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Plant calorimetry. Part 2. Modeling the differences between apples and oranges ☆

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Abstract

In a previous review we discussed calorimetric methods for the study of plant metabolism. Since that review, a number of papers describing calorimetric measurements examining plant growth, stress responses and effects of temperature have appeared. This recent work is reviewed here.

In addition to the experimental work, a mechanistic model linking respiration rates to growth has been published. This model is derived from both mass and enthalpy balance equations. It describes specific growth rate and substrate carbon conversion efficiency 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. Application of this model to understanding the basis for variation in growth rates among individual genotypes in plants is reviewed.

The effects of environment on the plant respiration–growth relation has been an important focus for plant calorimetry studies. Climatic temperature is one of the most important variables determining growth. Extremes of temperature determine limits of growth, and diurnal variation and mean temperature have a major influence on growth rate. Calorimetric measurements of respiratory rates as a function of temperature can be used to relate the temperature influence on respiratory metabolism to the temperature influence on growth rate. These studies have also discovered the existence of an isokinetic point within the range

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of normal growth temperatures. Studies of temperature dependence are reviewed and the results analyzed in terms of the recently published mechanistic model.

Keywords: Calorimetry; Climate; Model; Plant; Respiration; Temperature

1. Introduction

Although much effort has been expended trying to find correlations between photosynthesis rates and growth rates of plants, no useful correlations have been found for predicting plant growth rates from measurements of photosynthesis of single leaves under normal growth conditions. In contrast, many positive and a few negative correlations have been found between plant growth rates and respiration rates, see, for example, Refs. [1–8] and reviews in Refs. [9–12], suggesting that respiration parameters, when properly interpreted, may be useful predictors of plant growth rates. The empirical correlations of growth with respiration suggest that research on plant respiration should be a particularly fruitful area for development of strategies to select plants with enhanced growth rates.

Despite recent progress, it is still true that "the precise nature of the relationship between growth and respiration in ... plants is unknown" [9], and "surprisingly little is known about the underlying physiological mechanisms causing the negative correlation between yield and respiration" [3]. Until the model using both energy and mass balance equations was derived [13], mechanistic models for plant growth were all based only on mass balance relations [14]. This limited their ability to test hypotheses about the relation between respiration rate and growth rate because they do not yield direct information on the efficiency of energy use by plants. The uncertainties in mass balance models have led to ongoing arguments in the literature about such simple questions as whether increased or decreased respiration rates will increase crop productivity [3,9,15,16].

Our previous review of plant calorimetry [17] discussed methodology available at that time and early applications of calorimetric techniques to the study of plant respiration. There are still only a few laboratories using calorimetry to study plant metabolism, but new developments in methods and theory have significantly enhanced the ability to collect meaningful data and interpret results. This paper is an attempt to review all the calorimetric methodologies developed and studies performed on plant metabolism since the earlier paper was written. The major focus of this review is, however, to go beyond a literature survey and use available respiratory rate data to develop a better understanding of the physiology of plant growth. We apologize beforehand for any work we may overlook. The mass- and energy-based model of Hansen et al. [13] linking calorespirometric measurements to plant growth is thus a central focus of this review.

Because the growth rate of plants is dependent on the environment, it is also necessary to determine how environmental variables affect respiration and the respiration–growth relation. Therefore, this review also addresses the effects of temperature on interpretation of calorimetric studies on plants.

2. Methods development

There have been several significant calorimetric methods developed and applied to plant tissues since the previous review [17].

Fontana [18] and Russel [19] attached gas chromatographs to large (> 50 ml), sealed, isothermal calorimetric vessels for the purpose of measuring O_2, CO_2 and N_2 rates simultaneously with heat rates. Another development uses pressure tranducers connected to the sealed calorimetric vessel by glass microcapillary tubing for simultaneous measurement of O_2 and CO_2 rates in 1-ml vessels [18]. Pressure changes are measured in the absence and presence of an NaOH solution used to trap CO_2. Similar methods were used previously with large (> 50 ml) calorimetric vessels [20], but the new developments make possible accurate measurements on small (< 250 mg wet weight) samples of plant tissue. Bäckman et al. [21] used a gas flow-through system to measure O_2 and CO_2 rates.

Criddle et al. [22] reported a simple method for modifying heat conduction calorimeter ampules to allow measurement of metabolic heat rates at gas pressures up to 16 MPa. The use of glass microcapillary tubing to connect the calorimeter ampules to a gas source allows temperature scanning as well as isothermal measurements of metabolic heat rate at various pressures and/or gas compositions.

Alyabyev et al. [23] have developed photocalorimetric methods to measure light "energy storage rate" under optimum and stress conditions. They have applied their method to algae and some crop plants. While only preliminary results are available at this time, it will be of great interest to learn how accurate their methods are for determining photosynthetic and respiration energies. Wadsö [24] has also reported some preliminary work on calorimetric methods for studying photosynthesis.

Feng et al. [25] examined metabolism in a variety of CAM plants. Because dark metabolism in these plants depends on CO_2 uptake, buffer bicarbonate solutions were added to the ampule to supply the tissues with a constant partial pressure of CO_2. This work demonstrates a method for supplying a gas phase substrate for metabolism.

