Determination of Plant Growth Rate and Growth Temperature Range From Measurement of Physiological Parameters

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Abstract—Many factors influence species range and diversity, but temperature and temperature variability are always major global determinants, irrespective of local constraints. On a global scale, the ranges of many taxa have been observed to increase and their diversity decrease with increasing latitude. On a local scale, gradients in species distribution are observable with increasing altitude. These gradients in species distribution have not previously been linked to physiology. In this communication, the gradients are proposed to be a consequence of the physical laws governing energy transduction, acting through natural selection in response to environmental temperature variability. Measurements of rates of energy production and its use in anabolic metabolism as a function of temperature show that respiratory rates and efficiency of green plants are closely adapted to diurnal temperature changes and mean temperatures of the native environment. Optimization of energy production and use by respiratory metabolism along global gradients in temperature and temperature variability is a genome x environment interaction, thus is a fundamental cause of the latitudinal/altitudinal gradients of species range and diversity.

Introduction

Gradients of species range and diversity with altitude and latitude are observed in some taxa of both endotherms and ectotherms (in other words, organisms, including plants, in which cellular temperature is determined by environmental temperature). In those taxa that exhibit an increase in species range and decrease in diversity with increasing latitude and altitude, an as yet unidentified fundamental mechanism linking geographical distribution, climate and physiology may exist (Gaston 1999; Pianka 1996). This paper develops a hypothesis that the physical laws governing energy transduction acting through natural selection in response to environmental variability, and on a global scale, specifically temperature variability is such a mechanism. Application of the laws of equilibrium and non-equilibrium thermodynamics and kinetics to the temperature dependence of respiratory metabolism in ectotherms leads to a prediction of range and diversity gradients in reasonable agreement with observations, and thus is proposed as a fundamental cause of these gradients. We show that under certain conditions species range is proportional to, and diversity is inversely related to, the magnitude of diurnal or short-term temperature changes.

Previous explanations or descriptions of species distributions have been based on observations that equatorial-lowland climates are more constant than climates at higher latitudes and altitudes (Dobzhanski 1950; Klopfer 1959; Fisher 1960; Saunders 1968; Rapoport 1975; Brown 1984; Stevens 1989; Hallam 1994; Hanski and Gyllenberg 1997) or on relations among species number, land area and niche size (Wilson 1943; Preston 1948; MacArthur and Wilson 1967; Stehli and others 1969; Levinton 1982; McIntosh 1985; Rosenzweig 1995). Differences in mutation rates in temperate versus tropical zones, faster selection due to increased physiological rates at higher temperatures, nonsaturation of habitats, non-equilibrium conditions, and temporal and latitudinal gradients of light intensity have been postulated to contribute to species diversity (Connell 1978; Hubbel 1979; Huston 1979; Rohde 1992, 1997). Water, soil conditions, day length, symbiotic mechanisms, and so forth, are all important determinants of the existence of a species at any site, but local-scale environmental properties cannot explain the global-scale patterns of species range and diversity. Temperature is the only global-scale abiotic factor that could determine the global-scale distributions observed for ectotherms.

Our hypothesis may be summarized as follows. Survival and reproduction of an individual requires the ability to acquire and use energy and nutrients within a given environment (Harshman and others 1999). Because this ability varies with temperature and temperature variability, a boundary will exist somewhere along the global-scale temperature gradient, and inversely correlated global scale of short-term temperature variability, beyond which an organism is unable to exist and another organism adapted to the prevailing range of temperature conditions will occupy the succeeding temperature niche. Theoretical considerations and experimental measurements show that metabolic rates are adapted to mean environmental temperature while energy use efficiency is adapted to temperature variability. Optimizing energy use (rate multiplied by efficiency) while maximizing probability of survival of extreme temperature

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events thus requires that the temperature responses of energy metabolism be matched to both the mean temperature and the short-term or diurnal range of environmental temperature (Preston 1948). Ectotherm distribution emerges from the requirement for maintaining near constant intracellular ATP concentration and energy charge (phosphorylation potential, Wrigglesworth 1997) as conditions change.

A fundamental assumption of the paradigm developed in this paper is that the temperature range of adaptation is inversely related to mean growth rate defined as the rate of accumulation of energy in structural biomass. Thus, for organisms in which growth rate is important for survival or competitiveness, optimal adaptation requires adaptation to no broader range of temperatures than necessary, although this presents major risks to survival of the individual (Stiling 1999). The growth rate compromise between opposing needs to tolerate temperature extremes and to maximize energy use efficiency so as to compete for available resources is reflected in the rates and efficiency of ATP generation and use within a temperature regimen. The short-term (hours to days) variability of temperature and the absolute temperatures during the growth season thus determine the optimum energy strategy for many ectotherms. However, local and historical conditions (Rohde 1997) may override full expression of ecological consequences. Thus, for example, other reasons must be sought for the low diversity observed in some relatively constant temperature environments (for example, high latitude aquatic species) and in environments where scarcity of a necessary resource (for example, water) may play a more important role.

Because of the availability of plant experimental data and to avoid the complications introduced by animal behavior (for example, mobility), this paper is focused on plants. However, the principles apply directly to growth and distribution of all aerobic, ectothermic organisms and to homeotherms to the extent that their distributions are determined by the distribution of ectothermic symbionts, hosts, and food sources. The paper discusses first the response of energy metabolism to temperature, second, the respiratory variables that must be measured to characterize the metabolic response to temperature and temperature variability of an individual plant or species and the relationship of respiration to growth, third, the effect of temperature on growth rates as derived from measurements of temperature effects on respiration, and last, the predictions of the effects of temperature and temperature variability on species ranges and diversity.

