

Temperature-Dependent Respiration-Growth Relations in Ancestral Maize Cultivars

Bruce N. Smith
Jillian L. Walker
Rebekka L. Stone
Angela R. Jones
Lee D. Hansen

Abstract—Shoots from 4- to 6-day old seedlings of seven ancestral or old cultivars of *Zea mays* L. were placed in a calorimeter. Dark metabolic heat rate (q) and CO_2 production rate (R_{CO_2}) were measured at nine temperatures (5, 10, 15, 20, 25, 30, 35, 40, and 45 °C). Temperature dependencies of q and R_{CO_2} were used to model response of both growth and substrate carbon conversion efficiency. Responses at 5 °C were similar, but differences were noted at warmer temperatures. Upper temperature limits for growth were: Minipopcorn (26 °C), Black popcorn (30 °C), Black Mexican Sweet (31 °C), Pula Janku (32 °C), Santo Domingo White (32 °C), Loncho (39 °C), and Santa Ana Blue (45 °C). This study of seedling metabolism reveals climatic adaptation among cultivars that may prove beneficial to maize production across the globe.

Maize (*Zea mays* L.) is an important crop originating in the Americas, now 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 production could result from a better understanding of the effects of temperature on metabolism and growth (Bandolini and others 2000; Greaves 1996; Miedema 1982; Singletary and others 1994).

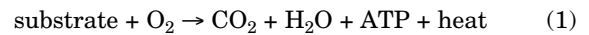
All life depends on photosynthesis, however despite much effort to correlate photosynthesis with growth rates, no meaningful results have been obtained, only correlations (Nelson 1988). Respiratory rates of plants have frequently been empirically correlated with growth rates (Amthor 1989; Hay and Walker 1989; Loomis and Amthor 1999; Thornley and Cannell 2000), and a recent model allows predictions of growth rates from metabolic rate measurements. This model and rapid methods for measurement allow definition of responses to subtle changes in environmental factors, including temperature (Hansen and others 1994).

In an earlier study of maize (Taylor and others 1998), seed was purchased from commercial sources for nine cultivars of both flint and dent varieties, and five newer cultivars were

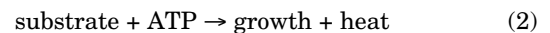
supplied by Pioneer Hi-bred International. Metabolic heat rates and CO_2 rates were measured at just two temperatures, and these values were used to model the temperature dependences of both growth and substrate carbon conversion efficiency (Taylor and others 1998). Some cultivars were found to grow better at low temperatures, while others were better at higher temperatures.

For this study we obtained ancestral or old cultivars of maize and made metabolic measurements at nine temperatures (from 5 to 45 °C at 5 °C intervals) so that the curves presented are measured rather than calculated.

Respiration has two aspects: catabolism and anabolism. In catabolism organic substrates are oxidized to produce CO_2 . Part of the energy produced by oxidation is used to convert ADP and inorganic phosphate to ATP, the rest is lost as heat.



ATP produced in catabolism is transient, but is used for cellular work, including anabolism as shown below:



In anabolism, heat and new plant tissue are produced. A calorimeter measures the rate of heat loss from both catabolism and anabolism (q). The rate of CO_2 production measures the rate of catabolism (R_{CO_2}).

Materials and Methods

The specific predicted growth rate of structural biomass or rate of anabolism (R_{SG}) is related to the two measured variables as in equation (3).

$$R_{\text{SG}}\Delta H_{\text{B}} = 455R_{\text{CO}_2} - q \quad (3)$$

where ΔH_{B} is the enthalpy change for the formation of biomass from photosynthate and Thornton's constant ($-455 \pm 15 \text{ kJ mol}^{-1}$ of O_2) is incorporated.

Seven ancestral or older cultivars of *Zea mays* L. were obtained (table 1). (After considerable searching in library and web sites, we conclude that the experts disagree as to which cultivars resemble old or ancestral types). Seeds were germinated at room temperature and about 100 mg fresh weight of shoot tissue from 4- to 6-day old seedlings was placed in each of three ampules of the calorimeter (Hart Scientific model 7707 or Calorimetry Sciences Corporation MCDSC model 4100). After 15 to 20 minutes thermal equilibration at the desired temperature, the metabolic

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Bruce N. Smith is a Professor, Jillian L. Walker and Rebekka L. Stone are Undergraduate Students, and Angela R. Jones is a Graduate Student, Department of Botany and Range Science; Lee D. Hansen is a Professor, Department of Chemistry and Biochemistry, Brigham Young University, Provo, UT 84602.

