

Modelling temperature effects on growth–respiration relations of maize

D. K. TAYLOR¹, D. R. RANK², D. R. KEISER¹, B. N. SMITH³, R. S. CRIDDLE² & L. D. HANSEN¹

¹Department of Chemistry and Biochemistry, Brigham Young University, Provo, Utah 84602, USA, ²Section of Molecular and Cellular Biology, University of California, Davis, CA 95616 USA and ³Department of Botany and Range Science, Brigham Young University, Provo, UT 84602 USA

ABSTRACT

The temperature dependence of plant growth rate is related to the temperature dependence of respiratory metabolism. To determine how the effects of temperature on respiration rate and efficiency are transmitted to growth, this study measured the dark metabolic heat rate (q) and CO₂ production rate (R_{CO_2}) in excised shoots of seedlings of 14 maize cultivars (*Zea mays* L.) at several temperatures. The temperature coefficients of q and R_{CO_2} differ within a given cultivar and also differ among the cultivars. Both q and R_{CO_2} exhibit an isokinetic temperature of 20 ± 3 °C. The measured temperature dependences of q and R_{CO_2} were used to model the temperature dependences of both growth and substrate carbon conversion efficiency. This procedure may be useful in determining the suitability of cultivars for growth in a given climate and in understanding metabolic adaptation to climate.

Key-words: *Zea mays*; maize; calorimetry; efficiency; growth rate; respiration; temperature.

INTRODUCTION

Maize (*Zea mays* L.) is an important crop grown for both biomass and grain production in a variety of climatic conditions around the world. Because small differences in climatic temperature significantly affect maize growth, increased biomass production could result from a better understanding of the effects of temperature on metabolism and growth rates of maize (Miedema 1982; Singletary, Banisadr & Keeling 1994; Greaves 1996). The goal of this study is to model how differences in respiratory properties among cultivars affect growth responses to temperature changes.

Respiratory rates of plants are frequently correlated with growth rates (Amthor 1989; Hay & Walker 1989; Lambers 1985), but the relationship has not been adequately quantified. Growth and maintenance compartment models of respiration are difficult to apply to

studies of large numbers of cultivars or accessions at multiple temperatures. A recently derived model (Hansen *et al.* 1994) provides a more experimentally accessible description of the relation between respiration rates and relative specific growth rates. This model gives the specific growth rate R_{SG} as

$$R_{\text{SG}} = [-q - R_{\text{CO}_2}(1 - \gamma_p/4)\Delta H_{\text{O}_2}]/\Delta H_{\text{B}} = R_{\text{CO}_2}[\varepsilon/(1 - \varepsilon)], \quad (1)$$

where R_{SG} is the specific rate of conversion of substrate carbon into structural biomass in moles of C per unit time per mass of tissue, q is the specific metabolic heat rate in watts (or joules per second) per mass of tissue, R_{CO_2} is the specific rate of CO₂ production in moles per unit time per mass of tissue, γ_p is the mean chemical oxidation state of the substrate carbon (the $1 - \gamma_p/4$ thus has units of moles O₂/mole CO₂), ΔH_{O_2} is the constant from Thornton's rule (in this study assumed equal to -455 ± 15 kJ mol⁻¹ of oxygen), ΔH_{B} is the enthalpy change per mole of carbon for conversion of substrate to biomass, and ε is the substrate carbon conversion efficiency, i.e. the fraction of substrate carbon that is incorporated into structural biomass. The definition of ε used here appears similar to, but is not the same as, the traditional definition of growth efficiency (Hansen *et al.* 1998). The second part of Eqn 1 shows that R_{SG} is proportional to respiration rate, specifically R_{CO_2} , multiplied by a function of the efficiency, ε . Because q and R_{CO_2} are easily measured as functions of temperature, the growth rate and substrate carbon conversion efficiency can both be modelled as functions of temperature.

In the range of temperatures for which the Arrhenius equation describes the temperature dependence of respiration rates, and assuming only q and R_{CO_2} are temperature dependent, substitution of Arrhenius rate equations into Eqn 1 gives

$$R_{\text{SG}} = [-A_q e^{-\mu_q/T} - (1 - \gamma_p/4)\Delta H_{\text{O}_2} A_{\text{CO}_2} e^{-\mu_{\text{CO}_2}/T}]/\Delta H_{\text{B}}, \quad (2)$$

where μ_q is the temperature coefficient for the metabolic heat rate, μ_{CO_2} is the temperature coefficient for the CO₂ rate, T is the absolute temperature, and A_q and A_{CO_2} are the pre-exponential terms in the respective Arrhenius equations. Equation 2 allows prediction of relative values of specific growth rate as a continuous function of temperature from q and R_{CO_2} values measured at two or more temperatures.

Correspondence: Lee D. Hansen. Fax: 801 378 5474; e-mail: Lee_Hansen@BYU.edu

The ratio of metabolic heat rate to CO₂ rate is related to ε as:

$$q/R_{\text{CO}_2} = -(1 - \gamma_p/4)\Delta H_{\text{O}_2} - [\varepsilon/(1 - \varepsilon)]\Delta H_B. \quad (3)$$

With the same assumptions as above, the temperature dependence of q/R_{CO_2} , and thence of ε , is given by

$$q/R_{\text{CO}_2} = [A_q e^{-\mu_q/T}]/[A_{\text{CO}_2} e^{-\mu_{\text{CO}_2}/T}]. \quad (4)$$

Equations 3 and 4 allow prediction of relative values of the function $[\varepsilon/(1 - \varepsilon)]$ as a continuous function of temperature.

