Regular paper

Acclimation of photosynthesis to temperature in eight cool and warm climate herbaceous C$_3$ species: Temperature dependence of parameters of a biochemical photosynthesis model

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Abstract

To determine how parameters of a Farquhar-type photosynthesis model varied with measurement temperature and with growth temperature, eight cool and warm climate herbaceous crop and weed species were grown at 15 and 25 °C and single leaf carbon dioxide and water vapor exchange rates were measured over the range of 15 – 35 °C. Photosynthetic parameters examined were the initial slope of the response of assimilation rate (A) to substomatal carbon dioxide concentration (C$_i$), A at high C$_i$, and stomatal conductance. The first two measurements allow calculation of V$_{Cmax}$, the maximum rate of carboxylation of ribulose bisphosphate carboxylase and J$_{max}$, the maximum rate of photosynthetic electron transport, of Farquhar-type photosynthesis models. In all species, stomatal conductance increased exponentially with temperature over the whole range of 15 – 35 °C, even when A decreased at high measurement temperature. There were larger increases in conductance over this temperature range in the warm climate species (4.3 ×) than in the cool climate species (2.5 ×). The initial slope of A vs. C$_i$ exhibited an optimum temperature which ranged from 20 to 30 °C. There was a larger increase in the optimum temperature of the initial slope at the warmer growth temperature in the cool climate species than in the warm climate species. The optimum temperature for A at high C$_i$ ranged from 25 to 30 °C among species, but changed little with growth temperature. The absolute values of both the initial slope of A vs. C$_i$ and A at high C$_i$ were increased about 10% by growth at the warmer temperature in the warm climate species, and decreased about 20% in the cool climate species. The ratio of J$_{max}$ − V$_{Cmax}$ normalized to 20 °C varied by more than a factor of 2 across species and growth temperatures, but differences in the temperature response of photosynthesis were more related to variation in the temperature dependencies of J$_{max}$ and V$_{Cmax}$ than to the ratio of their normalized values.

Introduction

Models of C$_3$ photosynthesis based on that of Farquhar et al. (1980) are widely and successfully used in many applications. Two key parameters of Farquhar-type photosynthesis models, V$_{Cmax}$ and J$_{max}$, the maximum rate of carboxylation of ribulose bisphosphate carboxylase, and the maximum rate of photosynthetic electron transport, respectively, can be obtained from the initial slope of the response of assimilation rate (A) to substomatal carbon dioxide concentration (C$_i$), and A at high C$_i$, respectively (Farquhar et al. 1980; Wull-

schleger 1993). However, the temperature dependence of these parameters has been experimentally determined in only a few cases. Leuning (1997) summarized the wide variation in the temperature dependencies of these parameters reported in the three studies he identified which provided experimental values. Farquhar and Von Caemmerer (1982) pointed out that variation in the optimum temperature for photosynthesis among species or growth conditions could result from variation in the relative values of the two parameters, V$_{Cmax}$ and J$_{max}$. Given that the optimum temperature for photosynthesis varies widely among species and

with growth temperature (Berry and Bjorkman 1980), it is therefore perhaps surprising how tightly correlated V_{Cmax} and J_{max} are in species comparisons (Wullschleger 1993; Leuning 1997). It could be that the data surveyed by Wullshcleger and reanalysed by Leuning cover too small a temperature range to reflect differing optimum temperatures of photosynthesis, that quite small changes in the ratio of the two parameters result in substantial changes in the optimum temperature for photosynthesis, or that acclimation of photosynthesis to temperature primarily involves changes in the temperature dependencies of V_{Cmax} and J_{max}, rather than the ratio of their absolute values.

Another variable which can affect the response of photosynthesis to temperature is stomatal conductance. For a given set of V_{Cmax} and J_{max} values, the optimum temperature for photosynthesis increases with C_i (Farquhar and Von Caemmerer 1982), and therefore depends on stomatal conductance for a fixed value of external carbon dioxide concentration. Stomatal conductance has sometimes been reported to have an optimum temperature similar to that of photosynthesis, such that the C_i is relatively constant across temperatures, and stomatal conductance has little influence over the response of photosynthesis to temperature. However, in some cases, stomatal conductance decreases more than photosynthesis at high temperature and C_i decreases substantially (e.g. Berryman et al. 1994). Measurements of stomatal conductance at high temperatures are often confounded with high water vapor pressure deficits, and when this is avoided, stomatal conductance may increase with temperatures above the optimum temperature for photosynthesis (e.g. Raschke 1970; Hall et al. 1976) and C_i may thus increase with temperature (e.g. Bunce 1998). It can not, therefore, be ruled out that changes in stomatal conductance with temperature could affect C_i and the optimum temperature of photosynthesis.

