

# Misconceptions About the Relation Between Plant Growth and Respiration

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**Abstract:** The relation between plant growth rate and respiration rate is readily derived from the overall chemical reaction for aerobic metabolism. The derived relation can be used to show that separation of respiration into growth (*g*) and maintenance (*m*) components is not a useful concept. *g* and *m* cannot be unambiguously measured or defined in terms of biochemical processes. Moreover, because growth yield calculations from biochemical pathway analysis, from biomass molecular composition, from biomass heat of combustion, and from biomass elemental composition have not included all of the energy costs for biosynthesis, they are not accurate measures of the carbon cost for plant growth. Improper definitions of growth-respiration relations are impeding the use of physiological properties for prediction of plant growth as a function of environmental variables.

**Key words:** Efficiency, growth, maintenance, respiration.

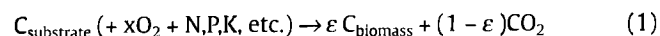
## Abbreviations:

*g*: growth coefficient, unitless  
*GE*: growth efficiency  
*GV*: glucose value, grams glucose/gram biomass  
*m*: maintenance respiration rate  
*R<sub>CO<sub>2</sub></sub>*: specific CO<sub>2</sub> rate, moles/time/mass  
*R<sub>SG</sub>*: specific growth rate, moles C/time/mass  
*ε*: substrate carbon conversion efficiency

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## Introduction

The literature contains many correlations establishing that the rate of respiratory metabolism is directly related to the growth rate of plants (Amthor, 1989). The mathematical form of the relation between growth rate and the rate of CO<sub>2</sub> evolution during respiration is easily derived from the overall chemical equation for aerobic growth shown in equation 1



where  $\epsilon$  is the substrate carbon conversion efficiency. (The symbol  $\epsilon$  is used here to avoid confusion with various symbols and definitions used previously by others.) The quantitative relation between the specific CO<sub>2</sub> rate (*R<sub>CO<sub>2</sub></sub>* in moles/time per

mass) and specific growth rate (*R<sub>SG</sub>* in moles of C going into structural biomass/time per mass) of a plant or tissue, derived by inspection of equation 1, is

$$R_{SG} = R_{CO_2} [\epsilon / (1 - \epsilon)] \quad (2)$$

where  $[\epsilon / (1 - \epsilon)]$  is simply the ratio of coefficients in equation 1. Note  $\epsilon$  is a variable, not a constant, and that structural biomass as defined here includes all products of respiration-driven biosynthesis.

Equation 2 accurately describes plant growth rate as a function of the respiratory CO<sub>2</sub> rate, but has not been widely applied in plant growth studies because of the difficulty of determining  $\epsilon$ . If properly used, equation 2 provides a basis for a physiological model to predict plant growth rate as a function of abiotic and biotic factors (Hansen et al., 1996). Reformulation of equation 2 in terms of readily measurable parameters provides an invaluable means for developing models and methods leading to rapid and less expensive selection of crop plants and for better ecological modeling if  $\epsilon$  could be determined across the range of growth conditions (Hansen et al., 1994). Progress in developing useful forms of equation 2 is presently being impeded by misconceptions that have become deeply entrenched in plant sciences and ecology.

## Photosynthesis

Rather than focusing on respiration rate as a measure of growth rate, many plant physiologists have assumed photosynthesis is the major determinant of growth rate. This assumption requires that plant growth rate be determined by the availability of photosynthate, and thus photosynthesis parameters are predictive of plant growth rates. This view has long been questioned (Evans, 1975) and much of the evidence is tautological or equivocal (Demetriades-Shaw et al., 1992 and 1994). The absence of a general correlation between photosynthesis rate and growth rate has caused some authors to focus on the rate of loss of assimilated carbon leading to a conclusion that "... further increase in production will require greater rates of canopy photosynthesis or reduced respiration or longer duration of crop and photosynthesis" (Lawlor, 1995). Such conclusions unfortunately do not further our understanding of  $\epsilon$  or of the relation between carbon assimilation and plant growth. Although plant growth is absolutely dependent on photosynthate and may be limited by photosynthesis

under some conditions, under many conditions growth is limited by the availability of other nutrients or by the ability of the plant to use available photosynthate (Evans, 1975; Hansen et al., 1996 and 1997a).

