Plant Respiration

Roger Gifford
CRC for Greenhouse Accounting
CSIRO Plant Industry

Introduction

This paper concerns calculation of plant autotrophic respiration rate, which may emit about half of the CO_2 fixed by photosynthesis (Ryle 1984). At the same time it generates chemical energy and reducing power as well as metabolites that are used as the building blocks for synthesis of organic molecules. It does this through multi-step biochemical pathways - glycolysis, the TCA cycle and pentose phosphate pathway and a mitochondrial electron transport chain. Even though about half the gross photosynthate produced is dissipated by respiration our capacity to model it falls well short of our capacity to model photosynthesis.

Mechanistic carbon cycle models are concerned with calculating the CO_2 emitted by whole plant respiration to subtract from photosynthetic fixation by the leaves. To do this, understanding of the "logic" of its regulation should be helpful. The dynamic regulation of respiration is complex. The over-arching logic behind the regulation of the rate of respiration at the cellular level is determined by the relative requirements for chemical energy and reducing power, and C-skeletons for biosynthesis of complex molecules. At the level of electron transport in the production of ATP it is the local supply of ADP and AMP that may be in control.

Respiration may sometimes, however, be controlled by the supply of its substrate – translocated sucrose. Thus respiration can be controlled by the photosynthetic source, the utilization sink, or by a combination of both. A complexity is that, within the electron transport chain, there is also the potential for an alternative oxidase to be engaged that has the effect of allowing respiratory CO_2 release without concurrent generation of ATP. The function of this apparently CO_2-wasting respiration is unclear and its regulation is not understood (Affourtit ***et al.*** 2001)

Considered mechanistically from the bottom up, control of respiratory CO_2 release seems hopelessly complicated to capture in productivity models. Accordingly, simplifying notions about the high level logic of respiration have had to be devised. Several approaches have been adopted.

Respiration-modelling approaches in productivity models

Non-explicit treatment of respiration

The simplest way to represent respiration is to embed it implicitly in parameters of empirical growth functions that don't explicitly recognise photosynthesis. Many vegetation production models calculate net primary productivity (i.e new tissue growth rate) by functions that are calibrated to relate primary production directly to the environmental drivers and modulators of plant growth like radiation, water supply, temperature, nutrition and stress factors. A popular approach to such models is to calculate NPP as the amount of solar radiation intercepted or absorbed by green leaves multiplied by an efficiency of conversion of solar energy into plant dry matter. The efficiency term may be taken to be constant or to be a function of some variables such as temperature. Such models do not need to represent respiration as they enter the biological hierarchy at a higher level than that of process physiology, respiration being built into the empirical parameterisation of the growth functions.

Specific respiration

Models that do attempt to include representation of physiological and biochemical mechanisms of CO_2 exchange need to calculate respiration separately for subtraction from photosynthesis to determine growth. Thus:

$$R = R_s(T) \cdot W \qquad (1)$$

where R is respiration rate per plant, W is the dry weight per plant and R_s is the specific respiration rate that varies with temperature, T. However, it was found that specific plant respiration is far from a constant at any given temperature.

Growth and maintenance

Specific respiration rate is high in young fast growing tissues and small in non-growing tissues and can respond quickly to change in environmental factors. This fact led to recognition that there could be a background or basal rate of specific respiration combined with a respiration rate that was linked to the rate at which the tissue or plant was photosynthesising or growing. This idea was formulated at the whole plant level by

McCree (1970) and by Thornley (1970). McCree suggested that the dynamic component be related to the rate of plant photosynthesis

$$R = mW + pP \quad (2)$$

where R is the respiration rate per plant or per unit ground area, P is the photosynthesis rate per plant or per unit ground area, m is a respiratory maintenance coefficient and p is a coefficient for respiration related to photosynthesis rate.

Thornley (1970) showed that the dynamic part could equivalently be related to new growth (i.e. to photosynthesis minus respiration)

$$R = mW + gG = R_m + R_g \quad (3)$$

Where G is the growth rate per plant or per unit ground area calculated as (P-R), and g is the growth coefficient.

At the same time it was also recognised that respiration linked to the rate of growth was mainly that required to energise synthesis of the new complex molecules (proteins, membranes, cell walls etc) that constitute growth (Beevers 1970).