This study measured q and R_{CO_2} at two to six temperatures for shoots of 14 maize cultivars. A_q , A_{CO_2} , μ_q and μ_{CO_2} are calculated directly from these data. Then, assuming that ΔH_B and γ_p are independent of temperature, relative values of R_{SG} and $[\varepsilon/(1 - \varepsilon)]$ are obtained as functions of temperature from Eqns 2 and 4. To test these predictions and assumptions, seedling growth at three temperatures was measured for some of the cultivars. Growth, q , and R_{CO_2} measurements were made on the same plants.

Attempts to define the temperature dependence of ε from carbon balance during seedling growth (Yamaguchi 1978; Penning de Vries 1972) have not given a definitive answer. Data compiled in Penning de Vries (1972) show ε to both increase and decrease with temperature. Yamaguchi reported ε constant for maize, rice and soybean. These studies show that it would be extremely laborious and time consuming to obtain sufficient data to accurately define the temperature dependence of ε for several cultivars at narrow intervals over a wide temperature range by measurements of carbon balance in seedlings.

Another approach to determining ε and its temperature dependence is to obtain values for the maintenance rate and the growth coefficient (or construction cost) and combine these values to calculate ε . Construction cost (Penning de Vries, Brunsting & van Laar 1974) is considered by most workers to be independent of temperature and maintenance rate to increase with temperature, and most previous discussions of the effects of temperature on respiratory efficiency have been couched in terms of models dividing

respiration into growth and maintenance components. But the relationship between these parameters and ε is such that the direction of change of ε with temperature cannot be predicted without knowledge of the temperature dependence of the growth rate as well as of the growth and maintenance coefficients. Thus, compartment models are not well suited for describing plant growth as a function of temperature *a priori*. Furthermore, the relation between the growth and maintenance coefficients and plant biochemistry is not clear (Chiariello, Mooney & Williams 1989; Breeze & Elston 1983; Shinano, Osaki & Tadano 1996); there are theoretical arguments indicating construction cost is not independent of temperature (Stucki 1989), and theoretical as well as experimental results showing that meaningful maintenance rates have not been measured for plants (Breeze & Elston 1983; Shinano *et al.* 1996; Hansen *et al.* 1998).

MATERIALS AND METHODS

Maize (*Zea mays* L.) cultivars exhibiting a wide range of morphology and temperature-dependent growth characteristics were selected for this study. The selected cultivars include some long-established flint and dent varieties, some standard inbred cultivars, and some newer cultivars supplied by Pioneer Hi-bred International. The 14 cultivars are described in Table 1.

Plant growth

The non-Pioneer cultivars were grown and studied at Brigham Young University. Seedlings were grown hydroponically at 25 °C. Seeds were suspended at water level on a cheese cloth covered metal screen and grown under a 12 h light/dark cycle. Radicals 3–5 cm long from 4- to 6-d-old seedlings were cut at the base of the radical and further cut to 1 cm lengths, and the entire radical was immediately placed in the calorimeter.

The Pioneer cultivars were grown and studied in an independent study carried out at the University of California, Davis (Rank 1995). There, seedlings were grown in the

Variety	Source
Baby (miniature popcorn)	Lilly Miller
Northstine Dent (dry field corn)	Johnny's Selected Seeds
Fiesta F-1 (hybrid ornamental)	Johnny's Selected Seeds
Garland Flint (dry field corn)	Johnny's Selected Seeds
Jubilee Supersweet (hybrid sweet corn)	Nichol's Garden Nursery
Kandy Korn (hybrid sweet corn)	Lilly Miller
Squaw (Indian flint)	Nichol's Garden Nursery
Early Sunglow (hybrid sweet corn)	Lilly Miller
Tom Thumb (miniature popcorn)	Johnny's Selected Seeds
Pioneer 814	Pioneer
Pioneer G17	Pioneer
Pioneer T10	Pioneer
Pioneer K46	Pioneer
Pioneer W91	Pioneer

Table 1. Characteristics of maize used in this study

dark in incubators at three temperatures, 32, 25, and either 22 or 15 °C, and all harvested when about 5 cm long (80–100 h at 25 °C). Seeds were imbibed for 2 h, then wrapped in paper toweling and placed in a beaker of water so the seeds were just above water level. At the measurement time, the entire shoot was excised at the scutellum, cut into 1 cm lengths and immediately placed in calorimeter ampules.

Calorimetric methods

Calorimetric data were collected with Hart Scientific model 7707 differential scanning calorimeters according to previously published procedures (Criddle *et al.* 1991). The heat rate and CO₂ rate data, corrected for blank values, were divided by the dry weight of the tissue (70 °C vacuum oven for > 24 h) to obtain specific rates.