Lamprecht et al. [26] published a description of a calorimeter with a volume of about 2.75 l, suitable for study of whole plants. Even larger volume (up to about 1 m^3) heat conduction calorimeters for studies of whole plants and large plant parts, such as cauliflower heads, have been constructed in our laboratories but none of this work has been published. Our and others' [27] experience shows that a baseline stability of about 100 μW can be achieved in these large calorimeters.

3. Recent calorimetric studies on plants

Though calorimetry offers a rapid and convenient means for examining salt stress in plants, little work on this problem has been reported since the initial studies of NaCl inhibition of barley (*Hordeum vulgare* L.) root metabolism [28]. Studies have been done on forage kochia (*Kochia prostrata* L.) [29,30], a salt-tolerant species, and on cottonwood (*Populus fremontii*) [30], a less salt-tolerant species. Both

studies show that NaCl decreases the metabolic heat rate of root tissue with increasing concentration. Cottonwood root tissue shows a similar, but less abrupt, sigmoidal drop in metabolic heat rate in response to NaCl when compared to barley root tissue. The total decrease in the metabolic heat rate is about the same in cottonwood and barley root, i.e. $\approx 50\%$. The decrease occurs between about 0.2 and 0.3 M NaCl in the cottonwood and between 0.02 and 0.1 M NaCl in barley root. Mannitol, which is excluded from root tissue and hence measures only the effects of osmotic pressure, produces similar responses in cottonwood and barley root, but the response is different from the response to NaCl. In contrast, the responses of kochia root to NaCl and mannitol are similar. It was concluded that the strategy used by cottonwood and barley to avoid salt damage is to prevent salt from entering the roots. Kochia uses a different strategy that allows NaCl to exchange freely between soil water and roots. The two strategies are consistent with the ecological niches occupied by these plants.

Recent work in our laboratories has examined the effects of aqueous aluminum ions on metabolic activity and energy-use efficiency in barley plants. Decreases in metabolic heat rate with increasing aluminum concentration parallel decreases in root elongation and biomass accumulation. Decreases in leaf metabolic rate and increases in the ratio of metabolic heat rate to CO_2 production rate both indicate that aluminum is transported to and inhibits metabolism in leaf as well as root tissues.

Further work on the effects of high and low temperatures on metabolic heat rate in tomato (*Lycopersicon esculentum*) tissue [31] verifies that there are no simple, critical temperature extremes for inactivation of plant cell activity in this chilling sensitive plant. Rather, inactivation is a continuous function of time and temperature at both high and low temperatures as described in Refs. [32,33]. In addition, the effects of pressure on inactivation of tomato tissue [22] provide further results consistent with a hypothesis that extreme temperatures damage lipid membranes by irreversible phase separation or higher order phase transition. The results of the pressure studies are consistent with the time–temperature studies of inactivation rates [31,33]. To date, no calorimetric evidence for a first-order phase transition associated with temperature-dependent activity changes in whole plant tissues has been observed.

Studies have examined potato (*Solanum tuberosum*) tuber slices to define the time course of changes in respiratory parameters associated with wound healing [21,34,35]. Simultaneous measurements of metabolic heat rate and CO_2 rate were made to define the kinetics of changes in respiration rate and in the change of respiratory substrate from lipids to carbohydrates as wound healing progresses.

Nevo et al. [36] measured metabolic heat rates for young seedlings of the wild progenitors of wheat (*Triticum aestivum*) and barley from different climatic zones before and after exposure to chilling temperatures. Accessions from cold climates showed a greater increase in metabolic rate in response to chilling than did accessions from warm climates. These are interesting findings, but the results were interpreted incorrectly as a mechanism used by the plants to increase metabolic heat rate and thereby avoid the effects of low temperature by heating the tissues.

Calculations using the data from Ref. [36] show the measured increases in metabolic rate would produce a negligible increase in the temperature of the plant tissues. Metabolic heat rates of plant tissues are sufficiently large to be readily measured with high-sensitivity calorimetric methods even at low temperatures, but only in rare cases is the metabolic heat rate large enough to significantly increase plant tissue temperatures above ambient.

At the time of flowering, some plants do show a significant increase in temperature of some specialized tissues as a result of metabolic heating [37,38]. In these tissues, oxidative phosphorylation becomes completely uncoupled and the respiration rate may increase several hundred fold. The purpose of heating these special thermogenic tissues is apparently to volatilize attractants for insect pollinators [37]. The metabolic heat rate in arum lilies and in cycads during flowering has been studied calorimetrically [38–41]. The results show that the metabolic rate in core sections of voodoo lily (*Sauromatum guttatum* Schott) appendix tissue appears to be limited only by the rate of diffusion of oxygen into the tissue [39].

Uncoupling of oxidative phosphorylation leads to only a slight increase in heat production in these plants. The major cause for the heat rate increase is almost entirely a greatly enhanced metabolic rate. Salycilates produced during anthesis are secondary effectors causing uncoupling of respiration and allowing the increase in metabolic rate. The study on cycads [41] presents data that were interpreted to indicate temperature cycling in the reproductive tissues of these species. However, this study and the study on voodoo lily by the same author [40] did not include proper controls and the data probably contain systematic instrumental and data interpretation errors and hence should be repeated before the conclusions unique to these two studies can be accepted.