Only under photosynthate-limited conditions can measurements of photosynthetic rates be used to predict plant growth rates. In contrast, equation 2 holds for all conditions of aerobic metabolism, and thus measurements of  $R_{CO_2}$  and  $\epsilon$  can accurately predict plant growth rates (i.e. the rate of increase in structural biomass) no matter what ultimately limits growth. Because of the focus on photosynthesis, the important contribution that knowledge of  $\epsilon$  can make to understanding the energetics of plant growth has often not been appreciated.

### Growth Efficiency

In the past, growth efficiency has usually been calculated from equation 3 (Tanaka and Yamaguchi, 1968)

$$GE = (\Delta W_B / \Delta t) / (\Delta W_B / \Delta t + \Delta W_R / \Delta t) \quad (3)$$

where  $\Delta W_B / \Delta t$  is the increase in total biomass dry weight over a given time  $\Delta t$  and  $\Delta W_R / \Delta t$  is the dry weight loss due to respiration over the same time period. Uncritical use of equation 3 gave rise to the idea that decreasing respiration would increase growth (Hopkins, 1995). But equation 2 shows that a high rate of respiration is required for a high rate of growth (assuming  $\epsilon / (1 - \epsilon)$  does not decrease). The direct proportionality between growth rate and respiration rate in equation 2 is consistent with the fast respiration rates found in rapidly growing tissues and plants and the slow rates found in slowly growing tissues and plants. The few exceptions to this rule (Amthor, 1989) are probably explained by variations in  $\epsilon$ . The idea that decreasing total respiration rate will increase growth has largely been discredited, but vestiges of this misconception remain, particularly in considerations of carbon balances in ecology and in statements that decreasing maintenance respiration will increase growth.

Rearrangement of equation 2 into the form of equation 3 gives equation 4.

$$\epsilon = R_{SG} / (R_{SG} + R_{CO_2}) \quad (4)$$

Even though equations 3 and 4 appear to be equivalent, they are not. Furthermore, GE and  $\epsilon$  are not equivalent.  $R_{SG}$  includes only the rate of increase in the non-storage or structural portion of the biomass, but  $\Delta W_B / \Delta t$  includes stored photosynthate.  $\Delta W_B / \Delta t$  in equation 3 does not always correctly represent the rate of increase in growth mass. Consider growth of plants at night when the total mass of the plant is decreasing as stored photosynthate is converted into structural biomass by respiration-driven biosynthesis. Even though the plant grows, GE is negative at night;  $\epsilon$  is always positive as required during growth. Furthermore, because  $\Delta W_B / \Delta t$  and  $\Delta W_R / \Delta t$  are defined in terms of mass, not moles of carbon, the value of GE depends on the oxidation states of the respiratory substrate and the biomass. The value of  $\epsilon$  does not depend on oxidation states in this way.

### Compartment Models of Respiration

Another misconception is that substrate carbon conversion efficiency can be simplified and understood by apportioning the loss of carbon from respiration between growth costs and maintenance costs. Definitions of growth and maintenance respiration are summarized by: (1) Maintenance respiration is that component of respiration not used to directly support growth, and (2) growth respiration is that component of respiration used directly for growth, i.e. not used for maintenance. Such a partitioning is expressed in equation 5

$$R_{CO_2} = gR_{SG} + m \quad (5)$$

where  $g$  is defined as a unitless growth coefficient and  $m$  is defined as the maintenance rate (Penning de Vries, 1972; Amthor, 1989; Thornley and Johnson, 1990). Several methods for determining  $g$  and  $m$  have been proposed (Penning de Vries, 1975a; Chiariello et al., 1989). Some of the serious problems with these methods have been discussed (Breeze and Elston, 1983; Amthor, 1989; Chiariello et al., 1989; Shinano et al., 1996).

