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Kinetics of plant growth and metabolism

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Abstract

Direct measurements of plant growth rates in terms of volume, length, net photosynthate, etc. provide little information concerning the mechanism of adaptation of metabolism to an environment. To derive the mechanism, metabolic properties must be measured as functions of environmental variables. Growth rates may be limited by the availability of nutrients including fixed carbon, by climate, by other environmental factors including toxins, or by the genetically determined properties of the plant. But in all cases, growth rate is equal to a function of respiration rate and efficiency. For a plant to thrive, its respiratory metabolism as well as its photosynthetic metabolism must be closely adapted to the seasonal and daily variations in the environment. Thus, measurement of respiratory properties is necessary for understanding plant adaptation.

In terms of readily measurable respiratory variables, the rate law for growth driven by aerobic respiration is

$$R_{SG} = R_{CO_2}\left[\frac{\epsilon_C}{1-\epsilon_C}\right] = rR_{O_2}\left[\frac{\epsilon_C}{1-\epsilon_C}\right] = -R_{CO_2}\Delta H_{CO_2}\frac{\eta_H}{\Delta H_B} = \frac{-\Delta H_{CO_2}R_{CO_2} - R_q}{\Delta H_B}$$

where R_{SG} is the specific growth rate, R_{CO_2} the specific rate of CO_2 evolution, ϵ_C the fraction of substrate carbon converted into structural biomass or the substrate carbon conversion efficiency, r the respiratory quotient, R_{O_2} the specific rate of O_2 uptake, ΔH_{CO_2} the enthalpy change for combustion of substrate per mole of CO_2, η_H the fraction of enthalpy produced by oxidation of substrate that is conserved in the biomass synthesized through anabolism (i.e. the enthalpic efficiency), and ΔH_B is the enthalpy change for conversion of substrate into structural biomass per C-mole. ΔH_{CO_2} can be obtained from Thornton's rule, and ΔH_B from either heat of combustion or composition data or from growth measurements. Calorespirometric measurements can then be used to obtain values for ϵ_C and η_H. Measurements of R_{CO_2}(or of r and R_{O_2}) and the metabolic heat rate, R_q, as functions of environmental variables thus, can be used to rapidly ascertain the growth and metabolic responses of plants to environmental variables.

This model and calorespirometric measurements are used to predict the responses of plant growth to differing climates, to predict the global gradient of plant species ranges and diversity, and to predict global treeline temperature conditions. Growth-season temperature and temperature variability are found to be major determinants of growth rates and distributions of plants. These findings may be useful in predicting the response of plants to climate changes.

Keywords: Plants; Respiration; Photosynthesis; Calorespirometry; Distribution; Treelines; Alternative oxidase

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Nomenclature

r	respiratory quotient, i.e. the ratio R_{CO_2}/R_{O_2}
R_{CO_2}	specific rate of CO_2 evolution from respiration
R_{O_2}	specific rate of O_2 uptake by respiration
R_q	specific metabolic heat rate
R_{SG}	specific growth rate
T	absolute temperature
ΔH_B	enthalpy change for conversion of substrate into structural biomass per C-mole
ΔH_{CO_2}	enthalpy change for combustion of substrate per mole of CO_2
ΔT	range of environmental temperature
ϵ_C	the fraction of substrate carbon converted into structural biomass by respiration, or the substrate carbon conversion efficiency
η_H	fraction of enthalpy produced by oxidation of substrate that is conserved in the biomass synthesized through anabolism, or the enthalpic efficiency

1. Introduction

Plants grow at widely differing rates, from the ornamental succulent that adds but one leaf per year to the bamboo shoot that grows meters per day. Growth rate is determined by both the genetic nature of the plant and the nurture given by the environment. Because plants are immobile ectotherms, a plant may have the genetic potential to grow rapidly, but in the wrong environment may grow very slowly or not grow at all. A plant must receive the right environmental cues for growth and life cycle stages to occur in the proper seasons, and in addition, the plant's metabolism must respond properly to short-term changes in the environment that occur on a daily basis. Determination of the potential growth rate as a function of environmental variables is thus important for development of new crops and for ecological understanding. In current practice, growth and development are measured in several different environments, a slow and costly practice. Although empirical field methods will probably never be entirely replaced by laboratory methods for these determinations, this paper shows that calorespirometric methods could be used to direct, and thus, greatly speed field trials.

