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REVIEW

The McCree–de Wit–Penning de Vries–Thornley Respiration Paradigms: 30 Years Later

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To grow, an organism must respire substrates to produce C-skeleton intermediates, usable energy (i.e. ATP), and reducing power [i.e. NAD(P)H] to support biosynthesis and related processes such as active transport of substrates. Respiration is also needed—mainly as a supplier of ATP—to maintain existing biomass in a functional state. As a result, quantifying links between respiration, growth, and maintenance are needed to assess potential plant productivity, to understand plant responses to environmental factors, and as the basis of cost-benefit analyses of alternative uses of photosynthate. Beginning 30 years ago, and continuing for about 5 years, rapid advances were made in understanding and quantifying relationships between respiration and the processes it supports. Progress has continued since then, though often as refinements rather than novel advances. The simplest framework (i.e. paradigm) for relating respiration to other processes divides respiration into growth and maintenance fractions. This often involves a combination of empiricism and mechanism. A three-component framework (growth, maintenance and wastage) has also been considered, although quantifying wastage (theoretically or empirically) remains problematic. The more general and flexible framework, called the *general paradigm* (GP, herein), relates respiration to any number of individual processes that it supports. The most important processes (from C and energy balance perspectives) identified to date that require respiration are: biosynthesis of new structural biomass, translocation of photosynthate from sources to sinks, uptake of ions from the soil solution, assimilation of N (including N_2) and S into organic compounds, protein turnover, and cellular ion-gradient maintenance. In addition, some part of respiration may be associated with wastage (e.g. futile cycles and mitochondrial electron transport uncoupled from oxidative phosphorylation). Most importantly, the GP can (semi-)mechanistically relate respiration to underlying physiology and biochemistry. The GP is more complicated than other approaches to describing or modelling respiration because it is more realistic, complete and mechanistic. This review describes a history of the GP and its present state. Future research questions are suggested.

Key words: Review, growth, history, maintenance, model, paradigm, respiration.

INTRODUCTION

Respiration is a complex, pivotal metabolic process in higher plants. It produces C-skeleton intermediates, usable energy (ATP), and reducing power [NAD(P)H] needed for most growth and maintenance processes. As a result, it converts a large fraction of photosynthate back to CO_2 (Appendix 1). Despite the importance of respiration to plant metabolism and C balance, some of its key facets are still poorly understood and quantifying relationships between photosynthesis, respiration and growth is an area of active research.

Thirty years ago (September 1969) at the International Biological Programme section of Production Processes (IBP/PP) Technical Meeting in Třeboň, Czechoslovakia, K. J. McCree (1970) presented the following empirical[1] equation relating whole-plant respiration to photosynthesis and dry mass:

$$R = k_1 P + cW \quad (1)$$

where R is daily respiration [g CO_2 m^{-2} (ground) d^{-1}], P daily 'gross' photosynthesis [g CO_2 m^{-2} (ground) d^{-1}], W living dry mass [g CO_2 equivalents m^{-2} (ground)], k_1 a dimensionless ratio, and c a rate (d^{-1}). The term $k_1 P$ was later associated with 'growth respiration' and cW with 'maintenance respiration'. Equation (1), based on laboratory experiments, is noteworthy because it triggered (or catalyzed) a series of advances in a larger programme of understanding and modelling respiration, with many key advances published by 1975. The programme was driven by modellers because they needed better respiration algorithms to accurately simulate C balances. The importance of the

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[1] Progress in understanding and modelling respiration can be judged in part by whether a treatment is mechanistic or empirical. *Empirical* models describe data, but do not explain it (Loomis *et al.*, 1979). Fitted lines are empirical models. Although they can be powerful, they contain no information beyond the data (Thornley and Johnson, 1990). Conversely, *mechanistic* models are reductionist and explain data based on knowledge of processes at lower levels of biological organization. A mechanistic model of physiology is therefore generally based on biochemical principles such as enzyme kinetics and reaction stoichiometries. In turn, a mechanistic model of biochemistry is based on chemical or physical principles, and on and on 'down' levels of complexity, with the 'lowest' level *always* described empirically.

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TABLE 1. *Number of times key plant 'growth and maintenance respiration' publications from 1969–75 were cited in subsequent journal articles*

Original publication	Number of journal articles citing publication
McCree (1969, 1970)*	258
Thornley (1970)	135
Hesketh *et al.* (1971)	80
Penning de Vries (1972)	131
McCree (1974)†	213
Penning de Vries (1974)	63
Penning de Vries *et al.* (1974)	385
Penning de Vries (1975*a*)	333
Penning de Vries (1975*b*)	173

Citation counts are from the printed version of *Science Citation Index* for 1970–72 and from the world wide web version of *Science Citation Index Expanded*® for 1973 to February 2000. These counts include only the journals covered by *Science Citation Index*. All these articles except Hesketh *et al.* (1971) and Penning de Vries (1974) were cited in 1999.

* These are two forms of a 'single' article, with the 1970 form usually cited.

† This paper was chosen as a *Citation Classic*® in 1985 for the Agriculture, Biology & Environmental Sciences edition of Institute for Scientific Information® *Current Contents*® (McCree, 1985).

major 1969–75 publications advancing this programme is indicated by extent of their citation in journal articles (Table 1).

This review presents a history of models of higher-plant respiration related to eqn (1), and outlines relationships between respiration and processes that it supports, such as growth and maintenance. It then briefly discusses the ratio of respiration to photosynthesis, considers effects of rising temperature and CO_2 concentration on respiration, and closes with questions posed to guide further research.

RESPIRATION PARADIGMS

Three paradigms—meaning theoretical frameworks for research—are considered in this review. They are each based on relationships between respiration and different, distinguishable processes that it supports by producing C-skeleton intermediates, NAD(P)H and ATP. The two most general (i.e. at high levels of biological organization) distinguishable processes are growth of new biomass and maintenance of existing biomass. That is, there is a fundamental difference between adding to the total amount of proteins, lipids, cellulose, minerals, etc. in cells (i.e. growth) and turning over proteins and lipids or pumping mineral ions back across membranes through which they have leaked (i.e. maintenance). This difference is the basis of the first paradigm, which I call the *growth-and-maintenance-respiration paradigm* (simply GMRP hereafter). It recognizes that growth and maintenance are fundamentally different, and assumes that all metabolic processes supported by respiration can be included under either 'growth' or 'maintenance' rubrics, although growth and maintenance share some biochemical reactions. The GMRP is usually associated with empirical studies, though it has a theoretical underpinning and can be treated (semi-) mechanistically. Equation (1) can be interpreted within the GMRP, as outlined below.

The second paradigm I call the *growth-and-maintenance-and-wastage-respiration paradigm* (simply GMWRP hereafter). It recognizes that some respiration may occur without benefit to a plant. It is a simple extension of the GMRP in which some respiration supports growth, some supports maintenance, and some may be wasted. Wasted respiration produces CO_2 and/or heat, but does not contribute directly to growth or maintenance. Futile cycles of ATP production and hydrolysis are supported by 'wastage respiration'. Activity of the mitochondrial alternative oxidase might also contribute to wastage. Equation (1) can be interpreted within the GMWRP if some fraction of k_1 and/or c account for CO_2 release not contributing to growth or maintenance.

The third paradigm is more general; I call it the *general paradigm* (simply GP hereafter). The GP recognizes that individual relationships exist between respiration and each distinguishable biochemical process that it supports, including wastage. The GP represents the larger research program relating rates of respiration to rates of other processes. To use eqn (1) within the GP, relationships between photosynthesis and other processes (such as growth) must be established and both k_1 and c must be decomposed to account for individual biochemical processes. Most importantly, the GP relates respiration (defined in its broadest sense of CO_2 or O_2 exchange) to underlying biochemistry and physiology and provides opportunities to do this mechanistically and quantitatively, although many aspects of biochemistry underlying respiration and processes it supports remain uncertain. This is in contrast to empirical approaches that merely describe (rather than explain) observed respiration rates. Thus, the GP (but not empirical models) can address the question 'How much growth *could* occur from a unit of photosynthesis?' from the perspective of hard science.

The title of this review is meant to suggest that all the paradigms are related and that work within all three began in earnest about 30 years ago. Indeed, the GMRP and the GMWRP are subsets of the GP.

For many reasons, photosynthesis is an important consideration for all three paradigms. In broad terms, photosynthesis supplies C substrates used in respiration, growth and maintenance, but relationships between photosynthesis and respiration can be more direct than this. For example, photosynthesis might directly supply ATP, NAD(P)H, and C-skeletons to processes 'normally' supported by respiration, obviating some respiration in photosynthesizing cells. This complicates extrapolations of night-time respiration measurements to daytime, and calculations of daytime respiratory requirements, in photosynthetic cells. It also affects interpretations of photosynthetic production as measured by daytime CO_2 uptake because photosynthesis may at the same time be assimilating inorganic N and S, directly supporting biosynthesis in growing photosynthetic cells (though most growth occurs

outside photosynthetically active cells), and driving phloem transport (e.g. Penning de Vries, 1975*b*).

BACKGROUND AND BASIC EQUATIONS

The 1969 Třeboň meeting, and its 1970 proceedings (Šetlík, 1970), provided the first major venue for discussions of the paradigms (e.g. Beevers, 1969, 1970; de Wit and Brouwer, 1969; McCree, 1969, 1970; Canvin, 1970*a*,*b*; de Wit *et al*., 1970; Evans, 1970; Lake and Anderson, 1970; Loomis, 1970; Monsi and Murata, 1970; Tooming, 1970). An earlier, notable interaction that contributed to the importance of the Třeboň meeting occurred among McCree, C. T. de Wit, and R. S. Loomis during spring 1968 at the University of California in Davis, USA. De Wit was trying to quantify respiration and relate it to appropriate variables in his ELementary CROp Simulator (ELCROS, a computer program) while McCree was analysing CO_2 exchange data for *Trifolium repens* L. obtained as follow-up to earlier work (McCree and Troughton, 1966*a*,*b*). The significance of those data for modelling respiration became obvious to the group, including the concept that respiration related to growth was 'separate' from respiration related to maintenance (McCree, 1985; R. S. Loomis, pers. comm., 1990). De Wit then invited McCree to present his data at Třeboň (McCree, 1985) and incorporated them into ELCROS (de Wit *et al*., 1970). As a result, eqn (1) initiated important *quantitative* uses of all three paradigms, but there was an even earlier, underlying foundation.