Cellular Energy Metabolism Response to Temperature

Figure 1 shows the reactions of respiratory metabolism. A fraction of substrate carbon is catabolized via oxidative pathways to form CO_2 and the energy thus obtained is used to synthesize ATP. Some ATP and the remainder of the substrate carbon are used for formation and maintenance of structural biomass. The phosphatase catalyzed reaction(s), the ADP disproportionation reaction(s), and alternative oxidase (or uncoupling proteins, Laloi and others 1997) pathway(s) shown in figure 1 are commonly not

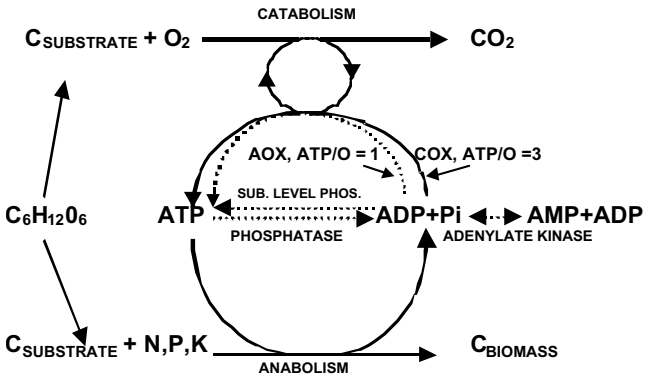

Figure 1—Coupled metabolic energy reactions in biomass production.

included in diagrams of respiratory energy metabolism as they are viewed as "futile" or wasteful reactions, not integral parts of properly functioning energy metabolism (Stryer 1988). However, the phosphatases and alternative oxidases must be included in proper representations of respiratory metabolism as they are absolutely necessary for controlling [ATP] and phosphorylation potential, particularly during changes in temperature or other reaction conditions. ADP disproportionation by adenylate kinase-type reactions with equilibrium constants near 1.0 is also necessary to buffer ATP concentration and maintain the proper [ATP]/[ADP] ratio (Stucki 1989). The requirement that the phosphorylation potential (in other words, the ratio [ATP]/[ADP] [Pi]), which is directly related to the free energy change for hydrolysis of ATP), must remain in a narrow range has been discussed extensively by Atkinson (1977), largely in terms of the energy charge.

Thus, equation 1 must obtain where n is the number of moles of ATP and t is time.

$$(dn/dt)_{synthesis} = (dn/dt)_{loss} \text{ and } (dn/dt)_{synthesis}/(dn/dt)_{loss} = 1 \quad (1)$$

The static representations in figure 1 do not clearly convey the message that relative rates of parallel pathways of the ATP cycle, and therefore overall reaction stoichiometries between energy production and use, change continuously with reaction conditions (Stucki 1989; Gnaiger and Kemp 1990; Kemp and Guan 1997). The principles of energy coupling in biological systems elucidated by Stucki's (1989) studies of ATP metabolism in mammalian mitochondria at isothermal conditions also apply to intact ectotherms with variable temperature. Thus, the energy use efficiency of any coupled pair of reactions is defined by the ratio of Gibbs free energies $(-\Delta G_{driving\ reaction})/(\Delta G_{driven\ reaction})$ (Stucki 1989; Gnaiger and Kemp 1990; Kemp and Guan 1997). The efficiency is 100 percent when this ratio = 1, but the overall rate is zero because the system is at equilibrium. The greater the ratio above 1, the faster the rate, but the lower the efficiency because the excess energy from the driving reaction is lost from the system. Thus, there is an optimum value of the ratio at which the system can operate at the rate required to accomplish growth and reproduction within the time constraints of the environment while maximizing the efficiency to the range of environmental conditions.

Cellular growth rates can be expressed in terms of the relative rates of ATP synthesis and its anabolic use (Kemp 1996), equation 2.

$$(dn/dt)_{synthesis} = (dn_G/dt) + (dn_F/dt) \quad (2)$$

(dn_G/dt) is the rate of synthesis of that portion of ATP used for biosynthesis reactions including maintenance, and (dn_F/dt) is the rate of synthesis of the portion of ATP used in futile reactions. The rates (dn_G/dt), (dn_F/dt), and $(dn/dt)_{synthesis}$ vary with temperature, including variability in the coupling of oxidative phosphorylation, in the coupling of ATP hydrolysis to energy requiring reactions, and in the ATP buffering reactions. Thus, the fraction of ATP used for biosynthesis varies with temperature. The second law of thermodynamics defines the upper limit of the efficiency of ATP use by requiring that $(dn_F/dt) > 0$. At the low limit of efficiency, ATP use in biosynthesis goes to zero, in other words, $(dn_F/dt) = (dn/dt)_{synthesis}$.

The driving force for evolutionary adaptation of energy metabolism in ectothermic organisms is optimization of the efficiency of ATP for biosynthesis within the limits of a niche defined by the environmental variables. This suggests that fitness for a thermal niche may be quantified by measurements of rates of ATP reactions as a function of temperature.

