_{pl}}{dt} \]

kg carbon d\(^{-1}\). By formulating the cost of ion uptake in this way, nitrogen is used as the basic unit. However, this may be readily converted to any other ion. In deriving eqn 4c, it is assumed that the respiratory cost for active ion uptake is independent of the particular ion.

**Growth respiration**

The location of respiration associated with plant growth will depend on whether the source of nitrogen is nitrate or ammonium, since nitrate reduction need not occur at the site of utilization for protein synthesis, whereas ammonium is immediately incorporated into amino acids. Therefore, the two cases will be treated separately.

### Nitrate supplied

When nitrate is supplied,

\[ \xi = 1 \]

The respiration required for the growth of plant structure has the following components: non-degradable structural synthesis (protein), degradable structural synthesis (cellulose), and ion uptake. These are, in turn

\[ \left( 1 - \frac{Y_{ge}}{Y_{ap}} \right) \frac{f_n}{f_d} \frac{dW_{pl}}{dt} + \left( 1 - \frac{Y_{gp}}{Y_{ap}} \right) \frac{f_d}{f_d} \frac{dW_{pl}}{dt} \]

The total growth respiration for the plant is, therefore,

\[ R_{g, pl} = \left( 1 - \frac{Y_{ge}}{Y_{ap}} \right) \frac{f_n}{f_d} \frac{dW_{pl}}{dt} + \left( 1 - \frac{Y_{gp}}{Y_{ap}} \right) \frac{f_d}{f_d} \frac{dW_{pl}}{dt} \]

Using eqn 3i, the respiration associated with the growth of degradable structure may be written

\[ \left( 1 - \frac{Y_{gp}}{Y_{ap}} \right) \frac{f_d}{f_d} \frac{dW_{pl}}{dt} + \left( 1 - \frac{Y_{ge}}{Y_{ap}} \right) \frac{f_n}{f_d} \frac{dW_{pl}}{dt} \]

where the terms on the right hand side represent the nitrate to amino acid and amino acid to protein stages, respectively. If the proportion of the total nitrate reduction and amino acid synthesis that occurs in the shoot is \(\theta\), then it follows that the growth respiration observed in the shoot is

\[ R_{g, sh} = \left( 1 - \frac{Y_{ge}}{Y_{ap}} \right) \frac{f_n}{f_d} \frac{dW_{sh}}{dt} + \theta \left( 1 - \frac{Y_{ge}}{Y_{ap}} \right) \frac{f_n}{f_d} \frac{dW_{pl}}{dt} \]

where \(W_{sh}\) is the shoot mass (kg carbon). Equations 5c and 5e define the observed growth respiration in the whole plant and shoot respectively. The proportion of nitrate reduction which is required for shoot growth which actually occurs in the shoot is

\[ \overline{f_{sh}} \]

with \(f_{sh}\) defined by

\[ f_{sh} = \frac{W_{sh}}{W_{pl}} \]

Consider plants growing in uniform conditions where the shoot, root and whole plant have the same specific growth rate, \(\mu\) (d\(^{-1}\)). This means that

\[ \frac{1}{W_{pl}} \frac{dW_{pl}}{dt} = \frac{1}{W_{sh}} \frac{dW_{sh}}{dt} = \mu \]

* The term 'specific growth rate' is used in preference to 'relative growth rate' (which is often used in plant growth studies) since, in SI units, specific is defined as divided by mass (Royal Society, 1975).
so that, expressed as respiration per unit mass, eqns 5c and 5e becomes

\[ r_{g, pt} = \left( \frac{1 - Y_{gp}}{Y_{gc}} \right) f_n + \left( \frac{1 - Y_{pp}}{Y_{ap}} \right) f_d + \frac{\alpha}{\lambda} F_N f_d \mu, \]  