Microbiologists concerned with production efficiency of fermentation processes were first to distinguish energy use in growth from use in maintenance, beginning with Duclaux (1898; see Pirt, 1965, and Penning de Vries, 1972). The first comprehensive discussion of the GMRP for plants (of which I am aware) was by Wohl and James (1942). Their insightful work was 30 years ahead of its time, however, with little apparent impact on respiration research, and even James (1953, p. 257) later understated their penetrating analysis. By the early 1960s it was clearer that respiration was linked causally to plant growth and that factors stimulating growth simultaneously enhanced respiration (e.g. Audus, 1960; Beevers, 1961, pp. 185–197; Gaastra, 1963). A role for respiration in maintenance was also appreciated (e.g. Olson, 1964; Yemm, 1965). This exalted respiration to a process doing more than just releasing CO_2 and heat—it was needed for growth and maintenance (Tanaka and Yamaguchi, 1968; Beevers, 1970)—and the GMRP was included in early C-balance models by Hiroi and Monsi (1964) and Monsi (1968). At about the same time, Warren Wilson (1967) outlined the GMWRP when he identified three components of respiration: (1) 'maintenance respiration', 'to maintain existing organization, for example in the uptake of salts to replace those passively lost, and in the continuous turnover of protein'; (2) 'constructive respiration', to synthesize 'new structures in growth'; and (3) 'substrate-induced respiration', occurring 'when sugar levels have been raised', and presumably unrelated to growth or maintenance. Warren Wilson then produced a hypothetical mass balance for plants indicating that maintenance plus substrate-induced respiration was about equal in magnitude to growth respiration, but no mechanistic basis for this assertion was presented.

Other references could be cited, but this is sufficient to show that before the Třeboň meeting the GMRP, the GMWRP, and precursors of the GP existed in several forms. It could have been expected, therefore, that once a body of quantitative experimental data (from McCree, 1970, and shortly thereafter others) and mechanistic calculations (mainly from F. W. T. Penning de Vries during the early 1970s) were applied to plants within the paradigms, that uses of the paradigms would increase. This was the case, and follows directly from Yemm's (1965) point that 'a deeper understanding of the significance of respiration in the metabolism and energy economy of plants [would] *require quantitative information*, not only of the catabolic mechanisms, but also of the anabolic systems with which they may be coupled' (italics added).

Early GMRP equations for plants were published by de Wit *et al*. (1970), McCree (1970), Thornley (1970), and Hesketh *et al*. (1971). The simplest was:

$$R = R_G + R_M = g_R G + m_R W \qquad (2)$$

where R was respiration rate (e.g. mol CO_2 s^{-1}), R_G was growth respiration rate (e.g. mol CO_2 s^{-1}), R_M was maintenance respiration rate (e.g. mol CO_2 s^{-1}), G was growth rate (e.g. g new biomass s^{-1}), W was living biomass (e.g. g dry mass), g_R was a growth respiration coefficient (amount of CO_2 released *due to growth* per unit growth; e.g. mol CO_2 (g new biomass)$^{-1}$), and m_R was a maintenance respiration coefficient (amount of CO_2 released *due to maintenance* per unit existing biomass per unit time; e.g. mol CO_2 (g living biomass)$^{-1}$ s^{-1}). Growth was defined in many ways; the most useful definition was conversion of reserve materials (e.g. nonstructural carbohydrates) into new structure (i.e. structural carbohydrates, lignins, proteins, lipids, organic acids, etc.) rather than change in total dry mass (Warren Wilson, 1967; de Wit *et al*., 1970; Penning de Vries *et al*., 1979). That is the definition used herein. Importantly, g_R was a ratio representing the CO_2 by-product of growth, whereas m_R was a rate associated with maintenance activities. Both g_R and m_R can be estimated empirically by simultaneously measuring R and other variables, or calculated mechanistically from underlying process data. Both methods are used, with the mechanistic approach (based on the GP) first quantitatively articulated by Penning de Vries (1972, 1974, 1975*a*,*b*) and Penning de Vries *et al*. (1974) (see below). It should be made clear at the outset that g_R and m_R are variables, not constants.

The GMRP also formed the basis of a simple whole-plant growth equation (Thornley, 1970):

$$G = Y_G(P - R_M) = Y_G P - Y_G m_R W \qquad (3)$$

where Y_G was the yield of growth processes (i.e. amount of growth per unit substrate used *in growth processes*, including that part of substrate retained in new structure) and photosynthesis (P) had the same units as R. With consistent units, $Y_G = 1/(1 + g_R)$. Equation (3) applies to

whole plants in a *steady state* of substrate production in photosynthesis and use in growth and respiration. In that steady state, $G = P - R$ and McCree's (1970) $k_1 = 1 - Y_G$ and $c = Y_G m_R$ (Thornley, 1970). Equation (3) can be applied to an individual organ/tissue if P is replaced with the rate of substrate import and no net change in reserve material amount occurs in that organ/tissue. Monsi's (1968) earlier model contained forms of eqns (2) and (3), but it apparently played only a minor role in GMRP advances.

The issue of priorities for photosynthate use is sometimes raised. For example, is a fixed rate of maintenance respiration required, with growth then supported by the substrate 'left over'? Equation (2) does not specify priorities; it simply states that both R_G and R_M contribute to respiration in growing plants. On the other hand, some rate of maintenance is continuously needed in living cells and maintenance therefore probably entails some minimal priority for substrate use, but because m_R and g_R (and Y_G) are variables with respect to time and environmental conditions, apparent priorities may also vary. Plants dynamically balance substrate use between maintenance and growth activities depending on environmental conditions, physiological state, and developmental state. Implications of substrate-use priorities for maintenance *vs.* growth within the context of mathematical models were recently assessed by Thornley and Cannell (2000).

Thornley (1971) extended the GMRP by formalizing the GMWRP shortly after the Třeboň meeting [compare this to 'substrate-induced respiration' of Warren Wilson (1967) and 'idling respiration' of Beevers (1970)]. De Wit *et al.* (1970) thought it difficult to separate idling from maintenance. Thornley (1971) noted that wastage respiration could increase apparent g_R and/or m_R, depending on its biochemical nature. If mechanistic calculations determine what g_R and m_R 'should' be, these values could be compared to measurements of those coefficients [e.g. based on eqn (2)] to estimate the degree of wastage. To the extent that some respiration is 'wasted', the GMRP is incomplete.

An important point is that maximum productivity from a unit of photosynthate would be achieved if ATP and NAD(P)H produced by respiration were used only in reactions 'directly contributing to growth and maintenance' (Beevers, 1970). A related point is that the ratio of ATP production (from ADP and P_i) to CO_2 release in respiration should be related to productivity per unit photosynthesis. Herein, the ratio ATP produced per CO_2 released in the biochemical pathways of respiration is symbolized $Y_{ATP,C}$ [mol ATP (mol CO_2)$^{-1}$]. Note that $Y_{ATP,C}$ is a complicated variable, not a constant. The importance of $Y_{ATP,C}$, and being able to estimate it mechanistically (Appendix 2), arises from the points that most maintenance respiration probably involves ATP production and a considerable fraction of g_R is related to ATP production. Indeed, m_R is inversely related to $Y_{ATP,C}$, so an understanding of maintenance respiration rate relies directly on an understanding of $Y_{ATP,C}$. One aspect of respiratory efficiency (i.e. $Y_{ATP,C}$) that receives considerable attention is engagement of the alternative oxidase (e.g. Lambers, 1979; Millar *et al.*, 1998) which reduces the number of protons pumped across the inner mitochondrial membrane per NAD(P)H oxidized there. This in turn reduces $Y_{ATP,C}$, as quantitatively accounted for in Appendix 2.

The maximum value of $Y_{ATP,C}$ may be a little less than 5 (Appendix 2), whereas most previous mechanistic studies assumed that $Y_{ATP,C}$ was as large as 6 to 6·3 (e.g. Penning de Vries *et al.*, 1974; Penning de Vries, 1975*a*; McDermitt and Loomis, 1981; Williams *et al.*, 1987; Thornley and Johnson, 1990). Thus, modest amendments to many previous theoretical estimates of m_R and g_R (and other 'respiratory coefficients') are needed.

MAINTENANCE AND MAINTENANCE RESPIRATION

Defining maintenance is tricky, but the definition by Penning de Vries (1975*a*) remains useful: maintenance includes processes that maintain cellular structures and intracellular gradients of ions and metabolites, along with cellular acclimation (phenotypic adjustment) to environmental changes. Replacement of one set of enzymes with another during ontogeny may also be considered maintenance. Dominant maintenance processes are macromolecular turnover (i.e. simultaneous breakdown and 're'-synthesis) and active transport that offsets membrane leaks. The 'purpose' is to maintain cellular functionality. 'Maintenance respiration' is CO_2 release resulting from maintenance activities. Maintenance processes may consume mainly ATP rather than C-skeletons or NAD(P)H.

As outlined by Wohl and James (1942), maintenance respiration rate R_M can be calculated from rates of underlying processes if the metabolic costs and stoichiometries of CO_2 release of those processes are known. The questions then become, what are the rates of maintenance processes and what are their metabolic costs in CO_2 units? Answering these questions is a mechanistic approach to evaluating the maintenance respiration coefficient m_R. Penning de Vries (1975*a*) made the first comprehensive attempt to do this, considering mainly turnover and intracellular transport processes.

The coefficient m_R is decomposed to explicitly account for different maintenance processes with:

$$m_R = \Sigma_{processes,X}\, m_{R,X} = \Sigma_{processes,X}\, c_X a_X \qquad (4)$$

where X is a maintenance process, $m_{R,X}$ is the maintenance respiration coefficient for process X, c_X is cost of process X (in CO_2 per unit activity of X), and a_X is rate of process X per unit biomass (i.e. specific activity). Three processes—protein turnover, lipid turnover and active intracellular ion transport—are considered below. Equation (4) is 'complete' when all quantitatively important processes are included. But, until better estimates of *in situ* costs and activities of maintenance processes are obtained, mechanistic estimates of m_R will remain crude.

Turnover of cellular components

Most protein breakdown is catalyzed by proteases under metabolic regulation. Protein turnover allows cells to alter their enzyme makeup in response to ontogeny and/or

environmental changes, and it facilitates removal/replacement of abnormal or damaged proteins (Vierstra, 1993). Without turnover, protein requirements would be greatly increased because plants would need the full complement of proteins required to function across a range of environmental conditions and all stages of development. Rapid response (including acclimation) to environmental change or stress may require rapid turnover, though evidence that background turnover rate must be rapid is lacking.

ATP required per amino acid for protein turnover is estimated in Table 2; conversion to protein turnover cost c_{pt} in CO_2 per amino acid depends on the ratio of CO_2 release per ATP formed, or $1/Y_{ATP,C}$. The minimum (i.e. most efficient) value of $1/Y_{ATP,C}$ is about 0·2 CO_2/ATP (Appendix 2). This gives $c_{pt} \approx 0{\cdot}9$–$1{\cdot}6$ CO_2/amino acid for the case of complete amino acid recycling and with an ATP cost of 4·7–7·9 per amino acid (see Table 2); c_{pt} is larger with amino acid turnover [Table 2, note (b)]. Note that c_{pt} includes mRNA turnover cost (Table 2). Turnover of other RNAs is probably an even smaller fraction of c_{pt}.