It has also been recognised that a substantial part of the energy requirement for maintenance may be for protein turnover. Thus another way to express the concept is as:

$$R = m_n W_n + gG \quad (4)$$

where W_n is the N content of the plant and m_n is the maintenance expressed on a nitrogen basis. While it was conceived that a major energy demand for plant tissue maintenance would be protein turnover it has also been recognised that maintenance of membrane integrity and solute gradients must contribute (Penning de Vries *et al.* 1983).

A problem with growth and maintenance formulations is that they are purely notional constructs. Growth and maintenance are not biochemically distinct. The concept does not withstand close scrutiny. They are defined only operationally by the measurement approach adopted and the assumptions involved in such measurements. There are several approaches to measuring growth and maintenance components; each involves different assumptions and therefore measures different properties of respiration.

Growth and maintenance coefficients measured even by the same method are not necessarily constant (Amthor 2000) for several reasons. One is that their values depend on the composition of the plant being grown and maintained. Maintenance of wood that is mostly lignocellulosic cell wall requires much less energy than maintenance of leaves containing a high fraction of functional enzyme-proteins and membranes, for example. And the energy for wood growth is very different from the energy requirement for growing oily or proteinaceous tissues. Penning de Vries *et al.* (1983) addressed the compositional question in determining the growth coefficient by substituting organic synthesis respiration for growth respiration assuming that these processes occur at maximum efficiency and are uninfluenced in their energy requirement by temperature and stress. They calculated theoretical energy requirements to synthesise the variety of compounds found in plants to estimate the synthesis respiration for a diversity of species.

A second reason why growth and maintenance coefficients are not constant is that there are carbon (energy) utilizing plant process that are not readily classified as either growth or maintenance. Under the growth and maintenance concept such respiration-requiring processes are forced into one or other of the coefficients by whatever means is adopted to determine them. For example, where environmental conditions trigger operation of the alternative oxidase, which may act as a C wasting valve, the CO_2 emitted does not logically fall under either growth or maintenance; its classification under a technique that breaks down respiration into just those two components is not obvious. Phloem loading for long distance transport of photoassimilate is energy demanding but services the carbohydrate requirements of both growth and maintenance. Similarly, nutrient uptake by the root system consumes energy; how it should be classified under the growth and maintenance concept is unclear. Accordingly, van Veen (1980) suggested that ion uptake requires separate consideration. However, there are also other energy requiring processes occurring in plants such as N-fixation in some species, and nitrate reduction which can occur in roots or leaves the proportion varying with species (Thornley and Cannell 2000).

Although for a period it became conventional to relate maintenance respiration closely with protein turnover, the case is not, however, strong for modelling maintenance respiration based on the assumption that it is best related to plant N content.

An alternative way to treat components of respiration – the "process-residual" approach

To deal with the unavoidable fuzzy boundaries between maintenance and growth, Cannell and Thornley (2000)

proposed a different approach in which each respiration-demanding process is regarded as an independently acting process which can be assessed individually. In this approach, the model would first calculate the respiration of each individual process that can be quantified. For example, there might be data that would allow calculation of the energy demand of new synthesis of N-fixation, of N-uptake, of nitrate reduction, of other ion uptake, and of phloem loading. Then any other processes not explicitly calculated would be lumped into the residual respiration. The approach is called the "process-residual" approach. It is adopted in Thornley's Hurley Pasture Model (HPM) and the Edinburgh Forest Model (EFM) (Thornley and Cannell 2000). The HPM and EFM were run with the process-residual approach for a full year or full forest rotation, respectively. It was found that the energy requirements of mineral nutrition are minute compared with those of new materials synthesis, phloem loading and the residual components that cover protein turnover, C-wasting respiration and maintenance of ion and other gradients in cells and tissues.

Respiration:photosynthesis ratio

It has been found in practice that for whole plants and ecosystems the ratio of respiration to gross photosynthesis is conservative over a wide range of plant sizes and growth rates, CO_2 concentrations and temperatures. This is equivalent to conservatism in carbon use efficiency, CUE (NPP/GPP) and in respiration to GPP ratio. In practice measurements have shown that at the whole plant level R:P ratio is typically within the range 0.35-0.6. Utilization of this approach in models has experienced a resurgence over the last few years (Gifford, 1994; 1995, Waring *et al* 1998).