Changes in respiratory rates during dormancy and development of grape (*Vitus vinifera*) buds were studied calorimetrically by Gardea et al. [42]. Respiratory rate was at a minimum in mid-winter after which it rose steadily through budbreak in the spring. The ratio of heat rate to CO_2 rate was lowest in ecodormant buds, increased at initial bud swelling, and thereafter declined through budbreak. The temperature dependence of respiration was shown to be a function of temperature and stage of bud development. These data suggest major changes occur in metabolic pathways during bud development. The information may be agronomically useful for the purpose of predicting, and perhaps controlling, the date of budbreak. Moreno-Simunovik [43] showed that the degree of vernalization of peach (*Prunus persica* var. *persica*) seeds can be followed by calorimetry. Temperature scans on shoot tissue were used to determine the metabolic rate as a continuous function of temperature by the method of Hansen and Criddle [44]. The temperature at which the maximum metabolic heat rate is achieved decreases and the respiration rate increases with degree of vernalization.

CO_2 fixation into malate is the main metabolic process occurring in CAM plants during the night. CAM plants open their stomates to collect CO_2 during the night and thus avoid water losses during the day. It is of interest to identify CAM species with low temperature capability because of the possibility of moving such CAM genes into crop plants such as pineapple (*Ananas comosus*), and thus increasing the

range in which these crops can be economically produced. Feng et al. [25] determined the rate of crassulacean acid metabolism as a function of temperature in nine species of CAM plants by a scanning calorimetric method [44]. The results show that CAM is chilling sensitive, showing an abrupt increase in the negative slope of an Arrhenius plot below the chilling temperature. The chilling temperature varies from 17°C down to 8°C in the species studied.

Periodic spraying with methanol has recently been reported to greatly increase crop production and/or decrease water usage in irrigated crops grown in desert lands [45]. However, field tests of methanol spraying done by other workers [46,47] have been unsuccessful in reproducing the reported results, showing that the original study must have contained uncontrolled variables. Calorimetric methods to rapidly examine plant responses to methanol under a variety of conditions have been developed [48]. Studies of the effects of methanol on respiration in petunia (*Petunia hybrida*), pepper (*Capsicum annuum*) and tomato leaf and root tissues show that methanol increases the metabolic rate of leaf tissues when applied at low doses, is toxic of high doses, and may increase respiratory efficiency over a narrow range of dose rates and application conditions. Thus, methanol may increase or decrease growth rates depending on concentration, means of application, and growth conditions. These results have not yet been related to growth rate effects, but the variable responses observed may explain the inconsistencies in results of field studies.

Respiratory rates in radish (*Raphinus sativus*) leaf tissue have recently been studied in our laboratories at limiting levels of the three nutrients, N, P and K, by calorespirometric methods. The results show that growth rates, metabolic heat rates, CO_2 rates and ratio of heat rate to CO_2 rate are all altered by changing N, P, K concentrations. Nutrient limitation stresses are readily observed as an increase in the ratio of heat rate to growth rate. Both growth rate and stress responses (as indicated by changes in the metabolic heat rate) depend on the absolute concentrations of mineral nutrients and on their ratios.

The Arrhenius temperature coefficient of respiratory metabolism (μ) for plants growing in a common garden was shown to be linearly related to a linear combination of latitude and altitude of origin for three woody shrubs in a calorimetric study by Criddle et al. [49]. Plants from low latitude and low elevation have higher temperature coefficients than congeneric plants from high latitude and high elevation. The linear relation between μ and the combination of latitude and altitude with 1° latitude $\equiv$ 85 m elevation was shown to hold in general for perennial, woody plants, but not for annuals. Isothermal data collected at several temperatures in a multi-sample DSC allowed rapid screening of large numbers of samples to provide north–south and high–low comparisons on numerous species. The significance of these results to considerations of selection criteria for plant growth in different climates is discussed later in this review.

Several studies since the last review have reported strong correlations between calorimetrically measured respiratory rates in meristem tissues and plant growth rates. Smith et al. [50] reported that metabolic heat rate was a much better predictor of growth rates of cold desert shrubs than was isotopic fractionation of carbon. In a series of papers Anekonda et al. [1,51–54] showed that growth rates

of coast redwood (*Sequoia sempervirens*) genotypes were strongly correlated with metabolic heat rates, CO_2 production rates and the ratios of metabolic heat rate to CO_2 production rate. These respiratory parameters and the high temperature at which metabolic heat rate began to rapidly and irreversibly decrease were also shown to be related to the location and climate of origin of the genotype. Workers at Union Camp have begun metabolic heat rate studies on loblolly pine (*Pinus taeda*) with the goal of improving the rate of biomass production [55].

A short report by Criddle et al. [56] discusses the selection of plants with increased energy use efficiency as a means of increasing productivity.

In a series of papers, Anekonda and coworkers [2,57–60] have used a number of temperature-dependent parameters determined by calorespirometry to select eucalyptus (*Eucalyptus*) species and genotypes for rapid biomass production in specific climates. The parameters used in making the selections were metabolic heat rate, Arrhenius temperature coefficient of metabolic heat rate, the high temperatures at which particular heat stress responses become apparent as a negative deviation from Arrhenius behavior, and the ratio of heat rates to CO_2 rates. The effects of temperature, seed origin, and plant age on growth rates were investigated with calorespirometric measurements. With climatic temperature included as an environmental variable in the study, selection of trees best matched to a growth climate can be made. These selections may be different from that of the common garden in which the trees are growing. These methods greatly reduce the time for selection of superior trees, and provide rationales for identifying trees that may be expected to yield superior progeny in a breeding program.