(6b)

and

\[ r_{g, sh} = \left( \frac{1 - Y_{gc}}{Y_{gc}} \right) f_n + \left( \frac{1 - Y_{pp}}{Y_{ap}} \right) f_d + \theta \left( \frac{1 - Y_{ga}}{Y_{ga}} \right) f_d \mu. \]  

(6c)

Comparing these equations with eqn 1b applied to the shoot and whole plant, \( \alpha \) and \( \theta \) are given by

\[ \alpha = \frac{F_C}{F_N f_d} \left( g_{pt} - \left( \frac{1 - Y_{gc}}{Y_{gc}} \right) f_n - \left( \frac{1 - Y_{pp}}{Y_{ap}} \right) f_d \right), \]  

(6d)

and

\[ \theta = \frac{f_{sh} \left( \frac{Y_{ga}}{1 - Y_{ga}} \right) \left( g_{sh} - \left( \frac{1 - Y_{gc}}{Y_{gc}} \right) f_n - \left( \frac{1 - Y_{pp}}{Y_{ap}} \right) f_d \right)}{f_{sh} \left( \frac{Y_{ga}}{1 - Y_{ga}} \right) \left( g_{sh} - \left( \frac{1 - Y_{gc}}{Y_{gc}} \right) f_n - \left( \frac{1 - Y_{pp}}{Y_{ap}} \right) f_d \right)}. \]  

(6e)

Equations 6d and 6e may be used to estimate \( \alpha \) and \( \theta \) from experimental data.

**Ammonium supplied**

Since the ammonium which is taken up by the roots is immediately incorporated into amino acids,

\[ \theta = 0. \]  

(7a)

Proceeding as above, but with

\[ 0 < \xi < 1, \]  

(7b)

the equations corresponding to 6b and 6c for \( r_{g, pt} \) and \( r_{g, sh} \) are

\[ r_{g, pt} = \left( \frac{1 - Y_{gc}}{Y_{gc}} \right) f_n + \left( \frac{1 - Y_{pp}}{Y_{ap}} \right) f_d + \frac{\alpha \xi}{\lambda} F_N f_d \mu, \]  

(7c)

and

\[ r_{g, sh} = \left( \frac{1 - Y_{gc}}{Y_{gc}} \right) f_n + \left( \frac{1 - Y_{pp}}{Y_{ap}} \right) f_d \mu. \]  

(7d)

With nitrate supplied, the approach is to calculate the growth efficiencies from the energetics of the biochemical pathways, using measured values of plant structure, an estimated value for \( \lambda \), and subsequently evaluate \( \alpha \) and \( \theta \). Here, all the parameters in eqn 7d are prescribed, but eqn 7c involves \( \alpha \) and \( \xi \). One possible strategy is to obtain \( \alpha \) from the nitrate model and use this to estimate \( \xi \); eqn 7d may be used to check the accuracy of the model, in particular the values of the growth efficiencies \( Y_{gc} \) and \( Y_{pp} \).

**Maintenance respiration**

As mentioned earlier, when maintenance respiration is regarded as being associated with the re-synthesis of degraded protein and the active transport of ions across membranes within the plant, these processes do not account for the observed greater maintenance costs of roots.

Using labelled nitrogen techniques, Jackson, Volk & Israel (1980, Fig. 6) observed the diurnal efflux to be of the order of one third of uptake in corn, and one half in millet. If there is an efflux of ions, then there must be a corresponding influx to maintain the internal concentrations. Since efflux is likely to be related to the concentration gradient between the external medium and the plant, it is quite plausible that this process is related directly to plant dry mass.