Plant growth can be and is defined in a number of different ways. Volume, length and mass, either fresh or dry, are commonly used measures. Total carbon or nitrogen content from elemental analyses, or protein or cellulose or lignin content from proximate analyses are also used. Harvest yield, the amount of desired product, such as grain or wood is frequently used. Energy content is also used as a measure of plant growth in this paper. Growth rate is usually expressed as the specific growth rate. Thus, some property x is measured as a function of time, t, and the relation between $\ln x$ and t is expressed as an arbitrary function, often a second order polynomial. The derivative of this function then provides a quantitative description of the specific growth rate, R_{SG}, as a function of time:

$x =$ volume, length, mass, etc.

$$= f(\text{time}), \text{ then } \frac{d \ln x}{dt} = \left(\frac{1}{x}\right)\left(\frac{dx}{dt}\right) = R_{SG} \qquad (1)$$

Direct measurement of growth rate as a function of environmental variables is an inherently slow and complex process, because the plant or clones must be grown at many different sets of conditions. But, if the metabolic properties, which can be measured rapidly as a function of environmental variables, can be used to reliably predict growth rates, the process can be greatly accelerated.

Because green plants are autotrophs, growth rate has often been assumed to be related to the rate of photosynthesis. The linear correlation between integrated net photosynthesis rate and growth has been given as proof of this relationship. However, because growth is proportional to total carbon, the integrated net photosynthesis rate is simply another measure of growth, so this is a tautology [1]. Photosynthesis provides the necessary substrate and fuel to power the growth process, but the rate of growth is limited to the rate and efficiency with which photosynthate is processed through respiration. Photosynthate is often stored in a polymeric form, such as starch and then used later, maybe even in a different season, in the growth process.

Over the past 30 years, many attempts have been made to express plant growth rate as a function of respiration rate expressed as the CO_2 production rate (R_{CO_2}) or as the O_2 uptake rate (R_{O_2}) [2–5], but with a notable lack of success [6,7]. Although several rapid

methods for determining R_{CO_2} and R_{O_2} were developed, no generally applicable method for determining the respiratory efficiency emerged until calorespirometric methods and an enthalpy balance model for the relation between respiration and growth were applied to plants [8,9]. This model and supporting calorespirometric methodology now provide a means for rapid determination of the kinetics of plant growth as a function of environmental conditions, and are beginning to provide insights into the mechanism of adaptation of plant metabolism to the environment.

2. Theory

Whether the growth rate is limited by the input rate of a necessary material such as carbon, nitrogen, iron, etc., by other environmental conditions, or whether it is limited by the inherent properties of the respiratory system, measurements of respiratory rate and efficiency can be used to calculate the growth rate of a plant or of plant tissues. The equation for growth by aerobic respiration in terms of carbon is:

$$C_{substrate} + x(\text{compounds and ions of N, P, K, etc.}) + yO_2 \rightarrow C_{structural\ \ biomass} + (1-\epsilon)CO_2 \quad (2)$$

which leads by inspection to the fundamental rate law for growth:

$$R_{SG} = R_{CO_2}\left[\frac{\epsilon_C}{(1-\epsilon_C)}\right] = rR_{O_2}\left[\frac{\epsilon_C}{(1-\epsilon_C)}\right] \quad (3)$$

where R_{SG} is the specific growth rate, R_{CO_2} the specific rate of CO_2 evolution, ϵ_C the fraction of substrate carbon converted into structural biomass or the substrate carbon conversion efficiency, r the respiratory quotient, and R_{O_2} is the specific rate of O_2 uptake. Note that the definition of structural biomass used here arises from Eq. (2). That is, structural biomass is that part of the total biomass that is synthesized through anabolic reactions. Photosynthate is not a part of the structural biomass in this definition.

The value of ϵ_C can be calculated from the mass balance of carbon during growth [10,11], but because it must be known as a function of environmental variables, this involves growing the plant at many different conditions. Also, ϵ_C cannot be measured by this method under conditions where the plant will not grow. As an alternative, ϵ_C can be calculated from simultaneous measurements of R_{CO_2} and the metabolic heat rate, R_q:

$$\frac{R_q}{R_{CO_2}} = -\Delta H_{CO_2} - \left[\frac{\epsilon_C}{(1-\epsilon_C)}\right]\Delta H_B \quad (4)$$

ΔH_{CO_2} is the enthalpy change for combustion of substrate per mole of CO_2, and ΔH_B is the enthalpy change for conversion of substrate into structural biomass per C-mole. ΔH_{CO_2} can be obtained from Thornton's rule, if the mean oxidation state of carbon in the substrate is known. Since the substrate in plants is usually sucrose or another sugar in aqueous solution, the substrate oxidation state is usually zero and $\Delta H_{CO_2} = -470$ kJ mol^{-1} [12,13], it is less exothermic for amino acids and fatty acids. An estimate of the substrate oxidation state can be obtained from the respiratory quotient, R_{CO_2}/R_{O_2}, if it is not known from the biochemistry [14]. ΔH_B can be obtained from the heat of combustion of the biomass [15], from the composition of the biomass [15], or from a combination of growth and respiration measurements. The last method is a new method discussed below that we are currently testing.

