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The relation between plant growth and respiration: A thermodynamic model

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Abstract. A thermodynamic model describing the relation between plant growth and respiration rates is derived from mass- and enthalpy-balance equations. The specific growth rate and the substrate carbon conversion efficiency are described as functions of the metabolic heat rate, the rate of CO_2 production, the mean oxidation state of the substrate carbon produced by photosynthesis, and enthalpy changes for conversion of photosynthate to biomass and CO_2. The relation of this new model to previous models based only on mass-balance equations is explored. Metabolic heat rate is shown to be a useful additional measure of respiration rates in plant tissues because it leads to a more explicit description of energy relations. Preliminary data on three *Zea mays* (L.) cultivars are reported. The model suggests new rationales for plant selection, breeding and genetic engineering that could lead to development of plants with more desirable growth rates.

Key words: Energy efficiency – Growth – Metabolic heat rate – Model (thermodynamic) – Respiration – *Zea*

Introduction

Existing literature contains many positive and a few negative correlations between plant growth rates and respiration rates (e.g. see Geider and Osborne 1989; Hansen et al. 1989; Poorter et al. 1990; Anekonda 1992; Hansen et al. 1992; Kraus et al. 1993; Anekonda et al. 1994; and reviews in Ryle 1984; Fitter and Hay 1987; Amthor 1989; Hay and Walker 1989). These correlations suggest that research on plant respiration should be a particularly fruitful area for development of means to increase or control plant growth rates. However, "the precise nature of the relationship between growth and respiration in ... plants is unknown" (Amthor 1989), and "surprisingly little is known about the underlying physiological mechanisms causing the negative correlation between yield and respiration" (Kraus et al. 1993). Existing growth-respiration models may closely simulate aspects of plant growth and are therefore useful, but are limited in their ability "to test hypotheses about respiration and its links to growth and productivity" (Amthor 1989). These failures of existing models are reflected in ongoing arguments about whether increased or decreased respiration will increase crop productivity (Beevers 1970; Lambers 1985; Amthor 1989; Kraus et al. 1993).

Most respiration-based models for plant growth are simply empirical equations fitted to experimental data. Such equations are useful as a database, but cannot provide further insight into the relation between growth and respiration until they can be placed into the context of an accurate and complete mechanistic model. Two mechanistic models relating plant growth to respiration are frequently cited in current literature.

The first of these models equates growth rate to the difference between photosynthetic and respiration rates,

$$\dot{G} = \dot{P} - \dot{R} \qquad \text{(Eq. 1)}$$

(see *Appendix* for explanation of symbols). Although the equation is true when integrated over a growth season, the equation is incorrect when expressed as instantaneous rates, because it assumes growth rate is equivalent to carbon accumulation rate and thus does not distinguish between stored photosynthate and photosynthate processed into new cell material. Equation 1 implies all respiration diminishes growth; but respiration is certainly required for growth. A rapidly growing tissue must respire at a high rate to produce the energy and intermediates at the high rate necessary to sustain the high rate of biosynthesis. Therefore Eq. 1 does not accurately describe the growth rate-respiration rate relation.

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The second model, which was developed as an empirical equation (McCree 1970) at about the same time it was derived theoretically (Thornley 1970), separates the dual roles of respiration in growth and maintenance:

$$\dot{R} = g\dot{G} + \dot{m} \quad \text{(Eq. 2)}$$

where g is the growth coefficient (Amthor 1989) and $\dot{m}$ is the rate of maintenance respiration, is one form of this model (Thornley and Johnson 1990; Amthor 1989). Use of Eq. 2 and related models presents several difficulties, however. Determination of g and $\dot{m}$ values with Eq. 2 requires that g be constant and that $\dot{m}$ be negligible or constant while $\dot{R}$ and $\dot{G}$ are varied, severe experimental restrictions. There are many situations of interest that cannot meet these criteria. Even when the restrictions are apparently met, it does not prove that accurate (as opposed to precise) values of g and $\dot{m}$ are obtained from the slope and intercept of a plot of $\dot{R}$ versus $\dot{G}$, since any linear function would describe data that can be fit by Eq. 2. This colinearity problem is quite likely to occur because the plots of $\dot{R}$ versus $\dot{G}$ always must contain a hidden variable, e.g. age, light intensity, nutrient level, used to vary $\dot{R}$ and $\dot{G}$. Independent measurement of g or $\dot{m}$ requires questionable assumptions and/or severe experimental difficulties as discussed by Amthor (1989), and there is no means of verifying the interpretation of linear $\dot{R}$ versus $\dot{G}$ plots made with this model. Furthermore, this model is incomplete. Equation 2 does not give explicit information on how $\dot{m}$ and g are related to specifics of plant metabolism. For example, it does not consider the effect of biomass composition on the growth-respiration relation and it implies numerical equivalence of the various measures of respiration rate even though different measures of respiration rate may be affected differently by the hidden variable in such studies. Although the consensus from limited data on g and $\dot{m}$ as a function of temperature is that g is independent of temperature and $\dot{m}$ increases with temperature (Amthor 1989), there is no theoretical basis for a quantitative prediction of the dependence of g and $\dot{m}$ on environmental factors. A more complete model with more accessible and better-defined experimental variables is needed.

Although both previous mechanistic models have been used as a basis for discussions of energy use in plants, they are both mass-balance models which use the law of conservation of matter as the only basis for their derivation and thus cannot be explicit concerning energy. The second law of thermodynamics requires energy efficiency to be less than 100% in all processes, biological as well as mechanical, a fact also not included in previous models. Based on known biochemistry and using solely stoichiometric considerations, Penning de Vries et al. (1974) calculated a maximum possible substrate carbon conversion efficiency of 90%, but this value represents an unachievable 100% energy-use efficiency. Highly developed crop plants may achieve actual yields as high as 50% substrate carbon conversion efficiency over a growth season, but many plants use more than half of their photosynthetically fixed carbon in respiration. The two commonly used measures of respiration rate, i.e. CO_2 production rate and O_2 use rate, taken together measure the stoichiometry of respiration, i.e. the respiratory quotient, but do not contain any direct information on energy. The metabolic heat rate measures respiratory energy loss (Wohl and James 1942), and the ratios of metabolic heat rate to the CO_2 and O_2 rates are both related to energy-use efficiency, but through somewhat different parameters. The purpose of this paper is to explore the advantages of adding metabolic heat rate to the list of readily available measures of plant respiration. Metabolic heat rate in plant tissues is easily measured with commercially available calorimeters, and supplies the necessary information for use of an energy-balance equation. When considered together, simultaneously measured values of CO_2 production rate, O_2 use rate and metabolic heat rate provide an experimental link between cellular biochemistry and whole-plant processes. Although measurements of metabolic heat rate are commonly done on animals and microorganisms, very little data on metabolic heat rates of plants have been reported until recently (Wadsö 1988; Criddle et al. 1991b).

