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Growth temperature can alter the temperature dependent stimulation of photosynthesis by elevated carbon dioxide in *Albutilon theophrasti*

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Stimulation of photosynthesis in response to elevated carbon dioxide concentration [CO_2] in the short-term (min) should be highly temperature dependent at high photon flux. However, it is unclear if long-term (days, weeks) adaptation to a given growth temperature alters the temperature-dependent stimulation of photosynthesis to [CO_2]. In velveltleaf (*Albutilon theophrasti*), the response of photosynthesis, determined as CO_2 assimilation, was measured over a range of internal CO_2 concentrations at 7 short-term measurement (12, 16, 20, 24, 28, 32, 36°C) temperatures for each of 4 long-term growth (16, 20, 28 and 32°C) temperatures. In vivo estimates of V_{Cmax}, the maximum RuBP saturated rate of carboxylation, and J_{max}, the light-saturated rate of potential electron transport, were determined from gas exchange measurements for each temperature combination. Overall, previous exposure to a given growth temperature adjusted the optimal temperatures of J_{max} and V_{Cmax} with subsequently greater enhancement of photosynthesis at elevated [CO_2] (i.e., a greater enhancement of photosynthesis at elevated [CO_2] was observed at low measurement temperatures for *A. theophrasti* grown at low growth temperatures compared with higher growth temperatures, and vice versa for plants grown and measured at high temperatures). Previous biochemical based models used to predict the interaction between rising [CO_2] and temperature on photosynthesis have generally assumed no growth temperature effect on carboxylation kinetics or no limitation by J_{max}. In the current study, these models over predicted the temperature dependence of the photosynthetic response to elevated [CO_2] at temperatures above 24°C. If these models are modified to include long-term adjustments of J_{max} and V_{Cmax} to growth temperature, then greater agreement between observed and predicted values was obtained.

Introduction

Because of the kinetic properties of Rubisco, it is generally anticipated that the stimulation of photosynthesis by rising [CO_2] will increase strongly with temperature (Long 1991, Kirschbaum 1994). The potential interaction between higher temperature and increasing carbon dioxide has clear implications with respect to global vegetation as atmospheric carbon dioxide increases. For the cooler climates a lower stimulation of photosynthesis and growth might be anticipated, while a greater stimulation would be expected in tropical climates.

The dependence of the CO_2-induced stimulation is related both to temperature induced changes in CO_2/O_2 solubility and the kinetic characteristics of the ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) enzyme. Increasing temperature reduces the ratio of [CO_2]/[O_2] in solution, shifting Rubisco specificity to oxygenase and a subsequent enhancement of photorespiration. Since photorespiratory carbon loss increases with temperature, and since rising [CO_2] shifts Rubisco activity toward carboxylase, rising [CO_2] should stimulate net photosynthesis more as temperature rises. Because Rubisco characteristics are, in general, conservative, the photosynthetic response to rising [CO_2] is anticipated to demonstrate a consistent temperature dependence among C_3 species. A number of studies show that the predicted temperature dependence of photosynthetic stimulation with increasing carbon dioxide is consistent with the kinetic characteristics of Rubisco (e.g., Idso et al. 1987, Long 1991, Sage et al. 1995).

Abbreviations – A, photosynthetic CO_2 assimilation rate; J, potential rate of electron transport; J_{max}, light saturated potential rate of electron transport; PPF, photosynthetic photon flux; TPU, triose phosphate utilization; V_{Cmax}, maximum RuBP saturated rate of carboxylation; Wj, RuBP limited rate of carboxylation; Wc, RuBP saturated rate of carboxylation.

However, there have also been a number of studies indicating that some species can have greater or lesser than expected photosynthetic stimulation by elevated carbon dioxide at low or high temperatures (Ziska and Bunce 1994, Greer et al. 1995, Tesky 1997, Bunce 1998). While it is recognized that differences in the degree of long-term photosynthetic acclimation to elevated [CO_2] can obscure the interaction of temperature and [CO_2] (e.g., Ziska and Bunce 1994, Bunce 1998, Tjoelker et al. 1998), inconsistencies in the temperature dependence of photosynthetic stimulation with additional [CO_2] have also been reported with short-term temperature exposure (cf., Bunce 1998).