A method based on analysis of  $^{14}CO_2$  release rate and residual  $^{14}C$  in biomass fractions following a pulse label of plants has been used to obtain values for  $g$  and  $m$  (Ryle et al., 1976; Breeze and Elston, 1983). While this method showed early promise, recent studies show that the method fails because the slow and fast release pools measured do not correspond to maintenance and growth fractions as was assumed (Shinano et al., 1996).

Determination of  $g$  and  $m$  with equation 5 and simultaneous measurements of growth and respiration is also flawed. Extraction of  $g$  and  $m$  from application of equation 5 requires the assumption of a linear relation between growth rates and  $CO_2$  (or  $O_2$ ) rates of similar tissues of different ages or conditions on a plant, and thus that  $g$  and  $m$  are constants. But both the assumption of linearity and the assumption of constant  $g$  and  $m$  are false, and linear regression thus does not give valid  $g$  and  $m$  values. For such a plot of experimental data to be linear, equation 2 requires that the function  $\epsilon / (1 - \epsilon)$  be constant or covariant with  $R_{CO_2}$ . The first condition is impossible among plants or tissues varying over a wide range of growth rates (by definition  $\epsilon = 0$  when  $R_{SG} = 0$  and  $\epsilon$  increases as growth rate increases, see equation 4) and the second condition indicates variable  $g$  and  $m$ . Data fitting of respiration and growth rates and extrapolation with equation 5 thus leads to meaningless values for the intercepts ( $m$ ) and slopes ( $g$ ) of such plots. Most plots of specific  $R_{CO_2}$  vs. specific growth rate are distinctly non-linear and have only been fitted with a straight line because the model requires constant  $g$  and  $m$  (e.g. Wullschlegel et al., 1995; Mata et al., 1996). Use of the regression method thus requires both the difficult task of proving the linearity of the data over the entire range of  $\epsilon$  including the extrapolation to zero for obtaining  $m$  (Oreskes et al., 1994), and proving that  $m$  and  $g$  are constant instead of covariant with growth rate. Contrary to the assumptions required for linear regression determination of  $g$  and  $m$ , Amthor (1989) stated "The maintenance (respiration) coefficient tends to increase as the growth rate increases." Also, there is increasing evidence that  $m$  varies with growth rate (Amthor, 1998; Lavigne and Ryan, 1998).

Direct determination of  $m$  by equating  $m$  to the respiration rate of non-growing tissues is also incorrect. The biochemistry of mature and starved tissues, and hence  $m$ , is not the same as in growing tissues (Breeze and Elston, 1983). Likewise, equating the energetic cost of a stress to differences in  $m$  values produces meaningless numbers.

Many workers have recognized the conceptual and experimental difficulties with determination of  $m$  (e.g. see Amthor, 1989; Chiariello et al., 1989; and Thornley and Johnson, 1990). The discussion above shows that neither  $g$  nor  $m$  can be obtained from regression of respiration-growth data, from data on starved or mature tissue, or from  $^{14}\text{C}$  release data. Most workers have been confident, however, that stoichiometric calculations (i.e. calculation of growth coefficients from reaction pathways and molecular composition, elemental composition, and heat of combustion of biomass) have provided accurate values for  $g$  (Gary et al., 1995). But the results of these determinations have been interpreted incorrectly. Application of stoichiometric methods to open systems does not correctly include total energy costs and therefore the carbon requirements for biomass synthesis. Methods based on composition and heats of combustion were originally developed, and have been correctly applied to, growth of micro-organisms in closed culture (e.g. Battley, 1998), but these methods were incorrectly extended to plants growing in open systems. This fundamental misunderstanding of the difference between closed and open systems causes an error in  $g$  as large as a factor of 2. Calculations of growth yield by the stoichiometric methods give values around 0.88 moles of  $\text{C}_{\text{biomass}}$ /mole of  $\text{C}_{\text{substrate}}$  while measurements show that "approximately half of the carbon assimilated in photosynthesis is eventually lost by respiration" (Hopkins, 1995).