The purpose of this work was to determine the temperature dependencies of the initial slope of A vs. C_i, A at high C_i, and stomatal conductance in some common C_3 crop and weed species adapted to warm and cool temperate climates, and to determine the extent to which the temperature dependencies varied with growth temperature.

Materials and methods

Studies were conducted on eight species, *Abutilon theophrasti* M. (velvetleaf), *Brassica rapa* L.

cv. Purple Globe (turnip), *Chenopodium album* L.(lamb's-quaters), *Glycine max* L. Merr. cv. Kent (soybean), *Helianthus annuus* L. cv. Mammoth (sunflower), *Hordeum vulgare* L. Cv. Brant (barley), *Lycopersicon esculentum* Mill. cv. Rutgers (tomato) and *Vicia faba* L. Cv. Longpod (broadbean). The weed species, *Abutilon theophrasti* and *Chenopodium album*, were collected from local Beltsville MD populations. *B. rapa, C. album, H. vulgare* and *V. faba* were considered 'cool climate' species, based on our observations of higher relative growth rate at 17 rather than at 30 °C in these species, but not in the others (not shown). All plants were grown from seed, one plant per pot, in 15 cm diameter pots filled with 1.8 dm^3 of vermiculite and flushed daily with a complete nutrient solution containing 13.5 mM nitrogen. Plants were grown in a single controlled environment chamber set at either 15 or 25 °C constant air temperature. The lower growth temperature was chosen as the lowest temperature at which all of the warm climate species could be grown. The higher growth temperature was chosen as an approximation of the highest long-term mean temperature likely to be encountered in temperate climates. Constant temperatures were used to avoid complications of acclimation to day, night or mean temperatures (Bunce 1985). The relative humidity of the chamber air was 65% and there were 14 h per day of light from 'cool white' fluorescent lamps at a photosynthetic photon flux density (PPFD) of 500 μmol m^{-2} s^{-1}. The carbon dioxide concentration [CO_2] of chamber air was controlled between 350 and 380 μmol mol^{-1} by injection of carbon dioxide or carbon dioxide-free air under the control of an infrared CO_2 analyzer which sample chamber air continuously. Each temperature regime was run twice, and combined data for the two runs is presented.

Measurements of leaf gas exchange were made on the most recently fully expanded leaves of plants which were grown for up to 24 d at 25 °C and up to 35 d at 15 °C. Leaves at the same nodal positions were measured for both growth temperatures. Leaf gas exchange measurements were conducted in a separate controlled environment chamber. Measurements of net CO_2 assimilation rate and stomatal conductance to water vapor were made using a CIRAS-1 portable gas exchange system (PP Systems, Haverhill, Massachusetts) which was entirely inside the controlled environment chamber. The gas exchange system was used with a cuvette with programmable light, temperature and [CO_2] control and used an infrared sensor to measure leaf temperature. Water vapor content of
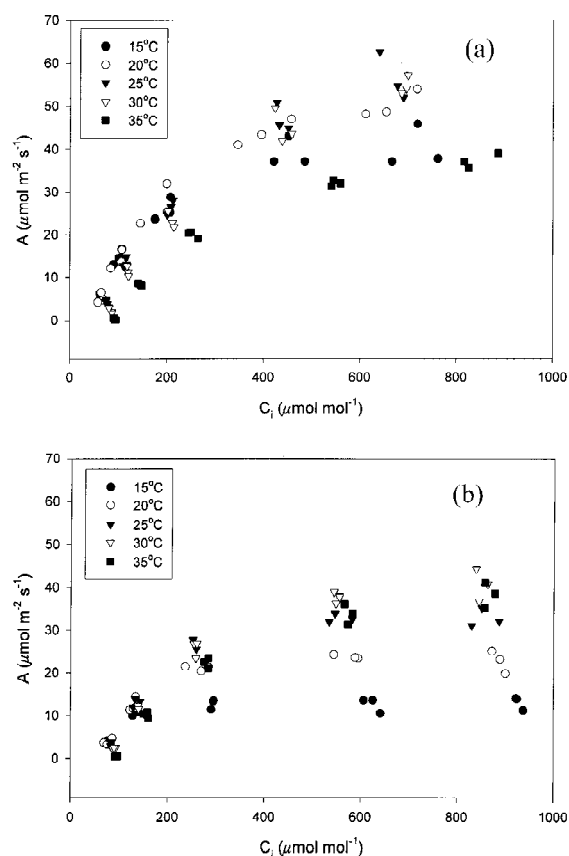
Figure 1. Carbon dioxide assimilation rate (A) as a function of sub-stomatal [CO_2] (C_i) at various temperatures for leaves of *Hordeum vulgare* grown at 15 °C (A) and for *Lycopersicon esculentum* grown at 25 °C (B). Each point represents a measurement on an individual leaf.

