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BRIEF COMMUNICATION

Photosynthetic acclimation to temperature is affected by night temperature in *Zea mays*

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Abstract

In this study, *Zea mays* L. was grown in indoor controlled environment chambers with a uniform daytime temperature of 30°C, and night-time temperatures of 30, 25, 20, or 15°C. Responses of net photosynthesis (P_N) of mature leaves at high PPFD to intercellular CO_2 concentrations (C_i) were measured at 20, 25, and 30°C using a new method that generates a complete P_N *vs.* C_i curve in less than four minutes. Results indicated that photosynthesis measured at both C_i values of 25 and 150 μmol mol^{-1} increased strongly with measurement temperature in plants grown with night temperatures of 25 and 30°C, but there was a much smaller change in photosynthesis with temperature in plants grown with night temperatures of 15 or 20°C. These results indicate that the acclimation of photosynthesis to temperature in this C_4 species is substantially affected by night temperature.

Keywords: C_4 photosynthesis; CO_2 response of photosynthesis; night temperature; temperature acclimation.

Some recent studies and reviews about the acclimation of photosynthesis to temperature in C_4 species have ignored any possible role of night temperature (*e.g.*, Massad *et al*. 2007, Smith and Dukes 2017, Yamori *et al*. 2014). The rate of photosynthesis of a mature leaf in a given environmental situation depends on the light and temperature regime during the development of that leaf (*e.g.*, Bunce 1985a). Acclimation of photosynthesis to temperature may affect only the maximum rate of P_N at ambient CO_2, or it may also shift the optimum temperature for P_N, depending upon the species (Yamori *et al*. 2014). Independent control of day and night temperature indicated than maximum rates of P_N were affected primarily by night temperature in *Glycine max*, but by both day and night temperature in *Helianthus annuus* and *Amaranthus hypochondriacus*, a C_4 species (Bunce 1985b). In outdoor environments, the difference in temperature between day and night varies with climate, being larger in less humid climates. Climate warming has shown a larger increase in night than day temperature on a global scale, although the opposite pattern has been observed in some drier environments (Cox *et al*. 2020). Effects of nocturnal warming on crops such as maize (Niu *et al.* 2021) and rice (Peng *et al.* 2004) are receiving increased attention. Because differences between day and night temperature vary, and may change as the climate changes, predictions of photosynthetic properties of leaves, both C_3 and C_4, might benefit from careful consideration of effects of both day and night temperatures on photosynthetic acclimation. In this work, based on the response of *Amaranthus hypochondriacus* to mean temperature (Bunce 1985b), the hypothesis that photosynthetic thermal properties would be affected by night temperature in *Zea mays*, the most agronomically important C_4 crop species, was examined, using controlled environment chambers.

Highlights

- Described a new rapid method for photosynthetic CO_2 response curves
- Grew maize with constant day, various night temperatures
- Low night temperatures flattened photosynthetic temperature curves

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Abbreviations: C_i – intercellular CO_2 concentration; g_s – stomatal conductance; P_N – net photosynthesis; PPFD – photosynthetic photon flux density; V_{Cmax} – the maximal rate of Rubisco carboxylation; V_{Pmax} – the maximal rate of phospho*enol*pyruvate carboxylase carboxylation.

Conflict of interest: The author declares no conflict of interest.

Plants of *Zea mays*. L., cultivar Fisher's Earliest, were grown from seed in three identical controlled environment chambers with different temperature treatments. This cultivar is adapted to cool climates. In all temperature treatments light was provided for 12 h per day at a PPFD of 800 µmol m^{-2} s^{-1} above the plants, from a mixture of high-pressure sodium and metal halide lamps.The concentration of CO_2 was controlled at 400 ± 25 µmol mol^{-1} by injection of pure CO_2 or CO_2-free air under the control of an infrared CO_2 analyzer which sampled chamber air continuously. Plants were grown in 20-cm diameter pots filled with vermiculite and flushed daily with a complete nutrient solution containing 14.5 mM nitrogen. Plants were widely spaced, and there was no overlapping of leaves among plants. Daytime temperature was 30°C, and night-time temperatures of 15, 20, 25, and 30°C were randomly assigned to the chambers. Experiments were repeated, with the night temperature conditions rotated among chambers. Leaf gas-exchange measurements were conducted on the sixth leaf from the bottom of the plant, within a few days after full expansion of that leaf.