Protein turnover rates may vary significantly among species, organs and environments, as well as temporally. For example, Zerihun *et al.* (1998) summarized literature indicating that between 6·5 and 21 % of total protein turns over daily, though data from plants in the field are limited. As a hypothetical example, biomass with 10 % protein turning over with a rate of 0·15 d^{-1} [i.e. $a_{pt} = 0{\cdot}1$ kg protein (kg biomass)$^{-1}$ × 0·15 d^{-1} = 0·015 kg protein (kg biomass)$^{-1}$ d^{-1}] would cycle amino acids through protein at a rate of 130 mmol (kg biomass)$^{-1}$ d^{-1} (for 0·119 kg mol^{-1} mean molecular mass of amino acids, i.e. $a_{pt}/0{\cdot}119$). [Hereafter, (kg biomass)$^{-1}$ is written kg^{-1}.] This gives 120–210 mmol CO_2 kg^{-1} d^{-1} as the maintenance coefficient for protein turnover $m_{R,pt}$ with c_{pt} as above. Bouma *et al.* (1994) estimated experimentally that 17–21 % of darkened, detached mature-leaf respiration was associated with protein turnover (equivalent to $m_{R,pt} \approx 200$ mmol CO_2 kg^{-1} d^{-1}).

Membranes (including their proteins) also turn over. The plasmalemma of some cells may turn over every few hours, though no metabolic cost of this rapid process was estimated (Steer, 1988). If lipids are catabolized during membrane turnover, biosynthesis of new lipids is required. The maintenance coefficient for membrane lipid turnover (i.e. $m_{R,lt} = c_{lt}a_{lt}$) can hardly be evaluated from available data: Penning de Vries (1975*a*) speculated that membrane turnover might have a respiratory cost of 60 mmol CO_2 kg^{-1} d^{-1}, whereas calculations in Thornley and Johnson (1990, pp. 365–366) lead to a respiratory cost of lipid turnover of 8 mmol CO_2 kg^{-1} d^{-1} (for $1/Y_{ATP,C} = 0{\cdot}2$ CO_2/ATP).

Turnover of other macromolecules (e.g. DNAs, chlorophylls, hormones) was estimated to be unimportant to m_R (Penning de Vries, 1975*a*). Nonetheless, rates and pathways (i.e. costs) of turnover are largely unknown for most macromolecules (see e.g. Matile *et al.*, 1999, for chlorophyll).

TABLE 2. *Estimated specific costs of component processes of protein turnover*

Process	Metabolic cost (ATP per amino acid)[a]
Protein breakdown (to amino acids)	0·13–2
Protein synthesis (from amino acids)[b]	
Amino acid activation	2[c]
Editing for misaminoacylation of tRNAs	0–0·15
Polypeptide initiation and elongation	$2 + 1/n$[d]
Editing noncognate aminoacyl-tRNA	0–0·01
Methylation, acetylation, glycosylation, etc.	0·1[e]
Phosphorylation	0·1–0·3[e]
mRNA turnover[f]	0·16–0·36
Signal sequences	0·18–1·0
Total synthesis	4·5–5·9[g]
Total (breakdown + synthesis)	4·7–7·9

Based on Zerihun *et al.* (1998); some values are speculative.

[a] Cost is expressed as ATP cleavage to ADP and P_i.

[b] Some amino acids produced by protein breakdown are recycled (i.e. repolymerized in subsequent protein synthesis) and some are catabolized. Synthesis of amino acids to replace those catabolized increases the cost of protein turnover (not shown); according to Zerihun *et al.* (1998), resynthesizing all the amino acids would increase total protein turnover cost by more than 83 % (see also Penning de Vries, 1975*a*; de Visser *et al.*, 1992).

[c] One ATP is cleaved to AMP and PP_i per amino acid. This is equated with 2 ATP through the action of adenylate kinase (i.e. ATP + AMP→2 ADP). Note that PP_i might serve as an energy source in other maintenance processes (e.g. active transport through tonoplasts).

[d] n is number of amino acid residues in a protein.

[e] From de Visser *et al.* (1992).

[f] mRNA turnover accounts for mRNA 'lifetime', i.e. number of protein molecules polymerized before an mRNA molecule is broken down.

[g] Assumes n is large (i.e. cost of polypeptide initiation and elongation is 2 ATP/peptide).

Intracellular ion-gradient maintenance

Active ion transport to counteract membrane leaks (or regulate pH or osmotic potential) is part of maintenance; the 'original' ion compartmentation is part of growth. To evaluate active ion transport cost (c_{ion}, CO_2/ion), CO_2 release must be related stoichiometrically to the transport energy source. That source can be ATP, but also PP_i at tonoplasts and perhaps NAD(P)H at plasmalemmas (Marschner, 1995, pp. 21–25). Using ATP, with H^+:ATP = 1:1 and ion:H^+ = 1:1, c_{ion} is $1/Y_{ATP,C}$. [Different values for c_{ion} may arise for PP_i or NAD(P)H use with the same ion:H^+.] Based on ion flux data from artificial conditions, Penning de Vries (1975*a*) gave 2 mol ion kg^{-1} d^{-1} as an order of magnitude of specific active transport a_{ion}. With $c_{ion} = 0{\cdot}2$ CO_2/ion (from maximum $Y_{ATP,C}$), the intracellular ion-gradient maintenance coefficient $m_{R,ion}$ ($=c_{ion}a_{ion}$) would be 400 mmol CO_2 kg^{-1} d^{-1}.

The possibly large contribution of ion-gradient maintenance to R_M does not fit well into the 'recycling' model of growth and maintenance respiration proposed by Thornley (1977). In that model, 'degradable' biomass is broken down over time and added to the pool of substrate (also supplied

by photosynthesis) used for biosynthesis and respiration (and see Thornley and Johnson, 1990; Thornley and Cannell, 2000). Substrate is simultaneously converted to biomass with efficiency Y_G, with $(1 - Y_G)$ of the substrate oxidized to CO_2. The fraction of CO_2 release associated with resynthesis of degraded biomass is called maintenance, but a difficulty arises because leaking ions may not contribute to the substrate pool nor does ion-gradient maintenance occur with efficiency Y_G. Although the recycling model is well posed to address the macromolecule-turnover component of maintenance, it is an incomplete model of respiration because it lacks ion-gradient maintenance.

The enclosed, multicellular nature of higher plants, along with the presence of much of their body in air, greatly limits ion leakage to the environment. (Roots grown hydroponically can be an important exception.) In contrast, bacteria in chemostats—which formed the basis of much early work on growth and maintenance principles—experience large ion gradients, with rapid leakage and consequently greater maintenance needs. This is seen in large values of bacterial m_R (typically ten–100 times plant values) determined in the laboratory. In soils, however, bacterial m_R is greatly reduced (as inferred from soil respiration rate).

Measuring m_R

In addition to calculating m_R (or its components) from costs and rates of underlying processes with eqn (4), it can be estimated by measuring respiration rate R. For example, eqns (1), (2), or (3) can be solved experimentally. When this is done for crop species at moderate temperatures, m_R falls in the range 110–4600 mmol CO_2 kg^{-1} d^{-1}, with root values often exceeding shoot/leaf/fruit values (Amthor, 1989, pp. 78–79). Caution is needed when using individual results because several factors can compromise accuracy (Amthor, 1989).

Measuring R/W during extended dark periods was proposed by Penning de Vries (1972) and McCree (1974) as another method of estimating m_R. McCree wrote: 'when a plant is placed in darkness, it uses up its reserves . . . and growth eventually stops. At this point, the efflux of CO_2 is entirely due to maintenance'. Because of its simplicity, this method was often used, but it may be unreliable. During extended dark periods, physiological functionality can decline (e.g. Challa, 1976; Breeze and Elston, 1983) and growth may continue (e.g. Robson and Parsons, 1981; Moser *et al*., 1982; Denison and Nobel, 1988), invalidating the assumption that respiration then reflects normal maintenance costs. Thus, this 'starvation method' of estimating m_R fell out of favour (McCree, 1986).

Another method of evaluating m_R is to measure R/W in 'mature' tissues/organs. The assumption is that mature organs do not grow so $R_G = 0$ and $R_M = R$. A complication is that even in mature organs non-maintenance processes may occur. For leaves—a favourite organ of study—the clearest difficulty concerns respiration supporting translocation (de Wit and Brouwer, 1969; Irving and Silsbury, 1988). Also, respiration supporting senescence and mobilization (including translocation) can be important in old leaves (de Wit and Brouwer, 1969). This 'mature-tissue method' is nonetheless popular for estimating leaf m_R (e.g. Ryan, 1995). Its appeal is that it does not involve special treatments or experimental conditions, simply intact-organ respiration measurements. It is used in winter to estimate tree-stem m_R based on the assumption that wood growth is halted then (e.g. Ryan, 1990; Sprugel, 1990; Ryan *et al*., 1995; Edwards and Hanson, 1996; Lavigne *et al*., 1996; Lavigne and Ryan, 1997; Maier *et al*., 1998; Stockfors and Linder, 1998). To apply these winter estimates of tree-stem m_R to other seasons, a temperature response function is used to account for seasonal (and diurnal) temperature changes. Mean annual tree-stem m_R in eight boreal forests estimated in this way ranged from 1·9 to 9·7 mmol CO_2 $(kg\ sapwood)^{-1}$ d^{-1} (Lavigne and Ryan, 1997), or one to three orders of magnitude smaller than crop-plant m_R values estimated with eqns (1), (2), or (3) (see above). (Heartwood is metabolically inactive.) Potential acclimation of sapwood maintenance processes to seasonal temperature patterns is a possible, but poorly understood, weakness in this application of the mature-tissue method. Moreover, it has not been established whether winter maintenance processes are well related to summer maintenance processes in sapwood.

General principles related to m_R

Two common generalizations about m_R—both first spelled out by de Wit *et al*. (1970)—are that it responds strongly to temperature and is positively related to plant N content (N; e.g. kg N). For short-term (hours to days) changes in temperature, the Q_{10} of m_R is typically about 2 (e.g. McCree, 1974; Penning de Vries, 1975*a*; Jones *et al*., 1978; McCree and Silsbury, 1978; McCree and Amthor, 1982; Marcelis and Baan Hofman-Eijer, 1995). It is possible that long-term (days to years) temperature changes lead to adaptation (genotypic adjustment) and/or acclimation of maintenance processes, but only a few data address this possibility. Whole-plant m_R of the perennial herb *Reynoutria japonica* was adapted to temperature at different altitudes (700 *vs*. 2420 m) (Mariko and Koizumi, 1993). Similarly, leaf m_R was greater at a given temperature for boreal and subalpine trees and shrubs compared with typical values from temperate-area plants (Ryan, 1995). Conversely, neither *R. japonica* whole-plant m_R (Mariko and Koizumi, 1993) nor *Cucumis sativus* L. fruit m_R (Marcelis and Baan Hofman-Eijer, 1995) acclimated to temperature changes imposed artificially for several weeks.