Measurements of heat rates on non-Pioneer cultivars were made at 25, 20, 15, 10 and 5 °C and on Pioneer cultivars at 32, 28, 25, 22, 19 and 15 °C. Replicate data on each cultivar were averaged for each temperature. The average values were plotted as $\ln q$ versus reciprocal absolute temperature (Fig. 1). The slope of such an Arrhenius plot is equal to μ_q in units of kelvins, or more conveniently, kilokelvins (kK), and the intercept is equal to $\ln(A_q, \mu W \text{ mg}^{-1})$. R_{CO_2} was measured by the method of Criddle *et al.* (1991) at 32, 28, 25, 22, 19 and 15 °C for the Pioneer cultivars, but only at 25 and 15 °C on the others. The temperature

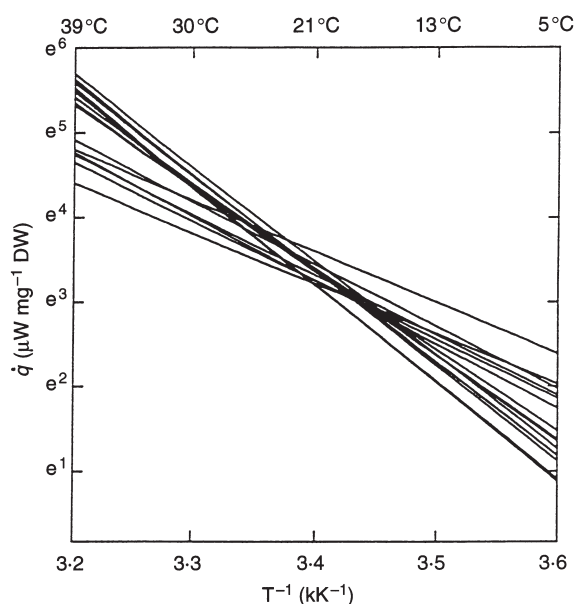


Figure 1. Arrhenius plot for q showing an isokinetic temperature at 20 ± 3 °C. The vertical scale is given as powers of e , the natural logarithm base. Heat rates were measured at 25, 20, 15, 10 and 5 °C for non-Pioneer cultivars and at 32, 28, 25, 22, 19 and 15 °C for Pioneer cultivars. Data points at the extreme temperatures were not used in computing the least squares line if they deviated significantly from the linear fit. Lines may be identified with the cultivars by use of the μ_q values in Table 3.

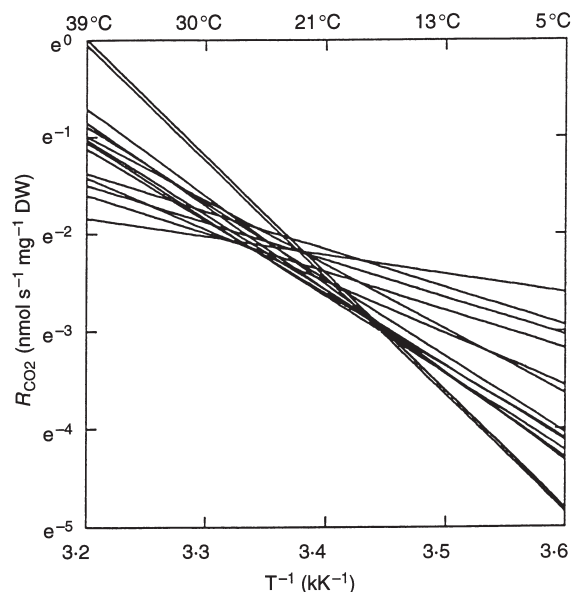


Figure 2. Arrhenius plot for R_{CO_2} showing an isokinetic temperature at 20 ± 3 °C. The vertical scale is given as powers of e , the natural logarithm base. R_{CO_2} was measured at 32, 28, 25, 22, 19, and 15 °C for the Pioneer cultivars, but only at 25 and 15 °C on the others. The data point at 32 °C was not used in constructing the least squares line if it fell significantly below the linear fit to the rest of the data. Lines may be identified with the cultivars by use of the μ_{CO_2} values in Table 3.

dependence of R_{CO_2} , i.e. μ_{CO_2} in kK, and $\ln(A_{\text{CO}_2}, \text{nmol mg}^{-1} \text{ s}^{-1})$ were determined from the slope and intercept, respectively, of Arrhenius plots of R_{CO_2} data averaged at each temperature (Fig. 2).

Growth rate

Growth rates were measured on the same tissues used for calorimetric measurements. Growth rates were calculated as (dry weight of shoot) \times (fractional carbon content)/(age at harvest). The carbon content of dried, ground samples was determined by a commercial laboratory. Age at harvest was time at harvest minus time of planting.

RESULTS

Data for q and R_{CO_2} at 15 and 25 °C are given in Table 2. The Arrhenius plots in Figs 1 and 2 show that the lines fitted to both q and R_{CO_2} data mostly cross at a temperature near 20 °C. Most of the cultivars have nearly the same metabolic heat and CO₂ rates at this temperature and thus it is a unique temperature, commonly referred to as an isokinetic temperature. The μ_q , μ_{CO_2} , A_q and A_{CO_2} values derived from the data in Figs 1 and 2 are given in Table 3. Intercultivar variation is large for both μ_q and μ_{CO_2} . The μ_{CO_2} values derived from data taken at 15 and 25 °C range from 2 to 12 kK and μ_q values range from 6 to 11.5 kK ($Q_{10} = 2$ corresponds to $\mu \approx 6$ kK). It is highly significant that the values of μ_q and μ_{CO_2} are generally not equal for a

Table 2. Specific metabolic heat and CO₂ production rates measured at 15 and 25 °C^a