Since the predicted response of photosynthesis to interactions of temperature and elevated [CO_2] is based on the kinetic properties of Rubisco, inconsistencies in the short-term response suggest potential long-term adjustments of Rubisco properties to growth temperature. Temperature-dependent changes in Rubisco properties could include changes in Rubisco specificity or V_{Cmax} (Bunce 1998). Inconsistencies could also be related to non-Rubisco properties as well, such as the temperature dependence of RuBP regeneration and J_{max}, which is assumed to be non-limiting in some biochemical models (Long 1991, Bunce 1998). Recent results from Niinemets et al. (1999) indicate that temperature can vary with canopy depth for deciduous trees with J_{max} being more responsive to lower temperatures relative to high temperature acclimated leaves. This result suggests long-term temperature-related adjustments in photosynthetic properties. Whether a similar result occurs in conjunction with prior exposure to a range of growth temperatures is unclear.

To determine whether long-term exposure at a given growth temperature can alter photosynthetic properties with subsequent changes in the dependence on measurement temperature of photosynthetic stimulation with increasing [CO_2], Velvetleaf (*Albutilon theophrasti*), a warm season weedy annual, was grown at 4 growth temperatures and at measurement temperatures from 12 to 36°C.

Materials and methods

Experiments were conducted in controlled environment chambers located at the Climate Stress Laboratory USDA-ARS, Beltsville, MD using Velvetleaf (*A. theophrasti* L.). Seed for Velvetleaf was obtained from local populations at the Beltsville experimental farm.

For each controlled environment chamber (EGC Corp., Chagrin Falls, OH, USA), the CO_2 concentration was controlled by continuous flushing with CO_2-free air, then re-injection with CO_2 to maintain the desired CO_2 concentration. Injection of CO_2 was controlled by an absolute infra-red gas analyzer (WMA-2, PP Systems, Haverhill, MA, USA), which sampled air continuously. The set point for CO_2 was 370 μmol mol^{-1}. Actual [CO_2] for an average 24-h period was 381 ± 16 μmol mol^{-1}. Since only one pair of chambers was available, the same experiment was repeated 4 times at constant day/night growth temperatures of 16, 20, 28 and 32°C. In all experiments, plants received 14 h of 1000 μmol m^{-2} s^{-1} photosynthetic photon flux (PPF) at the upper leaf level from a mixture of incandescent, high pressure sodium and metal halide lamps (GE Corp., Glen Ellen, VA, USA). At temperatures up to 32°C, average daily relative humidity (RH) exceeded 60%, whereas above 32°C, average daily RH was $\sim$45%. Temperature, [CO_2] and RH were monitored and recorded at 1-min intervals by an EGC network datalogger (EGC Corp.) in conjunction with a PC.

Two to 3 seeds were sown in 15-cm-diameter plastic pots filled with $\sim$1.8 l of vermiculite. All pots were thinned to one seedling within 2–3 days following emergence. Eight new pots were planted at 5–10-day intervals (depending on growth temperature) until 7 cohorts were established. When Velvetleaf began initiation of the fourth leaf stage (Huan index of $\sim$3.5) for a given cohort, 8 pots were transferred to a second environmental growth chamber maintained at one of 7 measurement temperatures, 12, 16, 20, 24, 28, 32 or 36°C. Pots were arranged to avoid shading each other. All pots were watered daily to the drip point (twice daily at 36°C) with complete nutrient solution containing 13.5 m*M* nitrogen (Robinson 1984).

All gas-exchange measurements were made initially (4–6 h) after transfer from a given growth temperature to a measurement temperature for leaves which had developed completely under the prior temperature regime and again (5–10 days later) for younger leaves, which had completely developed under the new measurement temperature. At the end of 5–10 days, the measurement temperature was changed and the next cohort was introduced to a new measurement temperature and the gas exchange measurements repeated. This was done for all 7 measurement temperatures for growth temperatures of 16, 20, 28 and 32°C.

Both initial and later measurements of single leaf photosynthesis (measured as A, the rate of CO_2 assimilation) were determined on the uppermost fully expanded leaf for 3 plants at each measurement temperature for a given growth temperature. Measurements were made using a portable open gas exchange system incorporating infra-red CO_2 and water vapor analyzers for determining net photosynthetic CO_2 uptake rate and stomatal conductance (CIRAS-1, PP Systems, Haverhill, MA, USA). PPF was supplied by a separate light unit, which produced a constant value of 1640 μmol m^{-2} s^{-1} for all measurements of gas exchange. The water vapor pressure surrounding the leaf during all measurements was less than 2.0 kPa. Leaf temperature was maintained within 1°C of the measurement temperature. All data were collected on a PC using the remote-controlled operating system software supplied by CIRAS. To determine assimilation for a wide range of values, different [CO_2]s were obtained using the internal CO_2 mixing system (with CO_2 cartridge) provided with the CIRAS-1 system. The response of leaf assimilation rate (A) to intercellular carbon dioxide concentration (C_i) was determined at 5 external CO_2 concentrations (C_a), 50, 100, 150, 370 and 740 μmol mol^{-1}. Initially, leaves were measured at ambient [CO_2] (i.e., 370 μmol mol^{-1}), then the C_a was lowered to 50 μmol mol^{-1} and increased in steps to 740 μmol mol^{-1}. In changing to a new [CO_2], sufficient time was given (10–15 min) to allow for a steady-state condition prior to the measurement of assimilation rate.