Combining Eqs. (3) and (4) gives:

$$\Delta H_B R_{SG} = -\Delta H_{CO_2} R_{CO_2} - R_q \quad (5)$$

which provides values of $\Delta H_B R_{SG}$ from an estimate of ΔH_{CO_2} from Thornton's rule and measurements of R_{CO_2} and R_q. Division of $\Delta H_B R_{SG}$ by R_{SG}, measured independently on the same tissue by the methods outlined previously in this paper (Eq. (1)), gives the value of ΔH_B. The major advantage of this method of evaluating ΔH_B over the methods based on measurements of heat of combustion or composition is that the value of ΔH_B obtained applies to the conditions in the living tissue, not in a dry state. Because the tissue has to be dried for combustion, and Thornton's rule is based on data for the enthalpy content in the dry state, both of the previously available methods give ΔH_B values for the dry state. Thus, we hope we will soon be able to provide an answer to the longstanding question of the difference in enthalpy between the hydrated and dehydrated states of cells.

Eq. (3) can also be written in terms of the enthalpic efficiency instead of the efficiency of use of substrate carbon:

$$R_{SG} = -R_{CO_2}\Delta H_{CO_2}\frac{\eta_H}{\Delta H_B} \quad (6)$$

where η_H is the fraction of enthalpy produced by oxidation of substrate that is conserved in structural biomass. The value of η_H can be calculated by combining Eq. (5) and (6) to eliminate R_{SG}, and then applying Thornton's rule to get ΔH_{CO_2} and combining the result with measured R_q and R_{CO_2} values. Although Eq. (6) is intuitively more apparent than Eq. (3), Eq. (6) is more difficult to relate to actual biochemical reactions.

Eq. (5) provides a means for rapid laboratory determinations of growth rate and the responses of growth rate to environmental variables. Since ΔH_{CO_2} and ΔH_B depend only on substrate and biomass composition, which normally only vary with ontogeny and not with environmental conditions, it will often be the case that only R_{CO_2} and R_q need to be determined as functions of environmental variables to calculate $\Delta H_B R_{SG}$. If ΔH_B is known, R_{SG} can of course be obtained. But the product $\Delta H_B R_{SG}$ itself provides a very useful measure of growth rate in terms of the rate of enthalpy deposition in structural biomass. One of the useful features of using $\Delta H_B R_{SG}$ as a measure of growth rate is that it does not depend on the composition of the biomass; tissues of differing composition (e.g. with differing ratios of lignin and cellulose or of lipids and carbohydrates) can be directly compared. However, it must be kept in mind that ΔH_B is approximately equal to zero for conversion of sugars from photosynthesis into starch or other carbohydrate polymers during a biological process such as loading of seeds or tubers with carbohydrate polymers. If the absolute value of ΔH_B is too small, Eqs. (5) and (6) become indeterminate for practical purposes.

3. Effects of growth conditions

The effects of environmental variables on plant growth are often complex. The effects of environmental variables are typically described as shown in Fig. 1 (e.g. see [16–18]) where, for example, too little or too much of a nutrient, or too low or too high temperature causes a large decrease in growth rate. In the optimal range of the environmental variable, growth rate is typically illustrated as going through a low maximum, being changed relatively little by large changes in the environmental variable. One might reasonably have expected instead that growth rate would increase exponentially with temperature and perhaps linearly with an increasing nutrient concentration. However, changes in growth rate with changes in environmental conditions are much smaller than these expectations. Fig. 1, thus, captures the essence of the response of diverse species, including both plants and animals, to various environmental factors, and may explain why diverse species can coexist on a single site.

In the optimal range, growth rate changes relatively little, and respiration rate may increase or decrease with increasing growth rate (e.g. see [19–22]). Also, different measures of the respiration rate, e.g. R_{CO_2} and R_q, may respond differently. Observations of only one measure of the respiratory rate as a function of an environmental variable have thus caused much confusion in the literature on plant ecophysiology. But application of the calorespirometric methods described here has made it clear that changes in respiration rate are often opposed by changes in efficiency, thus keeping the growth rate near constant, see

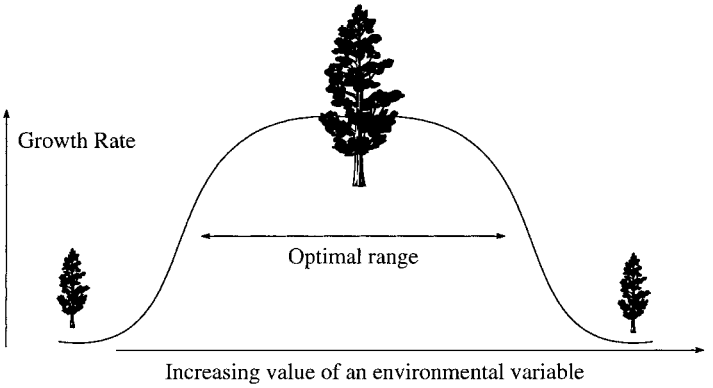

Fig. 1. A generalized view of the effects of environmental factors on the growth rate of plants.