Variety	q at 15 °C [$\mu\text{W (mgDW)}^{-1}$]	q at 25 °C [$\mu\text{W (mgDW)}^{-1}$]	R_{CO_2} at 15 °C [$\text{nmol (mgDW)}^{-1} \text{ s}^{-1}$]	R_{CO_2} at 25 °C [$\text{nmol (mgDW)}^{-1} \text{ s}^{-1}$]
Baby	13.1 \pm 1.1(5)	46.9 \pm 1.3(8)	0.0479	0.120 \pm 0.013(3)
Northstine Dent	13.9 \pm 2.4(5)	44.8 \pm 3.9(10)	0.0611	0.132 \pm 0.016(7)
Fiesta F-1	15.5 \pm 1.7(4)	40.4 \pm 3.0(9)	0.0428	0.102 \pm 0.011(7)
Garland Flint	16.2 \pm 1.2(3)	40.4 \pm 2.9(7)	0.0869	0.137 \pm 0.021(11)
Jubilee Supersweet	16.2 \pm 2.6(4)	39.4 \pm 3.8(4)	0.0363	0.142 \pm 0.039(2)
Kandy Korn	11.2 \pm 1.6(6)	38.7 \pm 2.8(8)	0.0564	0.105 \pm 0.031(5)
Squaw	15.4 \pm 2.6(4)	50.4 \pm 4.5(4)	0.0944	0.118 \pm 0.040(5)
Early Sunglow	11.4 \pm 1.9(4)	37.7 \pm 3.1(6)	0.0688	0.109 \pm 0.083(7)
Tom Thumb	13.8 \pm 1.6(5)	45.2 \pm 3.1(5)	0.0434	0.107 \pm 0.019(5)
G17	17.8	38.2	0.0774	0.125
T10	14.9	36.2	0.0351	0.116
814	13.7	34.5	0.0370	0.117
K46	14.6	37.8	0.0378	0.144
W91	12.8	48.6	0.0332	0.154

^aUncertainties are given as the standard deviation of the mean with number of observations in parentheses.

given cultivar. For some cultivars $\mu_q > \mu_{\text{CO}_2}$ and for others $\mu_q < \mu_{\text{CO}_2}$, as shown by the μ_q/μ_{CO_2} ratios given in Table 3. Figure 3 shows there is no significant correlation ($R^2 = 0.36$ with negative slope) between μ_q and μ_{CO_2} .

The ratio q/R_{CO_2} was obtained in two ways. In the first, values of q and R_{CO_2} were measured at 15 and 25 °C and ratios calculated (Table 3). In the second, the ratio was calculated from the A_q , A_{CO_2} , μ_q and μ_{CO_2} values (see Eqn 4). Values of A_q and μ_q were calculated from q values measured at several temperatures but with R_{CO_2} measurements only at 15 and 25 °C. The temperature dependence of the q/R_{CO_2} ratios measured directly agrees with the dependence calculated from the A_q , A_{CO_2} , μ_q and μ_{CO_2} values. The two methods were used in some cases for measurements on different plants of the same cultivar grown at different times over a 2 year period, thus demonstrating the reproducibility of the methods. Figure 4 shows plots of q/R_{CO_2} versus

temperature for the Pioneer cultivars. Note that the cultivars do not all show the same pattern of change with temperature. Values of the function $[\varepsilon/(1 - \varepsilon)]\Delta H_B$, which is related to q/R_{CO_2} by Eqn 3, were calculated as a function of temperature from Eqns 3 and 4 and the μ_q , μ_{CO_2} , A_q and A_{CO_2} data in Table 3. The results are shown in Fig. 5. There is significant variation of this function among the cultivars.

Values of the product $R_{\text{SG}}\Delta H_B$ were calculated as functions of temperature by use of the μ_q , μ_{CO_2} , A_q and A_{CO_2} data in Table 3 and Eqn 2 (Fig. 6a). The $R_{\text{SG}}\Delta H_B$ values are respiration-predicted, specific growth rates in terms of the rate of storage of chemical energy in structural biomass with substrate as the reference energy state. On this basis, Fig. 6a predicts that the order of growth rates at 10 °C is nearly opposite the order at 40 °C: i.e. the fastest growing plants at 10 °C are predicted to be the slowest growing at 40 °C. An approximate isokinetic temperature for the

Table 3. Temperature dependence of maize metabolism

Variety	$\ln(A_q)$ [$\mu\text{W (mgDW)}^{-1}$]	μ_q , [kK]	$\ln(A_{\text{CO}_2})$ [$\text{nmol (mgDW)}^{-1} \text{ s}^{-1}$]	μ_{CO_2} , [kK]	μ_q/μ_{CO_2}	q/R_{CO_2} at 25 °C [kJ mol^{-1}]	q/R_{CO_2} at 15 °C [kJ mol^{-1}]	T cross [°C]	455 $R_{\text{CO}_2} > q$
Baby	41.70	11.273	24.33	7.882	1.430	343 \pm 67(3)	338	28	below
Northstine Dent	40.83	11.013	20.16	6.611	1.666	321 \pm 18(7)	284	29	below
Fiesta F-1	37.91	10.157	22.73	7.453	1.363	349 \pm 55(7)	393	25	below
Garland Flint	36.14	9.631	11.12	3.907	2.465	326 \pm 44(11)	280	30	below
Jubilee Supersweet	27.51	7.117	38.36	12.003	0.593	260 \pm 320(2)	242	15	above
Kandy Korn	42.63	11.599	15.65	5.334	2.172	321 \pm 45(5)	232	27	below
Squaw	41.11	11.068	4.29	1.915	5.780	347 \pm 45(5)	216	25	below
Early Sunglow	42.09	11.440	11.04	3.949	2.897	292 \pm 41(7)	221	27	below
Tom Thumb	37.16	9.943	23.75	7.745	1.284	322 \pm 55(5)	297	28	below
G17	28.48	7.366	10.82	3.849	1.914	237	235	32	below
T10	23.46	5.956	24.29	7.922	0.752	314	429	10	above
814	28.99	7.571	28.26	9.051	0.930	292	380	1	above
K46	27.01	6.988	26.70	8.611	0.812	263	386	6	above
W91	24.08	6.027	38.58	12.054	0.500	299	388	19	above