V_{Cmax} and J_{max} were calculated from the low and high C_i regions of the A versus C_i response using the methods of Bunce (1998) and Wullschleger (1993), respectively. Estimating J_{max} by this method included using A at elevated [CO_2] where C_i was still limiting to A. This reduced the possible influence of TPU limitation on the estimate of J_{max}. For V_{Cmax} the calculation requires assumptions regarding the temperature dependencies of other kinetic parameters of Rubisco and the relationship of O_2 to CO_2 flux in photorespiration (see Harley et al. 1992). Measurements of V_{Cmax} and J_{max} were obtained for leaves, which had developed completely under each measurement temperature for all growth temperatures.

A biochemical model of C_3 photosynthesis was used to help clarify the observed experimental results in relation to the temperature dependence of photosynthesis at elevated [CO_2]. The model was based on that of Farquhar et al. (1980) incorporating the dependency functions for the solubilities of oxygen and carbon dioxide and the kinetic characteristics of Rubisco used by Long (1991) with either W_c or W_j as the limiting factor to A. The equation is given as follows:

$$A = [1 - \Gamma^*/C_i] \times \min[W_c,\ W_j] - R_d$$

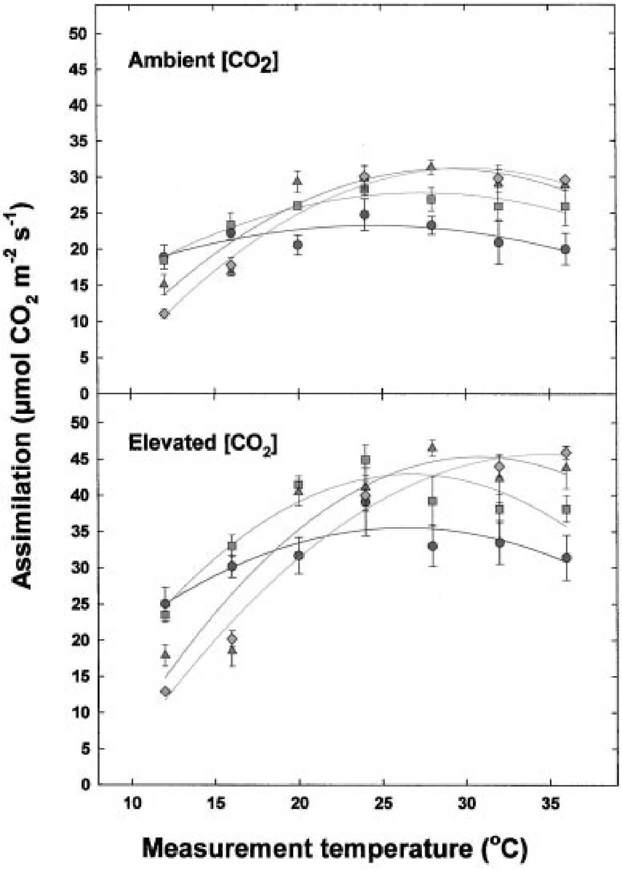

Fig. 1. The temperature dependence of the carbon dioxide assimilation rate (A) at ambient (370 μmol mol^{-1}) and elevated (740 μmol mol^{-1}) [CO_2] for *A. theophrasti* grown at 4 growth temperatures, 16°C (circles), 20°C (squares), 28°C (triangles) and 32°C (diamonds). Each point is the mean of 3 measurements on different leaves.