Let \( m_{sh} \) (d\(^{-1}\)) and \( m_r \) (d\(^{-1}\)) be the observed maintenance coefficients in the shoot and root, as in eqn 1b. Assume that the cost of maintaining plant structure (protein) and ionic gradients is the same for the shoot and root, and denote this by \( m \) (d\(^{-1}\)). If the respiratory cost of ion uptake per unit root dry mass to balance efflux is \( m_r \) (d\(^{-1}\)), it follows that

\[ m = m_{sh} + m_r - m. \]  

(8a)

The absolute respiration rate associated with ion uptake to balance leakage is therefore \( m W_r \) (kg carbon d\(^{-1}\)), where \( W_r \) (kg carbon) is the root dry mass. Thus, the total respiration associated with ion uptake is, using eqn 4b

\[ m W_r + \frac{\alpha \xi}{\lambda} F_N f_d \frac{d W_{pt}}{dt}, \]  

(8b)

kg carbon d\(^{-1}\).

To assess the validity of this approach, consider nitrate leakage where nitrate is the only source of nitrogen (so that \( \xi = 1 \)). Assume that a fraction \( \lambda \) of ions leaked are nitrate, where \( \lambda \), as defined above, is the nitrate proportion of ions which are actively taken up. Consequently, the ratio of nitrate taken up to balance efflux to the total nitrate taken up is

\[ \zeta = \frac{\lambda m_r f_r}{\lambda m_r f_r + \alpha \frac{F_N}{F_C} f_d \mu}, \]  

(8c)

where

\[ f_r = \frac{W_r}{W_{pt}}. \]  

(8d)

Equation 8c may be used to compare with experimental data of nitrate uptake and efflux.

**Estimation of \( \alpha \) and \( \theta \) (nitrate supplied)**

Recall that \( \alpha \), kg carbon (kg nitrogen\(^{-1}\)), is the respiratory cost for ion uptake, expressed on a nitrogen basis, and \( \theta \) is the proportion of total nitrate reduction and amino acid synthesis that occurs in the shoot.

The model described here requires quite an extensive set of data in order to calculate these parameters. As well as the respiration coefficients, the quantities
also required are: the plant composition in terms of substrate, degradable and non-degradable structure; the carbon and nitrogen fractional content of structure; and the shoot: root ratio. The most complete set of data for this exercise that I am aware of is that reported by Szaniawski & Kielkiewicz (1982): the only piece of information not available from their paper is the substrate concentration, \( f_c \). In their experiment, Szaniawski & Kielkiewicz maintained the shoot temperature at 25/20 °C during the light/dark periods. Three constant root temperature regimes of 10, 20 and 30 °C were studied. The respiration coefficients of eqn 1b (\( g \) and \( m \)) and the shoot: root ratio \( (W_{sh}/W_r) \) they observed are presented in Table 1. The variation in the \( g \) parameters is not significant, and so in the following illustrations, the values \( g_{sh} = 0.28 \) and \( g_{pt} = 0.33 \) are used.

The parameters for the composition of degradable structure (protein) are

\[
F_c = 0.54 \text{ kg carbon (kg protein)}^{-1} \quad \text{and} \quad F_N = 0.17 \text{ kg nitrogen (kg protein)}^{-1},
\]

which may be evaluated from Thornley & Johnson (1990, Table 12.1). (Note that this value for \( F_N \) corresponds to that used by Szaniawski & Kielkiewicz.) The parameters for the composition of plant dry mass, \( f_s \), \( f_d \) and \( f_n \) which are in carbon equivalents (that is, dry mass and its components are expressed in carbon units), are taken to be

\[
f_s = 0.2, \quad f_d = 0.3, \quad f_n = 0.5.
\]

In deriving these values, the protein content of plant dry mass is 0.25 kg protein (kg dry mass)

\( ^{-1} \) for each root temperature regime, as calculated by Szaniawski & Kielkiewicz; the carbon fractions of glucose and cellulose may be calculated directly as 0.4 and 0.44, respectively; the substrate fraction of dry mass (which was not presented by Szaniawski & Kielkiewicz) is taken to be 0.23 kg substrate (kg dry mass)

\( ^{-1} \), which is a reasonable value for \( C_3 \) plants (J. R. Wilson, personal communication) (since this was not measured, no variation in response to temperature is included).