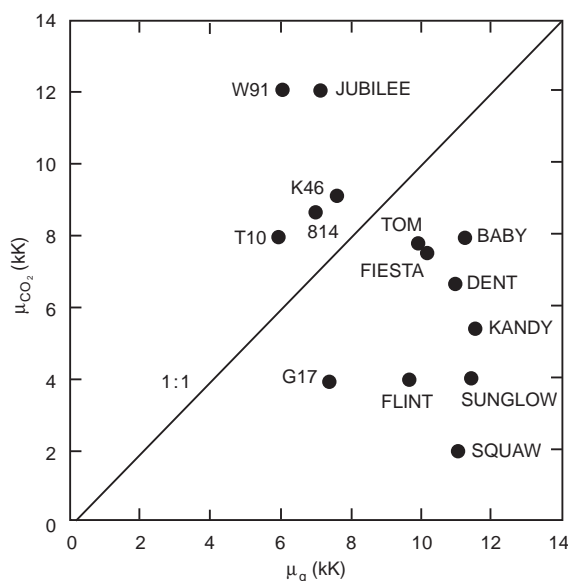


Figure 3. Plot of μ_q versus μ_{CO_2} demonstrating the inequality and absence of significant correlation ($R^2 = 0.36$ with negative slope) between these two quantities. The line of equality is shown for reference.

predicted growth rate is observed at 23 °C for most of the cultivars (see Fig. 6).

For some cultivars, $R_{SG}\Delta H_B$ increases approximately exponentially with increasing temperature. For others, $R_{SG}\Delta H_B$ increases, goes through a maximum and then decreases approximately exponentially. Negative values of $R_{SG}\Delta H_B$ indicate regions of temperature where the plants are predicted to be unable to grow unless acclimation is possible. A rate of storage of chemical energy in structural

biomass of < 0 is associated with decay of structural integrity. Figure 6b shows that, as a difference between two exponentials with different exponents (see Eqn 2), $R_{SG}\Delta H_B$ does not give a linear plot on Arrhenius axes.

Figure 7 shows an Arrhenius plot of the temperatures where $q = 455R_{CO_2}$. These crossover temperatures (T_{cross}) are also given in Table 3. Note that the difference, $455R_{CO_2} - q$, is positive at temperatures above T_{cross} for some cultivars (closed circles) and negative for others (open circles). This plot ranks the cultivars according to the minimum (closed circles) or maximum (open circles) temperature that is predicted to allow growth. The data points in Fig. 7 fall on a straight line on an Arrhenius plot as a consequence of the existence of isokinetic behavior at the same temperature for q and R_{CO_2} .

Figure 8 compares measured growth with specific growth rates calculated with Eqn 1 and measured values of q and R_{CO_2} . The figure demonstrates agreement between predicted and measured values for seedlings of five cultivars grown at temperatures from 15 to 32 °C. The agreement shows that the model in Eqn 1 is capable of accurate predictions of seedling growth rates.

DISCUSSION

The agreement between predicted and measured growth rates indicates that the assumptions of constant γ_p and ΔH_B made in applying Eqn 1 are reasonable, though variation in these values may be responsible for some of the scatter in Fig. 8. From measurements of q and R_{CO_2} , Eqn 1 thus successfully (correlation slope = 0.93) predicts relative values of seedling growth rates of the five Pioneer cultivars across a wide range of temperatures (15–32 °C). The results of this part of the study thus show that respiratory traits are

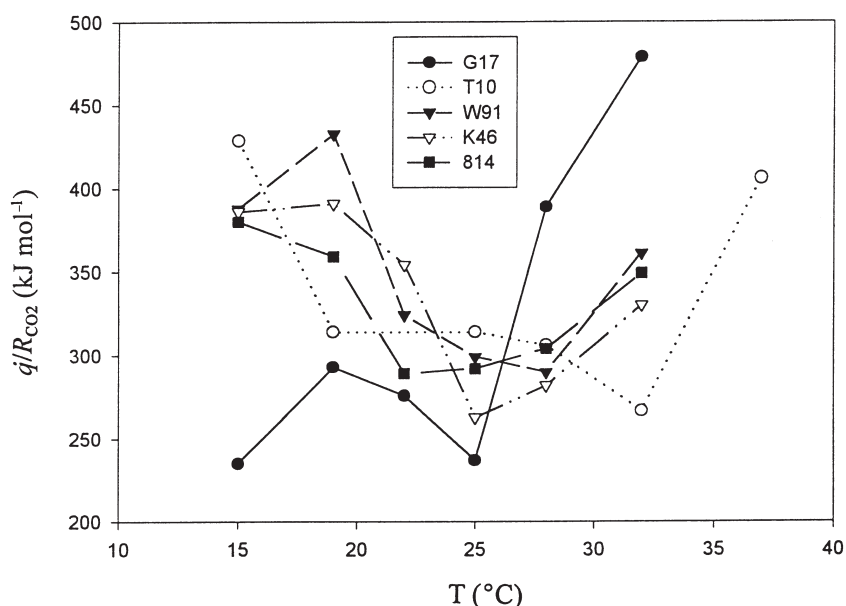


Figure 4. Plot of q/R_{CO_2} versus temperature for the Pioneer cultivars.