In the first part of this study, equations relating CO_2 production rate, O_2 use rate and metabolic heat rate to growth rate and substrate carbon conversion efficiency are derived. Such a model requires logical proof, and must be consistent with experimental data if it is to be useful. The value of such a purely mechanistic model that is consistent with experimental data lies in explaining and relating previously disparate observations, in identifying misconceptions, and in suggesting directions for future research. The equations derived in this study are capable of accurately describing the relation between plant respiration and growth rates, and when applied to experimental data, lead to new questions about the mechanisms controlling plant growth rates.

The many strong correlations found between growth rate and respiration rate imply that respiration rate reflects the rate of growth regardless of whether respiration is the rate-limiting step, is demand-driven by maintenance and biosynthesis, or is limited by photosynthate supply. Within a species, considerable variability exists among individual genotypes in all three measures of respiratory rate considered here as well as in substrate carbon conversion efficiency (e.g. Wilson 1975; Yamaguchi 1978; Robson 1982; Wilson 1982; Wilson and Jones 1982; Amthor 1989; Geider and Osborne 1989; Poorter et al. 1990; Anekonda 1992; Hansen et al. 1992, 1989; Anekonda et al. 1994). These traits have rarely been used as selection criteria, however, because previous methods for their measurement are difficult to apply. The theory presented in this paper provides the basis for development of more suitable techniques for evaluation of respiration rates and efficiencies and their effects on growth rates among individuals in large populations of plants. These techniques are thus of potential use in breeding and genetic engineering programs. Since it is cast in terms of well defined stoichiometric and thermodynamic variables, the model also provides a natural means for including the effects of environmental variables on growth rate.

Derivation of equations relating growth and respiration

The equations presented in this paper describe the relation between respiration and growth rates of plants in the absence of light. Respiratory metabolism in plants has three inputs, i.e. photosynthate, oxygen and mineral nutrients (e.g. N, P, K) and three outputs, i.e. heat, carbon dioxide, and biomass. A model relating the inputs to the outputs can be derived from the general chemical reaction for plant respiration and growth,

$$C_{in} + aO_2 + bN_{in} + cP_{in} + dK_{in} + \ldots \rightarrow \varepsilon C_{bio} + (1-e)CO_2 + bN_{bio} + cP_{bio} + dK_{bio} + \ldots \quad \text{(Eq. 3)}$$

where C_{in} represents the substrate carbon input or photosynthate, N_{in}, P_{in}, and K_{in} respectively represent the inputs from the environment of nitrogen, phosphorous and potassium, C_{bio}, N_{bio}, P_{bio} and K_{bio} represent the average chemical form of each of the elements in the biomass, and ε is the substrate carbon conversion efficiency.

The specific metabolic heat rate, $\dot{q}$, i.e. the heat rate from reaction 3 per mass of tissue, is given by

$$-\dot{q} = R_{CO_2}\,\Delta H_{CO_2} + R_{SG}\,\Delta H_{SG} + \Sigma R_E\,\Delta H_E \quad \text{(Eq. 4)}$$

where R_{CO_2} is the specific rate of CO_2 production, ΔH_{CO_2} is the enthalpy change per mole of carbon for conversion of photosynthate to CO_2, R_{SG} and ΔH_{SG} are respectively the specific rate and enthalpy change for conversion of photosynthate to biomass, and R_E and ΔH_E are respectively the specific rates and enthalpy changes for conversion of elements other than carbon from the input form to the biomass form. The summation is taken over all elements other than carbon. However, only major elements need be considered in the summation, since only these contribute significantly to the metabolic heat rate. At 13–15% of total dry mass, nitrogen must be included, and may be the only significant element in the summation. ΔH_N will vary significantly with the form of nitrogen supplied to the plant.

Assuming unchanging elemental composition of plant dry matter over the time of the experiment, Eq. 4 further reduces to

$$-\dot{q} = R_{CO_2}\,\Delta H_{CO_2} + R_{SG}(\Delta H_{SG} + \Sigma r_E\,\Delta H_E) = R_{CO_2}\,\Delta H_{CO_2} + R_{SG}\,\Delta H_B \quad \text{(Eq. 5)}$$

where r_E is the proportionality constant between R_E and R_{SG}, and ΔH_B is the total enthalpy change per mole of carbon incorporated into biomass. ΔH_B includes redox reactions involved in biomass production, as well as polymerizations, transport, and all other biosynthetic and maintenance processes. In situations where ΔH_B is equal to zero or in mature, nongrowing tissues where R_{SG} is equal to zero, Eq. 4 reduces to a simple proportionality between $\dot{q}$ and R_{CO_2}. Since R_{CO_2} and R_{O_2} are also directly proportional (Eq. 3), $\dot{q}$ and R_{O_2} are also directly proportional. The coefficients of proportionality between $\dot{q}$ and R_{CO_2}, i.e. ΔH_{CO_2}, and between R_{CO_2} and R_{O_2}, i.e. the respiratory quotient, are variable, but the proportionality coefficient between $\dot{q}$ and R_{O_2}, i.e. ΔH_{O_2}, is an empirical constant called the oxycaloric ratio or the constant from Thornton's rule.