Eqs. (3) and (6). Further, we now understand that this approximate homeostasis of the growth rate is a necessary consequence of the mechanism of coupling of the catabolic reaction, i.e. the exergonic oxidation of substrate by oxygen, to the anabolic reaction, i.e. the endergonic synthesis of structural biomass from substrate.

The overall reaction for aerobic growth, reaction (2), defines the thermodynamic system, which is the sum of two coupled processes, the very exothermic catabolic reaction (7):

$$C_{substrate} + yO_2 + n\mathrm{ADP} + n\mathrm{P}i + a\mathrm{NAD}^+ \rightarrow CO_2 + n\mathrm{ATP} + a\mathrm{NADH} + \mathrm{H}^+ \quad (7)$$

and the nearly thermoneutral reaction (8):

$$C_{substrate} + x(\text{compounds and ions of N, P, K, etc.}) + m\mathrm{ATP} + b\mathrm{NADH} + b\mathrm{H}^+ \rightarrow C_{\text{structural biomass}} + m\mathrm{ADP} + m\mathrm{P}i + b\mathrm{NAD}^+ \quad (8)$$

Reactions (7) and (8) occur in the condition-dependent ratio $(1-\epsilon_C)/\epsilon_C$ where ϵ_C is the substrate carbon conversion efficiency. Reactions (7) and (8) are energy-coupled through cyclic production and hydrolysis of ATP and redox cycling of NADH. Because the rates of reactions (7) and (8) have different dependencies on temperature and other conditions, the coefficients of ATP and NADH n and m and a and b, are generally not equal for the two reactions. In plants, the variable stoichiometry between reactions (7) and (8) is primarily a consequence of variable coupling between the oxidation reaction and ATP synthesis, although substrate level phosphorylation, ATP hydrolysis by phosphatases uncoupled to any synthesis or transport reactions, and ADP disproportionation catalyzed by adenylate kinases play smaller, but nonetheless important roles. The ATP cycles and alternate paths coupling the catabolic and anabolic reactions are shown diagrammatically in Fig. 2.

Three principles, concerning the coupling of the oxidative catabolic reaction to anabolic use of ATP must be recognized. First, the rate of ATP turnover is extremely high, i.e. most organisms synthesize about half their body weight in ATP per day [14], but cellular concentrations of ATP are only in the millimolar range. Any discrepancy between the two rates would quickly lead to either depletion of, or a large excess of, ATP. Thus, the overall rates of ATP synthesis and hydrolysis must be precisely controlled to be equal under all conditions of viability to maintain near-constant intracellular ATP concentration and phosphorylation potential. The fact that the optimal range of temperature for growth, as measured by calorespirometry, matches the range of environmental temperature for plants adapted to their environment [23–26], demonstrates that the limits of control of the phosphorylation potential establishes the upper and lower bounds of the optimal range in Fig. 1 [23,24]. (The phosphorylation potential, which is the free energy change for hydrolysis of ATP to ADP and P_i, is, on a practical basis, similar to what is called the energy charge in most biochemical literature [27].).

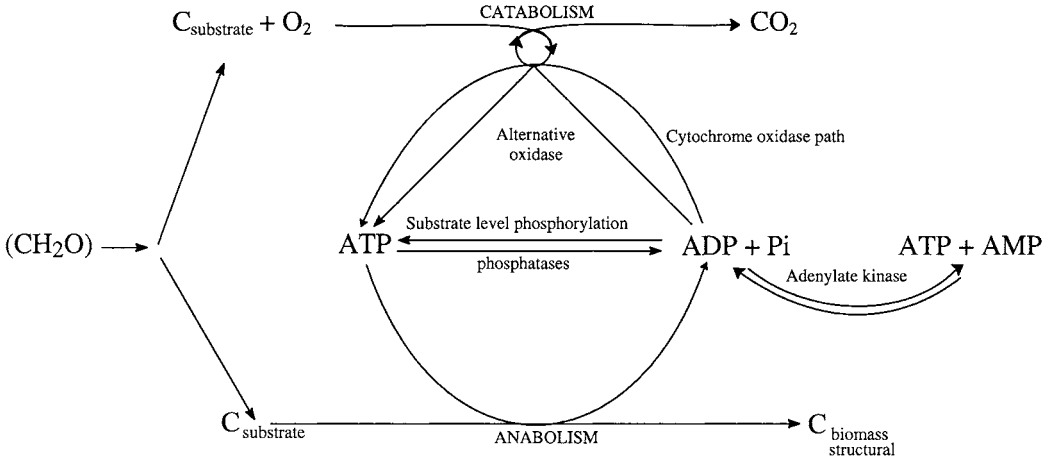

Fig. 2. ATP cycle coupling catabolism and anabolism in plant respiration.