Respiratory CO_2 and Heat Production Are Measures of ATP Metabolism, Metabolic Efficiency, and Growth Rate

$(dn/dt)_{synthesis}$ and (dn_F/dt) and the temperature dependencies of these rates can be estimated from measurements of respiratory heat and CO_2 production rates. The rate of release of Gibbs energy (dG) in the coupled processes of catabolism and anabolism at constant pressure is described by

$$dG = dw + dQ - TdS \quad (3)$$

where dw, the pdV work, is negligibly small. Under steady-state conditions, dG is proportional to $(dn/dt)_{synthesis}$, which in aerobic cells is proportional to CO_2 production rates (Kemp 1996). dQ, the rate of heat dissipation, is a measure of dn_F/dt. Thus, equation 3 shows that TdS closely approximates the rate of energy accumulated in structural biomass (in other words, growth rate). Since TdS = (dG – dQ) therefore

$$\text{Growth rate} = k(dn_G/dt) = k\,[(dn/dt)_{synthesis} - (dn_F/dt)] \quad (4)$$

where k is a proportionality constant. Equation 5, previously developed by Hansen and others (1994) is equivalent to equation 4.

$$R_{SG}\Delta H_B = -[R_{CO2}\,(1-\gamma_p/4)\,\Delta H_{O2}] - q \quad (5)$$

R_{SG} is the specific growth rate (mol C s^{-1} g^{-1}) and ΔH_B is the enthalpy change for the reaction $C_{substrate} \rightarrow C_{biomass}$ (kJ mol C^{-1}). Therefore, $R_{SG}\Delta H_B$ is specific growth rate expressed as the rate of storage of chemical energy in structural biomass with units of kJ $s^{-1}g^{-1}$. R_{CO2} is the specific CO_2 production rate (mol $s^{-1}g^{-1}$), ΔH_{O2} is approximately constant with a value of –455 kJ mol^{-1} (Erickson 1987; Hansen and others 1997), γ_p is the mean chemical oxidation state of the substrate carbon, and q is the specific metabolic heat production rate (kJ s^{-1} g^{-1}).

Because ΔH_B is normally positive, it follows that q/R_{CO2} is a measure of efficiency, in other words,

$$q/R_{CO2} = K[(dn_F/dt) / (dn/dt)_{synthesis}] = K(1-\varepsilon_{ATP}) \quad (6)$$

where K is a ratio of proportionality constants relating q to (dn_F/dt) and R_{CO2} to $(dn/dt)_{synthesis}$ and ε_{ATP} is efficiency of ATP use.

Experimental measurements on many plants (and insects, fish eggs, yeast, and so forth) show that the temperature dependence of q and the temperature dependence of R_{CO2}, and therefore the temperature dependencies of (dn_F/dt) and $(dn/dt)_{synthesis}$, differ within individuals, among individuals, within a species, and among species (Criddle and others 1994, 1996a, 1997; Anekonda and others 1996). Consequently, $(dn_F/dt)/(dn/dt)_{synthesis}$, and q/R_{CO2}, are functions of temperature.

Energy use efficiency can be extremely sensitive to small differences in temperature, emphasizing the importance of temperature in determining which organisms can survive, compete, and reproduce in a particular niche. The efficiency of ATP use, ε_{ATP}, is not directly measurable, but is related to the substrate carbon conversion efficiency, ε, which is also related to q/R_{CO2} (Hansen and others 1994).

Temperature Dependence of Growth Rates and Temperatures Allowing Growth

The temperatures at which experimentally determined temperature functions of q and $(1-\gamma_p/4)455R_{CO2}$ cross define the limits to the growth temperature range (equation 5). As examples, figure 2 shows plots of q and $455R_{CO2}$ and $R_{SG}\Delta H_B$ versus temperature for cultivars of tomato, as a representative warm climate plant, and cabbage, as a representative cool adapted species (Criddle and others 1997). The curves for q are approximately Arrhenius functions over the temperature range allowing growth. R_{CO2} increases exponentially only up to about 20 °C (tomato) and 16 °C (cabbage). At higher temperatures R_{CO2} decreases. Tomato has a larger temperature dependence for $455R_{CO2}$ than for q over much of the growth temperature range. The difference between $455R_{CO2}$ and q [and therefore between $(dn/dt)_{synthesis}$ and (dn_F/dt)] is positive only in the temperature range above 13–14 °C and below about 37 °C. For cabbage, the temperature dependencies of q and R_{CO2} are more similar, and $455R_{CO2} \geq q$ (in other words, $R_{SG}\Delta H_B$ is positive) only at temperatures below about 20 °C. Figure 2C shows that temperature ranges with positive values of $R_{SG}\Delta H_B$ correspond to the growth temperature ranges for these two cultivars.

Because the temperature dependence of q is typically greater than the temperature dependence of R_{CO2} in cold adapted plants (Criddle and others 1996a,b, 1997; Anekonda and others 1996; Hansen and others 1997; Earnshaw 1981) efficiency of cabbage growth decreases as temperature increases and a temperature is reached where $q > 455R_{CO2}$, in other words, the temperature at which the rate of energy production is exceeded by demands for ATP use is at the