From stoichiometric considerations, ΔH_{CO_2} can be expressed in terms of the average oxidation state of the substrate carbon, γ_P, and the enthalpy change for complete oxidation of C_{in} to CO_2 expressed per mole of O_2, i.e. ΔH_{O_2}:

$$\Delta H_{CO_2} = (1-\gamma_P/4)\,\Delta H_{O_2} \quad \text{(Eq. 6)}$$

The oxidation state is defined here as it is defined in chemistry, i.e. $\gamma_P = +4$ in CO_2, 0 in $C_nH_{2n}O_n$, -4 in CH_4, and $+1$ in H_2NCH_2COOH. For convenience, biologists sometimes use the degree of reductance (Erickson 1987) which is equal to 4 minus the oxidation state. ΔH_{O_2} is an empirical constant with a value of -455 ± 15 kJ·mol^{-1} of O_2 for the major compounds in plant metabolism (McDermitt and Loomis 1981; Loomis 1982; Erickson 1987; Williams et al. 1987). Carbohydrates are at the high end of the range (-468 kJ·mol^{-1}; Domalski 1972; Erickson 1987) and fats and proteins are at the low end of the range (-436 kJ·mol^{-1}; Erickson 1987). If end products of catabolism other than CO_2 (e.g. lactate and ethanol) are produced, the 1 in Eq. 6 must be modified to $\gamma_{\text{catabolic products}}/4$) to account for the average oxidation state of the catabolic products.

Substituting Eq. 6 into Eq. 5 and rearranging gives

$$R_{SG} = -[\dot{q} + R_{CO_2}(1-\gamma_P/4)\,\Delta H_{O_2}]/\Delta H_B \quad \text{(Eq. 7)}$$

This equation gives R_{SG}, the specific growth rate, in moles of carbon per unit time per mass of tissue. Conversion of R_{SG} to the more usual units of rate of mass produced per unit time per mass of tissue requires multiplying R_{SG} by the ratio of biomass mass to moles of carbon.

The substrate carbon conversion efficiency, ε, can also be expressed in terms of the same variables and parameters appearing in Eq. 7. The definition of ε is given by

$$\varepsilon = R_{SG}/(R_{SG} + R_{CO_2}) \quad \text{(Eq. 8)}$$

Note that ε includes both growth and maintenance terms and is identical with the "growth efficiency" as defined by Amthor (1989) and Yamaguchi (1978) and the "conversion efficiency" as defined by Thornley and Johnson (1990). Application of Thornton's rule to Eq. 8 converts it into the "enthalpic efficiency" commonly used in literature on microorganisms (e.g. Erickson 1987). Substituting Eq. 7 into Eq. 8 and simplifying gives

$$\varepsilon = [(\dot{q}/R_{CO_2}) + (1-\gamma_P/4)\,\Delta H_{O_2}]/[(\dot{q}/R_{CO_2}) + (1-\gamma_P/4)\,\Delta H_{O_2} - \Delta H_B] \quad \text{(Eq. 9)}$$

Equations 7 and 9 predict specific growth rates and substrate carbon conversion efficiencies from information on γ_P, ΔH_B and simultaneously measured values of $\dot{q}$ and R_{CO_2}.

Figure 1 is derived from Eqs. 7 and 9 and shows how R_{SG} varies with $\dot{q}$, ε, and R_{CO_2} under one particular set of conditions, i.e. $\gamma_P = 0$, and $\Delta H_B = 25$ kJ·mol^{-1}. Increas-

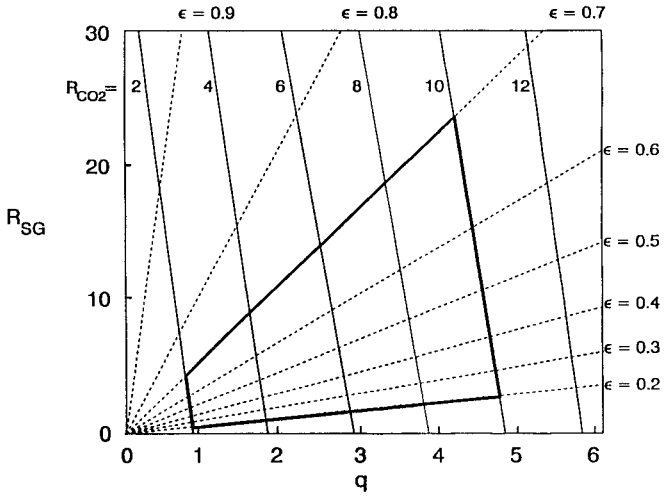

Fig. 1. Calculated specific growth rate (R_{SG}, pmol·(mg FW)$^{-1}$·s^{-1}) as a function of the metabolic heat rate ($\dot{q}$, μW·(mg FW)$^{-1}$) for various values of the rate of evolution of CO_2 (R_{CO2}, pmol·(mg FW)$^{-1}$·s^{-1}) and substrate carbon conversion efficiency (ε). Calculated on the basis of fresh weight assuming $\gamma_P = 0$, $\Delta H_{O_2} = -468$ kJ·mol^{-1} and $\Delta H_B = 25$ kJ·mol^{-1}. See Eqs. 7 and 9

ing metabolic rate at constant efficiency increases R_{SG} along the dashed lines and increasing efficiency at constant R_{CO_2} increases R_{SG} along the solid lines. The trapezoid encloses the area defined by the range of ε and $\dot{q}$ values typically observed for growing plants. Simultaneously increasing both metabolic rate and ε increases R_{SG} along the major diagonal of the trapezoid. Increasing metabolic rate while decreasing ε changes R_{SG} along the minor diagonal. Figure 1 could obviously also be drawn using R_{CO_2} as the horizontal axis and $\dot{q}$ as the third axis. The $\dot{q}$ axes then have a positive slope of the same magnitude as the negative slope of the R_{CO_2} axes pictured. R_{O_2} could likewise be used as the horizontal axis or third axis. Note that constant, arbitrary values for γ_P and ΔH_B have been assumed, but these parameters may not be constant within a collection of plants. Choosing other reasonable values for γ_P and ΔH_B alter the values on the axes but the trapezoid remains generally as plotted in Fig. 1. As the ΔH_B value changes from positive through zero to negative, the lines of constant R_{CO_2} rotate from negative slopes to positive slopes and the slopes of the dashed lines of constant e decrease continuously. Changing γ_P from positive through zero to negative values produces similar changes.