To define the parameter \( \lambda \) (the nitrate proportion of total active ion uptake, on a mole basis), assume that uptake is proportional to dry matter content. Taking the percentage components of plant dry mass of nitrogen, potassium, phosphorus and sulphur (those macronutrients requiring active uptake) to be 2.5, 1.0, 0.25 and 0.25, respectively, the value

\[
\lambda = 0.81
\]

is obtained.

With these parameter values and the growth efficiencies given by eqns 3f and 3m, eqn 6d gives, for the cost of nitrate uptake

\[
x = 0.66 \text{ kg carbon (kg nitrogen)}^{-1}.
\]

The proportion of nitrate reduction in the shoots, \( \theta \) (eqn 6e) is directly proportional to \( f_{sh} \), although the fraction of nitrate reduced in the shoot for shoot growth, \( \theta/f_{sh} \) is constant (since \( g_{sh} \) is observed to be constant for the experiment being considered here), and is given by

\[
\theta = 0.35
\]

so that, for these plants, the models suggests that the shoots reduce approximately one third of their nitrate.

Now consider maintenance and nitrate efflux. Since the shoots were measured at 20 °C whereas the roots were measured at 10, 20 and 30 °C, eqn 8a may not be applied directly, since maintenance is strongly temperature dependent. To account for this, assume that the temperature response of \( m \) (d

\( ^{-1} \)) may be described by the \( Q_{10} \) rule, with \( Q_{10} = 2 \) and a reference temperature of 20 °C (Amthor, 1984), so that

\[
m(T) = m(20) Q(T-20)/10.
\]

This enables \( m \) for the root temperatures to be calculated. From Table 1, it can be seen that there is a small variation in the shoot maintenance coefficient for different root temperature regimes. Since Szaniawski & Kielkiewicz observed no variation in protein content between the shoot and root, they suggested this may be related to the overall increase in plant growth rate in response to higher root temperatures. This is consistent with the present interpretation of maintenance, as ion transport across membranes is likely to increase as metabolic activity increases. Applying eqns 8a and 11a for each root temperature regime, the maintenance coefficients associated with the uptake of nitrate to balance efflux, \( m_e \) (d

\( ^{-1} \)), are

\[
m_e(T_r = 10) = 0.011, \quad m_e(T_r = 20) = 0.020, \quad m_e(T_r = 30) = 0.035.
\]

These values imply that there is greater leakage per unit of root dry mass at higher root temperatures.

The values for \( m_e \) may be used in eqn 8c with Table 1 to calculate the proportion of nitrate efflux to total nitrate taken up, \( \xi \). This is illustrated in Fig. 1 as a function of the specific growth rate, \( \mu \), for the parameters values above, where it can be seen that \( \xi \) decreases with increasing \( \mu \). This is reasonable since the concentrations of nitrate, and therefore leakage,
may only vary slightly with $\mu$, whereas the greater specific growth rates will be accompanied by greater overall nitrate uptake.

**Discussion**

The models described here incorporate the respiration associated with ion uptake and nitrogen assimilation into the traditional equation for plant respiration, for plants supplied with either nitrate or ammonium. Parameters for the cost of ion uptake, the site of nitrate reduction, and the uptake of ions to balance efflux are derived from respiration data. These components and where they occur are summarized in Fig. 2. Also shown are the percentage values of each component for the data analysed above (sunflower with nitrate supplied), with the specific growth rate taken to be $\mu = 0.15$ d$^{-1}$. The

![Figure 2](image-url)

**Figure 2.** Individual growth and maintenance respiration components in the shoot and root. The figures in parentheses are the percentage contributions to whole plant respiration as derived by the model (note that the figures on the left do not sum to 69%; this is due to rounding errors). These figures are specific to the particular data being considered here (see text for details).
values presented in the figure will be influenced by \( \mu \), and possibly by other genetic and environmental factors which may affect the parameters of the model. Nevertheless, it can be seen that amino acid synthesis (nitrate reduction) and ion uptake represent the major components of growth respiration, while the respiration required for the re-uptake of ions to balance leakage is a significant component of root maintenance respiration.