define the optimum temperature for photosynthesis for all species and growth temperatures. The controlled environment chamber was dark except for the illuminated area of a single leaf within the cuvette, in order to avoid water stress induced by high transpiration rates at high temperatures.

Leaves were routinely measured beginning at the lowest temperature and progressively increasing temperatures. Tests showed that this measurement sequence did not affect the results, probably because none of the measurement temperatures caused irreversible damage for any of the species. All measurement were made at a PPFD of 1500 μmol m^{-2} s^{-1}. The [CO_2] was initially set to 350 μmol mol^{-1}, and then sequentially to 200, 100, 700 and 1000 μmol mol^{-1}. At each [CO_2], steady-state rates of gas exchange were recorded, and A and C_i were calculated by the system software. Measurements were made on three leaves per species per growth temperature. The CO_2 exchange curves were primarily summarized as the initial slope of the A vs. C_i curve, and A at the highest C_i. Decreasing A at high C_i, which would be an indication of limitation by triose phosphate utilization rate (TPU) rather than V_{Cmax} or J_{max} (Harley and Sharkey 1991), did not occur in any species, although A at the highest C_i may have been limited by TPU in some cases. V_{Cmax} and J_{max} were calculated from the low and high C_i regions of the A vs. C_i curves, respectively, using the methods of Wullschleger (1993). In this method of estimating J_{max}, A at all the high C_i are utilized, including points where C_i was still limiting to A. This reduces the possible influence of TPU limitation on the estimate of J_{max}. For V_{Cmax}, this calculation requires assumptions about the temperature dependencies of other kinetic parameters of Rubisco and the relationship of O_2 to CO_2 flux in photorespiration, which were taken from Harley et al. (1992). These estimates of V_{Cmax} and J_{max} assume negligible diffusive resistance from beneath the stomatal pores to the site of CO_2 fixation. Including a mesophyll resistance to diffusion would affect the estimates of V_{Cmax} and J_{max} (e.g. Evans and Von Caemmerer 1996), but lack of information on mesophyll resistance for most of the species involved precluded such analysis.