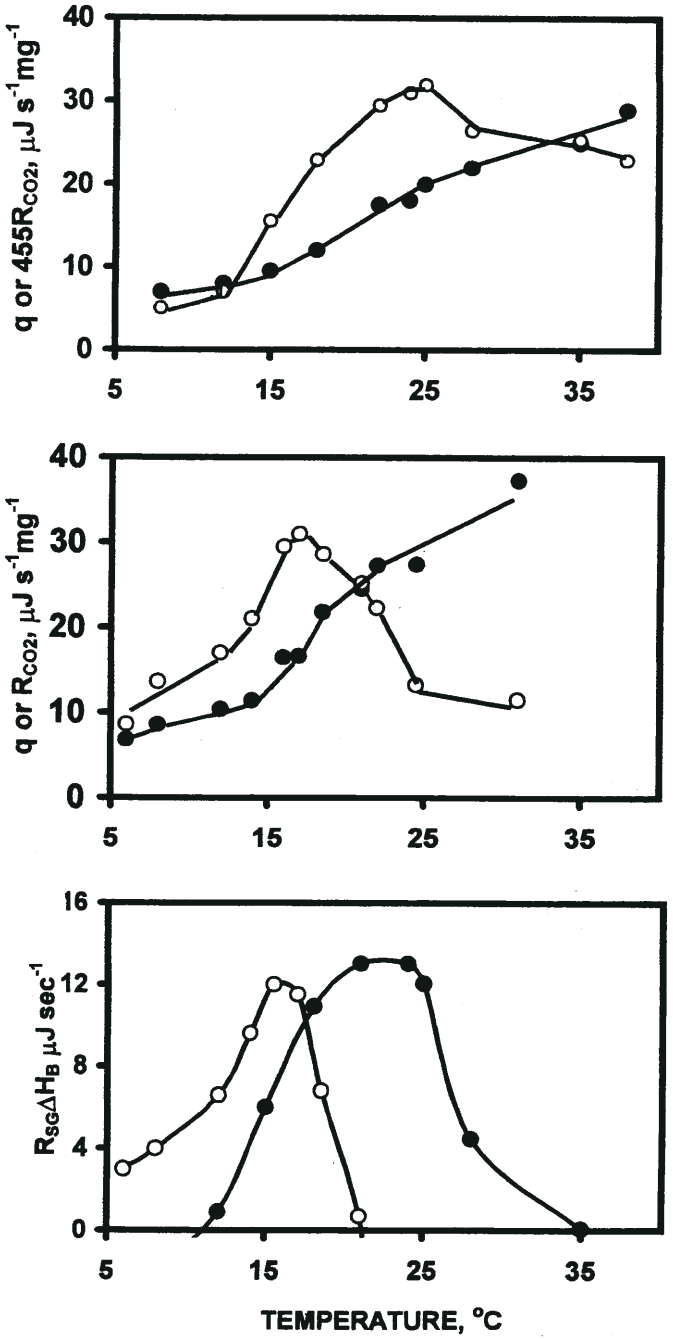

Figure 2—The temperature dependence of respiratory metabolism and growth rates of tomato and cabbage. Field observations show that the cabbage cultivar grows at low temperature, but growth ceases when the temperature is above about 20 °C. The tomato cultivar does not grow at temperatures below about 12 °C or above 35 °C. (A) Responses of $455R_{CO2}$ (open symbols) and q (solid symbols) values of tomato to changes in temperature. (B) Responses of the rate of CO_2 production (as $455R_{CO2}$) and heat rate (q) values of cabbage to changes in temperature. (C) Calculated values of the rates of deposition of respiratory energy in structural biomass ($R_{SG}\Delta H_B$) for tomato (solid symbols) and cabbage (open symbols) across their growth temperature ranges.

high temperature limits for these plants. At this temperature, the ATP/ADP ratio (and the phosphorylation potential) becomes too low to drive biosynthesis, and growth stops. At low temperature, growth rates of cold adapted plants will slow in spite of high efficiency because of the effect of temperature on metabolic rate.

In warm climate plants such as tomato where the temperature dependence of q ≤ the temperature dependence of R_{CO2}, efficiency decreases as temperature falls and the lower temperature limit to growth occurs at the temperature at which $[(1-\gamma_p/4)\ 455R_{CO2} - q]$ becomes zero (Criddle and others 1997). The high temperature decrease of tomato growth rate shown in figure 2C results from a rapid decrease in R_{CO2} that is not predicted by Arrhenius extrapolation of data collected at lower temperatures. Because the temperature coefficient of R_{CO2} is greater than that for q, the rate of ATP synthesis increases faster with increasing temperature than the rate of ATP loss, in other words, $d(dn/dt)_{synthesis}/dT$ becomes much greater than $d(dn_F/dt)dT$, and with increasing temperature, (dn_G/dt) approaches $(dn/dt)_{synthesis}$. Efficiency and metabolic rate both increase and growth rate increases. But, this can only continue to a maximum $(dn/dt)_{synthesis}/(dn_F/dt)$ (or $455R_{CO2}/q$) of about 1.4 (corresponding to an ε_{ATP} of about 0.75). Because a large ratio of [ATP]/[ADP] is incompatible with optimal economic growth (Stucki 1989; von Stockar and Marison 1993; Nath 1998; Ksenzhek and Volkov 1998) as the maximum value if this ratio is approached, the capacity of the ATP buffering enzyme systems is exceeded (Stucki 1989; Hoh and Cord-Ruwisch 1997), the ATP/ADP ratio becomes so large that the positive ΔG for ATP synthesis exceeds the negative ΔG from the oxidation reactions, ATP synthesis and correspondingly R_{CO2} is greatly reduced (as shown experimentally in fig. 2), energy use efficiency decreases to near zero, and growth stops.