Rather than attempt to calculate the growth efficiencies for structural synthesis, values derived from knowledge of the biochemical pathways of the reactions involved are used. The emphasis in the past has been to evaluate these efficiencies directly from respiration data and look for consistency between the two approaches. However, as is apparent from the present theory, such a strategy may be limiting in that the respiratory cost of ion uptake and differences between the site of nitrate reduction and the subsequent utilization of that nitrogen for protein synthesis may influence the analysis.

In modelling respiration and applying equations of the form described here, the respiration rate in the dark is generally measured and expressed on a per unit day basis, and the growth rate is estimated from sequential harvests of plant dry mass, which does not account for diurnal fluctuations. (Other methods are reviewed by Amthor [1984], but they all involve measuring respiration in the dark.) Implicit in this approach is the assumption that there is no difference in the mean metabolic activity during the light and dark periods, so that the estimated growth rate is equivalent to the growth rate during the dark (these models really relate the dark respiration rate to the dark growth rate). This is most likely to apply to plants growing in uniform conditions. Therefore, the models should be used to analyse data from plants growing in uniform conditions in order to obtain estimates of the underlying physiological parameters.

The respiration in the light (excluding photorespiration) will differ from that in the dark if energy from photophosphorylation is used directly for metabolic processes. The extent to which this occurs is difficult to assess. It is probably reasonable to assume that nitrate reduction in the leaves may use this source of energy, since otherwise there would seem to be little reason for plants to develop such a capacity. Also, leaf maintenance may use this source of energy on the basis that most leaf maintenance costs are likely to be for photosynthetic enzymes. Provided, as mentioned above, that there is no difference in the mean metabolic activity during the light and dark periods, respiration of this form during the light period will not affect the model. However, in models which predict daily carbon balance, it will be necessary to account for any reduction in dark respiration during the light period.

The cost for ion uptake has been calculated (by expressing on a nitrogen basis) as 0.66 kg carbon (kg nitrogen)\(^{-1}\) (eqn 10a). This is difficult to evaluate directly by experimental methods since measurements of respiration include the various other components. By supplying cowpea plants with an intermittent source of nitrate and observing the change in respiration rate, Sasakawa & LaRue (1986) measured the cost as 0.4 kg carbon (kg nitrogen)\(^{-1}\). In that experiment, there was a measured increase in reduced nitrogen throughout the plant, but little nitrate reductase activity was observed in the roots: it is possible that the shoot supplied the reduced nitrogen to the root. In a similar experiment on perennial ryegrass, G. J. A. Ryle (personal communication) has estimated the cost of nitrate uptake to be 0.76 kg carbon (kg nitrogen)\(^{-1}\). However, this may also include some cost for nitrate reduction as well as uptake (G. J. A. Ryle, personal communication). Veen (1981) regressed root respiration data with root growth rate, root volume and ion uptake and estimated the cost as 0.89 kg carbon (kg nitrogen)\(^{-1}\). In that analysis, Veen assumed \( \lambda = 0.9; \) with \( \lambda = 0.81, \) as used here, his data give 0.80 kg carbon (kg nitrogen)\(^{-1}\) for the cost of ion uptake. If nitrate was being reduced in the roots for shoot growth or vice versa, this may also affect Veen's analysis.

Simplified models of ion uptake and transport often assume that the ions cross one epidermal cell membrane, transport to the xylem is through the symplast continuum and a second membrane is crossed to the xylem (Pitman, 1982). Active transport across membranes, using ATP as an energy source, is understood to be facilitated either by carrier proteins, or by the production of electrochemical gradients produced by pumping protons out of the cell (Mengel & Kirkby, 1982). With the carrier model, on the assumption that the cost for transport across a membrane is one mole ATP per mole ion (Mengel & Kirkby, 1982, p. 119) and that one mole glucose produces 36 mole ATP, transport of nitrate across two membranes is equivalent to approximately 0.3 kg carbon (kg nitrogen)\(^{-1}\). However, it is possible that the proton pump mechanism must also be active and so it may be too simplistic to assume the only cost of ion uptake is that required to transport the ions across two membranes.