Survey of specific model treatments of respiration

Models that have plant productivity as output must deal with autotrophic respiration in some way, be it implicitly in some cases. Examples of models for which respiration is embedded implicitly in the parameters that relate growth to environmental variables include: the crop models of the APSIM farm-system suite of models, the rangeland production/management model GRASP, the ecosystem level forest model LINKAGES, the agricultural soil C model SOCRATES, the continental C-cycle model VAST and the forest productivity model G'Day when simulating water limiting conditions.

Models which assign values of specific respiration include the carbon cycle model CENTURY, and G'Day when water is not growth limiting during the growing season. In each case, specific respiration is expressed as a function of N-concentration and temperature. Models that utilise the growth and maintenance approach are the forest productivity model CenW (as one option) and the forest growth and yield model Promod. Use of constant values of either R:GPP ratio or NPP:GPP ratio as inputs are allowed as options in CenW and G'Day. They are the sole option in the simple terrestrial C-cycle models CQUEST and CQUESTN, and in the forest growth model 3PG. The forest carbon cycle model FullCAM uses 3PG as a sub-model and hence relies on the NPP/GPP ratio to expresses respiration.

Some unresolved issues in autotrophic respiration

There is a significant problem in whole-plant respiration studies of not being able routinely to measure autotrophic respiration of leaves by day when photosynthetic CO_2 uptake is occurring. Commonly it is assumed in whole plant studies and models that respiration continues by day at the rate it does at night, possibly responding to short term diurnal variation in leaf temperature. However, there is evidence both for and against a reduction of leaf autotrophic respiration in the light (Lambers 1997).

There are many papers reporting that plant respiration is partially suppressed by elevated atmospheric CO_2 concentration. Both short term reversible effects and long term irreversible effects have been described (Drake *et al*. 1999). While there are significant doubts about the validity of that conclusion under doubled CO_2 concentration, the reality or not of the phenomenon has not yet been resolved (Bunce 2001).

Most C-cycle and productivity modelling approaches adopt a high sensitivity of specific respiration to temperature with a Q_{10} > 2 (Ryan 1991). However, in the long term, plant respiration seems to acclimate to a temperature change over several days to a week (Gifford 1995). The acclimated Q_{10} may be much less than 2. For example, whole plant specific respiration of sorghum plants (Gifford 1992) grown and measured at a range of constant temperatures was only 1.3 whereas the short-term sensitivity (hours) of whole plant specific respiration to temperature was much greater (Figure 1a). When expressed as a ratio of 24 hour respiration to 24hr photosynthesis per plant, the sorghum plants showed a low response to growth temperature (Figure 1b).

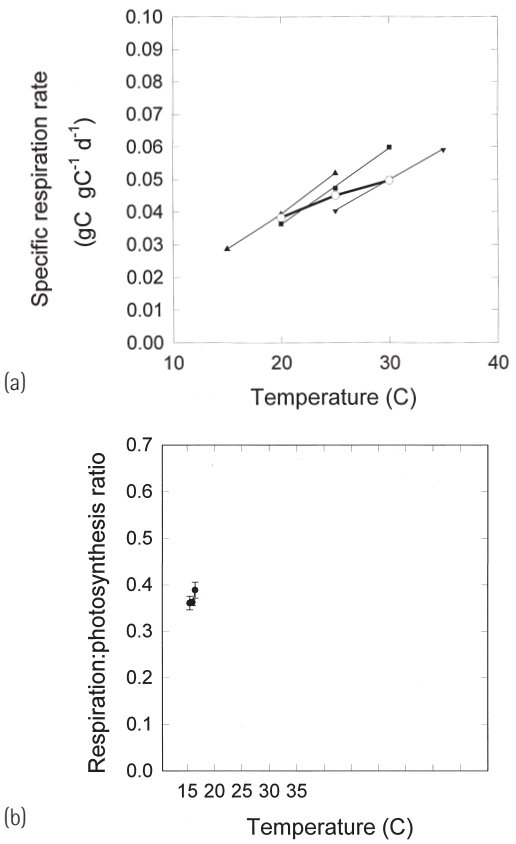

Figure 1. R*espiration of Sorghum bicolor plants.*

a) Specific respiration rates of whole plants (including roots in inert potting medium) grown and measured at the plotted temperatures (open symbols at 20, 25 and 30C), or grown at those three temperatures but measured at temperatures 5C above and below those growth temperatures as well as at the growth temperatures (solid symbols). The Q_{10} that best fits the temperature-acclimated response (open symbols) is 1.3 (Gifford 1992). Each point is a mean of 4 replicate plants.