With respect to N, m_R can be better related to it than to W (or plant area or volume) in some cases (e.g. Penning de Vries, 1972, 1975*a*; McCree, 1974, 1983; Jones *et al*., 1978; Ryan, 1991; Li and Jones, 1992; Ryan, 1995; Maier *et al*., 1998) but not others (Byrd *et al*., 1992; Ryan, 1995; Lavigne *et al*., 1996; Lavigne and Ryan, 1997). To emphasize an R_M–N link, eqn (2) is sometimes rewritten as:

$$R = g_R G + m_{R,N} N \qquad (5)$$

where $m_{R,N}$ is a maintenance coefficient in terms of N (i.e. with units R/N, such as mol CO_2 (kg N)$^{-1}$ s^{-1}), and $R_M = m_{R,N}N$ (de Wit *et al*., 1970; Barnes and Hole, 1978), but more work is needed to quantify how, when and where m_R is related to N.

In addition to links to short-term temperature patterns, and often to N, m_R can be positively related to overall metabolic rate, assessed as net CO_2 assimilation (Penning de Vries, 1974, 1975*a*; McCree, 1982; Amthor, 1989; Lavigne and Ryan, 1997). This property of m_R was included in models as a separate component of R_M (along with protein-turnover and ion-gradient-maintenance components) by Penning de Vries and van Laar (1977), de Wit *et al*. (1978), and Penning de Vries *et al*. (1989). From a mechanistic perspective, this characteristic of m_R may reflect increased macromolecular turnover and ion leakage with increased metabolic rate, rather than an additional component of maintenance. It might also reflect increased wastage respiration. To understand, and quantify, this aspect of respiration, better data on turnover and ion leakage rates as functions of overall metabolic activity are needed.

Maintenance processes are usually slow in developing storage organs such as tubers and seeds (Penning de Vries *et al*., 1983; Ploschuk and Hall, 1997). This is expected because proteins in those organs are mostly inactive storage molecules (i.e. slow turnover). Also, a_{ion} is probably slow there because of the chemical and physical properties of those cells. Whole-plant m_R (or $m_{R,N}$) may therefore decline during grain or tuber filling because of small m_R (or $m_{R,N}$) in developing storage organs. This has consequences for crop productivity and relationships between plant mass or N content and respiration during grain (McCree, 1988; Stahl and McCree, 1988) and tuber filling.

If substrate availability limits growth, and maintenance 'competes' with growth for substrate, a reduction in m_R will enhance growth, providing the reduction occurs without drawbacks (McCree, 1974; Robson and Parsons, 1981; e.g. if some part of maintenance is unnecessary or R_M includes wastage, in which case the GMWRP is more appropriate than the GMRP). For example, perhaps some protein turnover is superfluous in crops and could be eliminated (Penning de Vries, 1974). One promising (at least for a time) example of yield enhancement through m_R reduction was the negative correlation between growth and mature-leaf respiration rate in *Lolium perenne* L. genotypes (Wilson, 1975). Wilson noted that such respiration presumably reflected 'maintenance respiration, with a small proportion for growth-supporting processes such as translocation'. Many studies of those genotypes followed, with Kraus *et al*. (1993) eventually finding that the m_R-growth relationship held only with high plant density. They concluded that respiration could not 'be regarded as the primary factor determining differences in yield'. Still, some crop improvement might result (or have resulted) from inadvertent selection for reduced m_R and/or wastage (McCullough and Hunt, 1989; Earl and Tollenaar, 1998).

GROWTH RESPIRATION

In principle, calculating CO_2 released (i.e. g_R) and substrate consumed (i.e. $1/Y_G$) during unit growth is straightforward. It is done by summing all biochemical reactions of growth (weighted for biomass composition) and balancing net ATP and NAD(P)H requirements with an amount of respiration producing that ATP and NAD(P)H (Penning de Vries *et al*., 1974). This 'pathway analysis method' of calculating g_R (and Y_G) requires knowledge of (1) *substrates* (e.g. specific sugars and amides) used in growth, (2) *pathways* of biosynthesis and respiration used in growth, and (3) *composition* of biomass produced in growth. Both g_R and Y_G are temperature independent to the extent that substrates, pathways and biomass composition are temperature independent. Because the method does not predict growth rate G, separate knowledge of G is needed to calculate growth respiration rate R_G ($=g_R G$). Obviously, rapid G causes rapid R_G.

The method originated, for plants, with Loomis's comment to de Wit in 1968 that by tracing biochemical pathways on a Gilson Medical Electronics (Madison, WI, USA) chart of interconnected reactions, the amount of biomass end product and CO_2 by-product obtained from unit substrate could be calculated. Loomis also commented, however, that 'it is too big a job' (R. S. Loomis, pers. comm., 1999). After early calculations by Penning de Vries in 1969, C. Veeger (Agricultural University, Wageningen, The Netherlands) was consulted about prospects for the method; he also thought it was too ambitious, whereas A. H. Stouthamer (Free University, Amsterdam) encouraged it (F. W. T. Penning de Vries, pers. comm., 1999), and the analysis proceeded as described in Penning de Vries *et al*. (1974). [The method was applied early on to bacteria by Gunsalus and Shuster (1961)—although they ignored several subprocesses of growth—by Forrest and Walker (1971), and by Stouthamer (1973).] De Wit *et al*. (1970) summarized early calculations at Třeboň. The goal was to determine maximum *potential* efficiency of growth.[2] Later, it was concluded from experiments that actual efficiency in plants approaches the potential, at least under favourable conditions [except perhaps in roots (Lambers, 1979)], meaning that Y_G for a given biomass composition cannot be much improved through breeding or biotechnology (Penning de Vries, 1974; Penning de Vries and van Laar, 1977; Penning de Vries *et al*., 1983). Though this conclusion may be true, I believe it deserves further consideration because of its potential importance in improving crop yield and understanding ecosystem primary productivity.

The key aspect of the method is its calculation of g_R and Y_G from underlying biochemistry. As such, it explains growth costs and is central to the GP. A limitation is the difficulty of obtaining accurate, complete biomass composition data. Moreover, pathway knowledge is sometimes incomplete, especially for secondary compounds. In

[2] Based on an apparent early attempt to calculate potential efficiency, de Wit mentioned 'respiration associated with possible growth' in ELCROS code internally dated 16 May 1968 along with a growth respiration factor of 0·404 of substrate available for growth (from files of R. S. Loomis).

particular, Penning de Vries *et al.* (1974) were forced to estimate the pathway of lignin synthesis because complete descriptions were unavailable. Also, synthesis of hemicelluloses and some other biomass components were 'greatly simplified' in their analysis. Knowledge of biosynthetic pathways has progressed since then and the method has been applied to a broader range of biomass components (e.g. Chung and Barnes, 1977; Merino *et al.*, 1984; Williams *et al.*, 1987; Gershenzon, 1994), though questions remain about some pathways.

Growth subprocesses

In developing the pathway analysis method, Penning de Vries *et al.* (1974) identified five subprocesses of growth that consume energy and/or C-skeletons: (1) NO_3^- and SO_4^{2-} reduction; (2) active uptake of minerals and organic substrates into growing cells; (3) monomer synthesis from those substrates; (4) polymerization; and (5) tool maintenance. Additionally, (6) active mineral uptake by roots and (7) phloem loading in source organs support growth and use energy.

The chemical reduction of any NO_3^- and SO_4^{2-} taken up from the soil requires reducing agents. These are formed in respiration (and/or photosynthesis in photosynthetically active cells). Active uptake of minerals and substrates into growing cells presumably requires ATP, and that ATP is derived mainly from respiration. Monomer synthesis is an especially important part of growth and is outlined in more detail below. Polymerization of some monomers requires energy in the form of ATP or reducing agents. Those can be derived from respiration (and/or photosynthesis). For example, the outline of ATP requirements for amino acid polymerization given in Table 2 applies to growth as well as maintenance. 'Tool maintenance' is turnover of RNA and enzymes catalyzing growth. It is distinguished from maintenance outlined above, which was called 'structure maintenance' (Penning de Vries *et al.*, 1974), because it is growth-rate dependent. Its costs, which are probably a small fraction of total growth costs, are calculated as outlined in Table 2. The ATP requirements can be met by respiration. Active mineral uptake by roots requires energy (e.g. ATP), which is produced by respiration. Phloem loading in source organs also requires energy in the form of ATP, which is produced by respiration (and/or photosynthesis during the day).

Monomer synthesis is central to growth because it is the main use of substrates during growth and because it accounts for the conservation of C within new biomass. Phenylalanine is used to illustrate the monomer synthesis part of the method. Phenylalanine synthesis from glucose and NH_3 is divided into three stages herein (other substrates could be used, but the procedure is the same). First, phosphoenolpyruvate (PEP) is produced via glycolysis in nine reactions, summarized by:

$$\text{glucose} + 2\ NAD^+ + 2\ P_i \rightarrow 2\ PEP + 2\ NADH + 2\ H_2O$$

Second, erythrose 4-P (E4P) is formed by cycling glucose 6-P through the oxidative pentose phosphate network (OPPN) in nine reactions, summarized by:

$$\text{glucose} + ATP + 4\ NADP^+ + 2\ H_2O \rightarrow E4P + ADP + 4\ NADPH + 2\ CO_2$$

Third, the shikimate pathway (in plastids) combines PEP, E4P and NH_3 to form phenylalanine in 12 reactions, summarized by:

$$2\ PEP + E4P + 2\ ATP + NADH + NADPH + NH_3 \rightarrow \text{phenylalanine} + 2\ ADP + NAD^+ + NADP^+ + 5\ P_i + H_2O + CO_2$$

The overall summary is:

$$2\ \text{glucose} + 3\ ATP + NAD^+ + 3\ NADP^+ + NH_3 \rightarrow \text{phenylalanine} + 3\ ADP + NADH + 3\ NADPH + 3\ P_i + H_2O + 3\ CO_2$$

Nine of 12 C in glucose are retained in phenylalanine. Only two of the three CO_2 released per phenylalanine are from respiratory reactions (in the OPPN), but all three are part of 'growth respiration'. The three ATP required could come from additional glucose catabolism, but could also be produced during mitochondrial oxidation of the NADH and NADPH formed as co-products (assuming they have access to mitochondria). Indeed, up to six ATP *might* be formed from the four NAD(P)H [i.e. 1·5 ATP/NAD(P)H, see Appendix 2], giving a three ATP 'excess'. That excess is available to other processes *at the same time and place*, but would be insufficient to add the phenylalanine to an elongating polypeptide (Table 2). (In addition to protein, phenylalanine is also a precursor of other important macromolecules such as lignins and flavonoids.) This outline of phenylalanine biosynthesis differs slightly from summaries in Penning de Vries *et al.* (1974) and Thornley and Johnson (1990). In fact, for most compounds I calculate slightly different pathway stoichiometries, based on newer biochemical knowledge. Moreover, most previous analyses assumed that $Y_{ATP,C}$ was larger than is now thought (see above). Overall effects on g_R and Y_G are undetermined, but probably minor. Nonetheless, pathway analyses should be updated as biochemical knowledge advances.