where A is the net leaf rate of CO_2 uptake per unit leaf area, Γ^* is the CO_2 compensation point of photosynthesis in the absence of dark respiration, C_i is the intercellular concentration of CO_2 in the air, R_d is dark respiration rate and W_c and W_j are the RuBP saturated rate of carboxylation and RuBP limited rate of carboxylation, respectively. These limitations are determined as:

$$W_c = (V_{Cmax} \times C_i)/C_i + K_c\,[1 + O_i/K_o]$$

and

$$W_j = (J \times C_i)/(4.5C_i + 10.5\Gamma^*)$$

where V_{Cmax} is the maximum RuBP saturated rate of carboxylation, K_c and K_o are the Michaelis constants for CO_2 and O_2, respectively, O_i is the intercellular concentration of O_2 in air and J is potential rate of electron transport. A complete description of the equations and temperature dependency functions is given in Long (1991). The Long model was used to predict the temperature dependence of the response of photosynthesis to elevated [CO_2] with these values compared to observed experimental values. When short-term responses of photosynthesis to elevated [CO_2] at different measurement temperatures differed substantially from the predicted [CO_2] temperature interaction, the model was revised and run using experimentally derived values of V_{Cmax}, and J_{max} obtained from the A versus C_i response.

Results

The increase in A with measurement temperature varied as a function of growth temperature with the optimum temperature for A shifting from ~24 to 32°C for plants grown at 16 and 32°C, respectively (Fig. 1). The shift in the optimal temperature for A was similar for leaves measured at both ambient and 740 μmol mol^{-1} (elevated) [CO_2] (Fig. 1). In contrast to the Long model (1991) of higher optimal temperatures for A at elevated CO_2, nearly the same optimal temperature for A was observed at 370 and 740 μmol mol^{-1} (Fig. 1). The least amount of variation among growth temperatures in the values of A was observed at a measurement temperature of 24°C (Fig. 1). Minimal differences were observed between the temperature dependency of photosynthetic response to [CO_2] for leaves exposed in the short-term (i.e., hours) to a given measurement temperature and new leaves which actually developed at that temperature (Table 1). The relative photosynthetic enhancement from 370 to 740 μmol mol^{-1} did increase to a greater extent for the higher growth temperatures at the higher measurement temperatures; however, the relative response of A to measurement temperature was approximately the same for both groups at a given growth temperature (Table 1). Overall, the relative enhancement of photosynthesis for leaves measured at elevated [CO_2] only increased slightly (and not significantly) with increasing growth temperatures to 32°C (e.g., 1.35, 1.59, 1.49 and 1.48 after 5–10 days, Table 1).

Interestingly, at either low or high measurement temperatures, growth temperature influenced the response of A to

Table 1. Relative enhancement of single leaf photosynthesis (determined as assimilation, μmol CO_2 m^{-2} s^{-1}) as a function of growth and measurement temperature. Relative enhancement was determined as the ratio of A at a C_a of 740 μmol mol^{-1} to A at a C_a of 370 μmol mol^{-1}. Initial data were obtained 1–4 h after transfer to measurement temperature. Data from 5–10 days were obtained for leaves, which had developed after transfer to the new measurement temperature. *A significant increase in single leaf photosynthesis at the elevated relative to the ambient CO_2 condition (*t*-test) for a specific growth/measurement temperature.

Measurement temperature (°C)	Growth temperature (°C)			
	16	20	28	32
Initial response				
12	1.35*	1.29*	1.11	1.11
16	1.45*	1.32*	1.22*	1.06
20	1.47*	1.59*	1.35*	N/A
24	1.59*	1.65*	1.41*	1.26*
28	1.58*	1.64*	1.49*	N/A
32	1.59*	1.64*	1.51*	1.42*
36	1.38*	1.40*	1.68*	1.84*
After 5–10 days				
12	1.32*	1.27*	1.19	1.16
16	1.35*	1.41*	1.10	1.13
20	1.54*	1.59*	1.38*	N/A
24	1.58*	1.59*	1.38*	1.33*
28	1.42*	1.46*	1.49*	N/A
32	1.60*	1.47*	1.46*	1.48*
36	1.43*	1.47*	1.52*	1.55*

C_i (Fig. 2). As a consequence, the stimulation of carbon assimilation by short-term exposure to elevated CO_2 and measurement temperature was greatly influenced by the previous growth temperature. For example, at a measurement temperature of 12°C, *A. theophrasti* grown at 16 and at 32°C, showed a 32 and 16% photosynthetic stimulation, respectively, at elevated CO_2; whereas at a measurement temperature of 36°C, the greatest relative enhancement was observed for growth temperatures of 32°C compared with a growth temperature of 16°C (56 versus 43%, Fig. 3).