Rank et al. [61] report determination of substrate carbon conversion efficiency from calorimetric measurements on a collection of highly inbred maize (*Zea mays*) cultivars. Substrate carbon conversion efficiency is the most significant respiratory determinant of growth rate among these cultivars. Among a much broader range of maize genotypes, the Arrhenius temperature coefficient of metabolic heat rate (μ_q), and the metabolic heat rate below 10°C were also robust predictors of growth rates [62]. The latter study demonstrated that the maize cultivars from both this study and the study by Rank et al. [61] all had essentially identical specific metabolic rates, i.e. exhibit an isokinetic point [49], at about 20°C. Because the different maize varieties have different temperature coefficients, metabolic rates differ at all other temperatures. Plants with low μ thus grow faster than plants with high μ at growth temperatures below 20°C, and the order of growth rates is reversed above 20°C.

3.1. The relation of growth rate to respiratory variables in plants

The purpose of developing a thermodynamic model for plant growth was (a) to allow prediction of long-term productivity from rapid, early measurements on seedlings and (b) to provide a series of respirogenetic markers to be used in breeding and genetic engineering programs leading to improved growth rates and stress responses.

In developing a practical, useful model for these purposes, two principles must be understood. Firstly, supply of substrate carbon, i.e. photosynthate, does not limit

growth rate under normal growth conditions. The evidence for this is, in part, negative, but of sufficient quantity to be compelling: "There has ... rarely been an indication ... of a clear positive association between leaf photosynthetic rate and yield. In fact the reverse tends to be true" [63]. Further, the linear correlations between net photosynthesis or leaf area index and yield that are claimed to show that photosynthesis is the limiting process in growth [63,64] are in fact self-correlations that apply equally well to chickens and random numbers as to plants [65]. "Light interception will always be highly correlated with crop growth, even when light is not limiting. The level of correlation for the crop response to any cumulated quantity such as temperature (degree days), evapotranspiration, etc., is unimportant" [65]. Such correlations represent a failure to distinguish between the rate of a process and the amount of total accumulated product of the process as a function of time and are common in the literature of ecology [66].

Secondly, although the equations that form the thermodynamic model for plants are conceptually identical to those previously developed for describing the growth of micro-organisms, many of the approaches used in applying the models to micro-organisms cannot be used with plants or even with plant tissue cultures. For example, the rate of consumption of substrate is not readily accessible in plant studies, nor are the oxidation states of carbon in the substrate or the biomass. All mechanistic, thermodyanmic growth models require definition of the oxidation state of carbon in the substrate (γ_P), and while it is probable that photosynthate can, in general, be represented as carbohydrate with $\gamma_P = 0$, sufficient uncertainty exists in the knowledge of biochemical cycles in specific plants and in products linked to photorespiration, to place some doubt on this as a universal conclusion. Definition of the oxidation state of carbon in the biomass (γ_B) is even more uncertain in plants because it varies from tissue to tissue, with age of the tissue and with environmental variables.

In the model discussed here, plant respiration/biosynthesis is considered to have three inputs (photosynthate, oxygen and mineral nutrients including water) and three outputs (CO_2, biomass and heat). Because the rates of O_2 uptake (R_{O_2}), CO_2 production (R_{CO_2}), and heat production ($\dot{q}$) are the only variables in this list that can be unequivocally defined and readily measured for plants, any practical model must focus on the question of how to relate these three measures of respiration rate to growth rate.

Beginning with the assumption of strictly aerobic metabolism with CO_2 as the sole catabolic product, an equation relating specific growth rate, R_{SG}, to the respiratory variables $\dot{q}$ and R_{CO_2} was derived [13]

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

ΔH_{O_2} is the empirical constant from Thornton's rule or the heat of combustion expressed per mole of O_2 and is equal to -455 ± 15 kJ mol^{-1} for the major compounds in plant metabolism [67–70]. 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. The substrate carbon conversion efficiency, ε as

defined in Eq. (2), can also be expressed in terms of the same variables and parameters appearing in Eq. (1)

$$\varepsilon = R_{SG}/(R_{SG} + R_{CO_2})$$
$$= [(\dot{q}/R_{CO_2}) + (1 - \gamma_P/4)\Delta H_{O_2}]/[(\dot{q}/R_{CO_2}) + (1 - \gamma_P/4)\Delta H_{O_2} - \Delta H_B] \quad (2)$$

The respiratory quotient is definable with the same parameters

$$R_{CO_2}/R_{O_2} = [(1 - \gamma_P/4) + (\varepsilon/1 - \varepsilon)(\gamma_B - \gamma_P)/4]^{-1} \quad (3)$$

Eqs. (1)–(3) contain five unknown variables and three measurable variables. Any two of the five unknown variables, γ_P, γ_B, ΔH_B, R_{SG}, and ε, can be eliminated by combination of Eqs. (1)–(3). Thus, two parameters must be assigned values in order to calculate R_{SG} values from measurements of $\dot{q}$, R_{CO_2}, and R_{O_2}. Assuming carbohydrate as photosynthate, i.e. $\gamma_P = 0$, still leaves one parameter that must be estimated.