The difficulties with the experimental methods for partitioning of respiration into growth and maintenance are not surprising when the concepts underlying partitioning are analyzed. The fundamental problem is that there is no way to define unequivocal boundaries among the various functions of respiration because it is impossible to select a cellular process that is required for maintenance but not for growth. Every process that contributes to the viability of cells, whether it be turnover of cellular components, maintenance of ion gradients, or synthesis of cell walls, is absolutely required for, and cannot be separated from, growth. Even pathways such as the alternative oxidase of mitochondria and other so called "wasteful" pathways of respiration (Lambers and Rychter, 1989) should not be labeled as maintenance respiration. These pathways are likely to be found to be essential for cell viability, function, and growth under some conditions. The many varying literature definitions of the growth and maintenance compartments of respiration discuss ion gradients, protein turn-over, mRNA, etc. with no consensus. Literature statements in which each author includes a different list of which processes should be included in which respiration compartment (e.g. Lafitte and Loomis, 1988; Amthor, 1989; Chiariello et al., 1989; Nelson, 1994) when taken together are reminiscent of Alice's argument with the Red Queen in *Alice in Wonderland*.

We conclude that  $g$  and  $m$  are not constant as required for use of equation 5, cannot be accurately defined, and have not been measured for plants. The compartmental separation concept for respiration is impeding development of more

useful physiological models for plant growth. Treating respiration in the living system as a whole is the only way to avoid such difficulties.

### Growth Yield Calculations

Calculations of plant growth yield that have been done from biochemical pathway analysis and biomass molecular composition (Penning de Vries et al., 1974; Penning de Vries, 1975b; Penning de Vries and van Laar, 1977; Chiariello et al., 1989), from biomass elemental composition (McDermitt and Loomis, 1981; Chiariello et al., 1989), and from biomass heat of combustion (McDermitt and Loomis, 1981; Williams et al., 1987; Chiariello et al., 1989) are in agreement (Gary et al., 1995), but the results do not correctly describe the growth yield. Penning de Vries et al. (1974) defined "construction cost" as the stoichiometric ratio of biomass carbon to carbohydrate carbon necessary to form the biomass, but excluding maintenance costs. Penning de Vries et al. included both carbon lost in formation of carbon skeletons through disproportionation reactions and through oxidative phosphorylation for formation of the stoichiometric amount of ATP required for the biosynthesis reactions. Penning de Vries method in effect calculates a maximum theoretical value of  $\epsilon$  from stoichiometric calculations of the biochemical requirement for ATP and reducing equivalents. Glucose values (GV) obtained by the methods of McDermitt and Loomis (1981) or Williams et al. (1987) from elemental analysis or heat of combustion of biomass do not include the carbon cost for ATP production or maintenance. GV can be corrected to production values or Penning de Vries "construction cost" by dividing by  $0.884 \pm 0.010$  (McDermitt and Loomis, 1981) or by a number in the range 0.84 to 0.95 (Williams et al., 1987). Results from all three methods have led to the conclusion that "construction cost", and thence  $g$ , is independent of conditions. However, previous interpretations of these data have failed to consider that a plant is an open system. Matter and energy is exchanged across the boundaries of an open system, and thus not included in the above three methods for determining "construction cost".

The second law of thermodynamics defines the energy efficiency of open systems. Thus, the energy derived from respiration must be greater than, and not just equal to, the energy used for biosynthesis. (The excess energy discussed here is a consequence of the existence of indirectly coupled reactions, and cannot be labeled as maintenance energy.) This excess energy required for biosynthesis is not stored in biomass; it appears as metabolic heat, producing an increase in the entropy of the surroundings. This energy loss is not included in the growth yield calculated for an open system from biochemical pathway analysis and biomass molecular composition, or from biomass elemental composition, or from biomass heat of combustion. To illustrate the energy cost not included, consider a wood carving and a piece of firewood of the same mass and molecular and elemental composition. The heats of combustion are essentially the same, but the energy dissipated to produce the two is very different, and the difference depends on how fast and how efficiently the woodcarver works.