Penning de Vries *et al.* (1974) simplified this method of calculating growth costs by categorizing compounds (they considered 61) into five groups: nitrogenous compounds (mainly amino acids and proteins), carbohydrates (mainly structural), lipids, lignin, and organic acids. Differences in biosynthetic costs between compounds within groups were small, but differences between groups were large. Minerals formed a sixth group, which incurred transport costs only during growth. This simplification allowed application of the method to proximate biomass composition (i.e. fraction of biomass composed of carbohydrates, proteins, lipids, lignins, organic acids and minerals) rather than requiring more detailed, and difficult to obtain, composition data.

Local growth respiration

In eqn (2)—or any related GMRP equation—g_R is the amount of CO_2 released per unit of growth. For whole plants, all seven growth subprocesses are included in g_R, and thus R_G. For individual organs, however, g_R includes only active import, monomer synthesis from imported substances such as sucrose and amides, polymerization, and tool maintenance. It is therefore useful to consider a g_R describing growth respiration within growing organs, written $g_{R,local}$, where 'local' means 'in the growing organ' (see Cannell and Thornley, 2000; Thornley and Cannell, 2000). Growth-related processes excluded from $g_{R,local}$, such as NO_3^- assimilation, ion uptake from the soil, and phloem loading, can perhaps best be treated as separate respiratory components (Johnson, 1990; Amthor, 1994*a*; Cannell and Thornley, 2000; and see below).

A $g_{R,local}$ was the basis of the analysis of crop storage-organ growth costs by Penning de Vries *et al.* (1983). That analysis, the results of which are summarized in Table 3, encompassed a wide range of tissue composition and illustrated several important points. (1) Calculated values of $g_{R,local}$ across the organs were in the range 0·13 to 0·43 mol CO_2 (mol C added to structure)$^{-1}$, corresponding to $Y_{G,local}$ values of 0·89 to 0·70 mol C (mol C)$^{-1}$. That is, between 70 and 89 % of the C in imported substrate was retained in the products of growth. (2) Calculated values of $g_{R,local}$ were strongly, positively related to C content ($Y_{G,local}$ was strongly, negatively related to C content). And (3) $g_{R,local}$ was smallest in high-carbohydrate tubers/beets, intermediate in low-lipid shoot organs, and largest in lipid-rich organs.

Mass vs. *energy*

In terms of mass (dry) of product synthesized per unit mass (dry) of substrate used, lipids are 'expensive' whereas structural carbohydrates are 'cheap' (e.g. Table 10 in Penning de Vries *et al.*, 1989), but in terms of energy in products per energy in substrate, there is less difference among compounds (e.g. McDermitt and Loomis, 1981). And because biomass C content is positively related to energy content (through reduction state), biomass C content is inversely related to mass-based Y_G.

In some ecological contexts, a Y_G based on energy (e.g. $Y_{G,E}$, J J^{-1}; and see Thornley, 1971) can be more

TABLE 3. *Local growth respiration coefficient* $g_{R,local}$ *and corresponding true growth yield* $Y_{G,local}$ *[*$Y_G = 1/(1 + g_R)$*] for crop-plant storage organs estimated from biochemical pathway analysis (derived from Penning de Vries* et al.*, 1983, Table 4)*

Crop, organ	Composition (%: carbohydrate, protein, lipid, lignin, organic acid, mineral, C)	$g_{R,local}$ [mol CO_2 released (mol C added to structure)$^{-1}$]	$Y_{G,local}$ [mol C added to structure (mol C in substrate used)$^{-1}$]
Tubers and beets			
Cassava, tuber	87, 3, 1, 3, 3, 3, 45	0·13	0·89
Sugarbeet, beet	82, 5, 0, 5, 4, 4, 45	0·13	0·89
Potato, tuber	78, 9, 0, 3, 5, 5, 44	0·13	0·88
Yam, tuber	80, 6, 1, 3, 5, 5, 44	0·13	0·88
Sweet potato, tuber	84, 5, 2, 3, 3, 3, 45	0·14	0·88
Low-lipid shoot organs			
Wheat, inflorescence + grain	76, 12, 2, 6, 2, 2, 47	0·16	0·86
Rice, inflorescence + grain	76, 8, 2, 12, 1, 1, 49	0·17	0·86
Grain sorghum, inflorescence + grain	72, 9, 3, 12, 2, 2, 49	0·18	0·85
Maize, cob + grain	75, 8, 4, 11, 1, 1, 48	0·18	0·85
Millet, inflorescence + grain	69, 9, 4, 12, 3, 3, 48	0·18	0·84
Cowpea, pod + seed	61, 22, 2, 7, 4, 4, 47	0·19	0·84
Field bean, pod + seed	60, 23, 2, 7, 4, 4, 47	0·19	0·84
Sugarcane, shoot	57, 7, 2, 22, 6, 6, 48	0·19	0·84
Pigeonpea, pod + seed	60, 20, 2, 10, 4, 4, 48	0·19	0·84
Fava bean, pod + seed	55, 29, 1, 7, 4, 4, 47	0·19	0·84
Tomato, fruit	54, 17, 4, 9, 8, 8, 46	0·20	0·84
Chickpea, pod + seed	65, 19, 6, 4, 3, 3, 48	0·20	0·83
High-lipid organs			
Sunflower, inflorescence + grain	45, 14, 22, 13, 3, 3, 55	0·31	0·76
Soybean, pod + seed	29, 37, 18, 6, 5, 5, 53	0·32	0·76
Cotton, boll	40, 21, 23, 8, 4, 4, 54	0·33	0·75
Coconut	39, 4, 28, 25, 2, 2, 59	0·34	0·74
Groundnut, pod + seed	14, 27, 39, 14, 3, 3, 62	0·42	0·70
Oil palm, palm nut	37, 7, 48, 4, 2, 2, 61	0·43	0·70

Organs are arranged in order of $g_{R,local}$ (rounded values are shown). Growth is from glucose and amides. Both $g_{R,local}$ and $Y_{G,local}$ include only costs of biosynthesis/polymerization and substrate uptake into growing cells (1 ATP for each glucose, amide and mineral). Carbon contents of organs, needed to express g_R and Y_G on a C basis, were calculated from Penning de Vries *et al.* (1983, Table 3) and Penning de Vries *et al.* (1989, Table 9). Note that g_R and Y_G in kg kg^{-1} differ from g_R and Y_G in mol C (mol C)$^{-1}$ when C content of biomass differs from C content of substrate, as is usually the case.

important than a mass-based Y_G. Nonetheless, energy content (i.e. heat of combustion) is also an imperfect measure of the 'useful' yield of growth processes. For example, amino groups ($-NH_2$) in proteins cannot be oxidized by animals, so even though some of the energy in substrate is retained in them, that energy is not available to animals (although amino groups are required in animal nutrition). Also, cellulose has high Y_G and $Y_{G,E}$, but cannot be used as a source of C or energy by many animals.

Calculating and measuring g_R

It is critical to realize that growth cost estimates from pathway analysis—or related short-cut methods based on Vertregt and Penning de Vries (1987) or Williams *et al.* (1987), both of which followed from McDermitt and Loomis's (1981) theoretical analysis—are estimates of *minimum* cost for a specified substrate involving specified biosynthetic pathways. These methods are based on biomass composition, but composition is *not a measure of* the amount or type of substrate used in growth or the amount of growth respiration. These can be determined only through measurements of growth, respiration and/or substrate consumption. On the other hand, the pathway analysis and related short-cut methods will accurately estimate g_R and Y_G from plant composition if actual efficiency approaches potential efficiency and substrate is known. But it is also necessary to understand how composition may change with time (e.g. Mutsaers, 1976; Merino *et al.*, 1984; Thornley and Johnson, 1990, pp. 350–353; Walton *et al.*, 1990, 1999). For example, differentiation and secondary growth can occur after organs are normally considered 'mature'; in particular, synthesis of lignins and hemicelluloses may be important in leaves after 'full expansion' but before senescence. And when acclimation occurs (e.g. in leaves in response to environmental change during canopy development), tissue composition can change. Thus, composition measurements used to calculate g_R must reflect amounts of compounds synthesized during growth (not just net compound accumulation) to be meaningful. In addition, mobilization and senescence processes in old organs require energy, but they are not accounted for in pathway-based estimates of growth costs; Penning de Vries *et al.* (1983) outlined theoretical mobilization costs, which can be particularly important during grain filling in many crops.

In addition to estimating minimum g_R from biochemical pathway stoichiometries, other methods can be used to evaluate g_R. For example, R_G can be estimated by deriving a theoretical or experimental estimate of R_M (using methods listed above) and then subtracting that R_M from measured total respiration R (e.g. Sprugel, 1990). This R_G then defines g_R from the relationship $g_R = R_G/G$. This method is the 'reverse' of evaluating R_G from measurements of G and composition-based estimates of g_R and then subtracting that R_G from measured R to estimate R_M (e.g. Mutsaers, 1976).

Values of g_R can also be evaluated by solving experimentally eqns (1), (2), or (3), or similar equations. Each approach to solving these equations has drawbacks (Amthor, 1989), but measurements of G and R can provide a direct (rather than theoretical) estimate of g_R.

As with m_R, different methods of calculating or measuring g_R (or Y_G) can give different results (e.g. Irving and Silsbury, 1987; Williams *et al.*, 1987; Lafitte and Loomis, 1988; Sprugel, 1990; Walton and de Jong, 1990; Walton *et al.*, 1990, 1999; Marcelis and Baan Hofman-Eijer, 1995; Ploschuk and Hall, 1997; Stockfors and Linder, 1998). Difficulties in accurately measuring composition of growing cells, measuring respiration throughout the day and night, and measuring growth can all affect estimates of g_R (and Y_G).

THE GENERAL PARADIGM

In the GMRP, all respiration is divided between growth and maintenance. The GMWRP adds a third term for wastage. From a biochemical/physiological perspective, finer distinctions than these two or three processes can be made, and these finer distinctions can be central to explaining respiratory behaviour and are the basis of the GP. That is, it is important to consider individual processes requiring support from respiration because they can vary independently in response to development and environmental changes. The basis for finer distinctions is illustrated above in decompositions of m_R and g_R. The general equation describing the GP (applicable to cells, organs, or whole plants) is:

$$R = \Sigma_{\text{processes,Y}}\ c_Y A_Y \qquad (6)$$

(see also Thornley and Cannell, 2000), where Y is a process supported by respiration, c_Y is the metabolic cost of Y (in CO_2 per unit activity of Y), and A_Y is the rate (activity) of Y. [Note that activity A is used in eqn (6) whereas specific activity a was used in eqn (4) to define m_R.] Equation (6) is 'complete' when all quantitatively important processes supported by respiration are included.

Respiration associated with the processes of 'local growth' (i.e. $g_{R,local}G$), macromolecular turnover associated with structure maintenance [i.e. $(c_{pt}a_{pt} + c_{lt}a_{lt})W$], and ion-gradient maintenance associated with structure maintenance (i.e. $c_{ion}a_{ion}W$) were outlined above. Four other processes are considered briefly (see Cannell and Thornley, 2000; Thornley and Cannell, 2000): active mineral uptake by roots, NO_3^- reduction, symbiotic N_2 assimilation, and phloem loading. Other processes, including wastage, can be included in eqn (6) when appropriate.