Because there is no apparent way to measure γ_P, γ_B, ΔH_B or ε directly, an understanding of the behavior of these parameters must be developed from respiratory studies on plants under controlled conditions where R_{SG} can also be measured. Thus, the behavior of γ_P, γ_B, ΔH_B, and ε for plant metabolism among genotypes within a species, among species, as a function of the physiological state of the tissue, e.g. age, season, root vs. shoot, etc., and as a function of environment, e.g. temperature, nutrients, water, etc., is of immediate interest. Combining Eqs. (1)–(3) to eliminate any two of the four measurable variables R_{SG}, R_{O_2}, R_{CO_2}, or $\dot{q}$ results in Eqs. (4)–(8)

$$R_{SG}/R_{CO_2} = (\varepsilon/1 - \varepsilon) \quad (4)$$

$$\dot{q}/R_{SG} = [(1 - 1/\varepsilon)(1 - \gamma_P/4)\Delta H_{O_2} - \Delta H_B] \quad (5)$$

$$R_{O_2}/R_{SG} = [(\varepsilon/1 - \varepsilon)(\gamma_B - \gamma_P)/4 + (1 - \gamma_P/4)]/(\varepsilon/1 - \varepsilon) \quad (6)$$

$$\dot{q}/R_{CO_2} = -(1 - \gamma_P/4)\Delta H_{O_2} - (\varepsilon/1 - \varepsilon)\Delta H_B \quad (7)$$

$$\dot{q}/R_{O_2} = [-(1 - \gamma_P/4)\Delta H_{O_2} - (\varepsilon/1 - \varepsilon)\Delta H_B]/[(1 - \gamma_p/4) + (\varepsilon/1 - \varepsilon)(\gamma_B - \gamma_P)/4] \quad (8)$$

which are particularly useful for this purpose because they are all ratios of measurable quantities expressed in terms of the unknown parameters. Eq. (3) is also of this form. These equations, together with measured values of the ratios on the left side, can be used to determine the behavior of γ_P, γ_B, ΔH_B, and ε.

ε can be determined from Eq. (4) and measured values of R_{SG} and R_{CO_2}. R_{SG} is not easy to define or measure experimentally, however. R_{SG} has units of moles of carbon per unit time. Thus, the amount of carbon incorporated into biomass must be determined as a function of time. Note that biomass in this context does not include storage carbohydrates that will later be mobilized and consumed in respiration. Such problems make direct determinations of absolute ε values from Eq. (4) extremely difficult in practice. However, relative ε values can be determined from growth rates measured in any units, e.g. height/day, change in stem volume

index over time, etc. Having obtained an ε value from Eq. (4), there is still no way of combining independent equations to eliminate all but one remaining variable, i.e. γ_P is not separable from γ_B or ΔH_B. One solution to this dilemma, as mentioned above, is to assume $\gamma_P = 0$. Another is to make an assumption about ΔH_B, namely

$$\Delta H_B = (\gamma_B - \gamma_P)\Delta H_{O_2}/4 + \Delta H_{CB} + \sum r_E \Delta H_E \quad (9)$$

Here ΔH_{CB} is the enthalpy change for all non-redox processes necessary for incorporation of carbon into biomass, and $\Sigma r_E \Delta H_E$ is the total enthalpy change for incorporation of all other elements (E) into the biomass. The simplest assumption is that the last two terms in Eq. (9) are negligible. Such an assumption is probably valid for ΔH_{CB}. Because r_E, the molar ratio of each element to carbon, is small for all elements except nitrogen, nitrogen is probably the only element that need be considered significant in the last term. Studies to determine the values of $r_N \Delta H_N$ for NH_4^+, NO_3^-, NO_2^-, and N_2 as the source of nitrogen are currently underway in our laboratories. Other studies are aimed at establishing under what conditions γ_P can safely be assumed to equal zero.

Our hope when we began these studies was that ΔH_B and γ_B would be constants for closely related genotypes, but recent, unpublished data from our laboratories clearly indicate that both can, and often do, vary with genotype. Indeed, the ratio $\dot{q}/R_{CO_2}$ can be used in selection of eucalyptus trees according to their lignin to cellulose ratio, i.e. γ_B. Studies on radish also show that the value of ΔH_B is altered by changing concentrations of N and P in the suboptimal range. Thus, application of the respiratory growth model is more complex than initially hoped, but still has proven immensely valuable in guiding fundamental inquiries and in developing methods for rapid, early selection of plants, particularly trees, for increased biomass production.

In that context, the model discussed here suggests a new strategy for plant breeding for high vegetative productivity. This is illustrated in Fig. 1 which is derived from Eqs. (1) and (2). Fig. 1 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}. The trapezoid outlined in this figure encloses the area defined by the range of ε and $\dot{q}$ values typical of growing plants. Although constant, arbitrary values for γ_P and ΔH_B have been assumed to construct Fig. 1, and these parameters may not be constant within a collection of plants, choosing other reasonable values for γ_P and ΔH_B alters only the values on the axes while the trapezoid remains generally as plotted in Fig. 1. Data from Anekonda [4] and Anekonda et al. [2] and other data from this lab show that natural populations apparently contain only plants having $\dot{q}$ and ε values placing them in the lower left half of the trapezoid. Extraordinarily fast growing plants would appear in the upper right corner of the trapezoid. Such a plant may be obtained by combining traits of a plant with high ε with a plant having high metabolic rate, even though either may not be a particularly fast growing plant. This approach has not been deliberately used by plant breeders in the past because, intuitively, pairs of plants with high growth rates are selected for crosses to achieve progeny with high growth rates. The very rapid growing plants that would occupy the upper right portion of the trapezoid in Fig. 1 may never have existed or may be eliminated from naturally occurring populations by evolutionary