Another means of viewing the energy loss error comes from recognition that the stoichiometry of coupling between catabolic and anabolic reactions of metabolism is not con-

stant. The stoichiometric ratio varies with changes in the force-flux relationships between the reactions (Stucki, 1989) and therefore with intracellular and external reaction conditions that continually change with plant development and environmental conditions. Life requires the existence of energy gradients in the form of concentration gradients. Spontaneous flows of matter (molecules, ions, and electrons) down these concentration gradients (catabolism) in a living organism are coupled to, and thus provide energy for, driving the reactions of biosynthesis (anabolism and growth). These processes are accompanied by increasing entropy in the surroundings as a result of metabolic heat, i.e. the heat transferred to the environment. Metabolic heat is not specifically included in and only a minor portion of it is accounted for in the enthalpy changes derived from the calculations and methods of Penning de Vries (1974), McDermitt and Loomis (1981), and Williams et al. (1987).

Energy efficiency varies with the rate of the process and the reaction conditions and is subject to regulation by the organism (Stucki, 1989; Nath, 1997). Changing the ATP coupling constant as a means of changing energy efficiency in calculations of construction cost (Penning de Vries et al., 1974) is inappropriate as it does not address the fundamental error, i.e. failure to consider coupling inefficiency as a variable dependent on growth rate and conditions. Introducing alternative pathways of respiration to vary efficiency (Lambers et al., 1983; Chiariello et al., 1989) is, in effect, a means of changing the coupling constant.

The calculations of Penning de Vries et al. (1974) give the value of the enthalpy change for reaction 1 as a function of  $\epsilon$ . But, as explained above, the enthalpy change calculated in this manner does not include all of the energy necessary for biomass construction in an open system. Glucose values also are not a measure of the actual construction cost, but instead are related to the enthalpy change for the reaction:  $C_{\text{substrate}} \rightarrow C_{\text{biomass}}$  (Vertregt and Penning de Vries, 1987), i.e.  $\Delta H_B$  as defined in Hansen et al. (1994). Although they should be corrected for photosynthate, values for these enthalpy changes are valuable data for input into newer models (e.g. Hansen et al. 1994) that can correctly describe the actual energy cost for biomass construction.

Accurate values of  $\epsilon$  can be measured by at least two methods. Measurements must be made on living tissue or plants during the growth process, either by metabolic rate measurements (Hansen et al., 1994) or by integral methods (Penning de Vries and van Laar, 1977; Yamaguchi, 1978) that account for the total exchange of energy and/or mass with the surroundings over the duration of the growth process. By the integral method, Yamaguchi (1978) and Hansen et al. (1994) obtained an  $\epsilon$  value of approximately 0.6 for maize seedlings. Penning de Vries (1972, p. 341) also reported a value of 0.6 moles  $C_{\text{biomass}}/\text{mole } C_{\text{substrate}}$  for maize seedlings. The magnitude of the error made in determination of the conversion efficiency by pathway analysis (Penning de Vries et al. 1974), or the methods of McDermitt and Loomis (1981), and Williams et al. (1987) can be estimated by comparison of Penning de Vries et al. (1974) value of 0.88 moles  $C_{\text{biomass}}/\text{mole } C_{\text{substrate}}$  calculated for maize embryo tissue with the 0.6 experimental value. Even after correcting for maintenance (Penning de Vries and Van Laar, 1977, p. 226), a difference of 20 to 30% between calculated and measured seedling growth remained to be

explained. The authors offered leakage of carbohydrate as an explanation.