Ion uptake

Active ion uptake into roots is generally supported by respiration, and the CO_2 cost is directly related to $1/Y_{ATP,C}$ if ATP [rather than NAD(P)H, see Marschner, 1995] is the energy source. Extensions to the GMRP explicitly accounting for this process were described by, e.g. Johnson (1983, 1990) and Bouma *et al.* (1996). Ions taken up can leak out of roots (perhaps more so in laboratory hydroponic experiments than in soils), so gross uptake exceeds net uptake. Respiration is related to gross uptake. (Uptake to

replace ions leaked from roots borders on maintenance, but is herein designated a part of the 'separate' process of ion uptake from the soil.)

Estimating uptake cost from biochemical principles is straightforward, though basic data are incomplete. In the context of respiration models, NO_3^- uptake is usually emphasized, with a possible uptake cost (in CO_2/NO_3^-) of $2/Y_{ATP,C}$ (Bouma *et al.*, 1996). This is equivalent to about 0·4 CO_2/NO_3^- for maximum $Y_{ATP,C}$. Uptake of other ions, or NO_3^- in combination with other ions, may be considerably cheaper (Cannell and Thornley, 2000).

Nitrate reduction (and assimilation)

Costs of NO_3^- reduction can be paid by respiration (or photosynthesis in 'green cells' during the day). To reduce NO_3^- to NH_3 using respiration, a cytosolic NADH and three plastidic NADPHs are required. These might be produced by plastidic activity of the OPPN (coupled with the oxaloacetate/malate shuttle to produce a cytosolic NADH from a plastidic NADPH) at a cost of about $[2 + 1/(3Y_{ATP,C})]$ CO_2 per NO_3^- [see eqn (11) in Amthor, 1994*a*]. Additional respiratory costs, separate from local growth, may be incurred for assimilating NH_3 into amino acids. The ratio CO_2 released per NH_3 assimilated varies greatly depending on the fate of the N; indeed, for NH_3 assimilated into aspartate, glutamate, asparagine and glutamine, CO_2 *fixation* occurs (Pate and Layzell, 1990).

Equation (2) was extended to account separately for NO_3^- reduction and assimilation into amino acids by, e.g. Sasakawa and LaRue (1986). Their measurements indicated that 3·0 CO_2 were released per NO_3^- assimilated (assumed to be in asparagine) in *Vigna unguiculata* roots, but this cost probably included NO_3^- uptake as well.

Symbiotic N_2 fixation

Mahon (1977, 1979) expanded eqn (2) to include a respiratory component supporting N_2 conversion to NH_3 catalyzed by nitrogenase within symbionts. The *minimum* cost of N_2 fixation may be 2·36 CO_2 per NH_3 (Pate and Layzell, 1990). N_2 fixation requires both ATP and reductant, so its cost is related to $Y_{ATP,C}$. Nodule growth and maintenance, and the concomitant respiration, are also required for N_2 fixation. Of course, respiration supporting N_2 fixation occurs only in plants assimilating N_2.

Phloem loading

Loading of sugars, amides, and other substances into phloem for transport to sinks is an active process. Growth, maintenance, ion uptake, respiration-supported N assimilation, and other processes are thereby supplied with substrates. Exceptions might be 'nearly adult leaves' which can 'supply substrate for their own growth, for which no translocation costs are incurred' (Penning de Vries, 1972), and mature 'source' leaves supplying their own substrates for maintenance.

A range of phloem sugar-loading costs—including costs of mobilizing reserves (notably starch) in source organs—can be calculated from biochemical pathways of sugar (e.g. sucrose, sorbitol) 'delivery' to phloem and specific costs of phloem loading (e.g. apoplastic or entirely symplastic). For sucrose arising from chloroplast-starch mobilization with export of triose-P out of chloroplasts, three ATP are used per sucrose formed, whereas if maltose is the compound exported from chloroplasts, two ATP are needed per sucrose formed (Bouma *et al.*, 1995). With apoplastic phloem loading, one H^+ (symport) is required per sucrose; ATP produces the H^+ gradient used, perhaps with a 1:1 H^+:ATP stoichiometry. Thus, for mobilization of starch to sucrose, followed by apoplastic phloem loading, three–four ATP are used per sucrose. The CO_2 cost is therefore $3/Y_{ATP,C}$ to $4/Y_{ATP,C}$ (or 0·62–0·83 CO_2 with maximum $Y_{ATP,C}$) per sucrose, or 0·05–0·07 mol CO_2 (mol C translocated)$^{-1}$. Penning de Vries (1975*b*) estimated that energy for sugar translocation could be supplied by an amount of sugar equal to 5·3 % of the amount arriving in the sink [i.e. cost was 0·053 mol CO_2 (mol C translocated)$^{-1}$]. That estimate was based on $Y_{ATP,C} = 6{\cdot}3$. With $Y_{ATP,C} = 4{\cdot}8$ (Appendix 2), cost is 0·069 CO_2/C. That cost was equally divided between source and sink, with the sink half part of $g_{R,local}$. Loading of other compounds, such as amides, into phloem will increase total phloem loading costs.

Cost of phloem loading of sugars (including mobilization) in source leaves can be experimentally estimated by simultaneously measuring rates of leaf respiration and C export. Costs covering the wide range from 0·47 to 3·8 CO_2/sucrose (i.e. 0·039–0·32 CO_2/C) have been reported (Bouma *et al.*, 1995). For a number of experiments, respiration supporting phloem loading of sugars accounted for 7–55 % (mean = 29 %) of *Solanum tuberosum* L. and *Phaseolus vulgaris* L. mature-leaf dark respiration rates (Bouma *et al.*, 1995).

An important process related to translocation in some old vegetative tissue is protein breakdown to amides followed by translocation to growing organs. According to Penning de Vries *et al.* (1983), a net production of ATP occurs during the protein–amide conversion. That ATP can contribute to maintenance and transport processes, though it may be insufficient to fully support leaf maintenance needs.

THE RATIO RESPIRATION/PHOTOSYNTHESIS

Table A1 (Appendix 1) summarizes data-based estimates of the long-term (seasonal to annual) ratio respiration/photosynthesis (or R/P, where R and P have the same units) for whole plants or plant communities in the field. [Other R/P estimates are in references cited in Cannell and Thornley (2000).] Most values fall within the range 0·35–0·80, although it has been suggested that the ratio R/P is more conservative than this (references in Cannell and Thornley, 2000). But an important, related question is rarely asked: what is the 'possible' or 'allowable' range in R/P over a season or year? A minimum R/P is set by growth costs. Local growth for most higher plants may proceed with maximum Y_G of perhaps 0·80–0·85 mol C (mol C)$^{-1}$, which is equivalent to minimum R/P of 0·15–0·20 mol C

(mol C)$^{-1}$. When respiratory costs of ion uptake from the soil, active transport through phloem, and N assimilation are included, the minimum R/P may increase to about 0·20–0·30. Finally, some structure maintenance is essential, raising the *minimum* long-term R/P to perhaps 0·30–0·40 for most higher plants. At the other extreme, an R/P of unity means that no growth or biomass accumulation (including litter) occurs, which is never the case. Indeed, an R/P greater than, say, 0·75–0·85 would seem unlikely following the long evolutionary history of higher plants. Thus, I suggest that 0·35–0·80 is about the allowable range for R/P in whole plants over long periods. This full range is spanned by values in Table A1. But what if R/P is generally more conservative, say 0·45–0·60? That range is still as large as one third of the possible range. In short, available data are not precise, or comprehensive, enough to decide whether R/P is highly constrained across species and environments, and in fact, available data indicate that R/P covers a significant fraction of the possible range in values. Moreover, a decrease in R/P from 0·60 to 0·45 (25 %) reflects a large (37·5 %) increase in growth per unit photosynthesis (with no net change in amount of reserve material), so even apparently small variation in R/P can be significant.

Estimates of crop R/P are typically lower than values for 'natural' vegetation [compare Table 6.1 in Amthor, 1989 (which contains values of $1 - R/P$), to Table A1 herein]. Relatively small values of R/P in crops might be related to the following: (1) a large fraction of growth and biomass in crops is in storage organs such as seeds and tubers, compared to a small fraction in other plants; (2) theoretical $Y_{G,local}$ in storage organs of most tuber and grain crops is large [i.e. 0·83–0·89 (see Table 3)] so growth respiration is relatively small there; and (3) maintenance respiration in storage organs is probably usually slow. Thus, selecting crop genotypes for large harvest index may indirectly select for reduced whole-plant R/P.

Although R/P is probably a variable (not a constant), single-value summaries of R/P may sometimes be useful descriptions of general patterns. Single-value summaries will not, however, help explain relationships among photosynthesis, respiration and growth as they vary across environments and species.

EFFECTS OF RISING TEMPERATURE AND CO_2 ON RESPIRATION

Ongoing global environmental change raises the question, how will rising CO_2 and temperature affect plant respiration during the coming decades?

Temperature

A short-term (seconds to hours) temperature increase (over the physiologically relevant range) stimulates respiration rate, often with a Q_{10} of about 2·0–2·5, but over the long term (days to years), respiration may acclimate and/or adapt to temperature (e.g. Amthor, 1994*b*; Larigauderie and Körner, 1995; Arnone and Körner, 1997; Tjoelker *et al*., 1999*a*). Short-term changes in temperature probably affect respiration mainly through kinetic effects on the processes using respiratory products. Whether, and to what extent, processes supported by respiration acclimate and adapt to temperature probably determines effects of long-term temperature change on respiration. That is, in the long term, temperature probably affects respiration through its effects on growth and maintenance processes, and developmental state, rather than through changes in respiratory capacity or kinetics *per se*, though respiratory capacity may also be affected by long-term temperature change. As mentioned above, studies by Mariko and Koizumi (1993) and Marcelis and Baan Hofman-Eijer (1995) indicated that whole-plant and fruit m_R did not acclimate to temperature (and g_R was independent of temperature in those studies), but there are too few data available to make generalizations about temperature acclimation of m_R (if any).

Because of acclimation and/or adaptation, short-term responses of respiration to temperature need not reflect long-term responses. Stated another way, the 'long-term Q_{10}' of respiration will generally be smaller than the 'short-term Q_{10}' because of some degree of acclimation and/or adaptation.

Perhaps the most important issue is how growth will respond to warming. If warming enhances growth and plant size (for whatever reasons), it is likely that both growth respiration and maintenance respiration will be enhanced as well, though not necessarily in direct proportion. That is, the ratio R/P might be affected by warming. For example, Tjoelker *et al*. (1999*b*) found that R/P generally increased with warming in boreal-tree seedlings.

In the end, understanding effects of long-term warming on respiration will depend on knowledge of how warming affects: (1) rates of processes that require respiration as a source of C-skeletons, ATP and/or NAD(P)H; (2) specific respiratory costs of those processes; and (3) the value of $Y_{ATP,C}$ and extent of any wastage respiration. Unfortunately, such knowledge is presently limited.