The mean temperature and diurnal and short-term growth seasonal range of temperatures allowing growth, and therefore plant distribution, are thus explicitly determined by the kinetic laws of temperature dependence of chemical reactions and the thermodynamic laws governing energy coupled processes in changing environments. The functioning of these laws in plants is evident from measurements of q and R_{CO2} and their change with temperature in many species (Hansen and others 1994; Criddle and others 1994, 1996a,b, 1997; Anekonda and others 1996; Hansen and others 1997). If we assume an Arrhenius temperature dependence of q and R_{CO2}, the allowable growth temperature range (ΔT) can be calculated for various combinations of the temperature dependencies of q and R_{CO2}, as shown in figure 3. The temperature range over which $455R_{CO2}/q$ changes from 1 (zero efficiency) to 1.4 (maximum efficiency) is defined as ΔT. ΔT is plotted against the Arrhenius temperature coefficient for R_{CO2} (μ_{CO2}) for various fixed values of the temperature coefficient of q (μ_q). The region with μ_{CO2} from approximately 3 to 11 kK and ΔT from 5 to 37 °C includes essentially the entire physiological and environmental range. A similar set of curves could be drawn for $\mu_q > \mu_{CO2}$.

Figure 3 shows how the temperature dependencies of q and R_{CO2} (in other words, of (dn_F/dt) and $(dn/dT)_{synthesis}$,

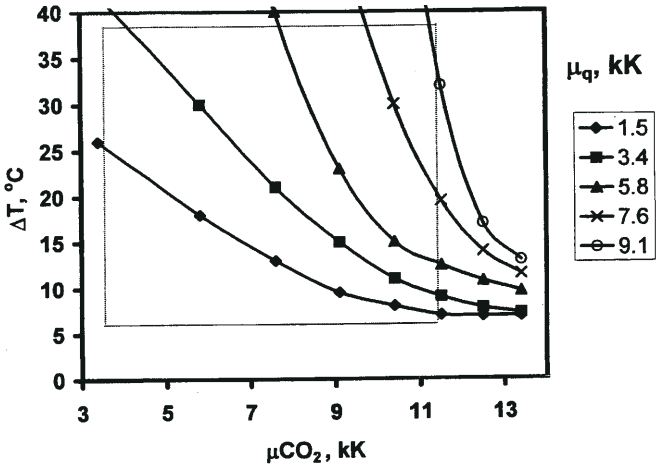

Figure 3—Dependence of the range of temperatures allowing growth (ΔT) on values of the Arrhenius temperature dependence of q and R_{CO2} (μ_q and μ_{CO2}). (A) Each curve represents ΔT dependence on μ_{CO2} at a different, constant μ_q. The μ_q values plotted are μ_q = 1.2 (open circles), μ_q = 1.5 (filled squares), μ_q = 2.0 (filled triangles), and μ_q = 2.5 (filled diamonds). The box insert includes the total range of experimentally observed combinations of μ_q and μ_{CO2}.

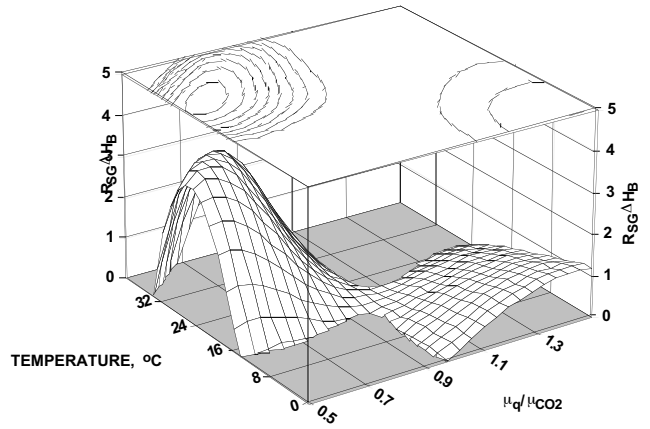

Figure 4—Growth rates for maize as a function of temperature and the ratio μ_{CO2}/μ_q calculated from data on maize cultivars.

respectively) determine fitness for a particular climate. If $\Delta T_{climate} > \Delta T (\mu_{CO2} - \mu_q)$ of the plant, the plant will not thrive if it spends too much time at the extreme temperatures where efficiency is zero. If $\Delta T_{climate} < \Delta T (\mu_{CO2} - \mu_q)$ of the plant, the plant will be less competitive than plants with $\Delta T(\mu_{CO2} - \mu_q)$ closer to $\Delta T_{climate}$. The minimum ΔT of about 5 °C is obtained only at large values of $(\mu_{CO2} - \mu_q)$. The maximum and minimum values of $(\mu_{CO2} - \mu_q)$ measured in our laboratories on ectotherms are about plus or minus 6 kK, (or a difference in Q_{10} values for R_{CO2} and q of about 2.0). When the absolute value of $(\mu_{CO2} - \mu q)$ is less than about 0.8 kK, ΔT reaches 32 to 37 °C and growth is possible in extremely variable climates, but efficiency for converting photosynthate into structural biomass is very low.

Figure 4 shows a three-dimensional model of the relations among growth rate (as $R_{SG}\Delta H_B$), the ratio of temperature coefficients μ_q/μ_{CO2} (varied from 1:2 to 2:1), and temperature from 0 to 40 °C, derived from experimental data on maize (Taylor and others 1998, and unpublished data). High growth rates are obtained when the ratio μ_q/μ_{CO2} is either very large or very small. When $\mu_q >> \mu_{CO2}$, the growth temperature range is small and growth rate maxima occur at low temperatures. When $\mu_q \approx \mu_{CO2}$, growth temperature range is large, but growth rate is small across the entire range. (In the limit where $\mu_q = \mu_{CO2}$, the temperature range is infinite, but growth rate is zero.) When $\mu_{CO2} >> \mu_q$, the growth temperature range is again small, but growth rate maxima occur at high temperature. Growth rate reaches a maximum where $455R_{CO2}/q = 1.4$ and rapidly declines with further increase in temperature. The higher the ratio μ_{CO2}/μ_q, the lower the temperature at which the optimum is obtained. The projected contour map at the top of figure 4 allows visualization of the decrease of growth rate at temperatures above optimum.