### Maintenance Energy

While maintenance energy cannot be associated with any particular metabolic process, the concept of maintenance is useful when discussing the need for plants to constantly replace and repair components and to respond to various stresses. It is therefore of value to arrive at an accurate definition of maintenance rate. Maintenance rate can be defined as the metabolic rate of an organism, tissue, or culture maintained in a steady state (i.e. perpetual stasis under a given set of conditions). However, the maintenance rates obtained are of limited value because they are valid only at the unique set of conditions employed to obtain the steady state. Extrapolation to other conditions is generally not possible. Thus, such data contribute little to understanding the biology of plants. Plants are autotrophic ectotherms living in constantly changing environments. They would seldom, if ever, experience the conditions of a steady state study.

This definition of maintenance rate does allow a definitive statement of the sequence of events that must happen in a plant if the metabolic rate becomes too low because of a lack of substrates or because of stressful conditions. First, the intracellular concentration gradients required for life will decay, then because the gradients are required to maintain tertiary structures, the organelles and cells will lose their membrane integrity, and the plant will die unless the gradients can be restored and the damage repaired (Criddle et al., 1997; Hansen et al., 1997b).

### Consequences of Using Compartment and Stoichiometry-Based Models of Plant Growth

More than twenty years of analyses of respiration data with compartment models have failed to produce a quantitative, predictive relation between plant growth and respiration. If the concepts embodied in compartment models are valid, why have they not been used for selection of crop plants? No successful introduction to agriculture of a plant with improved growth rate has been based on the misconceptions discussed here. Even the oft-cited work of Wilson (1975, 1982) and Wilson and Jones (1982) on perennial ryegrass populations with clear differences in respiration rates failed to result in an agronomic improvement (Kraus et al., 1993), although the initial interpretation of the data suggested the yield increase was due to a decrease in respiratory carbon losses. One hallmark of invalid concepts is that they appear to explain observed phenomena but do not lead to useful insights, no matter how much effort is expended (Kuhn, 1962).

Unsubstantiated answers to important questions regarding plant growth have become doctrine because of acceptance of the validity of compartment models. For example, it is commonly accepted that "temperature increase raises the cost of maintenance" (Penning de Vries, 1975a). (See also McCree, 1974; Penning de Vries, 1975b; McCree and Van Bavel, 1977.) There is also "little or no doubt that (respiration for) synthesis is independent of temperature" (Breeze and Elston, 1983) (see also McCree, 1974; Penning de Vries, 1975b; McCree and Van Bavel, 1977), and that maintenance respira-

tion is "proportional to the dry weight of the plant" and that "growth respiration rate is proportional to the growth rate or gross photosynthetic rate" (Chiariello et al., 1989). The substitution of an unmeasurable and nebulous "maintenance rate" for the energy losses required by the second law for an open system with indirectly-coupled reactions has led to these wrong explanations for experimental observations and thence to wrong conclusions about plant metabolic physiology. Neither the relation between respiration and growth nor the effects of environmental factors on growth can be correctly described with flawed measurements of improperly defined parameters. Even when apparent functional agreement exists between compartment respiration models and experiment, the results are misleading.

Despite expressing doubts about methods and assumptions in compartment models, many authors have then used a compartment model to explain their data. Compartment models apparently have been viewed as "good enough", or at least "the best means available" for analysis of growth energetics. Compartment models are not good enough. There is another means available for analysis of growth-respiration data. By combining enthalpy changes determined by the methods of Penning de Vries (1974), McDermitt and Loomis (1981), and Williams et al. (1987) with simultaneous measurement of metabolic heat and CO<sub>2</sub> rates, equation 2 can be used to predict growth rates from physiological measurements made as a function of environmental variables (Hansen et al., 1994; Hansen et al., 1996; Criddle et al., 1997). The energetics of respiration-driven growth cannot be understood without measurement of both the gas exchange rate and the metabolic heat rate. The CO<sub>2</sub> evolution rate or O<sub>2</sub> uptake rate is a measure of the rate of energy input into the tissue or plant. The metabolic heat rate is the rate of loss of energy from the tissue or plant. Trying to understand the relation between respiration and growth from measurements of only gas exchange rate is like trying to determine profit from income without knowledge of expenses.

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