Atmospheric CO_2 concentration

It is relatively easy to speculate on how (and why) rising CO_2 'should', according to the GP, affect respiration rate. It is well known that elevated CO_2 enhances photosynthesis and plant growth (at least in C_3 plants, though C_4 plant growth can also be stimulated, perhaps in part due to increased water use efficiency). Increased photosynthesis and growth also stimulate translocation. Elevated CO_2 should, therefore, result in greater whole-plant respiration supporting growth and translocation as well as respiration supporting ion uptake and N assimilation (assuming that bigger plants contain more minerals and proteins). The resulting increase in plant size should in turn stimulate whole-plant maintenance respiration. Finally, elevated CO_2 often results in a higher proportion of nonstructural carbohydrates (i.e. reserve materials), and this might enhance respiration associated with wastage (e.g. Azcón-Bieto and Osmond, 1983; Tjoelker *et al*., 1999*a*)—that is, 'substrate-induced respiration' of Warren Wilson (1967)—though it must be kept in mind that elevated nonstructural carbohydrate concentrations in source leaves may also

stimulate respiration through increased phloem loading and translocation. Thus, because elevated CO_2 stimulates photosynthesis, translocation, growth and nonstructural carbohydrates, it is expected that rising CO_2 will increase whole-plant respiration, and there is evidence for this response in elevated-CO_2 experiments (Amthor, 1997).

In addition to increased growth, elevated CO_2 can also cause lower protein concentrations, perhaps in part through 'dilution' by increased nonstructural carbohydrate levels. This response might be expected to reduce g_R and/or m_R (though not necessarily R_G and R_M, respectively), and there is evidence supporting these responses in several experiments (Amthor, 1997). [Many experimental estimates of g_R (and m_R) fail to distinguish structural mass from reserves (and see Warren Wilson, 1967), so g_R is typically based on dry mass accumulation rather than growth *per se*. Thus, changes in g_R caused by elevated CO_2 may be *apparent* only, rather than *actual*.] On the other hand, leaf respiration per unit N was increased by elevated CO_2 in several tree species, and this was related to more nonstructural carbohydrates (Tjoelker *et al*., 1999*a*). Reductions in g_R and/or m_R, or increases in nonstructural carbohydrate content, should reduce R/P, and there is evidence that this response is elicited in many experimental settings (Amthor, 1997). A reduction in R/P due to elevated CO_2 indicates that wastage respiration is not significantly increased.

As for temperature, the GP implies that rising CO_2 will influence respiration to the extent that it alters: (1) rates of processes supported by respiration; (2) stoichiometries between respiration and processes it supports; and (3) rates of futile cycling, alternative pathway activity, and other forms of wastage. And, as with temperature, the present database is limited. That is, generalizations made above are mainly based on simple correlations. There are too few simultaneous measurements of respiration and the processes it supports to draw firm conclusions or explanations.

Respiratory responses to elevated CO_2 brought about through changes in photosynthesis, translocation, growth, plant size, and/or plant composition are termed 'indirect' (Amthor, 1997) because the same respiratory responses would be expected if any other environmental factor (e.g. temperature, nutrient availability) caused the same changes in photosynthesis, translocation, growth, plant size, and/or plant composition. In addition to indirect effects of CO_2 on respiration, there has been considerable attention paid to 'direct' effects of CO_2 on respiration, in which CO_2 itself (in the dark for photosynthetic tissue) directly alters respiration rate (e.g. Amthor, 1997). Leaf, shoot, root, reproductive organ, and whole-plant respiration have all been reported to be directly inhibited by short-term increases in CO_2 concentration (reviewed in Amthor, 1997, with more recent research in Burton *et al*., 1997; Ceulemans *et al*., 1997; Reuveni and Bugbee, 1997; Clinton and Vose, 1999). Conversely, the respiration rate was independent of short-term CO_2 changes in many experiments (e.g. Amthor, 1997; Roberntz and Stockfors, 1998; Tjoelker *et al*., 1999*a*; Amthor, 2000; and references therein). Mechanisms of any direct effect of CO_2 on respiration are unknown, although an inhibition of cytochrome *c* oxidase activity could be partly responsible (Gonzàlez-Meler and Siedow, 1999). It is also possible that CO_2 directly affects some process(es) that uses the products of respiration, rather than affecting respiration *per se*.

In some cases, direct inhibition of respiration by elevated CO_2 may enhance C balance, implying that wastage respiration is reduced by elevated CO_2, whereas in other cases a direct inhibition of respiration by elevated CO_2 can reduce growth, implying that a useful fraction of respiration (or a useful process using the products of respiration) is affected (e.g. Bunce, 1995; Reuveni and Bugbee, 1997; Reuveni *et al*., 1997). Potential direct effects of CO_2 on respiration remain a puzzling topic. Additional experiments are needed, not only to establish mechanisms, but to better ascertain whether the response even occurs in most plants (Amthor, 2000).

STATE OF THE PARADIGMS AND FUTURE RESEARCH DIRECTIONS

By 1970, phenomenological equations summarizing the GMRP were applied to plants (Monsi, 1968; de Wit and Brouwer, 1969; McCree, 1969, 1970; de Wit *et al*., 1970; Sawada, 1970; Thornley, 1970), and by 1975, principles relating plant growth and maintenance processes to underlying biochemistry and the related respiration were worked out in considerable detail (Penning de Vries, 1972, 1974, 1975*a*,*b*; Penning de Vries *et al*., 1974). The latter formed a basis of quantitative research within the GP. Thus, while theoretical and experimental refinements continue today, the paradigms were relatively well developed 25–30 years ago.

Because the GP has firm physiological and biochemical underpinnings, it is the appropriate approach for explaining respiration rates (or amounts), and is in contrast to simple empirical relationships between respiration and factors such as temperature and plant dry mass or surface area. Although the two-component subset of the GP—i.e. the GMRP—is often useful (e.g. Marcelis and Baan Hofman-Eijer, 1995; Amthor, 1997; Kellomäki and Wang, 1998; and references therein), fuller versions of the GP (e.g. Johnson, 1990; Amthor, 1994*a*; Cannell and Thornley, 2000) enhance understanding of roles of respiration in plant growth and health and can better indicate specific targets for research.

While it is clear that respiration supports growth, maintenance and other processes at the biochemical level as outlined by Penning de Vries (1972, 1974, 1975*a*,*b*) and Penning de Vries *et al*. (1974, 1983), and more recently by Bouma *et al*. (1995, 1996) and Cannell and Thornley (2000) among others, it remains difficult to measure that support based on CO_2 (or O_2) exchange. Improved measurements of respiration and the processes it supports are needed. In particular, *simultaneous* measurements of rates of respiration and processes supported by respiration are needed to relate respiration to those processes. If those measurements can be made in the field, all the better, but field measurements must distinguish plants from any associated heterotrophic organisms. This is particularly difficult when studying root respiration. Moreover, simultaneous

photosynthesis complicates measurements of daytime respiration in 'green cells'. In any case, isolated respiration measurements are of limited value. For example, measurements of respiratory response to temperature without simultaneous measurements of processes using respiratory products do not contribute to explanations of respiration rate.

To the extent that metabolic costs of processes supported by respiration can be measured, they may differ from costs calculated from underlying biochemistry for several reasons, including ignorance of *in situ* biochemical stoichiometries. Nonetheless, discrepancies between measured and calculated metabolic efficiencies may indicate processes that could be targeted for improvement through breeding or biotechnology.

It is essential to consider g_R, m_R and other respiratory coefficients as variables, not constants (McCree, 1988). Although each may remain about constant during some periods, they change with time (during and among days, during and among seasons) in other circumstances. This follows directly from underlying biochemical principles. Thus, even if g_R or m_R (or other coefficients) are accurately measured at a point in time and space, that value may be inapplicable to other times/locations because efficiency of respiration and factors controlling g_R (e.g. nature of substrates and biomass formed) and m_R (e.g. rate of intracellular ion leakage) change in response to environment and during ontogeny (Penning de Vries, 1972; McCree, 1974; Mutsaers, 1976). Unfortunately, when respiration is included in models of plant growth and ecosystem primary production, a simplistic form of the GMRP is usually used (with constant g_R, and m_R responding only to temperature). Future modelling should include more detailed treatments of respiration to increase realism and to better match the models to underlying processes (see Thornley and Cannell, 2000).

It is usually implicit that the respiration rate is regulated by rates of processes that use respiratory products rather than by capacity of respiratory pathways or availability of respiratory substrates (e.g. Beevers, 1974). In some cases, however, substrate availability limits respiration rate (e.g. in mature *Spinacia oleracea* L. leaves studied by Noguchi and Terashima, 1997), and respiratory capacity in young, rapidly growing tissues might limit respiration rate in those tissues. In such cases, respiratory substrate availability or respiratory capacity may regulate rates of growth, maintenance, and other processes, rather than the converse. Too few data are available to determine whether stoichiometries between respiration and the processes it supports are affected by these various controls on respiration rates.

A question of practical import is, why haven't the paradigms been more useful in crop breeding? The same question applies to e.g. the successful C_3-photosynthesis model of Farquhar *et al.* (1980). The answer may be as simple as Evans's (1993, p. 266) claim that 'selection for greater yield potential has not, could not and never shall wait on our fuller understanding of its functional basis, despite the pleas of physiologists'. So although it is disappointing that the paradigms have so far been unsuccessful in contributing to major crop improvements—in spite of early hopes surrounding the work of Wilson (1975) with *Lolium perenne*—this does not alter their 'correctness' or explanatory power.

In summary, beginning 30 years ago, the models of McCree (1969, 1970), de Wit *et al.* (1970, 1978), Thornley (1970), Penning de Vries (1972, 1975*a*,*b*), and Penning de Vries *et al.* (1974) shed considerable light on the role of respiration in plant growth and health. They added a needed quantitative aspect to studies of respiration. Although the 1969–75 advances were large, and progress has continued to the present, research is still needed. Targets of future work include updating models with evolving biochemical knowledge and improving methods of measuring rates of respiration and the processes it supports. The following questions are offered as guides for research.

(1) Can robust, direct methods of measuring growth and respiration in intact plants be developed?
(2) What are magnitudes of *in situ* maintenance processes across plants and ecosystems, how are they affected by growth rate and environment, and in leaves, how much maintenance is supported directly by photosynthesis?
(3) What is *in situ* $Y_{ATP,C}$ and is there a widespread otiose component of respiration—as suggested by Reuveni *et al.* (1997) for conditions favourable for photosynthesis—and how do growth rate, ontogeny and environment affect them?
(4) Can non-growth-related respiration in crop plants be slowed (thereby enhancing productivity through improved substrate supply to growth) by reducing wastage respiration or eliminating some maintenance activities that are unnecessary, as proposed by Penning de Vries (1974)?
(5) Can the conclusion of Penning de Vries (1974), Penning de Vries and van Laar (1977), and Penning de Vries *et al.* (1983) that actual growth occurs with near maximum (potential) efficiency be re-evaluated in light of present biochemical knowledge and with new growth and respiration measurements designed specifically to test this notion, especially in the field?