R_{SG} may also be expressed as a function of only one of the respiratory variables $\dot{q}$, R_{CO_2} or R_{O_2} as shown in Eqs. 10–12:

$$R_{SG} = R_{CO_2}(\varepsilon/1-\varepsilon) \quad \text{(Eq. 10)}$$

$$R_{SG} = \dot{q}/[(1-1/\varepsilon)(1-\gamma_P/4)\,\Delta H_{O_2} - \Delta H_B] \quad \text{(Eq. 11)}$$

$$R_{SG} = R_{O_2}(\varepsilon/1-\varepsilon)/[(\varepsilon/1-\varepsilon)(\gamma_B-\gamma_P)/4 + (1-\gamma_P/4)] \quad \text{(Eq. 12)}$$

Equation 10 is simply a rearrangement of Eq. 8. Equation 11 results from combining Eqs. 7 and 9. Equation 12 results from combining Eq. 10 with Eq. 13 for the respiratory quotient

$$R_{CO_2}/R_{O_2} = [(1-\gamma_P/4) + (\varepsilon/1-\varepsilon)(\gamma_B-\gamma_P)/4]^{-1} \quad \text{(Eq. 13)}$$

where γ_B is the mean oxidation state of carbon in C_{bio}. Because they have different requirements for constancy of parameters required for linear correlations to exist, Eqs. 10, 11 and 12 are particularly useful for determing the variability of ε, ΔH_B, γ_P, and γ_B among a set of plants under study. Prediction of relative growth rates with Eq. 10 requires that ε be constant; Eq. 11 requires that ε be constant and γ_P and ΔH_B be negligible or constant; and Eq. 12 that ε be constant, γ_P be constant or negligible, and γ_B–γ_P be near zero or constant. When these approximations are valid, Eqs. 10, 11 and 12 predict a simple linear relation with zero intercept between growth rate and respiration rate.

Note that equations for the ratios $\dot{q}/R_{CO_2}$ and $\dot{q}/R_{O_2}$ are readily obtained from the ratios of Eq. 11 to Eq. 10 and Eq. 12, respectively. The equation for $\dot{q}/R_{O_2}$ and Eqs. 7 and 9 are independent relations containing five parameters (γ_P, γ_B, ΔH_{O_2}, ΔH_B, and ε) in addition to the directly measureable variables $\dot{q}$, R_{O_2}, and R_{CO_2} and the dependent variable R_{SG}. These three equations can be combined to eliminate any two of the five parameters. The result does not add to further understanding of the growth-respiration rate relation, but shows that the model developed here contains only three adjustable parameters. Which parameters to choose in formulating a final equation for growth rate and understanding the variability of these parameters among species, genotypes and physiological states must await further data.

Materials and methods

In order to gain some insight into the magnitude of ΔH_B, values of $\dot{q}$, R_{CO_2} and ε were determined for three corn (*Zea mays* L.) cultivars obtained from Pioneer Hi-bred International (Johnston, Iowa, USA). The methods for measuring $\dot{q}$ and R_{CO_2} are described in Criddle et al. (1991a) and Criddle et al. (1990). Data were collected with a Hart Scientific (Pleasant Grove, Utah, USA) model 7707 differential scanning calorimeter operated in isothermal mode with samples of three to five shoots excised at the scutellum and precisely cut to 1 cm length. Values for ε were obtained by the method of Yamaguchi (1978). Fifty kernels were dried at 80°C in vacuo, weighed and analyzed for carbon content. An additional 50 kernels were germinated and grown in the dark at 30°C on water-wetted filter paper for 7 d. The seedlings were harvested, divided into seedling axis and residual kernel and dried for determination of dry weight and carbon content. Carbon content was determined with a Leco (St. Joseph, Mich., USA) model CHN-800 analyzer. Mass conversion efficiency was calculated by taking the ratio of the root+shoot mass to the difference between the masses of the sprouted and unsprouted kernels. Substrate carbon conversion efficiency was calculated as the ratio of the same quantities multiplied by their respective carbon contents.

Results

Table 1 gives the results of determinations of ε, the ratio of $\dot{q}$ to R_{CO_2}, and calculated values of ΔH_B (assuming

Table 1. Substrate carbon conversion efficiency in corn (*Zea mays* L.) seedlings

Cultivar	Mass of unsprouted kernel (mg/kernel)[a]	Mass of sprouted kernel (mg/kernel)[a]	Mass of shoot+root (mg/kernel)[a]	Mass efficiency, (%)	C in unsprouted kernel (wt.%)[b]	C in sprouted kernel (wt.%)[b]	C in shoot+root (wt.%)[b]	Carbon efficiency, ε (%)	$\dot{q}/R_{CO_2}$ (kJ·mol^{-1})[c]	Calculated ΔH_B (kJ·mol^{-1})[d]
G-17-1	146.0 (50)	110.1 (39)	21.1 (39)	58.8	45.6±0.2	45.5±0.3	47.3±0.2	60.6	454	8
		109.7 (43)	23.4 (43)	64.5		45.8±0.3	47.5±0.1	68.1		
			Mean±SD	61.7±4.0				64.4±5.3		
W91-2	229.8 (50)	143.1 (49)	44.7 (49)	51.6	45.4±0.2	46.7±0.5	49.5±0.2	59.0	403	47
		143.8 (49)	43.6 (49)	50.7		46.5±0.8	48.8±0.4	56.8		
			Mean±SD	51.2±0.6				57.9±1.5		
K46-2	220.7 (50)	148.9 (41)	37.3 (41)	51.9	45.0±0.3	46.1±0.5	49.2±0.2	59.8	436	22

[a] Determined as total mass of all kernels divided by the number of kernels, given in parentheses
[b] From duplicate determinations on each sample
[c] Standard deviation is approximately ±7%, most of which is uncertainty in R_{CO_2}
[d] Calculated from carbon efficiency using Eq. 9 assuming $\gamma_P = 0$ and $H_{O_2} = -468$ kJ·mol^{-1} (Domalski 1972). Standard deviation is approximately ±16 kJ·mol^{-1}

$\gamma_P = 0$) for the three corn cultivars. The combined uncertainties in the experimental data result in a standard deviation of about ±16 kJ·mol^{-1} in the derived ΔH_B values. Thus, we do not know with any certainty whether or not ΔH_B differs significantly among these cultivars.