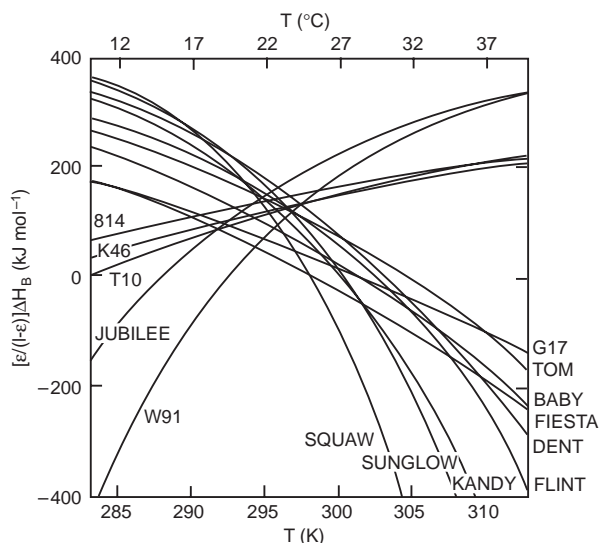


Figure 5. The efficiency function $[\varepsilon/(1-\varepsilon)]\Delta H_B$ calculated with Eqns 3 and 4 and plotted as a function of temperature for all the cultivars in this study.

predictive of the effects of temperature on growth of maize seedlings. This result further suggests the possibility of predicting suitability of a cultivar for growth in a particular temperature zone from laboratory measurements of q and R_{CO_2} .

Because $R_{SG}\Delta H_B$ values are correlated with measured growth rates, the growth versus temperature predictions made in Fig. 6 can be used to rank the maize cultivars according to their relative potential growth rate in different temperature zones. The result of such a ranking agrees well with empirically derived planting practices for the cultivars included in this study. Of the Pioneer cultivars, Fig. 6 predicts that W91 is the fastest grower in hot climates and G17 is the best cool climate grower. The Pioneer G17 cultivar was bred for its ability to grow well in cold temperatures where it is superior to the other Pioneer cultivars included in this study. While G17 will also grow in hot climates, the other Pioneer cultivars do better (Dr Barry Martin, Pioneer Hi-bred International, personal communication). Of the non-Pioneer cultivars, Fig. 6 predicts that Jubilee would outperform the other cultivars in a very hot climate, but would be the poorest choice in a cool climate. Likewise, Squaw is predicted to be the best grower in cool climates, but the poorest in a hot climate. In agreement with these predictions, Jubilee is commonly grown in the western US as a late summer variety and is known to do best in very hot weather. Squaw is commonly grown in Maine and south-eastern Canada.

The curves in Fig. 6 should not be considered to imply that growth rate will increase or decrease without limit as the temperature is increased or decreased. Recall that these curves are calculated from data taken largely at 15 and 25 °C. In another study (Criddle *et al.* 1997), we have shown that Eqn 1 can accurately predict temperature limits to growth from q and R_{CO_2} data measured as functions of

temperature. High and low temperature limits to growth are determined by either thermal events that damage cellular structures or by ε going to zero (Criddle *et al.* 1997). Such events place boundaries on the curves shown in Fig. 6. Also, the curves indicate only the potential for biomass accumulation, not yield of grain.

The similarities in the data presented in Figs 6a and 5 suggest that the substrate carbon conversion efficiency ε (or more precisely $[\varepsilon/(1-\varepsilon)]\Delta H_B$) is a major determinant of both specific growth rate and the temperature dependence