Second, control of the phosphorylation potential requires variable coupling between the rate of ATP production and the rates of O_2 use and CO_2 production [28]. The variation in coupling is probably accomplished in plants primarily by variable engagement of the alternative oxidase pathway [29,30]. An alternative path of low efficiency for making ATP or an uncoupling agent is probably necessary for survival of plants and other ectotherms that encounter variable temperature or large variation in other conditions. Third, the ratio between the rates of ATP formation and ATP use in biosynthetic reactions is also variable because of hydrolysis of ATP and oxidation of NADH in futile cycles, not coupled to biosynthesis [28,31]. To provide a means for flexible control as conditions vary, reaction (7) must always produce ATP and NADH at rates equal to, or in excess of, their rates of use in the biosynthetic reactions of anabolism, reaction (8). If ATP is synthesized faster than it is used for biosynthesis, the excess can be disposed of by hydrolytic reactions, but if ATP were to be synthesized slower than it is used, the phosphorylation potential would fall and cell death would ensue. Therefore, the excess ATP and NADH must be cycled through condition-dependent, uncoupled hydrolysis and oxidation reactions. Moreover, if the excess ATP and NADH were not disposed of in futile cycles, the phosphorylaton potential (i.e. the free energy change for hydrolysis of ATP) and redox potentials would become too large for cell viability.

A consequence of the necessity of constant phosphorylation potential, but variable coupling between the catabolic and anabolic reactions is that the rate of the catabolic reaction rises as the efficiency of ATP production falls [32,33] and vice versa. Because the phosphorylation potential, which is controlled in a narrow range, drives the endergonic anabolic reactions, these tend to run at a near constant rate unless the anabolic enzymes or pathways are altered. And, since the growth rate is proportional to the rate of anabolism, growth rate also changes little with conditions in the optimal range of Fig. 1 unless the anabolic enzymes or biochemical pathways change.

As stated above, the range of control of the phosphorylation potential matches the range of environmental temperature to which plants are adapted [23–25]. Plants adapt to the environmental temperature profile because of two opposing selective pressures. There is pressure to decrease the width of the optimal range of temperature (Fig. 1), because respiratory efficiency is inversely proportional to the width [29], and thus, the maximum potential growth rate increases as the optimal range narrows. The opposing selective force is the requirement that the environmental temperature extremes must be included in the optimal range. The range of temperature over which the phosphorylation potential can be controlled depends on the temperature dependencies (or activation energies) of the reactions catalyzed by the alternative and cytochrome oxidases. Thus, adaptation of plant respiration to the temperature of the environment evidently occurs by selection of those genotypes having the optimum amino acid sequence in these proteins.

4. Temperature effects on growth rate

Consideration of the effects of environmental temperature on growth rate as expressed in Eqs. (5) and (6) leads to increased understanding of plant ecology. These equations can be summarized as ''growth rate equals respiration rate times a function of respiratory efficiency for growth''. As expected for temperatures in the optimal range, the respiration rate increases with increasing temperature in an approximately linear manner. The efficiency function may increase or decrease with temperature [23], but must decrease as temperature variability increases, according to the application of the principles of non-equilibrium thermodynamics to the system of equations in Fig. 2 [29,32,33]. Assuming the efficiency function is proportional to the reciprocal of temperature variability gives:

$$R_{SG} = R_{CO_2} f(\text{efficiency}) = \frac{k(T - T_0)}{\Delta T} \tag{9}$$

ΔT is the short-term (e.g. diurnal) temperature range, T the absolute, mean-kinetic temperature (which depends on both the temperature of the environment and the temperature dependence of respiration) [34], and T_0 is the lower temperature limit for growth (e.g. 0 °C, where liquid water may become unavailable).

Eq. (9) predicts that growth rate should decrease as ΔT increases for plants growing at a common mean kinetic temperature. Just such a relation has been