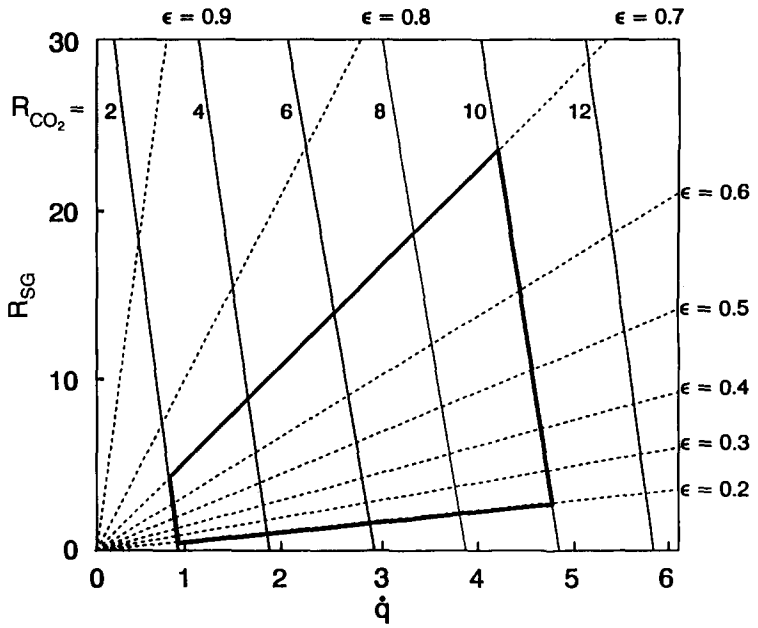

Fig. 1. Calculated specific growth rate (R_{SG} in pmol s^{-1} mg^{-1}) as a function of the metabolic heat rate ($\dot{q}$ in μW mg^{-1}) for various values of the rate of evolution of CO_2 (R_{CO_2} in pmol s^{-1} mg^{-1}) and substrate carbon conversion efficiency (ε). Calculated on the basis of fresh weight, assuming $\gamma_P = 0$, $\Delta H_{O_2} = -468$ kJ mol^{-1} and $\Delta H_B = 25$ kJ mol^{-1}. See Eqs. (1) and (2). (Reprinted with permission from Ref. [13].)

pressure. Such plants may require nutrient and water support by man to be maintained.

The mechanics of combining favorable respiratory traits may be complicated, however. Recent, unpublished observations in our laboratories suggest that mitochondrial genes are probably involved in some aspects of control of respiration rates and efficiencies. Because these genes are inherited from only one parent, new mitochondrial genotypes cannot be achieved through normal breeding. Variability in γ_B and ΔH_B must also be considered in breeding and selection programs. Practically, such selection requires rapid, easy means for measuring the desired traits. Simultaneous measurement of $\dot{q}$, R_{CO_2} and R_{O_2} may meet this need.

The commonly observed positive, but weak, correlations between growth rate and respiration rate for many plant species are readily explained by the model discussed here, see Eqs. (4)–(6). The weakness of the correlations is attributable to variation in ΔH_B, γ_B, and ε. Negative correlations are not so readily explained by the growth model, requiring a further condition that ε, ΔH_B or γ_B be linearly related to respiration rate within the study population. This is a possible, but unlikely condition. A much more likely explanation for both the occasionally observed negative correlations and the general weakness of all respiration–growth rate correlations is suggested by recent work on the temperature dependence of the

respiratory measures. Because plants cannot maintain their tissues at an optimum growth temperature, matching the Arrhenius temperature coefficient μ to the temperature profile experienced is an important mechanism for optimizing economic growth rate [71,72]. Furthermore, because biomass accumulation is an exponential function of growth rate, and growth rate is an exponential function of temperature, a small difference in μ can have a very large effect on total plant growth.

Similar to nearly all biological processes [73], metabolic heat, CO_2 and O_2 rates all closely follow the Arrhenius equation within a range of non-stress temperatures. In this temperature range, Eq. (1) can be expanded to Eq. (10)

$$R_{SG}(T) = [A_q\, e^{-\mu_q/T} - \Delta H_{CO_2} A_{CO_2}\, e^{-\mu_{CO_2}/T}]/\Delta H_B(T) \tag{10}$$

to describe the approximately exponential increase in growth rate with temperature [13]. Precise agreement between the responses of growth rate and respiration rate to temperature has been established in studies of eucalyptus genotypes with different μ values grown in controlled environment chambers [57].

μ values for $\dot{q}$ and R_{CO_2} are commonly not the same [62], vary widely both among and within species, are genetically determined, and vary in a definite pattern with season and mean growth temperature [49]. The absolute value of μ and the range of μ values achievable through adaptation of a plant are related to the climatic temperature to which the genotype is evolutionarily adapted [57]. Because μ for growth varies among genotypes, the curves relating growth to temperature for different plants must cross at some temperature. Surprisingly, Arrhenius plots for measured values of $\dot{q}$ and R_{CO_2}, as well as predicted values of R_{SG} (assuming constant ΔH_B) for genotypes of most species examined to date, cross in a narrow range of temperature within the range of non-stress temperatures at which the plants grow [49,57,62]. In this narrow temperature range, all genotypes of a species have the same respiration rate and growth rate, i.e. there is an isokinetic point. Thus, if both growth rates and respiration rates are measured at a temperature on one side of the isokinetic temperature, they will be positively correlated. But if growth rates and respiration rates are measured on opposite sides of the isokinetic temperature, negative correlation will be obtained. The latter situation can easily arise in studies with field grown plants if the average field growth temperature is on one side of the isokinetic temperature and laboratory respiration measurements are made on the other side of the isokinetic temperature. The presence of an isokinetic point in the normal range of growth temperatures and respiration measurements along with variability in μ among genotypes thus provides an additional explanation for the weak or non-significant growth–respiration correlations found in many studies. Variability in ΔH_B within the study population would cause further noise in the growth–respiration correlation and would widen the isokinetic range of temperature seen in an Arrhenius plot of growth rates.