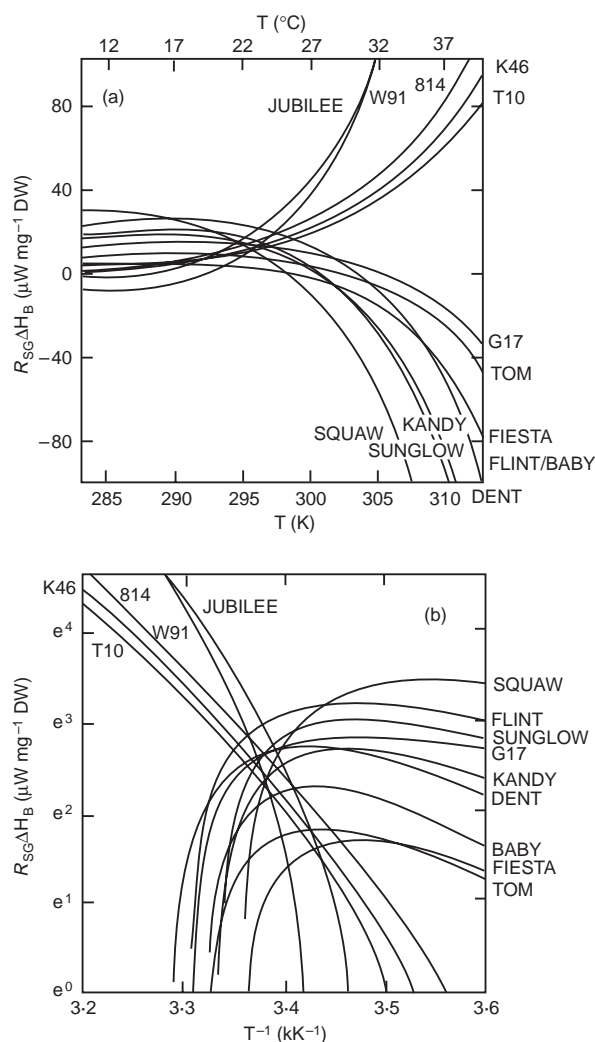


Figure 6. Values of the product $R_{SG}\Delta H_B$ calculated as a function of temperature from data in Table 3. (a) Plotted on linear axes. Negative values of $R_{SG}\Delta H_B$ indicate regions of temperatures where growth is predicted not to occur and tissue damage to occur. Note that these regions are at low temperatures for those cultivars with curves convex upwards and at high temperatures for those cultivars with curves convex downwards. (b) Plotted as an Arrhenius plot. The vertical scale is given as powers of e , the natural logarithm base. Low temperature stress is indicated by a downwards deviation from a linear extrapolation from the left for T10, 814, W91 and Jubilee. High temperature stress is indicated by a downwards deviation from a linear extrapolation from the right for the remaining cultivars.

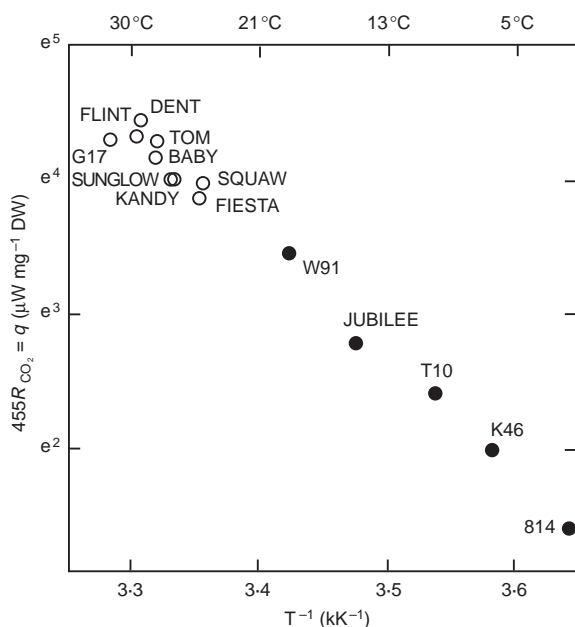


Figure 7. The temperature and q values at which $q = 455R_{CO_2}$ for each cultivar plotted on Arrhenius axes. The vertical scale is given as powers of e , the natural logarithm base. Values of ε and R_{SG} are positive at temperatures below the plotted temperature for open circles and above the plotted temperature for closed circles.

of growth rate. ε is related to the ratio q/R_{CO_2} as shown in Eqn 3 and the temperature dependence of this ratio is related to μ_q and μ_{CO_2} as shown in Eqn 4. Consideration of the large temperature dependence of the ratio q/R_{CO_2} (see Figs 4 & 5) and thus of ε (see Eqns 3 and 4) leads to an understanding of how selection for μ values can lead to accessions or cultivars optimized for a given climate (Criddle *et al.* 1994). The relative values of μ_q and μ_{CO_2} of a particular cultivar determine whether ε will increase or decrease with increasing temperature and the steepness of the temperature function of ε , and thus ultimately how growth rate depends on temperature. The location of any given data point in Fig. 3 indicates how the ratio of q to R_{CO_2} for each cultivar changes with temperature. If γ_p is constant or does not change so as to exactly compensate changes in $[\varepsilon/(1 - \varepsilon)]\Delta H_B$, Eqn 3 predicts that the product $[\varepsilon/(1 - \varepsilon)]\Delta H_B$ must change with temperature for cultivars not plotting on the 1 : 1 line in Fig. 3. For cultivars with data plotting above the 1 : 1 line, q increases faster than R_{CO_2} with temperature, and q/R_{CO_2} increases with temperature. If μ_q and μ_{CO_2} are equal, i.e. on the 1 : 1 line, q/R_{CO_2} is constant with temperature. For cultivars with data plotting below the 1 : 1 line, R_{CO_2} increases faster than q with temperature, and therefore q/R_{CO_2} decreases with temperature. In general, the farther a cultivar plots above or below the 1 : 1 line, the more suited it is for growth in a warmer or colder climate, respectively.