Table 1—Maize seedlings were grown from seven ancestral cultivars. Metabolic heat rate and CO₂ rate were measured every 5 °C from 5 to 45 °C. Low and high stress temperatures are indicated as well as the temperature for optimal growth.

Cultivar	Temperature response		
	Low stress	Optimal	High stress
Minipopcorn	<5	20	26
Black popcorn	<5	20	30
Black Mexican sweet	<5	25	31
Pula Janku	<5	20	32
Santo Domingo white	<5	20	32
Loncho	<5	25	39
Santa Ana Blue	<5	25	45

heat rate (q) was measured for another 15 to 20 minutes. The ampules were removed from the calorimeter and a small vial filled with 40 μ l of 0.4 M NaOH was placed in the calorimeter ampule with the tissue. Again a 15 to 20 minute thermal equilibration was necessary, followed by measurement of

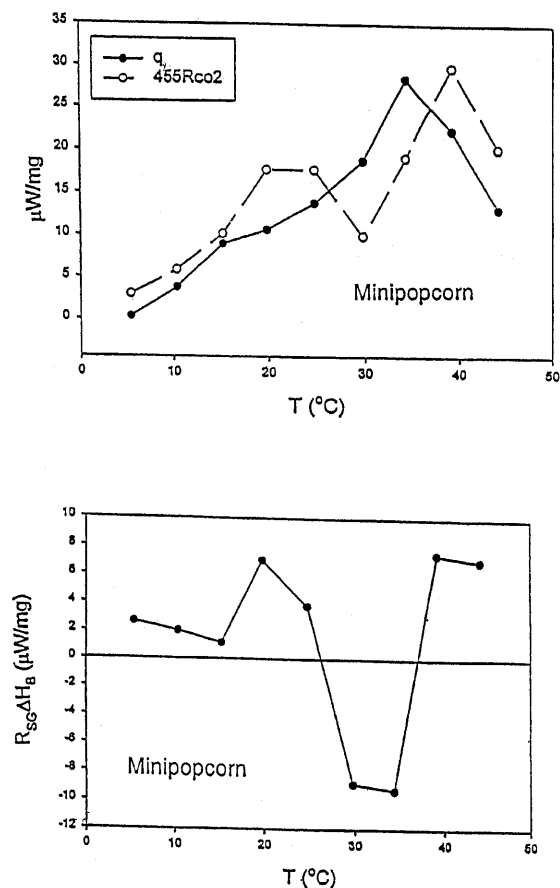


Figure 1—(A) Metabolic heat rate (q) and respiration rate ($455R_{CO_2}$) for the Minipopcorn cultivar of *Zea mays* L. was measured as μ W per mg dry wt. at 5 degree intervals from 5 to 45 °C. (B) Predicted specific growth rate ($R_{SG}\Delta H_B$) was calculated from the metabolic measurements in (A) according to equation 3.

the respiration rate (R_{CO_2}) for 15 to 20 minutes. As the CO₂ and NaOH react in solution, additional heat is produced ($-108.5 \text{ kJ mol}^{-1}$ is the heat of reaction for carbonate formation), giving the rate of CO₂ evolution (R_{CO_2}) by the plant tissue. Next the NaOH is removed and the heat rate (q) is measured as before (Hansen and others 1994; Criddle and Hansen 1999). The tissue was then run at another temperature. Measurements were made on each sample at 9 temperatures: 5, 10, 15, 20, 25, 30, 35, 40, and 45 °C. Three samples were used in each of the sequences: 15, 10, and 5 °C; 20, 25, and 30 °C; and 35, 40, and 45 °C.

Results and Discussion

For Minipopcorn (fig. 1), the calculated rate of energy production from catabolism ($455R_{CO_2}$) exceeded heat loss (q) at 5 through 26 °C, while at higher temperatures heat loss exceeded calculated energy available from oxidation of carbohydrate. Above 35 °C, heat rate declined with increasing temperature, indicating possible tissue damage. Thus, growth ($R_{SG}\Delta H_B$) was predicted to occur only at temperatures below about 26 °C. By contrast, the data on Black Popcorn indicated growth would continue up to about 30 °C (fig. 2), but not at higher temperatures. The calculated