The slope of the initial response of A versus C_i had an optimum temperature which ranged from ~24 to 36°C depending on growth temperature (Fig. 4). At lower measurement temperatures, lower growth temperatures produced plants with higher initial slopes. For example, at 12°C, the initial slope of the A/C_i response for a growth temperature of 16°C was approximately twice that of an initial slope for a growth temperature of 32°C (Fig. 4). Conversely, at a measurement temperature of 36°C, higher growth temperatures produce plants with higher initial slopes. For example, the initial slope of the A/C_i response for a growth temperature of 32°C, was twice that of an initial slope for a growth temperature of 16°C. The relative differences in initial slope were significantly different at measurement temperatures of 12 and 36°C for growth temperatures of 16 and 32°C according to a *t*-test. No signifi-

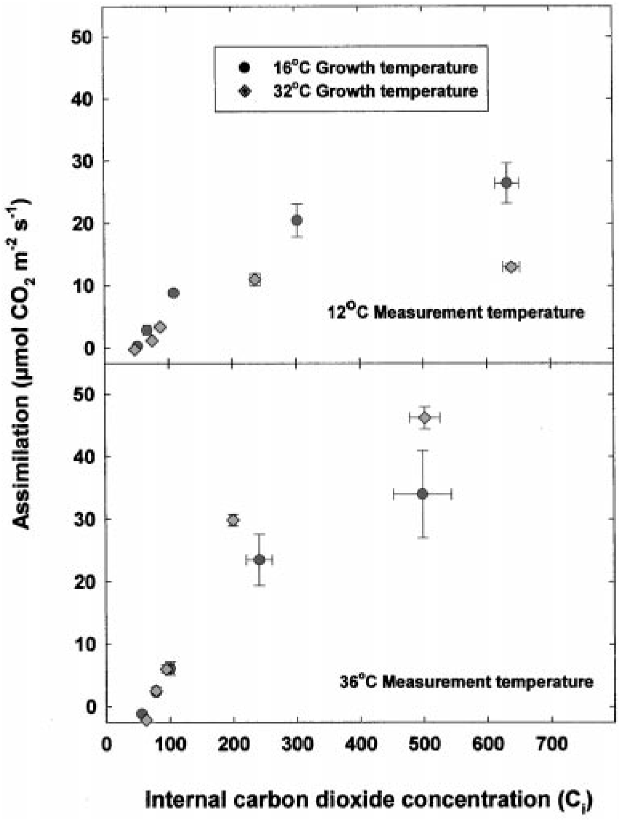

Fig. 2. The response of carbon dioxide assimilation (A) as a function of internal carbon dioxide concentration (C_i) for *A. theophrasti* at two extreme measurement temperatures (12 and 36°C) for plants at growth temperatures of 16 and 32°C. Data were taken for leaves, which had been allowed to develop at the measurement temperature. Each point is the mean of 3 measurements on different leaves.

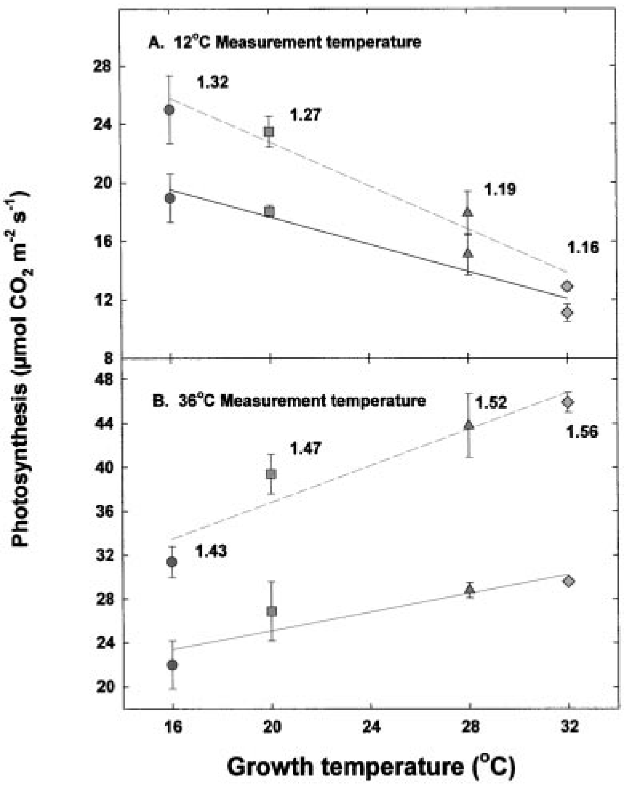

Fig. 3. Same as Fig. 1, but for leaves grown and measured at the same temperature. Dashed and solid lines indicate elevated and ambient [CO_2] conditions, respectively. Values above the dashed line represent the relative enhancement (E/A) with elevated [CO_2]. Relative enhancements for the full range of measurement and growth temperatures are given in Table 1. Each point is the mean of 3 measurements on different leaves.