b) *The 24 hr whole plant respiration to photosynthesis ratio of sorghum plants (including roots in inert potting medium) grown and measured at the plotted temperatures. Each point is a mean of 4 replicate plants. The error bars are ± the standard errors of the mean.*

Whether "wasteful respiration" occurs in plants is a moot point. The alternative oxidase (cyanide insensitive) pathway of respiration is only sometimes engaged and can vary in its degree of engagement. When it is engaged, it functions to generate much less ATP per unit CO_2 evolved than does normal cytochrome oxidase pathway. Yet it is a reasonable hypothesis that it becomes engaged to optimise overall plant performance in some way (Lambers 1997). Either way, since the underlying logic of regulation of the alternative pathway is not understood, expressing its functioning explicitly in productivity models is problematic.

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References

Affourtit C; Krabb K; Moore AL. (2001) Control of plant mitochondrial respiration. *Biochimica et Biophysica Acta /Bioenergetics*, **1504**:58-69.

Amthor JS (2000) The McCree-de Wit-Penning de Vries-Thornley respiration paradigms: 30 years later. *Annals of Botany* **86**: 1-20.

Bunce JA. (2001) Effects of prolonged darkness on the sensitivity of leaf respiration to carbon dioxide concentration in C_3 and C_4 species. *Annals of Botany* **87**: 463-468.

Beevers H (1970) Respiration in plants and its regulation. pp209-214 in *Prediction and measurement of photosynthetic productivity : proceedings of the IBP/PP Technical Meeting, Trebon, 14-21 September 1969.* International Biological Programme (ed). Wageningen, Centre for Agricultural Publishing and Documentation. 632p.

Cannell MGR and Thornley JHM (2000) Modelling the components of plant respiration: Some guiding principles. *Annals of Botany* **85**: 45-54.

Drake BG, Azcon-Bieto J, Berry J, Bunce J, Dijkstra P, Farrar J, Gifford RM, Gonzalez-Meler MA, Koch G, Lambers H, Siedow J, Wullschleger S (1999) Does elevated atmospheric CO_2 concentration inhibit mitochondrial respiration in green plants? *Plant Cell Environment* **22**: 649-657.

Gifford RM (1992) Impact of greenhouse effect temperature increase on the carbon balance of vegetation. *Energy Research and Development Corporation (Australia) Project Report No. 1402* (ISBN No. 06 421 71491).

Gifford RM (1994) The global carbon cycle: a viewpoint on the missing sink. *Australian Journal Plant Physiology* **21**: 1-15.

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.

Lambers H (1997) Oxidation of mitochondrial NADH and synthesis of ATP. pp200-219 in *Plant Metabolism.* DT Dennis, DH Turpin, DD Lefebvre and DB Layzell eds. 2nd Edition. Addison Wesley Longman, Harlow, UK. 529p.

McCree KJ (1970) An equation for the rate of respiration of white clover plants grown under controlled conditions. pp221-229 in *Prediction and measurement of photosynthetic productivity: proceedings of the IBP/PP Technical Meeting, Trebon, 14-21 September 1969.* International Biological Programme (ed). Wageningen, Centre for Agricultural Publishing and Documentation. 632p.

Penning de Vries FWT, van Laar HH and Chardon MCM (1983) Bioenergetics of growth of seeds, fruits, and storage organs. pp 37-59 in *Potential productivity of field crops under different environments.* International Rice Research Institute, Los Banos, Phillipines.

Ryan MG (1991) Effects of climate change on plant respiration. *Ecological Applications* 1: 157–167.

Ryle GJA (1984) Respiration and plant growth. In Palmer JM (ed) *Physiology and Biochemistry of Plant Respiration,* Cambridge University Press, Cambridge, UK.

Thornley JHM (1970) Respiration, growth and maintenance in plants. *Nature* **227**: 304-305.

Thornley JHM and Cannell MGR (2000) Modelling the components of plant respiration: Representation and realism. *Annals of Botany* **85**: 55-67.

van Veen BW (1980) Energy costs of ion transport. pp187-195 in *Genetic engineering of osmoregulastion. Impact on plant production for food, chemicals and energy.* (DW Rains, RC Valentine, A Hollaender, eds). New York, Plenum Press.

Waring RH, Landsberg JJ and Williams M (1998). Net primary production of forests: a constant fraction of gross primary production? *Tree Physiology* **18**: 129–134.