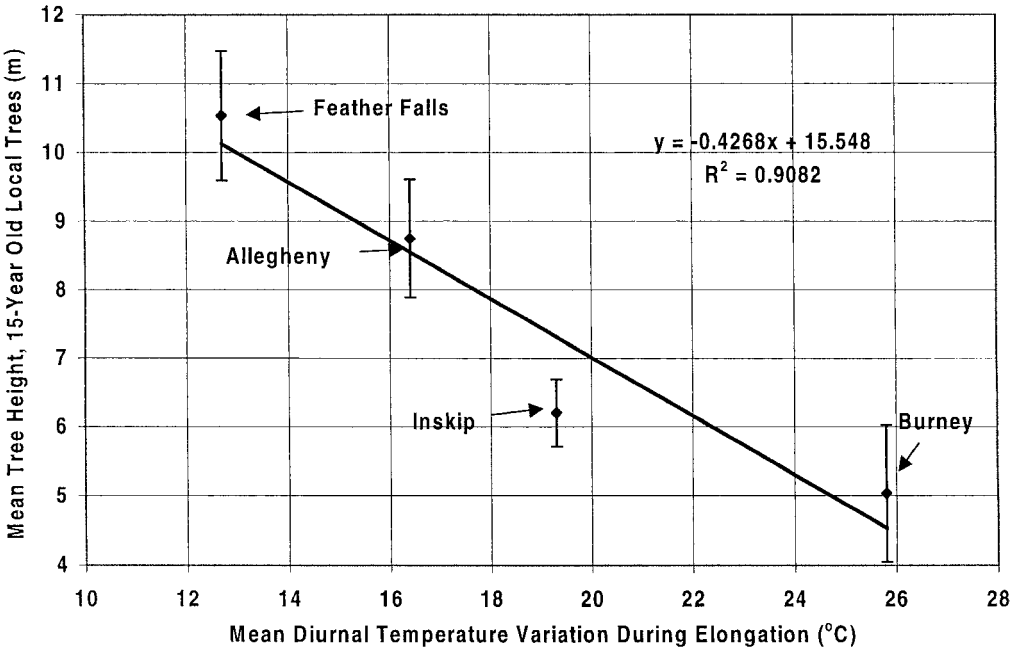

Fig. 3. Fifteen-year tree height of local *Pinus ponderosa* trees plotted vs. mean diurnal temperature variation during the shoot elongation period at four different elevations in the Sierra Mountains of California.

found for *Pinus ponderosa* families growing in plantations at different elevations and topographic conditions in the Sierra Nevada mountains of California (Fig. 3) [26]. In this species, spring growth of branches is triggered when daily high temperature reaches a minimum value, which generally occurs later in the season with increasing altitude, but may be influenced by local topography. Thus, growth occurs at similar temperatures irrespective of altitude or topography. But because ΔT increases with altitude and can vary with topography, Eq. (9) predicts growth will decrease with altitude and with topographic conditions that increase ΔT. Which is what was found for three of the plantations. No other environmental variable correlates nearly as well with the measured growth rates at these three plantations. Growth at the fourth plantation, Inskip, is lower than predicted from the correlation line for two reasons. Trees at Inskip receive more snowfall which causes more breakage, and this plantation was established with a seedlot collected at a lower elevation. Consequently, the trees at Inskip are not as well adapted to the local climate as the trees at the other plantations which were established with seed from local sources.

A second test of Eq. (9) was based on measurements of temperature at treelines around the world. The locations of treelines have been well documented. Below the treeline, normal tall forms of trees occur, at the treeline, the tall form abruptly disappears, and above treeline, the same tree species appear, but in a shrubby, Krummholz form. Assuming treeline occurs where the average annual growth equals the average annual loss, and that the growth and loss are about constant over the globe for treeline species, leads to the conclusion that the time averaged R_{SG} is approximately constant at treeline. Therefore, from Eq. (9):

$$\Delta T_{\text{treeline}} = k'(T_{\text{treeline}} - T_0) \tag{10}$$

where k' is a proportionality constant, $\Delta T_{\text{treeline}}$ is the temperature variation at the treeline, and T_{treeline} is the absolute, mean-kinetic temperature at the treeline. A plot of $\Delta T_{\text{treeline}}$ versus $T - T_0$ at the treeline (i.e. T_{treeline} is approximated as the mean temperature and given in degrees Celsius) should be linear. Data for locations above or at higher latitudes than treeline should plot above the line and data for locations below or at lower latitudes than treeline should plot below the line. Fig. 4 shows such a plot. The data points plot as

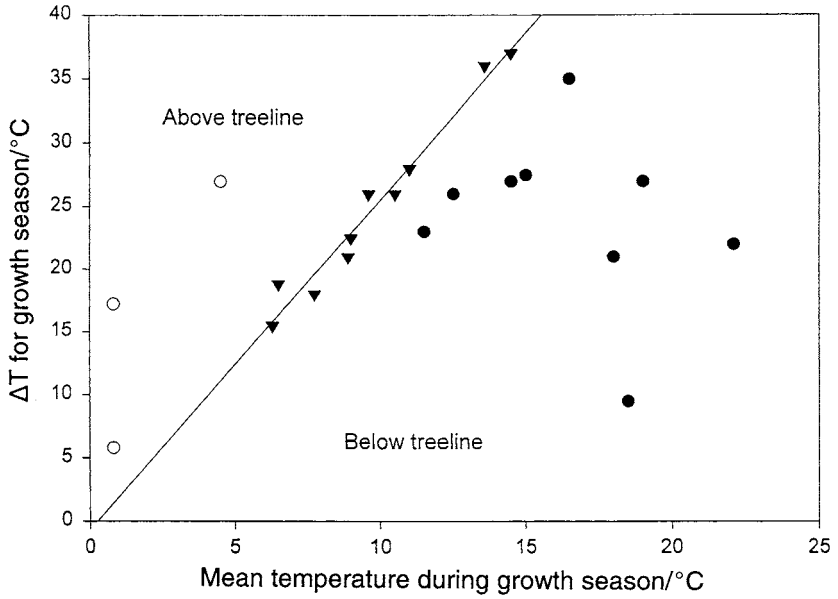

Fig. 4. Short-term temperature variation plotted against mean temperature for sites at treeline (▼), above treeline (○), and below treeline (●).

predicted for all locations where sufficient temperature data are available to estimate both T and ΔT.