Figure 4 shows that the penalty associated with an organism being adapted to a wider temperature range than required is a decreased growth rate. Plants adapted to a wide temperature range are capable of survival in a climate with little temperature variation, but to the extent that growth rate determines competitiveness, a widely adapted plant (a temperature generalist) will be out-competed by a narrowly adapted plant (a temperature specialist). However, plants adapted to too narrow a temperature range cannot tolerate the wide temperature range because much of the time they would be subjected to temperatures that disallow control of ATP metabolism.

An experimental test of the predicted inverse relation between environmental temperature range ΔT and growth rate has been done with 17 half-sib families of 15-year-old *Pinus ponderosa* planted at three or four sites with different latitudes and elevations (Church 2000). Plots of ΔT, the mean diurnal temperature variation during the growth season at each site versus height growth, show a linear decrease in height with increasing ΔT. Linear regression analysis of data for the 17 families gave an average regression coefficient (r^2) of 0.96 with a range from 0.88 to 0.99. Growth rate of these trees is not correlated with any other environmental variables except those co-correlated with ΔT.

A perfect adaptation of plants to temperature is not possible because climates vary from year to year. Thus, while individual plants are genetically limited in their response to temperature, a species evolves many genotypes with a range of responses. In addition, plants may alter their effective environmental growth temperatures simply by altering the time during the season when growth occurs. There is thus no "best" solution for adaptation of energy metabolism and growth rate to a location. Rather, plants with a range of properties exist both within and between species. However, the allowable ranges of energy metabolism and growth rate responses to temperature must change systematically with diurnal temperature range. Because of the covariance between diurnal temperature range ΔT and latitude/altitude, the relations among temperature, energy

use efficiency, and growth rate are a fundamental mechanism that may explain the observed latitudinal and altitudinal gradients of species range and diversity.

The relation between climate and respiration has been further tested with three *Eucalyptus* species from different native climates with approximately the same mean temperature, 16.4 °C, but different temperature variation ΔT. Plots of $R_{SG}\Delta H_B$ versus temperature for individual trees of each species, grown in, and therefore acclimated to, a common environment, are presented in figure 5. Differences between species are much larger than intra-species variation and the patterns shown are representative of the species. Because these species grow throughout the year, annual temperature data describe the growth temperature range. The native environmental temperature ranges are similar to, and give the same ranking of ΔT as the temperature range of positive values of $R_{SG}\Delta H_B$, which were calculated from measured q and R_{CO2} values (equation 5 with γ = 0). Acclimation of the trees to climate in the common growth environment is negligible because the temperature ranges allowing growth (positive $R_{SG}\Delta H_B$) are the same as the climatic temperature ranges at the different growth sites.

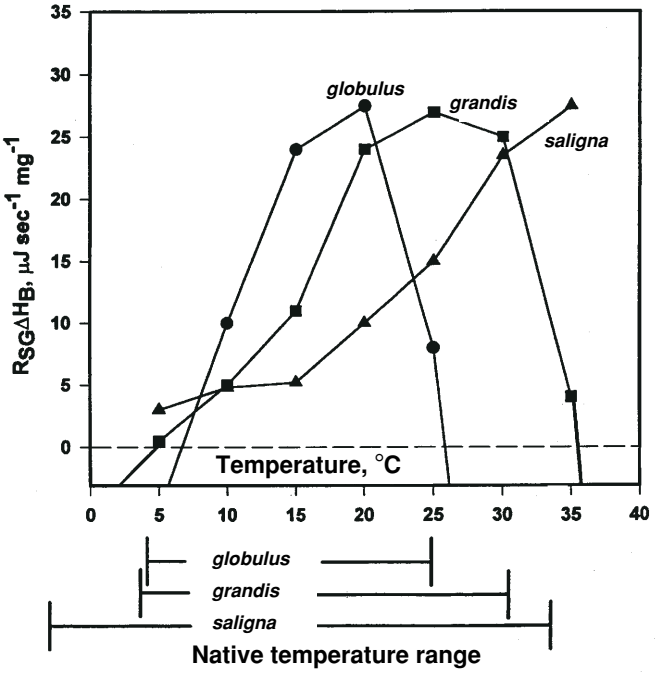

Figure 5—Growth rates of plants from three *Eucalyptus* species calculated as a function of temperature from q and R_{CO2} measurements and comparison with temperature ranges at the native growth sites of *E. Saligna* (Smith), *E. grandis* (W. Hill ex Maiden), and *E. globulus* (Labill. subsp. maidenii {F. Muell} Kirkpatr., commonly known as *E. Maidenii*) (Boland and others 1984). The trees tested were seedlings grown hydroponically in a common, controlled environment chamber. Measurements of q and R_{CO2} were made at several temperatures on small, expanding leaf tissues, followed by calculation of growth rates, $R_{SG}\Delta H_B$, by equation 8 with γ = 0 (Hansen and others1994). Lines at the lower portion of the figure connect the mean high temperature of the warmest month and the mean low of the coldest month at each site.