Leaf gas exchange was measured using a *CIRAS-4* portable photosynthesis system (*PP Systems*, Amesbury, MA, USA), with a *PLC-4* leaf chamber with a 2.5-cm^2 window and an air flow rate of 350 cm^3 min^{-1}. The measurement PPFD was 1,800 µmol m^{-2} s^{-1} from an equal mixture of red, green, and blue light-emitting diode lamps, which provide a close match to the solar spectrum. This PPFD was saturating to P_N. All gas-exchange measurements were conducted between 2 and 5 h after lights on, in a separate chamber controlled to 23°C, at the same PPFD and CO_2 as the plant growth conditions. Measurements were made at this chamber temperature so that the temperature of the rest of the plant during the leaf gas-exchange measurements would be constant for all growth temperature treatments and leaf measurement temperatures, and thus not cause different leaf photosynthetic responses. The leaf-to-air water vapor pressure difference for leaves in the *PLC-4* leaf chamber averaged 1.1 kPa at the 20°C leaf temperature, 1.4 kPa at 25°C, and 2.0 kPa at 30°C. P_N *vs*. C_i curves for each leaf were first measured at 30°C leaf temperature, followed by 25°C and then 20°C.

At each temperature, leaves were initially equilibrated using a reference CO_2 concentration of approximately 400 µmol mol^{-1} until P_N and stomatal conductance (g_s) were stable. The reference CO_2 concentration was then raised to 500 µmol mol^{-1} and then immediately programmed to decrease linearly at 150 µmol mol^{-1} per min to zero. By adding an extra volume (approximately 12 cm^3) to the reference air stream, a volume which depended on the air flow rate through the leaf chamber, the linear change in reference CO_2 could be made to result in zero difference between the sample and reference CO_2 concentrations in the absence of a leaf. Therefore, the difference in CO_2 concentration between sample and reference airstreams in the presence of a leaf directly indicated the net CO_2 exchange rate at that CO_2 concentration. This new method, a simpler and faster alternative to the RACiR method (Stinziano *et al.* 2017) thus allows the direct measurement of P_N *vs*. C_i curves, with no post-processing of the data or empty chamber measurements required. This new method produces real-time P_N *vs*. C_i curves, while the RACiR method requires a complete empty chamber P_N *vs*. C_i curve, subtraction of the curves with and without leaves, and recalculation of P_N and C_i values at each CO_2 concentration to correct for changes in instrument sensitivity to CO_2 with background CO_2. This later correction, for changes instrument sensitivity to CO_2 with background CO_2, is built into the *CIRAS-4* operating system. An example of comparing this rapid method of developing P_N *vs*. C_i curves with traditional steady-state measurements is given in Fig. 1. Nearly identical P_N values occurred at each C_i level using both methods (Fig. 1). For these P_N *vs*. C_i curves, where ambient CO_2 ranged from 500 to 0 µmol mol^{-1}, the new method took about 3.5 min per leaf at one temperature, compared with about 20 min to generate a steady-state P_N *vs*. C_i curve with eight steps in CO_2, under the same conditions. For each measured leaf, the P_N and C_i values of leaves initially equilibrated to a given temperature at a CO_2 of 400 µmol mol^{-1} were compared with P_N values at the same C_i obtained during the CO_2 ramp. No discrepancies occurred.