Discussion

To be useful, a mechanistic model such as the one derived here must not only be logically correct, but must also be consistent with experimental data. The first consistency test of our model is to ask if it accurately predicts what is known about growth rates of plants. A data set of simultaneously measured values of R_{SG}, ε, γ_P, γ_B, ΔH_B, $\dot{q}$, R_{CO_2} and R_{O_2} taken on a natural population of a plant species grown under common environmental conditions will be required to fully answer this question. No such complete data set in which all these parameters are systematically varied exists as yet, the major difficulty being the lack of direct methods for obtaining values for γ_P and ΔH_B. The results given in Table 1 give values for ΔH_B calculated with Eq. 9 by assuming $\gamma_P = 0$, a reasonable assumption for corn seedlings. In principle, γ_P and ΔH_B could both be determined by simultaneous application of Eqs. 7 and 9 if growth rate data in the correct units were determined simultaneously with ε. While such experiments are currently underway, measurements of R_{SG} with an acceptable reproducibility are not yet available. Values for γ_P and ΔH_B and an understanding of the variability of these parameters among genotypes and with environmental conditions will be necessary before Eq. 7 can be used to predict plant growth rates with confidence.

In the model presented here, γ_P is the mean oxidation state of photosynthetically fixed carbon entering the respiratory system, i.e. C_{in} in Eq. 3. Photosynthate is often assumed to be purely carbohydrate for which $\gamma_P = 0$. However, this assumption ignores transport of carbon in the form of amino acids and lipids from chloroplasts to mitochondria and from photosynthetic tissues to non-photosynthetic tissues. Thus, the value of γ_P applicable to a given tissue must be deduced from measurements on living tissue and probably can not be obtained from elemental analyses. The value of γ_P can be obtained from the respiratory quotient under certain conditions. If respiration is strictly aerobic with CO_2 as the sole catabolic product and the biomass formed has an average oxidation state of C equal to γ_P, the quantity $(1-\gamma_P/4)$ is numerically equal to the inverse of the respiratory quotient, i.e. R_{O_2}/R_{CO_2}. For formation of biomass with an average carbon oxidation state, γ_B, different from γ_P, the relation between the respiratory quotient and γ_P is more complex as shown in Eq. 13. Determination of γ_B in higher plants by elemental analyses or heat of combustion is also problematical because of the macroscopic differentiation of plant parts, i.e. γ_B may be different in stems, roots and leaves. In undifferentiated plants such as some algae, γ_B may be determinable from the elemental composition or heat of combustion of dry material.

ΔH_B is the total enthalpy change associated with the conversion of one mole of C from photosynthate into one mole of C in biomass. ΔH_B implicitly includes enthalpy changes for all of the processes required to generate new biomass, e.g. import of K^+, Ca^{2+}, nitrogen, water, etc.; transformation of small molecules into biopolymers; and redox reactions of S, N and C compounds. The sign and magnitude of ΔH_B is related to the difference between γ_P and γ_B by Thornton's rule because ΔH_{SG} depends on the difference in the energy contents of photosynthate and biomass,

$$\Delta H_B = \Delta H_{SG} + \Sigma r_E \Delta H_E = (\gamma_B - \gamma_P)\,\Delta H_{O_2}/4 + \Delta H_{CB} + \Sigma r_E \Delta H_E \quad \text{(Eq. 14)}.$$

Equation 14 makes it clear that ΔH_B is not equal to the difference between the heat of combustion of dried plant material and an equivalent amount of photosynthate which would be approximately equal to $(\gamma_B - \gamma_P)\Delta H_{O_2}/4$. The heat of combustion does not properly include the rest of the processes involved in growth

and photosynthesis, i.e. the enthalpy changes for incorporation of elements other than carbon, $\Sigma r_E \Delta H_E$, and for processes other than redox required to incorporate photosynthate carbon into biomass, ΔH_{CB}. Furthermore, such a procedure begs the question of defining exactly what is meant by photosynthate. Thus, ΔH_B must be obtained from experiments on live tissue or plants.

Equation 14 also shows that ΔH_B can reasonably have positive, negative or zero values. Both negative and positive values of ΔH_B predict positive values for R_{SG} and ε from Eqs. 7 and 9 because $\dot{q}$ and R_{CO_2} must invert their relative magnitudes at the same point ΔH_B goes through zero. A zero value of ΔH_B results in undefined, i.e. 0/0, predictions of R_{SG} and ε from Eqs. 7 and 9.

Although Eqs. 13 and 14 are useful in increasing our understanding, they do not provide means for evaluating γ_P and ΔH_B independent of Eqs. 7–9. Further understanding of the behavior of these parameters must be obtained from considerations of experimental data on $\dot{q}$, R_{CO_2}, R_{O_2} and R_{SG}.