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APPENDIX 1

Defining, and measuring, higher-plant respiration is difficult. Biochemically, respiration can be defined as the sum of glycolysis, the oxidative pentose phosphate pathway (or network), the tricarboxylic acid (TCA) or Krebs cycle, mitochondrial e^- transport, oxidative phosphorylation, and intimately related reactions. A physiological definition of respiration is non-photorespiratory CO_2 release (photorespiration being associated with photosynthesis), though photorespiration can contribute directly to mitochondrial e^- transport. Unfortunately, the biochemical and physiological definitions may be somewhat incongruous. The biochemical pathways of respiration need not account for all non-photorespiratory CO_2 release in plants because CO_2 is also released in biosynthetic reactions outside the respiratory pathways (e.g. in synthesis of tyrosine and phenylalanine from arogenate). In addition, anaplerotic dark CO_2 fixation by PEP carboxylase can mask some respiratory CO_2 release. It is also unfortunate that neither whole-plant nor plant-community CO_2 release can be directly measured during the course of a 24 h day, a season, or a year. This is because of simultaneous daytime respiration and photosynthesis, continuous CO_2 release by heterotrophic organisms (especially those oxidizing litter and soil organic matter), and, in many cases, inability to unobtrusively enclose whole plants in measuring cuvettes. Nonetheless, available estimates of respiration, and especially the ratio respiration/photosynthesis, made for plants in nature (Table A1) are useful in assessing the quantitative significance of respiration to plant C balance. But it must be kept in mind that such estimates are just that: estimates. Presentation of even two digits in Table A1 may imply greater precision than actually exists. For example, *Fagus sylvatica* L. root respiration was not measured by Möller *et al.* (1954), but simply set to 20 % of stem plus branch respiration estimates. In any case, as summarized in Table A1, respiration is a large component of a plant's seasonal or annual C balance, ranging from less than 50 % of photosynthesis in many crops to 65–75 % in some tropical and boreal trees and coastal marshes.

TABLE A1. *Estimates of annual (or seasonal) respiration as a fraction of annual (or seasonal) photosynthesis in intact ecosystems*

Ecosystem	Respiration/Photosynthesis	Reference
Crop		
Alfalfa	0·35–0·49	Thomas and Hill (1949)
Maize, rice, and wheat	*c.* 0·3–0·6	Amthor (1989, Table 6.1)
Grassland		
Shortgrass prairie	0·34	Andrews *et al.* (1974)
	0·51	Detling (1979)
Tallgrass prairie	0·61–0·65	Risser *et al.* (1981), range for three treatments
Forest		
Tropical moist		
Ivory Coast	0·75	Müller and Nielsen (1965)
Puerto Rico	0·88	Derived from Table 24 in Odum (1970)
Southern Thailand	0·66	Kira (1975)
Temperate		
Warm evergreen	0·72	Kira (1975)
Warm evergreen 'oak'	0·66	Kira and Yabuki (1978)
Abies sachalinensis	0·53	Kira (1975)
Castanopis cuspidata	0·575	Kira (1975)
Chamaecyparis obtusa plantation	0·62	Hagihara and Hozumi (1991)
Cryptomeria japonica plantation	0·71	Kira (1975), mean of five estimates
Fagus crenata	0·44,0·56	Kira (1975), secondary forest and plantation
F. sylvatica	0·39–0·47	Möller *et al.* (1954), range for four ages
Fraxinus excelsior plantation	0·37	Kira (1975)
Liriodendron tulipifera	0·66	Harris *et al.* (1975)
Picea abies plantation	0·32	Kira (1975)
Pinus densiflora plantation	0·71	Kira (1975)
P. ponderosa	0·55	Law *et al.* (1999)
P. taeda plantation	0·58	Kinerson (1975)
P. spp.	0·39–0·71*	Ryan *et al.* (1994)
Quercus-Acer (southern)	0·44–0·55	P. J. Hanson (pers. comm. 2000), 7 years
Quercus-Acer (northern)	0·54	M. L. Goulden (pers. comm. 1997)
Q.-Pinus	0·55	Whittaker and Woodwell (1969)
Q. spp.	0·61	Satchell (1973) (in Edwards *et al.*, 1981)
Q.-Carpinus	0·38	Medwecka-Kornas *et al.* (1974) (in Edwards *et al.*, 1981)
Subalpine		
Coniferous	0·72	Kitazawa (1977) (in Edwards *et al.*, 1981)
Abies	0·675	Kira (1975)
A. veitchii	0·61	Kira (1975), mean of three estimates
Boreal		
Picea mariana	0·72–0·77	Ryan *et al.* (1997)
Pinus banksiana	0·69–0·74	Ryan *et al.* (1997)
Populus tremuloides	0·64–0·67	Ryan *et al.* (1997)
Coastal salt marsh, temperate		
Spartina	0·77	Teal (1962)
Spartina-Distichlis	0·69	Woodwell *et al.* (1979)
Tundra, arctic	0·50	Reichle (1975)

Both respiration and photosynthesis have the same units (e.g. mol C m^{-2} ground $year^{-1}$) and photosynthesis is the balance of photosynthetic carboxylations with photorespiratory decarboxylations. To my knowledge, these estimates of respiration and photosynthesis assume that leaf respiration occurs at about the same rate in the light as in the dark, even though photosynthesis probably slows leaf respiration.

* Range of values for seven young (16–40-year-old) *Pinus* stands. Ryan *et al.* (1994) gave daily (24 h) stem, branch, and root respiration, but only night-time foliage respiration. To obtain total respiration here, night-time foliage respiration was doubled. To then obtain photosynthesis, night-time foliage respiration was added to daytime canopy net CO_2 assimilation. Both transformations assumed that daytime foliage respiration was similar to night-time foliage respiration in spite of differences in temperature and possible effects of photosynthesis on foliage respiration.

APPENDIX 2

The amount of ATP that can be produced per unit of respiratory substrate (e.g. hexose) oxidized is central to the efficiency of respiration. It is therefore desirable to mechanistically describe that ratio. With glucose as substrate, and assuming its complete oxidation by classical glycolysis and the TCA cycle along with oxidation of the resulting NADH by the respiratory chain, the amount of ADP phosphorylated (i.e. ATP formed) per glucose oxidized ($Y_{ATP,glucose}$, mol ATP (mol glucose)$^{-1}$) is (after Amthor, 1994*a*; and see Stryer, 1995, pp. 551–552):

$$Y_{ATP,glucose} = 4 + [(1 - a)(b\ 8\ H_I^+ + c\ 12\ H_{III,IV}^+) - 4]/(1 + H_{ATP}^+) \quad \text{(A1)}$$

where the left-most 4 is net substrate-level ADP phosphorylation per glucose, a is the fraction of protons pumped into the mitochondrial intermembrane space by the respiratory chain that re-enters the mitochondrial matrix through membrane 'leaks', b is the fraction of e^- from matrix NADH that pass through Complex I ($1 - b$ of e^- bypass Complex I via the rotenone-insensitive matrix-facing NADH dehydrogenase, which does not pump protons), 8 is the number of NADH formed (from NAD^+) per glucose by the TCA cycle, H_I^+ is the number of protons pumped into the intermembrane space when an e^--pair passes through Complex I, c is the fraction of e^- passed from ubiquinol to O_2 via Complexes III and IV ($1 - c$ of e^- are passed to O_2 via the alternative oxidase, which does not pump protons), 12 is cytosolic *and* mitochondrial NADH plus $FADH_2$ formed (from NAD^+ and FAD) per glucose, $H^+_{III,IV}$ is the number of protons pumped into the intermembrane space when an e^--pair passes through both Complexes III and IV, the right-most 4 is protons expended during symport into the mitochondrial matrix of two pyruvate plus the two P_i required for TCA-cycle *substrate-level* ADP phosphorylations, 1 in the denominator is the H^+ entering the matrix via $H^+ - P_i$ symporters with each P_i used in *oxidative* ADP phosphorylations, and H^+_{ATP} is the number of H^+ moving through ATP synthase per ADP phosphorylated. [Stryer (1995) noted pyruvate-H^+ symport into the matrix, but neglected it calculating $Y_{ATP,glucose}$.] Similar equations apply to other substrates and/or other respiratory pathways. For example, minor deviations possible in the pathway of glycolysis (see Plaxton, 1996) can be accounted for with simple modifications to eqn (A1). For glucose, the number of ATP produced per CO_2 released ($Y_{ATP,C}$, mol ATP (mol CO_2)$^{-1}$) is simply: $Y_{ATP,C} = Y_{ATP,glucose}/6$. Equation (A1) does not mean respiration normally yields only ATP (and heat and CO_2); it merely quantifies how much ATP *could* be produced during complete respiratory oxidation of glucose.

When $a = 0$ (no H^+ leaks), $b = 1$ (no rotenone-insensitive dehydrogenase activity), $c = 1$ (no alternative oxidase activity), $H_I^+ = 4$ (Nicholls and Ferguson, 1992), $H^+_{III,IV} = 6$ (Nicholls and Ferguson, 1992; Stryer, 1995), and $H^+_{ATP} = 3$ (Nicholls and Ferguson, 1992; Stryer, 1995), then $Y_{ATP,glucose} = 29$ mol ATP (mol glucose)$^{-1}$. (Most older textbooks give $Y_{ATP,glucose} = 36$ or 38.) With $c = 0$ (i.e. all e^- reducing O_2 via the alternative oxidase rather than cytochrome c oxidase) and other parameters as above, $Y_{ATP,glucose} = 11$, a 62 % decline from the 29 obtained with $c = 1$. There is no requirement for $Y_{ATP,glucose}$ (or a, b, or c) to take integer values.

ATP production from mitochondrial oxidation of *cytosolic* NAD(P)H [$Y_{ATP,cyt\text{-}NAD(P)H}$, mol ATP (mol cytosolic NAD(P)H oxidized)$^{-1}$] is:

$$Y_{ATP,cyt\text{-}NAD(P)H} = (1 - a)(c\ H^+_{III,IV})/(1 + H^+_{ATP}) \quad (A2)$$

With parameters as above, *maximum* $Y_{ATP,cyt\text{-}NAD(P)H}$ is 1·5 mol ATP (mol NAD(P)H)$^{-1}$.

The $Y_{ATP,glucose}$, $Y_{ATP,C}$, and $Y_{ATP,cyt\text{-}NAD(P)H}$ defined above all differ from 'Y_{ATP}' used in microbiology. Microbiologists Bauchop and Elsden (1960) defined Y^{ATP} (usually written Y_{ATP} since then) as 'dry weight of organism produced/mole ATP formed' in catabolism. That Y_{ATP} is estimated from measurements of growth and substrate consumption in conjunction with calculations (not measurements) of ATP produced per unit substrate consumed [e.g. with a form of equation (A1)].