Clearly, μ is an important determinant of relative metabolic and growth rates, and thus can affect a plant's ability to adapt to and compete with other plants in the environment. The value of μ must be matched to the climate at the growth site [57]. Climate–μ mismatch can explain why plants generally perform poorly when

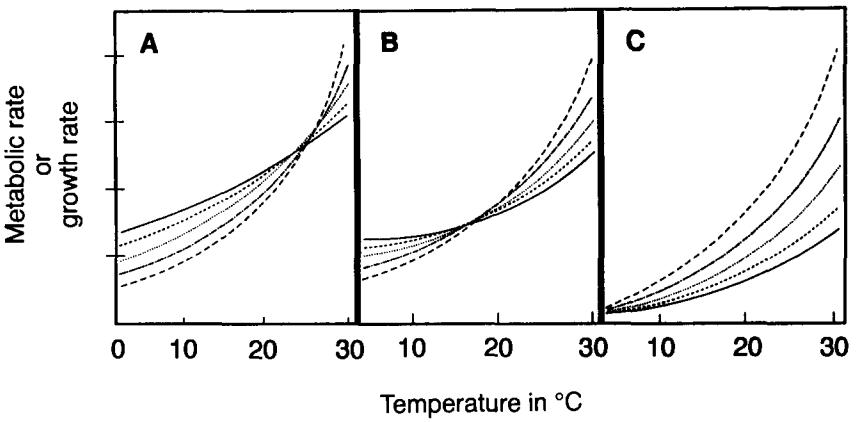

Fig. 2. Metabolic rate as a function of temperature for various Arrhenius temperature coefficients (μ) and isokinetic temperatures. A. These curves are presented to represent hypothetical plants having a distribution of μ values and an isokinetic temperature at 25°C similar to the pattern observed for bitterbrush, rabbitbrush, and sagebrush [49]. B. Hypothetical examples of curves for plants with an isokinetic temperature at 15°C, similar to that for maize. C. Hypothetical examples of curves for plants with a very low isokinetic temperature near 0°C as might exist for topical plants. The curves plotted in A, B and C have μ values of approximately 4 (—), 5 (– – –), 6 (· · ·), 7 (– · – · –) and 8 (— — —) kK.

removed to opposite ends of their latitude–elevation range. Both south-to-north and north-to-south plantings are frequently not successful, even within known temperature extreme limits for a given species' growth. The naturally occurring range of μ values shown by any species and the requirement that μ be matched to climate for optimum growth rate have important consequences upon a plant's ability to migrate and compete in communities during periods of climate change that do not exceed temperature limits for growth and reproduction.

Evaluation of the importance of high or low μ and the existence of an isokinetic point to relative plant growth rates is aided by the series of plots in Fig. 2. Fig. 2A illustrates temperature responses of metabolic rates for some hypothetical plants with varying μ values and a relatively high isokinetic temperature. These curves are plotted with μ values varying from 4 to 8 kK and identical metabolic rates per mg tissue near 25°C, the isokinetic temperature. Plants with temperature responses described by the curves of Fig. 2A, e.g. bitterbrush (*Purshia tridentata* Candolle and *Cowania stransburiana* Torrey), rabbitbrush (*Chrysothamnus nauseosus* (Tallas) Britt.), and sagebrush (*Artemesia tridentata* Nuttall) [49], spend the majority of their growing time at temperatures below the isokinetic temperature. At all temperatures below the isokinetic temperature, the metabolic rate (and thus total growth) is greater for those plants with lower μ values. At 10°C for example, the metabolic rate gets larger by a factor of about 2 for a doubling of μ. Temperate and arctic plants with their broad range of seasonal temperature exposures, relatively low average temperature, and large magnitude and rate of daily temperature variations would be expected to maximize relative growth rate by having low μ, relatively high

activity near 0°C and an isokinetic temperature near the maximum limit of thermal stability, i.e., like Fig. 2A.

When the isokinetic temperature is below the average climatic temperature, the relative metabolic rates of individual plants have a different dependence on the values of μ. Fig. 2C describes a hypothetical set of plants with approximately the same μ values as in Fig. 2A, but with an isokinetic temperature near 0°C. In this case, plants with higher values of μ metabolize faster than their lower μ counterparts at any temperature above 0°C. The anomaly then exists in this example that increasing values of μ translate into higher metabolic and growth rates. Temperature dependences of plants originating in subtropical and tropical environments are predicted to resemble the model of Fig. 2C in which plant growth at temperatures above the isokinetic temperature is more rapid for plants with higher μ. For plants that never experience low temperatures, this is an acceptable strategy.