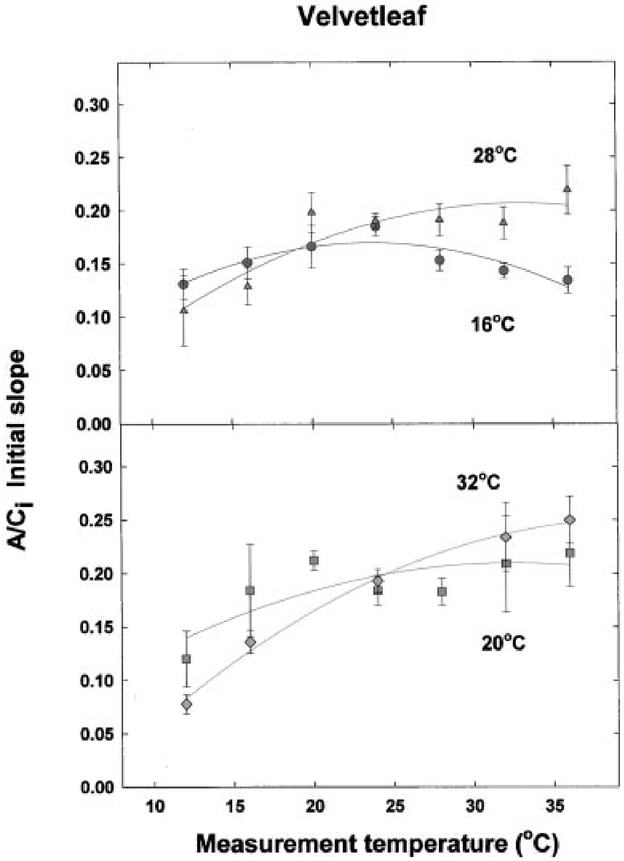

Fig. 4. The temperature dependence of the initial slope of the A versus C_i response for *A. theophrasti* grown at 4 different growth temperatures. Data are from leaves which developed after plant was transferred to new measurement temperature (5–10 days). Symbols are the same as Fig. 1. Each point is the mean of 3 measurements on different leaves.

cant differences were observed at a measurement temperature of 24°C for any growth temperature (Fig. 4).

The dependency of photosynthetic electron transport rates (J) to measurement temperature exhibited a trend similar to the initial A/C_i slope (Fig. 5). That is, the relative response at low or high measurement temperatures was a function of the previous growth temperature with significant increases in J at a measurement temperature of 12 for a growth temperature of 16 relative to 32°C; while significant increases in J at 36°C were observed for a growth temperature of 32 relative to 16°C ($P = 0.05$, *t*-test). Overall, values of J rose with increasing measurement temperature for the lower growth temperatures (i.e., 16, 20°C) up to an optimal value between 25 and 30°C; whereas for the higher growth temperatures (28, 32°C), J rose to an optimal value between 30 and 35°C (Fig. 5).

Discussion

The rather flat temperature dependence of photosynthetic stimulation at elevated [CO_2] observed here (Table 1) is similar to the interaction of elevated [CO_2] and temperature observed in some studies. Such studies do not demonstrate a strong increase in CO_2 stimulation at high temperatures, but indicate little change in the relative stimulation in photosynthesis by elevated [CO_2] over a range of temperatures (Jones et al. 1985, Sionit et al. 1987, Campbell et al. 1990, Ziska and Bunce 1994, Greer et al. 1995).

It is recognized that differences in the extent of long-term photosynthetic acclimation to elevated [CO_2] can obscure the interaction of temperature and [CO_2] on photosynthetic stimulation (e.g., Ziska and Bunce 1994); however, in the current study leaves were only exposed in the short term to elevated [CO_2] and the extent of photosynthetic stimulation was similar for leaves with immediate exposure to a measurement temperature, or for leaves which were allowed to develop at that measurement temperature (cf., Kirschbaum and Farquhar 1984).