Growth-respiration rate correlations in the literature are of two types. The first type makes comparisons among species or among genotypes within a species. These correlations usually have a positive slope, but show a large scatter around the correlation line. Equations 10–12 indicate the scatter occurs because any or all of ΔH_B, γ_P, γ_B, and ε are variable. The second type of correlation is obtained from data on a single genotype where some of these parameters might reasonably be expected to be constant. If all four parameters are constant, Eqs. 10–12 predict linear correlations with a zero intercept and a scatter within the experimental error for correlations between R_{SG} and any of the three measures of the respiration rate. Equation 10 requires that only ε be constant, Eq. 11 requires ε, γ_P and ΔH_B be constant, and Eq. 12 requires ε, γ_P and γ_B to be constant for a linear correlation with zero intercept to be obtained. Experimentally, correlations of this second type that have been reported are linear within experimental error, sometimes have an intercept that includes zero within the uncertainty, but usually have a positive intercept (Amthor 1989). Such correlations have been fit to and used as evidence for the accuracy of the McCree/Thornley model as given in Eq. 2. If the correlation has a zero intercept, $\dot{m} = 0$, and Eq. 2 collapses to an equivalent of one of Eqs. 10–12, depending on which measure of respiratory rate was used. Furthermore, g becomes equivalent to $\varepsilon/1-\varepsilon$, $[(1-1/\varepsilon)(1-\gamma_P/4)\Delta H_{O_2}-\Delta H_B]^{-1}$, or $(\varepsilon/1-\varepsilon)/[(\varepsilon/1-\varepsilon)(\gamma_B-\gamma_P)/4+(1-\gamma_P/4)]$ in this case. Only $g = \varepsilon/1-\varepsilon$ agrees exactly with the definition of g in the McCree/Thornley model.

If $\gamma_P = 0$ and ΔH_B and the term containing $(\gamma_B - \gamma_P)$ are negligible, Eqs. 10–12 collapse to essentially identical relations since $\dot{q} = R_{O_2}\Delta H_{O_2} = R_{CO_2}\Delta H_{O_2}$ in this case. Situations in which ΔH_B and $(\gamma_B-\gamma_P)$ are near zero and ε is constant may account for some of the simple linear correlations found between growth and respiration rates within a genotype. Variation in and nonzero values of γ_P, ΔH_B, and $(\gamma_B-\gamma_P)$ are required to account for the intergenotypic data and and other data in which respiration rate is only poorly correlated with growth rate.

The model derived here as Eq. 7 can be cast in the form of a linear equation with a nonzero intercept without the above assumptions if a linear relation between $\dot{q}$ and R_{CO_2} exists as described by

$$\dot{q} = \alpha R_{CO_2} + \beta \qquad \text{(Eq. 15)}$$

where α and β are constants. Substitution of Eq. 15 into Eq. 7 and rearranging results in

$$R_{CO_2} = -\Delta H_B[(1-\gamma_P/4)\,\Delta H_{O_2}+\alpha]^{-1} R_{SG} - \beta[(1-\gamma_P/4)\,\Delta H_{O_2}+a]^{-1} \qquad \text{(Eq. 16)}$$

which is a linear relation between R_{CO_2} and R_{SG} with a nonzero intercept if α, β, γ_P and ΔH_B are constants, a condition that may be expected for data taken on a single genotype, and if β is not zero. Experimentally, α and β have been found to be approximately constant even across genotypes in several recent studies, published (Hopkin 1991; Anekonda 1992; Anekonda et al. 1994) and unpublished from our laboratories. The literature contains several examples of data sets showing that R_{CO_2} and R_{SG} are linearly related for a genotype (Amthor 1989). Besides showing that the model derived here can describe existing correlations in the literature, these results suggest that values for γ_P and ΔH_B can be obtained from Eqs. 15 and 16 by linear regressions of $\dot{q}$, R_{CO_2} and R_{SG} data taken on a single genotype.

The correspondence of Eqs. 16 and 2 suggest Eqs. 17 and 18 when $\dot{R} = R_{CO_2}$ and $\dot{G} = R_{SG}$:

$$g = -\Delta H_B[(1-\gamma_P/4)\,\Delta H_{O_2}+\alpha]^{-1} \qquad \text{(Eq. 17)}$$

$$\dot{m} = -\beta[(1-\gamma_P/4)\,\Delta H_{O_2}+\alpha]^{-1} \qquad \text{(Eq. 18).}$$

Equations similar to Eq. 16 may also be written for the relation between $\dot{q}$ or R_{O_2} and R_{SG}. Equating corresponding coefficients in these cases gives Eqs. 19 and 20 for the R_{O_2} case

$$g = -\Delta H_B[(1-\gamma_P/4)\,\Delta H_{O_2}+\alpha]^{-1}[(1-\gamma_P/4) + (\varepsilon/1-\varepsilon)(\gamma_B-\gamma_P)/4] \qquad \text{(Eq. 19)}$$

$$\dot{m} = -\beta[(1-\gamma_P/4)\,\Delta H_{O_2}+\alpha]^{-1}[(1-\gamma_P/4) + (\varepsilon/1-\varepsilon)(\gamma_B-\gamma_P)/4] \qquad \text{(Eq. 20)}$$

and Eqs. 21 and 22 where $\dot{q}$ is the dependent variable:

$$g = -\alpha\Delta H_B[(1-\gamma_P/4)\,\Delta H_{O_2}+\alpha]^{-1} \qquad \text{(Eq. 21)}$$

$$\dot{m} = -\beta(1-\gamma_P/4)\,\Delta H_{O_2}[(1-\gamma_P/4)\,\Delta H_{O_2}+\alpha]^{-1} \qquad \text{(Eq. 22).}$$

Thornley's (1990) model is written in terms of CO_2 and is therefore directly comparable with Eqs. 17 and 18. Others have applied Eq. 2 with $\dot{R} = R_{O_2}$ most typically and a variety of measures of $\dot{G}$; resulting in inconsistent units when Eq. 2 was fit to the data. Equations 17–22 show that g and $\dot{m}$ values obtained with Eq. 2 depend on the respiratory parameter measured. The same conclusion can be reached by examination of Eqs. 10–13.