Predicted Magnitudes of Gradients of Species Range and Diversity

The principles developed above predict that range or niche size for growth of individual populations and species must increase with the magnitude of temperature fluctuations (ΔT) (equation 8)

$$A_T / N_T = c\ (\Delta T) \qquad (8)$$

where A_T is total area, N_T is total number of species, and A_T/N_T is the average species area. c is a proportionality coefficient. ΔT is related to latitude and altitude, in other words, ΔT = c' f(latitude, altitude). Through mid-range temperate latitudes and altitudes, the relation between ΔT and latitude or altitude is approximately linear so that in this range, species area, latitude/altitude, and ΔT are nearly linearly related.

Consider the effects of this relation on species areas in the northern hemisphere from 12° to 45° north latitude. The approximate mean temperature fluctuation (ΔT) at 45° latitude is about 3 times that at 12° latitude. Thus, the niche size increases (and number of thermal niches decreases) about threefold from 12 to 45°. However, if areas at the two latitudes are not constant, then the effect of area on species numbers also enters in.

An exponential relation exists between species number (N) and area (A), in other words, $N = kA^z$. z values from 0.1 to 0.6 have been reported (Rosenzweig 1998). For example, Hanski and Gyllenberg (1997) showed (for moth species) that plots of ln N versus ln A (of islands in an archipelago) yielded a line with slope, (or z value) near 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° north latitude. The species area relation predicts N should be $(1.5)^{0.4} = 1.2$ fold higher at 45°, a trend in species diversity opposite that observed. However, combination of the species area relation with equation 8 and the effects of latitude on species range yields equation 9,

$$N^{[(1/z)-1)} = c''\ \Delta T \qquad (9)$$

where c" is again a constant. Comparison of species numbers at 12 °C and 45 °C north latitude using the combined temperature and area gradient effects indicates a decrease in number of species per unit area by a factor of 2.08. Species diversity should thus decrease about twofold from 12° to 45° north latitude, which agrees reasonably well with relative values noted for species diversities at these latitudes (Rohde 1997).

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 examined limited areas where local climatic and geographical factors play important determinant roles in range and species numbers. Because ΔT is a 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 (Rosenzweig 1998).

Because optimization of metabolic properties with temperature within species must follow the same rules as for species, gradients of responses to temperature must exist within species. This intra-species variability helps ensure species survival during climate changes or influxes of competitors and provides the opportunity for farmers and plant scientists to select the best genotypes for optimal growth at a given site. These principles provide a unifying rationale for improving production by matching cultivars to environment. This paper has focused on plants, but the principles are applicable to ectothermic animals. Also, questions of ectotherm responses to climate change can be framed in more quantitative terms with an understanding of the underlying causes.

Summary

We conclude that the temperature responses of cellular energy metabolism are a fundamental determinant of latitudinal/altitudinal gradients of species range and diversity. To maximize the probability of growth, reproduction, and survival, organisms have been selected to optimize their ability to obtain and use energy throughout the range of ambient temperatures. Matching energy metabolism to climatic temperature is accomplished by variable engagement of "futile" reactions that are necessary to maintain efficient energy coupling with changing temperatures. Ectotherms growing in climates with a narrow temperature range can evolve high energy use efficiencies and enhance their ability to compete for resources, but in doing so they risk being damaged or killed by temperature excursions outside the normal range. Ectotherm adaptation to broad temperature ranges enhances survival during extreme temperature excursions, but at the cost of lower growth rates. Energy efficiency and survival requirements lead to species variability along latitudinal and elevational gradients of temperature range and diversity.

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References

Anekonda T. S.; Hansen, L. D.; Bacca, M.; Criddle, R. S. 1996. Selection for biomass production based on respiration parameters in eucalypts: effects of origin and growth climates on growth rate. Canadian Journal of Forest Research. 26: 1556–1568.

Atkinson, D. E. 1977. Cellular energy metabolism and its regulation in metabolism. New York: J. Wiley and Sons.

Boland, D. J.; Brooker, M. I. H.; Chippendale, G. M.; Hall, N.; Hyland, B. P. M.; Johnson, R. D.; Kleining, D. A.; Turner, J. D. 1984. Forest trees of Australia. Nelson, CSIRO Melbourne.

Brown, J. H. 1984. On the relation between abundance and distribution of species. American Naturalist. 124: 255–279.

Church, J. N. 2000. Tests of the ability of a respiration based model to predict growth rates and adaptation to specific temperature conditions: studies on Pinus ponderosa, Eucalyptus species and Sequoia species. Davis, CA: University of California. Thesis.

Connell, J. H. 1978. Diversity in tropical forests and coral reefs. Science. 199: 1302–1310.

Criddle, R. S.; Hopkins, M.; McArthur, E. D.; Hansen, L. D. 1994. Plant distribution and the temperature coefficient of metabolism. Plant, Cell and Environment. 17: 233–243.

Criddle, R. S.; Anekonda, T. S.; Hansen, L. D. 1996a. Selection for biomass production based on respiration parameters in eucalypts: acclimation of growth and respiration to changing growth conditions. Canadian Journal of Forest Research. 26: 1569–1575.

Criddle, R. S.; Breidenbach, R. W.; Fontana, A. J.; Henry, J-M.; Smith, B. N.; Hansen, L. D. 1996b. Plant respiration responses to climate determine geographic distribution. Russian Journal of Plant Physiology. 22: 913–936.

Criddle, R. S.; Smith, B. N.; Hansen, L. D. 1997. A respiration based description of plant growth rate responses to temperature. Planta. 201: 441–445.

Dobzhanski, T. 1950. Evolution in the tropics. American Scientist. 38: 209–221.