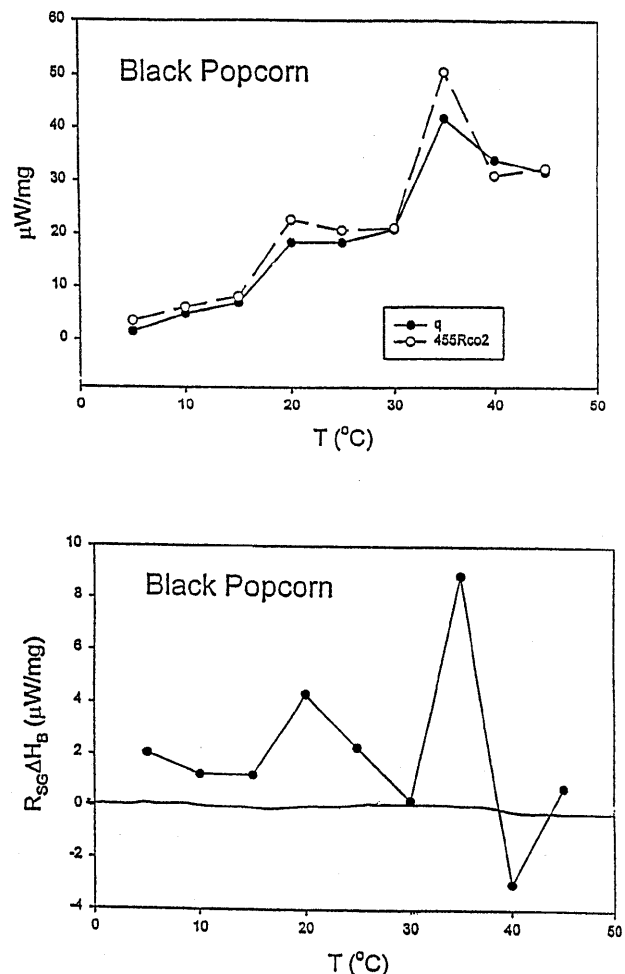


Figure 2—As in figure 1 but for the Black Popcorn cultivar.

growth rate of Black Mexican Sweet (fig. 3) had a temperature response a bit higher, to 31 °C. Pulu Janku (fig. 4) and Santo Domingo White (fig. 5) had very similar responses (to

32 °C). Loncho (fig. 6) was predicted to grow at temperatures below about 39 °C, while Santa Ana Blue (fig. 7) did well in warmer temperatures and would grow up to a temperature of about 45 °C.

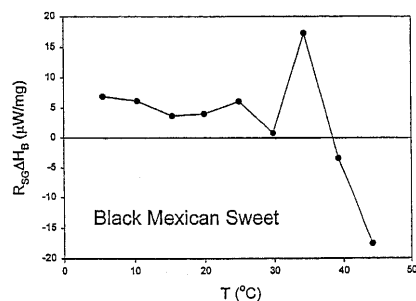
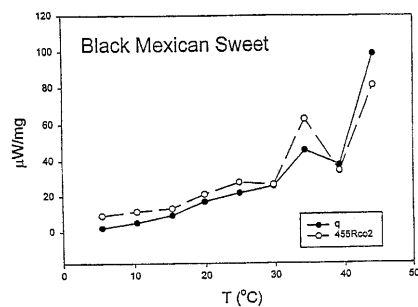


Figure 3—As in figure 1 but for the Black Mexican Sweet cultivar.

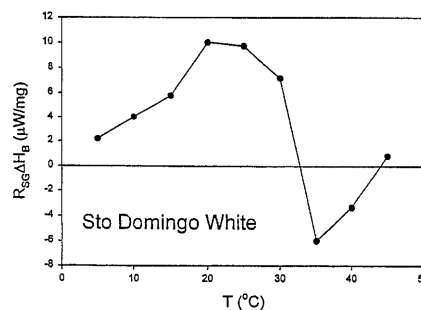
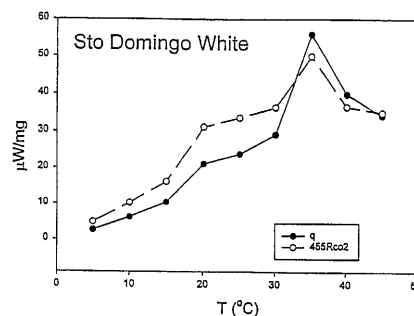


Figure 5—As in figure 1 but for the Santo Domingo White cultivar.