According to the model derived in this paper, the existence of a hidden linearity between any two respiratory measures must result in a linear relation between specific growth rate and either of the correlated respiratory measures. The values of g and $\dot{m}$ obtained from the $\dot{R}$ versus $\dot{G}$ correlation in such a situation do not necessarily correspond with the definitions used in deriving Eq. 2, however. Thus, Eqs. 17 and 18 can be numerically equal without being conceptually valid. One test of the conceptual validity of Eqs. 17 and 18 can be made by comparison of the signs and magnitudes of g and $\dot{m}$ predicted from Eq. 2 and from Eqs. 17 and 18. Equation 2 requires $0<g<1$ and $\dot{m} > 0$. The existence of several published data sets that resulted in positive $\dot{m}$ values (Amthor 1989) cannot be accepted as proof that $\dot{m}$ values obtained by application of Eq. 2 to real data are always positive. Data that produced negative $\dot{m}$ values may simply have been previously disregarded as bad data and not published. Data from our laboratories show β to be negative for coast redwood (Anekonda 1992; Anekonda et al. 1994) and positive for larch (Hopkin 1991) and eucalypts (Anekonda unpublished data from our laboratories), and α to be about 760 $kJ \cdot mol^{-1}$ for coast redwood, about 300 $kJ \cdot mol^{-1}$ for larch and about 200 $kJ \cdot mol^{-1}$ for eucalypts. (Because these values were collected on multiple genotypes, and because the values vary between half-sib families (Hopkin 1991), the actual values must be considered approximate, but they do provide semiquantitative data for examining the behavior of Eqs. 17 and 18.) Assuming γ_P to be near zero, the $\dot{m}$ values predicted from the right side of Eq. 18 are positive for all three species, in agreement with Eq. 2.

Under conditions where Eq. 15 is experimentally validated and R_{SG} is linearly correlated with R_{CO_2}, Eqs. 17–22 provide a means for relating the values of the intercept and slope of the correlation to parameters in our model that are measures of the physiology of the plant, i.e. γ_P, γ_B and ΔH_B. Unfortunately, no correlation was found between R_{CO_2} and growth rate in a study of larch (Hopkin 1991) and the units on the growth data for coast redwood and eucalypt make it impossible to quantitatively apply Eq. 16 even though strong correlations were found in those cases (Anekonda 1992; Anekonda et al. 1994; and unpublished data from our laboratories). Thus, we cannot obtain values for ΔH_B or γ_P, but we can predict that ΔH_B (averaged across genotypes) must be negative for coast redwood and positive for both larch and eucalypts if Eqs. 17 and 18 are conceptually valid.

Determination of the temperature dependence of the functions in Eqs. 17 and 18 is another way to test the conceptual validity of these equalities. Current consensus based on Eq. 2 (Amthor 1989) holds that g is at most a weak function of temperature and $\dot{m}$ must always increase with temperature. The temperature dependence of the functions on the right side of Eqs. 17 and 18 depend on the temperature dependencies of α and β which are unknown at present. The values of ΔH_B, γ_P and ΔH_{O_2} are not expected to be temperature dependent as long as the plant composition remains constant. The requirements of Eq. 2 predict the value of α to be independent of temperature (Eq. 17), but β to be temperature dependent (Eq. 18). However, other than the possible conceptual equality with $\dot{m}$, there is no apparent reason for the right side of Eq. 18 to have a particular temperature dependence.

Failure to appreciate the significance of temperature effects is a problem inherent in many earlier efforts to understand and obtain experimental correlations between growth and respiration rates. Recent data on the temperature dependence of $\dot{q}$ in woody shrubs (Criddle et al. 1993) show the specific metabolic rates of different accessions to all be the same at an isokinetic temperature within the growth range although plants from different accessions have different temperature dependencies. Thus, there is a temperature at which the metabolic rates, and presumably the growth rates, reverse their order among the accessions. Experimentally determined correlations of respiration and growth rates may thus have either a positive or negative slope depending on the time weighted average growth temperature and the temperature of the metabolic rate measurements. No correlation would be found if either respiration or growth measurements were made at the isokinetic temperature.

As an extension of the model predictions, consider the effects of temperature in the range where $\dot{q}$ and R_{CO_2} are described by the Arrhenius equation. With this substitution, Eqs. 7 and 9 become

$$R_{SG} = [A_q e^{-\mu q/T} - \Delta H_{CO_2} A_{CO_2} e^{-\mu CO_2/T}]/\Delta H_B \quad \text{(Eq. 23)}$$

and

$$\varepsilon = [A_q e^{-\mu q/T} - \Delta H_{CO_2} A_{CO_2} e^{-\mu CO_2/T}]/ \cdot [A_q e^{-\mu q/T} - \Delta H_{CO_2} A_{CO_2} e^{-\mu CO_2/T} - H_B] \quad \text{(Eq. 24)}$$

where A_q and A_{CO_2} are constants, μ_q and μ_{CO_2} are the apparent activation energies in kelvins for $\dot{q}$ and R_{CO_2}, and T is the Kelvin temperature. Recent experiments in our laboratories show that μ_q and μ_{CO_2} are not equal in maize. Also, $\dot{q}/R_{CO_2}$ for tomato has been shown experimentally to be dependent on temperature in the range between stress temperatures (Rank et al. 1991).

Over the range of temperature in which Eqs. 23 and 24 are valid, ΔH_{CO_2} will have only a very weak dependence on temperature and can be treated as a constant unless γ_P varies with temperature. ΔH_B will also have a weak temperature dependence unless the substrate or biomass oxidation state is temperature dependent, see Eq. 14. In agreement with experimental observations, Eq. 23 predicts an exponential dependence of growth rate on temperature for all reasonable values of μ_q and μ_{CO_2}. Equation 24 shows ε is equal to a ratio of exponentials in temperature, and thus could increase, decrease or remain constant with temperature within the temperature range permissive for growth. In agreement with this prediction, experimental ε values have been shown to have only a weak temperature dependence in rice and maize (Yamaguchi 1978). These results further indicate the model derived here has the correct mathematical functionality.