Overall, it was determined that photosynthetic adjustment to a given growth temperature involved changes in both the absolute values and the temperature dependencies of both the initial slope of A versus C_i (Rubisco activity) and A at high C_i (RuBP regeneration). Such changes imply that growth conditions such as temperature can affect the relative temperature sensitivities of carboxylation and other kinetic parameters of Rubisco or the PCR cycle with subsequent effects on the temperature response of photosynthesis. Although changes in J_{max} and V_{Cmax} are suggested by these measurements, such changes are often not taken into consideration by those utilizing Farquhar-type photosynthesis

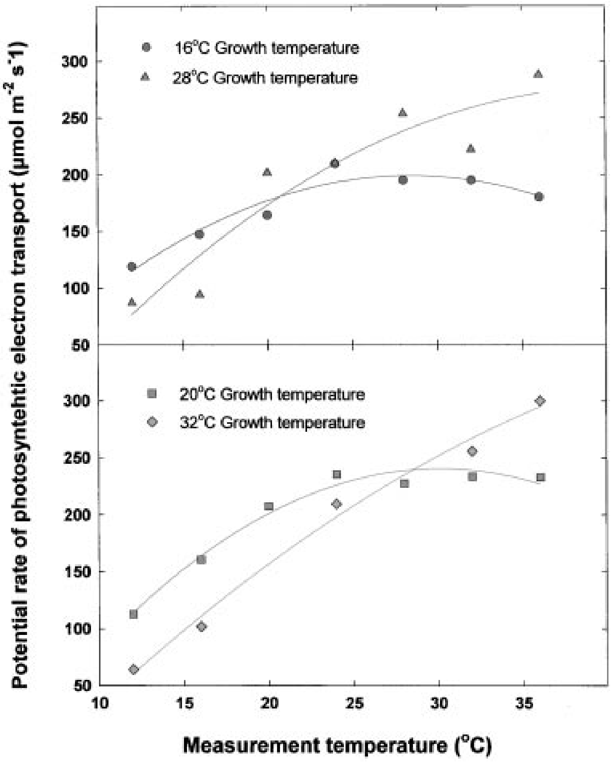

Fig. 5. The temperature dependence of photosynthetic electron transport rates (J) calculated from the response of A to C_i for a range of measurement temperatures for 4 growth temperatures (16, 20, 28 and 32°C). Symbols are as Fig. 1. Each point is the mean of 3 measurements on different leaves after development at the measurement temperature.

models to predict the temperature dependence of photosynthetic stimulation at elevated [CO_2] (e.g., Long 1991).

How well does a photosynthetic model based on the kinetic properties of Rubisco predict the temperature-dependent stimulation of A with short-term increases in [CO_2] for *A. theophrasti*? In the current study, such a model, modified using the temperature dependencies of Long (1991), agreed closely with the initial response of leaves to a new measurement temperature, but only for measurement temperatures up to ~24°C. At temperatures above 24°C the model deviated significantly from the observed results (Fig. 6A). If V_{Cmax} is varied as an input parameter, utilizing data generated from the A/C_i response, there is slightly less photosynthetic stimulation by elevated [CO_2] with increasing temperature, but agreement above measurement temperatures of 24°C is still poor (Fig. 6B).