Finally, Fig. 2B describes an additional hypothetical example, similar to that plotted in Ref. [9], illustrating plants with an isokinetic temperature equal to the mean temperature. The relative growth rates of individual plants, having different μ, but identical growth rates at 15°C, would be expected to differ as the average daily temperature increases and decreases through the season.

Available experimental data support the conclusions drawn from these hypothetical plots. The isokinetic temperature of maize [62], a warm climate crop, is lower than that of bitterbrush, sagebrush or rabbitbrush, all species originating from cooler climates [49]. Studies on eucalypts show a clear dependence of growth rate of different species in a common plantation on μ values [57]. Species with either too high or too low μ values grow poorly, while those with μ values matched to the climate at the growth site grow faster.

The correlation of μ with latitude and elevation of origin of woody perennials suggests that development of lower μ values with increasing latitude and elevation increases the survival and competitiveness of plants [49]. The observations can probably be extended to a general statement that within a given competitive niche, μ is related to the latitude and elevation, among species as well as within a given species.

One possible rationale for the evolutionary adaptation of low μ values during development of high latitude and high elevation plants is that wide variations of temperature cause relatively small variations in metabolic rate when μ is small. Limiting the temperature dependence of metabolic steps results in smaller changes in absolute and relative concentrations of intermediate metabolites due to differences in temperature responses of individual enzymes. Since these concentrations must be regulated to maintain balanced metabolism, low activation energies allow a smaller range of controls.

It would be incongruous to link μ and enzyme catalytic efficiency, i.e., interpretation in terms of activation energies of enzyme-catalyzed reactions, in the situation described in Fig. 2c. This would lead to a conclusion that increasing the μ of metabolism in a plant, i.e., apparently decreasing the enzyme catalytic efficiency, increases its metabolic rate relative to a related plant with lower μ. Values of μ must, therefore, be interpreted simply in terms of the temperature dependence of

some controlling process. This could be a direct temperature effect on kinetics or a temperature effect on binding of regulator molecules. The observed linear ln(heat rate) vs. $1/T$ dependence applies equally well to both. The Arrhenius equation ($\ln k = \text{constant} - E/RT$) and the van't Hoff equation ($\ln K_{eq} = \text{constant} - [\Delta H/RT]$) describing a temperature-induced shift in equilibria, have the same form. These are indistinguishable without knowing details of the chemistry.

In addition to describing how temperature influences biogeographic patterns of plants, the model discussed here may have important practical applications in improvement of crop productivity. The differing values of μ across the geographic range suggest that μ is as important in determining growth range as the maximum or minimum temperature limits for stability. The μ value is also a dominant factor in determining relative growth rates among genotypes of a species within a given environment. Because we have shown the variation in μ within a given species to be genetically determined, μ may be an excellent candidate for molecular genetic manipulation. Inheritable μ values differing quite widely among plants within a given species suggest the possibility of selection for this characteristic to optimize plant growth within a given environment and to extend ranges of plant growth.

The model presented here together with the methods of photocalorespirometry currently being developed may provide the means to predict specific growth rates of plants in the light, and thus answer one of the long-standing questions in plant biology, namely, how do respiration and growth in the dark differ from respiration and growth occurring at the same time as active photosynthesis? If $\dot{q}_m$ is the heat rate measured with light on a plant in a calorimeter, then

$$\dot{q}_m = \dot{q}_L + \dot{q}_P + \dot{q}_R \tag{11}$$

where $\dot{q}_L$ is the heat rate measured in the empty calorimeter with the light on (the baseline or blank), $\dot{q}_P$ is the heat rate due to photosynthesis reactions and $\dot{q}_R$ is the heat rate produced by respiration. Assuming that photosynthesis is simply the reaction of CO_2 and H_2O to form carbohydrates and O_2, then

$$\dot{q}_P = P_C \Delta H^P_{CO_2} \tag{12}$$

and

$$\dot{q}_R = -R_{CO_2} \Delta H^R_{CO_2} - R_{SG} \Delta H_B \tag{13}$$

where P_C is the rate of carbon fixation by photosynthesis, $\Delta H^P_{CO_2}$ is the enthalpy change per mole of carbon for the overall photosynthetic process, R_{CO_2} is the rate of CO_2 produced by respiration in the light, $\Delta H^R_{CO_2}$ is the enthalpy change per mole of CO_2 produced in respiration, and R_{SG} and ΔH_B are as defined above. Combining these equations and assuming $\Delta H^P_{CO_2} = \Delta H^R_{CO_2}$ results in

$$R_{SG} = [-\dot{q}_m + \dot{q}_L + \Delta H_{CO_2}(P_C - R_{CO_2})]/\Delta H_B \tag{14}$$

which can be used to predict relative specific growth rates for plants during photosynthesis as ΔH_{CO_2} is related to ΔH_{O_2} which is known, and the difference $(P_C - R_{CO_2})$ is simply the measured rate of change of CO_2 in the system.

4. Summary

A previous paper [17] reviewed the literature on applications of calorimetry to the study of plant metabolism. This paper reviews developments since that time. The major development has been in the derivation and testing of a respiratory model for plant growth. Use of this model has led to new understanding of the physiological determinants of plant growth and of the effects of temperature on plant growth and distribution. These discoveries have led to significant improvements in methods for rapid selection of plant genotypes with improved growth properties. Calorimetry will play an increasingly important role in future studies of plant metabolism.

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