The observation that q and R_{CO_2} have different temperature coefficients inevitably leads to the question: What change in metabolism with temperature leads to different

values of μ_q and μ_{CO_2} in the same plant? More than 90% of the metabolic heat from a cell is generated from reduction of oxygen in the mitochondria (Hopkin 1991). CO_2 is generated by the Krebs cycle, the pentose phosphate shunt, and by fermentation and decarboxylation reactions. For q and R_{CO_2} to have different temperature dependences, oxygen reduction and CO_2 production cannot be absolutely coupled. Thus, either the substrate carbon source or the ratio of anaerobic to aerobic products change with temperature. Changing substrate with temperature and the presence of significant levels of fermentation are both unlikely in maize seedling shoot tissues. Therefore, the temperature dependence of the ratio of glycolytic (anaerobic) products being oxidized to CO_2 in the Krebs cycle (aerobic) to those going into biomass synthesis is the most likely cause of the difference in temperature dependences of q and R_{CO_2} observed under the conditions of this study. In other words, we conclude that the branching ratio of the major biochemical pathways subsequent to pyruvate must be temperature dependent. The ratio of carbon being oxidized in the Krebs cycle to that going into new structural biomass is obviously related to ε . The measured differences in the temperature dependences of q and R_{CO_2} thus require that ε change with temperature (see Eqn 3 and Fig. 4).

The data of Yamaguchi (1978) reporting GE for maize seedlings from 15 to 40 °C show that GE changes systematically with temperature in the same manner found for the cold-climate cultivars included in this study, i.e. at 15 °C, GE = 55%; at 20 °C, GE = 65%; at 25 °C, GE = 67%; at 30 °C, GE = 64%; at 35 °C, GE = 61%; and at 40 °C, GE = 45%.

Demonstration of the existence of an isokinetic temperature for cultivars of an annual crop plant has significant

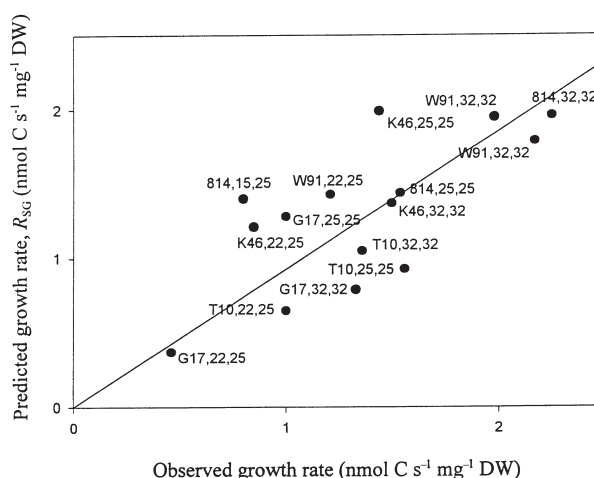


Figure 8. Comparison of measured shoot growth rates, i.e. (total C in shoot)/(age of shoot)/(mass of shoot), with growth rates predicted from respiration heat and CO_2 rates, i.e. $R_{SG} = (455R_{CO_2} - q)/(21 \text{ kJ mol}^{-1})$. Cultivars, temperatures of growth, and respiration measurement temperatures are given in the figure. The linear least square line passing through the origin and fitted to the data has a slope of 0.93.

consequences for the interpretation of empirical, linear correlations between growth and respiration. Empirical correlations between specific respiration rates and growth rates (often measured in the field at uncontrolled, variable temperatures) have sometimes been found to be strong, more often weak, usually positive, but sometimes negative (Hopkins 1995; Amthor 1989; Hay & Walker 1989; Lambers 1985). Positive correlations are usually found when rapidly growing tissues are measured. Negative correlations have been found when respiration rates are measured on mature tissues. Negative correlations are usually explained in terms of maintenance respiration, but the results in Figs 2 and 3 provide an alternative explanation for negative correlations obtained in studies performed without temperature control. If growth occurs at temperatures above an isokinetic temperature, but respiration data are measured below the isokinetic temperature, a negative correlation will be observed even for rapidly growing tissues. When both growth and respiration are measured at a temperature either above or below an isokinetic temperature, a positive correlation between growth and respiration will result. Furthermore, the temperature difference between the isokinetic temperature and the measurement temperature is a factor in the determination of the strength of the correlation. Only at temperatures well removed from an isokinetic temperature can a strong correlation be expected, and for the correlation to be meaningful, respiration measurements must be made at the growth temperature.

The concepts derived from this study are general, and therefore could be used to aid matching of cultivars of any species to growth climates. R_{CO_2} , q and their temperature dependences are heritable (Anekonda *et al.* 1994, 1996; Criddle *et al.* 1994, 1996). Therefore, it should be possible through breeding programmes to develop maize cultivars for rapid growth in cool or warm climates by selection for respiratory traits. The ability of species and cultivars to acclimate was not considered in this study, but acclimation could be characterized by the same techniques.

CONCLUSIONS

The model of Hansen *et al.* (1994a) is shown to predict observed growth of maize seedlings across a range of cultivars and growth temperatures. The measured temperature coefficients of q and R_{CO_2} are different for a given maize cultivar and also differ among cultivars. Based on these observations, growth rates of some of the cultivars are predicted by the model to increase at low temperature, go through a maximum in the normal growth range, and then decrease with further increases in temperature. Growth rates of other cultivars are predicted by the model to increase with temperature until tissue damage occurs if R_{CO_2} follows the Arrhenius equation extrapolation to high temperatures. The model predicts that changes in the substrate carbon conversion efficiency, ϵ , with temperature are the primary cause of changes in growth rate with temperature. The model predicts low and high temperature limits

for growth. Used in conjunction with measurements of q and R_{CO_2} at two or more temperatures, the model may aid in selection of cultivars and in understanding adaptation of plants to climate changes.

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