In addition to an understanding of the relations between predicted and measured variables and their dependence on environmental variables, using Eq. 7 for deter-

mination of R_{SG} requires careful consideration of experimental errors. Use of this equation involves obtaining a relatively small difference between two large numbers because ΔH_{O_2} is negative, $\dot{q}$ and R_{CO_2} are both positive and highly correlated, and $\dot{q}$ and the quantity $(1-\gamma_P/4)R_{CO_2}\Delta H_{O_2}$ are close in magnitude. Error analysis by partial differentiation of Eq. 7 gives

$$s_{RSG}/R_{SG} = [s_{\dot{q}}^2 + s_{R_{CO_2}}(1-\gamma_P/4)^2 \Delta H_{O_2}{}^2]^{0.5}/ \cdot[-\dot{q} - R_{CO_2}(1-\gamma_P/4)\Delta H_{O_2}] \quad \text{(Eq. 25)}$$

where s_x = the standard deviation in x. (Appropriate values of $\dot{q}$ and R_{CO_2} can be obtained from Fig. 1 for use in Eq. 25.) If $s_{RSG}/R_{SG} = 10\%$ is set as an acceptable error, $s_{\dot{q}}/\dot{q}$ and s_{RCO_2}/R_{CO_2} must both be $< 1\%$. Our experience is that the variablility inherent in plant tissues causes these errors to range from about 5% for field samples down to about 1% for carefully controlled, laboratory-grown samples (Hansen et al. 1989; Hopkin 1991; Anekonda 1992; Hansen et al. 1992; Anekonda et al. 1994).

Use of the model as given in Eq. 7 to predict relative values of specific growth rates in larch (Hopkin 1991), coast redwood (Anekonda 1992; Anekonda et al. 1994) and eucalypts (unpublished data from our laboratories) succeeded in the latter two cases, but failed in the case of larch because of experimental difficulties. More importantly, in all three cases the data show that ε, ΔH_B and possibly γ_P are variable among genotypes of the same species. This conclusion suggests that substrate carbon conversion efficiency, the composition of the biomass, and the quality of photosynthate as represented by γ_P, may be the ultimate determinants of growth rate in these species when growth rate is not nutrient- or carbon-limited. We do not know of any other studies addressing the question of variable ΔH_B or γ_P in plants. The model derived here thus indicates that determination of photosynthate and biomass oxidation states will be an important research topic in future studies of plant productivity. Herms and Mattson (1992) recently arrived at the same conclusion, but from an entirely different perspective based on evolutionary theory and life histories of plants.

The trapezoid in Fig. 1 suggests a new strategy for plant breeding for high vegetative productivity. Data from Anekonda (1992) and Anekonda et al. (1994) and other data from this laboratory show that natural populations apparently contain only plants having $\dot{q}$ and e values placing them in the lower left half of the trapezoid. A super-grower, i.e. a plant in the upper right corner of the trapezoid, may be obtained by combining traits of a plant with high ε with a plant with a high metabolic rate even though the latter may be a slow grower. This approach has not been deliberately done in the past because, intuitively, plants with high growth rates have been selected for crosses to achieve high growth rates. The very rapidly growing plants that would occupy the upper right portion of the trapezoid may never have existed or may have been eliminated from naturally occuring populations by evolutionary pressures. Such plants may be prepared and maintained in crosses and environments supported by man to overcome these limitations, however. If these hypotheses are correct, they suggest a new route to significantly increased production, possibly even in highly developed crop plants. The mechanics of combining these traits may be complicated, however if these parameters are significantly influenced by mitochondrial genes as suggested by recent, unpublished observations in our laboratories. Variability in γ_P and ΔH_B must also be considered in breeding and selection programs. Practically, such selection requires a rapid, easy means for measuring the desired traits. Equations 7 and 9 suggest simultaneous measurement of $\dot{q}$, R_{CO_2} and R_{O_2} may meet this need.

In conclusion, consideration of metabolic heat rate as an additional measure of respiration rate in plants leads to a thermodynamic model for plant growth rate in terms of clearly defined physiological parameters. Difficulties in practical application of the model arise from conceptual uncertainties in methods for determination of γ_P and ΔH_B and from the sensitivity of calculated parameters to experimental errors, but the model presented here can help experimentalists gain better control and understanding of the variables in experiments designed to quantify the relation between plant growth and respiration.

Appendix

Symbols are consistent with rules promulgated by IUPAC as listed in Quantities, Units and Symbols in Physical Chemistry by I. Mills, T. Cvitas, K. Homann, N. Kallay, and K. Kuchitsu, Blackwell Scientific Publications, Oxford, 1988. Units are self-consistent throughout and chosen to represent the units of measure typically used in studies in our laboratories. Symbols used at only one place in the text are defined in the text and not included in this list.

ε substrate carbon conversion efficiency (unitless)

$\dot{q}$ specific metabolic heat rate ($\mu W \cdot mg^{-1}$), the sign convention used here is that q is positive for exothermic processes

R_{CO_2} specific rate of CO_2 production ($nmol \cdot s^{-1} \cdot mg^{-1}$)

R_{O_2} specific rate of oxygen use ($nmol \cdot s^{-1} \cdot mg^{-1}$)

R_{SG} specific rate of conversion of substrate carbon to biomass carbon ($nmol \cdot s^{-1} \cdot mg^{-1}$)

ΔH_{CO_2} enthalpy change for combustion of one mole of substrate carbon to carbon dioxide ($\mu J \cdot nmol^{-1}$), negative for exothermic processes

ΔH_{SG} enthalpy change for the reaction to convert one mole of substrate carbon to one mole of biomass carbon ($\mu J \cdot nmol^{-1}$), negative for exothermic processes

ΔH_B total enthalpy change for incorporation of one mole of substrate carbon into one mole of biomass carbon, including enthalpy effects from all elements ($\mu J \cdot nmol^{-1}$), negative for exothermic processes

ΔH_{O_2} enthalpy change for the reaction to convert substrate carbon to carbon dioxide, expressed per mole of oxygen ($\mu J \cdot nmol^{-1}$), negative for exothermic processes

γ_P mean oxidation state of the substrate carbon

γ_B mean oxidation state of biomass carbon

$\dot{G}$ specific growth rate (unspecified)

$\dot{P}$ specific photosynthesis rate (unspecified)

$\dot{R}$ specific respiration rate (unspecified)

$\dot{m}$ specific rate of maintenance respiration (unspecified)

g growth coefficient (unitless), equal to the ratio of rate of carbon respired to produce biomass (not including maintenance respiration) to the rate of carbon going into biomass

α and β are constants in the relation $\dot{q} = \alpha R_{CO_2} + \beta$

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