Complete P_N *vs*. C_i curves at 30, 25, and 20°C were determined for leaves of four plants per species per night-time growth temperature. Because of the small plant to plant variation in leaf gas exchange, this was enough replication to statistically demonstrate effects of night temperature on parameters of the P_N *vs*. C_i curves. To summarize the curves, P_N rates at C_i values of 25 µmol mol^{-1} and at 150 µmol mol^{-1} were utilized. The P_N rates at 25 µmol mol^{-1} probably indicate the maximum rates of PEP carboxylation (von Caemmerer 2021), and the P_N rates at 150 µmol mol^{-1} probably indicate the maximum rates of Rubisco carboxylation (von Caemmerer 2021). The P_N rates measured at 150 µmol mol^{-1} were about 10% less than the CO_2-saturated rates. One-way analysis of variance was used to test separately for effects of measurement temperature on P_N rates measured at each of the two C_i values, for each growth temperature condition.

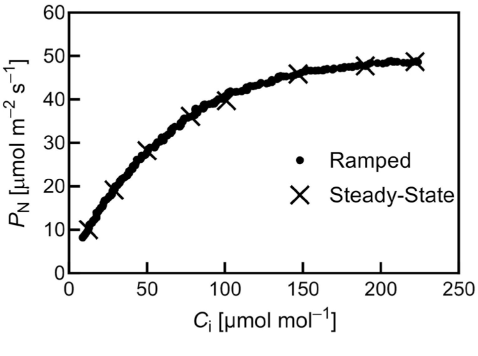

Fig. 1. Responses of net photosynthesis (P_N) to intercellular CO_2 concentration (C_i) measured on one leaf, using either linearly ramped CO_2, or steady-state CO_2. The leaf temperature was 30°C. Each symbol represents a single data point.

When P_{N} was measured at a C_{i} of 25 µmol mol^{-1}, P_{N} was increased very little, and not significantly, by increasing measurement temperature from 20 to 30°C in plants grown with night temperatures of either 15 or 20°C (Fig. 2). However, when plants were grown with either 25 or 30°C night temperatures, P_{N} at a C_{i} of 25 µmol mol^{-1} increased significantly with increasing measurement temperature from 20 to 30°C (Fig. 2).

Similarly, for P_{N} measured at a C_{i} of 150 µmol mol^{-1}, P_{N} was not increased significantly by increasing measurement temperature from 20 to 30°C in plants grown with night temperatures of 15 or 20°C but increased significantly with measurement temperature when grown with night temperatures of 25 and 30°C (Fig. 2).

However, despite these similar patterns, a clear difference in pattern occurred between P_{N} measured at C_{i} of 25 and 150 µmol mol^{-1}. When measured at the higher C_{i}, plants grown with the two lowest night temperatures had leaves with higher maximum P_{N} at 20°C. In contrast, when measured at the lower C_{i}, plants grown with the two highest night temperatures had leaves with higher P_{N} measured at 30°C (Fig. 2).

Another way of summarizing this data is that P_{N} at low C_{i} was strongly increased by higher night growth temperatures when P_{N} was measured at 30°C but not when measured at 20°C. In contrast, P_{N} measured at the higher C_{i} was strongly increased by low night growth temperature when P_{N} was measured at 20°C, but not when measured at 30°C.

Overall, the change in P_{N} over the range of 20 to 30°C measurement temperature was much greater in plants grown with higher night temperatures than in plants grown with cooler night temperatures in this experiment, where daytime temperature was a constant 30°C. Clearly, night temperature affected the acclimation of photosynthesis to growth temperature in this important C_4 species.

The responses found here differ in several ways from those reported by Smith and Dukes (2017) in which the several species were always grown with night temperature equal to day temperature, with plants that were exposed to altered temperatures for only five days. They did not test whether other changes occurred after five days. For the C_4 species, they found no evidence of acclimation of P_{N} measured at high C_{i}, taken as the maximum rate of Rubisco carboxylation (V_{Cmax}), to temperature. From their data in Fig. 2, the 'activation energy' (E_a) for V_{Cmax} was about 90 kJ mol^{-1} between 20 and 30°C, where activation energy (E_a) was calculated as the slope of $1/V_{\text{Cmax}}$ *vs.* 1/T (in °K). For P_{N} measured at low C_{i}, their estimates of the maximum capacity of PEP carboxylase (V_{Pmax}) increased to higher temperatures in plants treated with higher temperatures, but most of the V_{Cmax} responses to temperature peaked below 35°C (Smith and Dukes 2017; Fig. 2), suggesting that Rubisco was deactivated as measurement temperature increased (Farquhar *et al.* 1980).