It is apparent that there is some variation in the estimates for the cost of ion uptake. Each technique has its limitations but, at the same time, provides useful information. Furthermore, it is quite possible that ion uptake costs vary between different species and possibly in different environmental conditions. The advantage of the present approach is that it does not involve disturbing the plants, and so possibly affecting other respiratory processes.

The greater maintenance costs of root material has been explained in terms of replenishing the efflux of ions from the root to the external medium, and the extent to which this occurs depends on the root temperature. Since higher root temperatures are associated with higher specific root activity (Davidson, 1969), the substrate nitrogen concentration will rise...
(Bhat, Nye & Brereton, 1979), increasing the concentration gradient between the plant and external medium. This is likely to increase the efflux of nitrate from the root. The extent to which nitrate efflux occurs according to the present model is consistent with direct measurements of nitrate efflux (Jackson, Volk & Israel, 1980). As suggested by Amthor (1984), the greater root maintenance may also be due, in part, to the high costs of maintaining nitrate reductase which has a very short turnover time: however, this may equally well affect shoots with significant amounts of nitrate reductase.

The model gives a means of assessing the site of nitrate reduction from respiration data. For the data considered here, the model indicates that 35% of nitrate reduction required for shoot growth occurs in the shoot (eqn 10b). One value of using respiration data in this way is that it is non-destructive, unlike the two main methods currently used (as reviewed by Andrews [1986]). The first involves an *in vivo* assay which relies on the endogenous levels of nitrate and reductant. However, as emphasized by Andrews (1986), during this assay nitrate and photosynthate fluxes to the tissue cease and the local internal substrate concentrations are diluted. These disturbances may well alter the activity of nitrate reductase. The other approach is to examine xylem sap from decapitated plants and measure the proportions of reduced and nitrate nitrogen. Using this technique, Pate (1973) has analysed a large range of plants and has concluded that plants may reduce virtually all their nitrate in the roots, or all in the shoots, or have some intermediate strategy. However, it has been argued that this technique may not necessarily give a good indication of nitrate reductase activity (Pate & Atkins, 1983; Andrews, 1986). It is, nevertheless, established that the extent to which nitrate reduction occurs in different regions within the plant will vary between species and growing conditions (Pate, 1973; Andrews, 1986).

The strategy of reducing nitrate in the shoot may have considerable ecological significance. Nitrate reduction is energetically very expensive; approximately 81% of the energy required to synthesize protein is used for nitrate reduction and synthesis of the constituent amino acids. If some of this nitrate is reduced in the shoot, then during the light period energy may be used directly from photosynthesis rather than from fixed carbon. Although the model provides a means for estimating the amount of nitrate reduction in the shoot, this is likely to vary for different plants as well as for plants growing in different environments.

One component of respiration not included in the present model is the cyanide-resistant respiratory pathway, by which respiration occurs with a far lower yield of ATP than the usual cyanide-sensitive pathway. However, there is still considerable debate as to the possible extent to which this respiratory pathway is involved *in vivo*, as discussed by Farrar (1985). Furthermore, with this component not included, the behaviour of the model is consistent with experimental information.

The models described in this paper provide a basis for analysing experimental data of respiration in plants, and for understanding the respiration associated with growth, maintenance, ion uptake and nitrogen assimilation. While these processes occur simultaneously, they may be identified individually by using the models. This means that physiological parameters, such as the cost of ion uptake, may be estimated indirectly through an understanding of the major respiratory processes involved. One important advantage of the present technique is that it involves analysing data from undisturbed plants; this is a potentially powerful strategy which may complement attempts to make direct measurements of individual physiological processes.

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