Eq. (9) can also be used to predict the diversity and ranges of plant species as a function of latitude and altitude [29]. We propose that fitness is maximized in ectotherms having an optimal temperature dependence of the rate and efficiency of respiration. Because mean temperature is negatively correlated and, temperature variability positively correlated with latitude and altitude, natural selection will produce a gradient of metabolic phenotypes along latitudinal and elevational transects. Within the temperature range of viability, respiration rate increases with increasing temperature, but efficiency can either increase or decrease. However, increasing variability of temperature always decreases efficiency. The metabolic properties of ectotherms adapted to climates with more variable temperature allows survival over a broader temperature range and thus, over a broader geographical range than is possible for ectotherms adapted to a more constant temperature environment. Adaptation to low variability of temperature allows high efficiency of energy use, rapid growth, and thence high competitiveness, but only over a narrow temperature range. Gradients of ranges and diversity, with latitude and elevation thus arise from natural selection of enzymes with the optimum physicochemical responses of metabolic rate and substrate carbon conversion efficiency to temperature and temperature variability.

The principles developed above predict that range, or niche size, for populations and species must increase with the magnitude of temperature fluctuations. If A_T is total area, N_T is total number of species, then the ratio A_T/N_T is the average species area, which is proportional to T if the postulate above is correct, and the relation is linear.

$$\frac{A_T}{N_T} = c(\Delta T) \tag{11}$$

ΔT is related to latitude and altitude, i.e. $\Delta T = c'f$ (latitude, altitude). Through mid-range temperate latitudes and altitudes, the relation between T and latitude or altitude is approximately linear so that in this range, species area and latitude/altitude are predicted to be linearly related.

This relation (Eq. (11)) can be compared with known species diversity and seasonal temperature variation in the northern hemisphere at 12 and 45°N latitude. The approximate mean temperature fluctuation (ΔT) at 45° latitude is about three times that at 12° latitude. Thus, Eq. (11) predicts the niche size increases and number of thermal niches decreases about three-fold from 12 to 45° latitude. In comparison,

the actual species diversity at 12° latitude is only about twice that at 45°. However, because land areas at the two latitudes differ, the effect of area on species numbers must also be taken into account. An exponential relation exists between species number (N) and area (A), i.e. $N = kA^z$, and z values from 0.1 to 0.6 have been reported [35]. However the z values cluster around 0.4. Using this value and returning to our example, we find that the land area of the continents increases about 1.5-fold from 12 to 45°N latitude. The species area relation predicts N should be $(1.5)^{0.4} =$ 1.2-fold higher at 45°N than at 12°N. Combination of the species area relation with Eq. (11) yields Eq. (12):

$$N^{[(1/z)-1]} = c''\Delta T \tag{12}$$

where c'' is a constant. Comparison of species numbers at 12 and 45°N latitude using the combined temperature and area gradient effects indicates a decrease in number of species per unit area by a factor of 2.1 from 12 to 45°N latitude. This result agrees with species diversities at these latitudes [36].

The concept that temperature dependence of cellular energy production by respiration contributes to the gradient of species diversity thus predicts the correct direction and allows an a priori estimation of the magnitude of the temperature-linked portion of the gradient of species diversity with latitude and altitude. It should be noted that there is no clear test of this number available in the literature. All studies to date that have measured species numbers directly have examined limited areas, where local climatic and geographical factors are important determinants of range and species numbers. Further, because, on a global basis, ΔT is a non-linear function of latitude/altitude, the apparent value of the exponent, z, in species area curves will not be constant, but will increase with increasing latitude and altitude. This probably accounts for much of the observed variation between studies in values of z.

5. Adaptation of metabolism to environmental temperature to maximize growth

So far, this discussion has focused largely on the temperature limits illustrated in Fig. 1, i.e. the genetically determined biochemical limits that establish the high and low temperature limits within which a plant can grow. Respiratory efficiency as defined in Eq. (3) goes to zero at these limits [23,24]. Plant metabolism appears to adapt to these limits through natural selection for cytochrome and alternative oxidase enzymes that have the proper temperature response, i.e. activation energy [29]. Because altering the activation energy does not require changes at the active site of enzymes, significant variation in amino acid sequence of these proteins between plants adapted to different temperature regimes is thus expected. Furthermore, in all plants where it has been studied, there are two or more alternative oxidase isozymes [37]. Differential expression of these isozymes probably, has a role in maximizing plant growth in a given thermal environment.