In this experiment, calculating an activation energy (E_a), from the changes in P_{N} with temperature from 20 to 30°C for P_{N} measured at a C_{i} of 25 µmol mol^{-1}, yielded E_a values of about 40 to 50 kJ mol^{-1} for plants grown with night temperatures of 25 and 30°C, but about 10 to 15 kJ mol^{-1} for plants grown with night temperatures of 15 and 20°C. These values for E_a of V_{Pmax} are all much lower than value of 76 kJ mol^{-1} found by Massad *et al.* (2007) in maize grown at about 23/20°C day/night temperatures, and some are even much lower than the value of 50 kJ mol^{-1} reported by Boyd *et al.* (2015) for *Setaria viridis*.

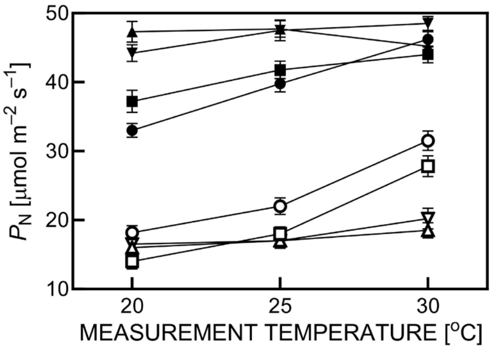

Fig. 2. Net photosynthesis (P_{N}) as a function of leaf temperature in leaves of maize grown with a daytime temperature of 30°C, with night-time temperatures of 30°C (*circles*), 25°C (*squares*), 20°C (*triangles*), or 15°C (*inverted triangles*). *Closed symbols* are for measurements at an intercellular CO_2 concentration (C_{i}) of 150 µmol mol^{-1}, and *open symbols* are for measurements at a C_{i} of 25 µmol mol^{-1}, as interpolated from ramped P_{N} *vs.* C_{i} plots, such as in Fig. 1. *Vertical bars* indicate SE for $n = 4$. Measurement temperature effects were significant for leaves of plants grown with night temperatures of 25 and 30°C, for both measurement C_{i} values.

For measurements of P_{N} at a C_{i} of 150 µmol mol^{-1}, the temperature response curves in this experiment did not increase exponentially between 20 and 30°C, so activation energy analysis is suspect. Nevertheless, the calculated E_a values were about 12 and 24 kJ mol^{-1} for night temperatures of 25 and 30°C, respectively, and 7 and –4 kJ mol^{-1} for plants grown at 15 and 20°C night temperatures, respectively. Assuming that P_{N} measured at $C_{\text{i}} = 150$ µmol mol^{-1} reflects Rubisco activity, typical values of E_a for C_4 plants are 50–78 kJ mol^{-1} (Massad *et al.* 2007), which is much higher than any of the values observed here for *Zea mays*, regardless of growth temperature. Similar discrepancies between Rubisco enzyme and P_{N} responses to temperature have been noted before and attributed to deactivation of Rubisco by increasing temperature (Dwyer *et al.* 2007). If deactivation of PEP carboxylase and Rubisco as temperature increases occurs commonly, and differs between growth temperature regimes, as indicated by these experiments, ecologically useful models of C_4 photosynthesis will need to be able to predict the activation status of both of these enzymes.

Regardless of the biochemical mechanisms responsible for the various responses photosynthesis to temperature, the results presented here clearly indicate that the night-time growth temperature can greatly affect photosynthetic responses to measurement temperature, supporting our hypothesis of an effect, and identifying another environmental variable that needs to be considered in photosynthetic acclimation to temperature in C_4 plants. In the case of maize observed here, increasing night temperatures would increase the sensitivity of photosynthesis to the measurement temperature.

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