Earnshaw, M. J. 1981. Arrhenius plots of root respiration in some arctic plants. Arctic and Alpine Research. 13: 425–430.

Erickson, L. E. 1987. Energy requirements in biological systems. In: James, A. M., ed. Thermal and energetic studies of cellular biological systems. Wright, Bristol: 14–33.

Fisher, A. G. 1960. Latitudinal variation in organic diversity. Evolution. 14: 64-81.

Gaston, K. J. 1999. Why Rapaport's Rule does not generalize. Oikos. 84: 309–312.

Gnaiger, E.; Kemp, R. B. 1990. Anaerobic metabolism in aerobic mammalian cells—Information from the ratio of calorimetric heat flux and respirometric oxygen flux. Biochimica et Biophysica Acta. 106: 328–332.

Hallam, A. 1994. An outline of phanerozoic biogeography. New York: Oxford University Press.

Hansen, L. D.; Hopkin, M. S.; Rank, D. R.; Anekonda, R. S.; Breidenbach, R. W.; Criddle, R. S. 1994. The relation between plant growth and respiration: a thermodynamic model. Planta. 185: 756–782.

Hansen, L. D.; Hopkin, M. S.; Criddle, R. S. 1997. A window to plant physiology and ecology. Thermochimica Acta. 300: 183–197.

Hanski, I.; Gyllenberg, M. 1997. Uniting two general patterns in the distribution of species. Science. 275: 397–400.

Harshman, L. G.; Hoffman A. A.; Clark A. G. 1999. Selection for starvation resistance in *Drosphila melanagaster*: physiological correlates, enzyme activities and multiple stress responses. Journal of Evolutionary Biology. 12: 370–379.

Hoh, C-Y.; Cord-Ruwisch, R. 1997. Experimental evidence for the need of thermodynamic considerations in modeling of anaerobic environmental bioprocesses. Water Science and Technology. 36: 109–115.

Hubbel, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical forest. Science. 203: 1299–1309.

Huston, M. 1979. A general hypothesis of species diversity. American Naturalist. 113: 81–101.

Kemp, R. B. 1996. Heat dissipation and metabolism in isolated mammalian cells. In: Principles of medical biology, volume 4, cell chemistry and physiology: part III. London: JAI Press: 303–329.

Kemp, R. B.; Guan, Y. 1997. Heat flux and the calorimetric-respirometric ratio as measures of catabolic flux in mammalian cells. Thermochimica Acta. 300: 199–211.

Klopfer, P. H. 1959. Environmental determinants of faunal diversity. American Naturalist. 94: 337–342.

Ksenzhek, O. F.; Volkov, A. G. 1998. Plant energetics. New York: Academic Press. 128–131.

Laloi, M.; Klein, M.; Reismeier, J. W.; Muller-Rober, B.; Fleury, C.; Bouillaud, F.; Ricquier, D. 1997. A plant cold-induced protein. Nature. 389: 135–136.

Levinton, J. S. 1982. Marine ecology. Englewood Cliffs, NJ: Prentice-Hall.

MacArthur, R. H.; Wilson, E. O. 1967. The theory of island biogeography. Princeton, NJ: Princeton University Press.

McIntosh, R. P. 1985. The background of ecology. Cambridge: Cambridge University Press.
Nath, S. 1998. A thermodynamic principle for coupled bioenergetic processes of ATP synthesis. Pure and Applied Chemistry. 70: 639–644.
Pianka, E. R. 1996. Latitudinal gradients in species diversity: a review of concepts. American Naturalist. 100: 33–46.
Preston, W. 1948. The commonness and rarity of species. Ecology. 29: 254–283.
Rapoport, E. H. 1975. Areografia: estrategias geograficas de las especies. Mexico: Fondo de Cultura Economica.
Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos. 65: 514–527.
Rohde, K. 1997. The larger area of the tropics does not explain latitudinal gradients in species diversity. Oikos 79: 169–172.
Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge: Cambridge University Press.
Rosenzweig, M. L. 1998. Preston's ergodic conjecture: the accumulation of species in space and time. In: McKinney, M. L.; Drake, J. A., eds. Biodiversity dynamics, turnover of populations, taxa, and communities. New York: Columbia University Press: 311–348.
Saunders, H. L. 1968. Marine benthic diversity: a comparative study. American Naturalist. 102: 243–282.
Stehli, F. G.; Douglas, R. G.; Newell, N. D. 1969. Generation and maintenance of gradients in taxonomic diversity. Science. 164: 947–949.
Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. American Naturalist. 140: 893–911.
Stiling, P. 1999. Ecology, theories and applications. NJ: Prentice-Hall.
Stryer, L. 1988. Biochemistry. New York: W. H. Freeman and Co.
Stucki, J. W. 1989. Thermodynamic optimizing principles in mitochondrial energy conversions. In: Sies, H., ed. Metabolic compartmentation. New York: Academic Press: 39–69.
Taylor, D. K.; Rank, D. R.; Keiser, D. R.; Smith, B. N.; Criddle, R. S.; Hansen, L. D. 1998. Modeling temperature effects on growth respiration relations of maize. Plant, Cell and Environment. 21: 1143–1151.
von Stockar, U.; Marison, I. W. 1993. The definition of energetic growth efficiencies for aerobic and anaerobic microbial growth and their determination by calorimetry and other means. Thermochimica Acta. 229: 155–172.
Wilson, C. B. 1943. Area and number of species. Nature. 152: 264–267.
Wrigglesworth, J. 1997. Energy and life. London: Taylor and Francis Ltd.