Maximizing growth in a given environment during a particular part of the season is a competitive strategy of many species. With respect to temperature, this strategy can be expressed as a ''minimal cost hypothesis''—adaptation of metabolism to environmental temperature maximizes vegetative growth rate and minimizes the entropy change in the surroundings per mass of vegetation produced. Expressing the specific growth rate as:

$$R_{SG} = f(T) \tag{11}$$

and the environmental temperature as:

$$T_{env} = g(t) \tag{12}$$

where $f(T)$ is a function of temperature and $g(t)$ describes the environmental temperature as a function of time, leads to:

$$R_{SG} = f[g(t)] \tag{13}$$

Total growth is then equal to the time integral of Eq. (13), i.e.

$$\text{Total growth} = \int f[g(t)]\mathrm{d}t \tag{14}$$

The rate of entropy increase, in the surroundings is given by:

$$\frac{\mathrm{d}S_{surr}}{\mathrm{d}t} = \frac{R_q}{T} = h(T,t) \tag{15}$$

where R_q is the metabolic heat rate and $h(T, t)$ is a function of temperature and time. Therefore, minimizing the ratio:

$$\frac{h(T,t)}{f[g(t)]} \tag{16}$$

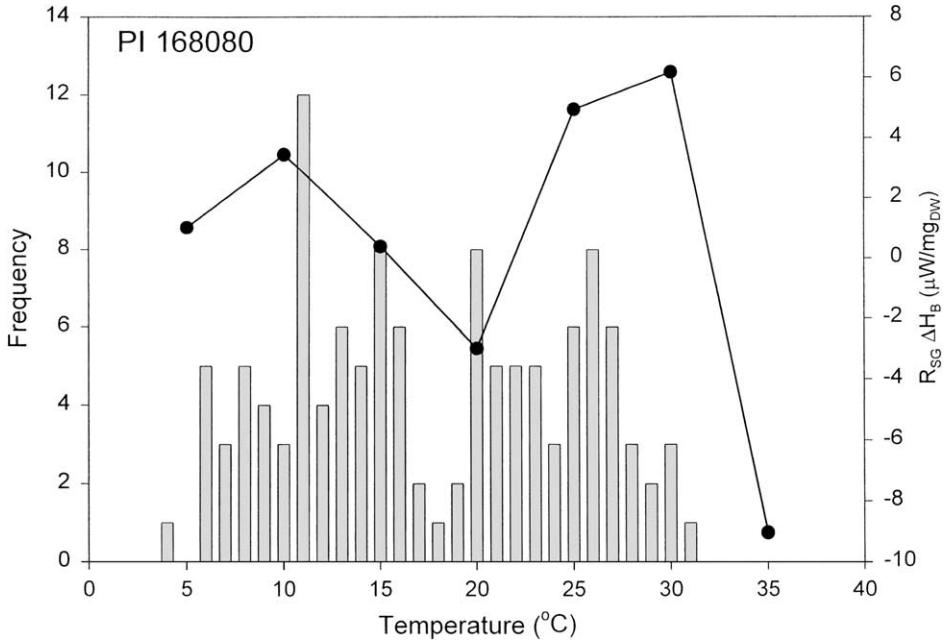

Fig. 5. Growth rate in terms of enthalpy (i.e. ΔH_B R_{SG}, (●)) for an accession of oats from Izmir, Turkey and temperature frequency (bar) at Izmir during the growth season plotted against temperature. Temperature frequency is given as relative number of hours at each temperature in one degree increments.

maximizes the ratio of total growth to ΔS_{surr}. Matching $f(T)$ to the distribution of environmental temperatures (e.g. number of hours at T_{env} versus T_{env}) minimizes the ratio in 16. We have observed such a concordance of measured growth rates and environmental temperature in a series of five oat (*Avena sativa*) accessions collected from different altitudes in Turkey [38]. An example of the data for one accession is shown in Fig. 5. In various cultivars, varieties, and accessions of other species, i.e. *Bromus tectorum* [39] and *Zea mays* [40], the temperature functions of $R_{SG}\,\Delta H_B$ have features that suggest the minimal cost hypothesis may be widely applicable, but much more work remains to be done to prove the general validity of this hypothesis.

6. Conclusion

Simultaneous measurements of metabolic heat and CO_2 production rates for plant respiration, and derivation of rate laws incorporating thermodynamic modeling of the catabolic and anabolic reactions of plant respiration have led to new insights into plant biochemistry and ecophysiology. These insights may make possible better predictions of plant responses to climate change. A further challenge is to relate respiratory efficiency for production of structural biomass to specific biochemical processes and to determine the effects of environmental variables on these processes. It may then be possible to relate differences in genes to metabolic adaptations to environmental variables.

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