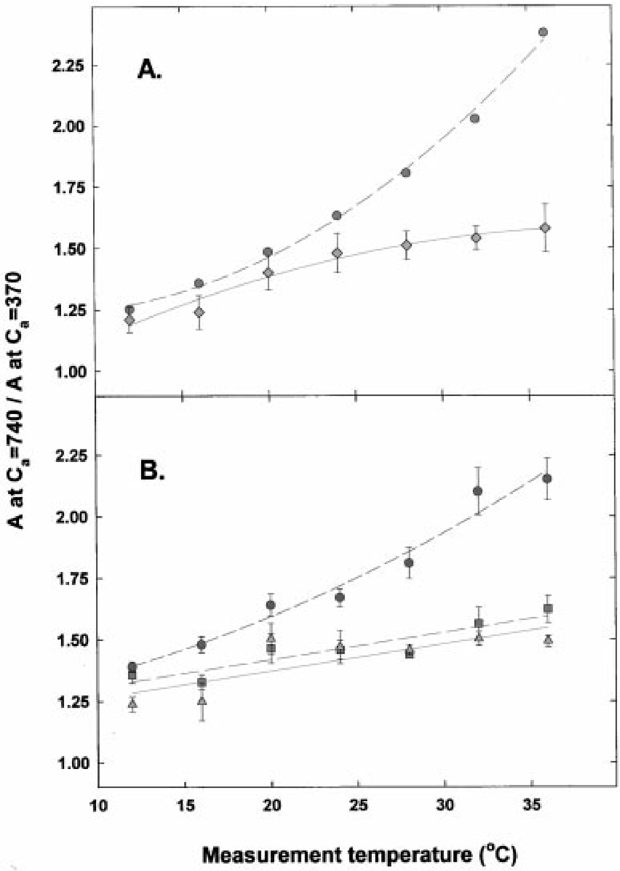

Fig. 6. The temperature dependence of the relative photosynthetic stimulation at elevated [CO_2] for *A. theophrasti*. Modeled (circles) and the immediate response to measurement temperature and elevated [CO_2] averaged over all growth temperatures (diamonds) are shown in (A). The model was based on that of Farquhar et al. (1980) incorporating the dependency functions for the solubilities of oxygen and carbon dioxide and the kinetic characteristics of Rubisco used by Long (1991). Variations of the standard model are shown in (B). If V_{Cmax} is varied as an input parameter, over prediction of the photosynthetic stimulation with elevated [CO_2] was still observed (circles); however, if V_{Cmax} and J_{max} are varied according to gas exchange data, consistent response between calculated (squares) and the relative stimulation at elevated [CO_2] for leaves allowed to develop at the measurement temperature was observed.

There are several reasons why the short-term relative stimulation of photosynthesis from 370 to 740 µmol mol^{-1} might be less than expected from the specificity of Rubisco. These include assimilation at elevated [CO_2] becoming limited by regeneration of RuBP (J_{max}) or limitation of assimilation rate by inorganic phosphate (TPU limitation). TPU limitations are indicative of low temperature and O_2 (or CO_2) insensitivity above ambient conditions (see Sage and Sharkey 1987, Wullschleger 1993). In the current experiment, however, decreasing relative stimulation of photosynthesis at high [CO_2] was not associated with CO_2 insensitivity above ambient conditions at high measurement temperature (see Fig. 2), suggesting that TPU limitation did not occur. This leaves J_{max} limitation as the likely explanation.

There is recent data for a tree species, *Populus tremula*, demonstrating temperature variation of photosynthesis within the canopy profile (Niinemets et al. 1999). Interestingly, the J_{max} of leaves, which have acclimated to colder temperatures, were more responsive photosynthetically to lower temperatures than that of high temperature acclimated leaves (Niinemets et al. 1999). Hikosaka et al. (1999) has also recently reported that growth temperature altered the temperature dependencies of RuBP carboxylation and regeneration in another tree species, *Quercus myrsinaefolia*. Similarly, in the current experiment with *A. theophrasti*, plants grown at lower temperatures had shifts in the optimal response of J relative to plants grown at higher temperatures (and vice versa, Fig. 5). In fact, if the temperature dependence of RuBP regeneration is accounted for, by inserting J as a controlling parameter in addition to V_{Cmax}, a significant correlation ($R^2 > 0.95$) is observed between the modeled response and the actual temperature dependence of photosynthetic stimulation with elevated [CO_2] for *A. theophrasti* (Fig. 6B).

It has also been shown recently that there are clear distinctions between cool and warm climate species in the direction of change in the absolute values of J_{max} and V_{Cmax} (Bunce 2000). The data presented here for *A. theophrasti* likewise suggest that within a given species, the optimal photosynthetic response adjusted as a function of climate. As a consequence of this adjustment, the temperature dependence of photosynthetic stimulation with exposure to elevated [CO_2] was altered as a function of growth temperature.

It has been demonstrated in a number of studies that the anticipated synergy between [CO_2] and temperature does not necessarily materialize at the whole plant level, due in part to temperature-dependent alterations in source/sink parameters (e.g., Rawson 1992, Lin et al. 1997). However, it has been assumed that variation in the temperature dependencies of J_{max} and V_{Cmax} was consistent among a wide range of C_3 species, and could be used to predict the extent of photosynthetic stimulation with concomitant increases in both temperature and [CO_2] (Long 1991). However, a number of recent studies (Bunce 1998, Niinemets et al. 1999, Bunce 2000) utilizing a biochemical approach to predict temperature/[CO_2] photosynthetic interaction indicate that the temperature dependence of photosynthetic stimulation may vary as a function of both species and growth conditions. Data from the current study for *A. theophrasti* suggest that inclusion of absolute values and temperature dependencies, particularly of J_{max}, in response to long-term adjustments in growth temperature could significantly improve the ability to predict the temperature dependence of photosynthetic stimulation with increased levels of atmospheric CO_2.

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