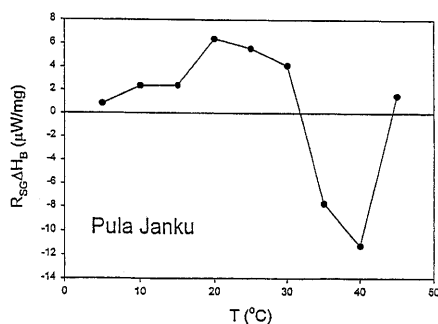
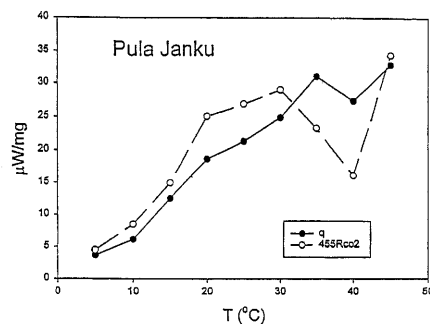


Figure 4—As in figure 1 but for the Pula Janku cultivar.

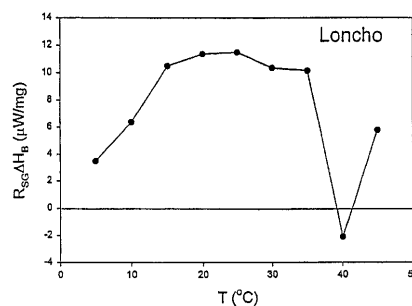
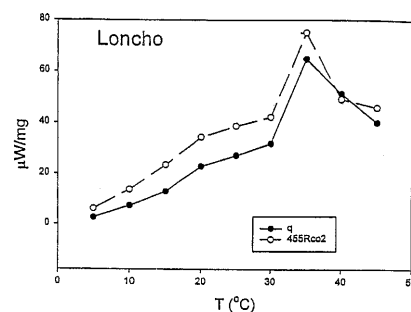


Figure 6—As in figure 1 but for the Loncho cultivar.

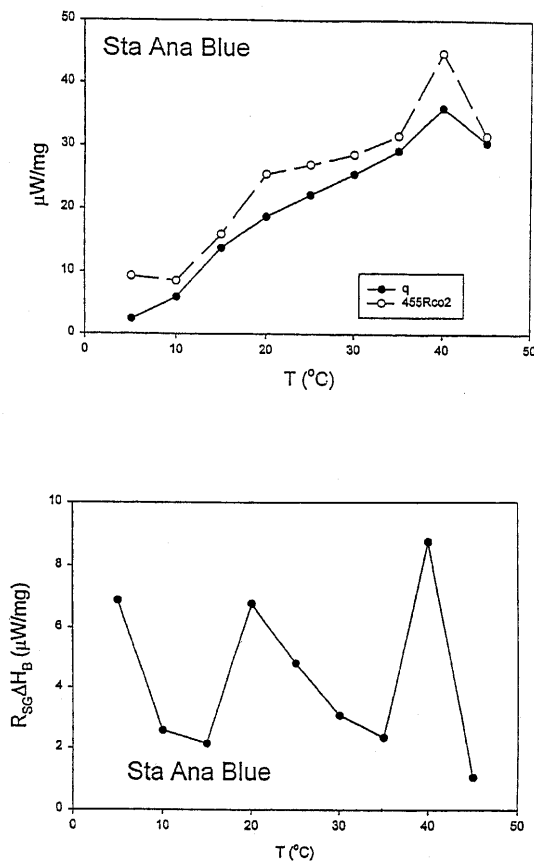


Figure 7—As in figure 1 but for the Santa Ana Blue cultivar.

Although no common cultivars were used in this and a previous study (Taylor and others 1998), the results show many similarities. Data obtained from metabolic measurements at nine temperatures is more definitive, and in essential agreement with the curves calculated from data at two temperatures, for example, Taylor and others 1998.

Different responses to temperature by cultivars (table 1) probably represents adaptation to different climates. All of the cultivars, except perhaps Black Mexican Sweet, exhibit a maximum in the calculated growth rate near 20 °C. Growth rates tend to decline at both higher and lower temperatures. The anomalous point at 5 °C for Santa Ana Blue is probably caused by tissue damage from chilling sensitivity in this cultivar.

Conclusions

- We studied older corn cultivars, however the experts disagree as to which cultivars resemble “old” or “ancestral” varieties. Metabolic measurements made in this and a previous study (Taylor and others 1998) indicate that the 21 cultivars examined have many similarities, and perhaps a common origin.
- Some cultivars are adapted to warm climates. Others are adapted to cooler climates.
- Data obtained from measurements at nine temperatures agrees with that obtained from modelling data at two temperatures, for example, Taylor and others 1998.
- With climatic information and calorimetric measurements, it is possible to quickly select the best cultivar for growth in a given location.

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