Results

A vs. C_i curves at the different measurement temperatures are shown in Figure 1a for a representative cool climate species grown at the cool temperature, and in
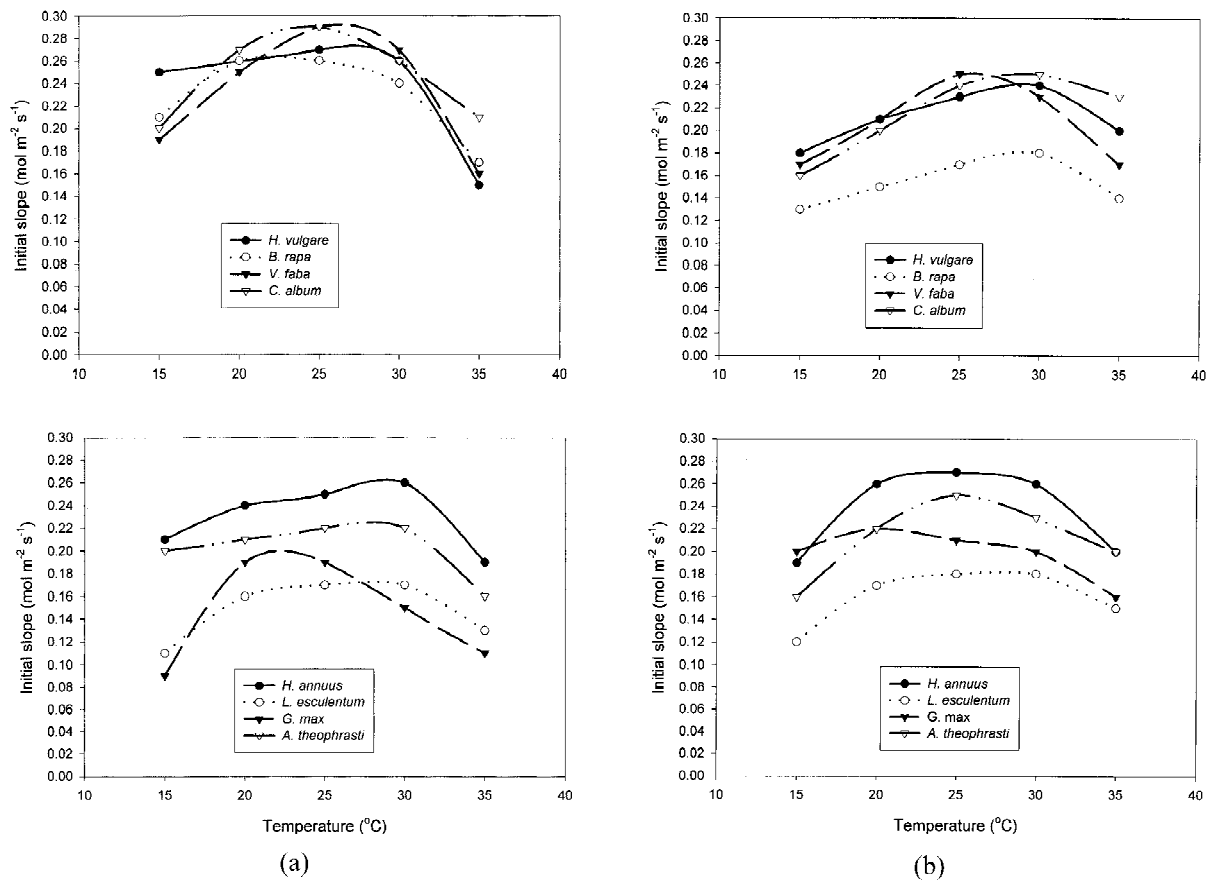
cuvette air was controlled by flushing the water vapor equilibrator of the gas exchange system with air supplied by a LI-610 dew point generator (Li-Cor Inc., Lincoln, Nebraska). The temperature of the controlled environment chamber was set a few degrees below the desired leaf temperature, so that the cuvette temperature control system would be in a heating mode. This avoided problems of condensation of water vapor within the cuvette. Condensation within the gas lines was prevented by keeping the dew point temperatures in the gas exchange system safely below the air temperature of the controlled environment chamber. The presence of condensation was tested by measuring transpiration rate for an empty cuvette. Using these procedures, it was possible to keep the leaf to air water vapor pressure difference below 1.5 kPa over the whole range of measurement temperatures of 15–35 °C. This temperature range was sufficient to

Figure 2. The temperature dependence of the initial slope of A vs. C_i for eight species grown at 15 °C (A) or at 25 °C (B). Each point represents a mean of 3 measurements on different leaves.

Figure 1b for a warm climate species grown at the warm temperature. These curves illustrate the shift of the initial part of the A vs. C_i curve with measurement temperature which occurred in all leaves, and the typical greater limitation of A at high C_i at low measurement temperature in the warm climate species and at high measurement temperature in the cool climate species.

The slope of the initial response of A vs. C_i had an optimum temperature which ranged from 20 to 30 °C (Figure 2). Growth at the warmer temperature generally decreased the absolute values of the initial slope for the cool climate species, and reduced the amount of decrease in slope which occurred at the highest measurement temperature. Initial slopes at the optimum measurement temperature were decreased on average 17% by growth at the warmer temperature in the cool climate species and increased on average 9% for the warm climate species. The relative changes were sig-

nificantly different at $P = 0.05$ between these groups, using a t-test.

A at high C_i had an optimum temperature which ranged between 25 and 30 °C (Figure 3). The decrease in A at high C_i at the highest measurement temperature was less when plants were grown at the warmer temperature for both groups of species. The absolute values of A at high C_i were reduced by growth at the warm temperature in the cool climate species, with the rates at the optimum measurement temperature decreased by an average of 25%, and increased by an average of 10% in the warm climate species. The relative changes were significantly different at $P = 0.05$ between these groups, using a t-test. The values of A at high C_i measured at 15 °C relative to the values at the optimum temperature were lower in the warm climate species as a group than in the cool climate species for both growth temperatures (Table 1).

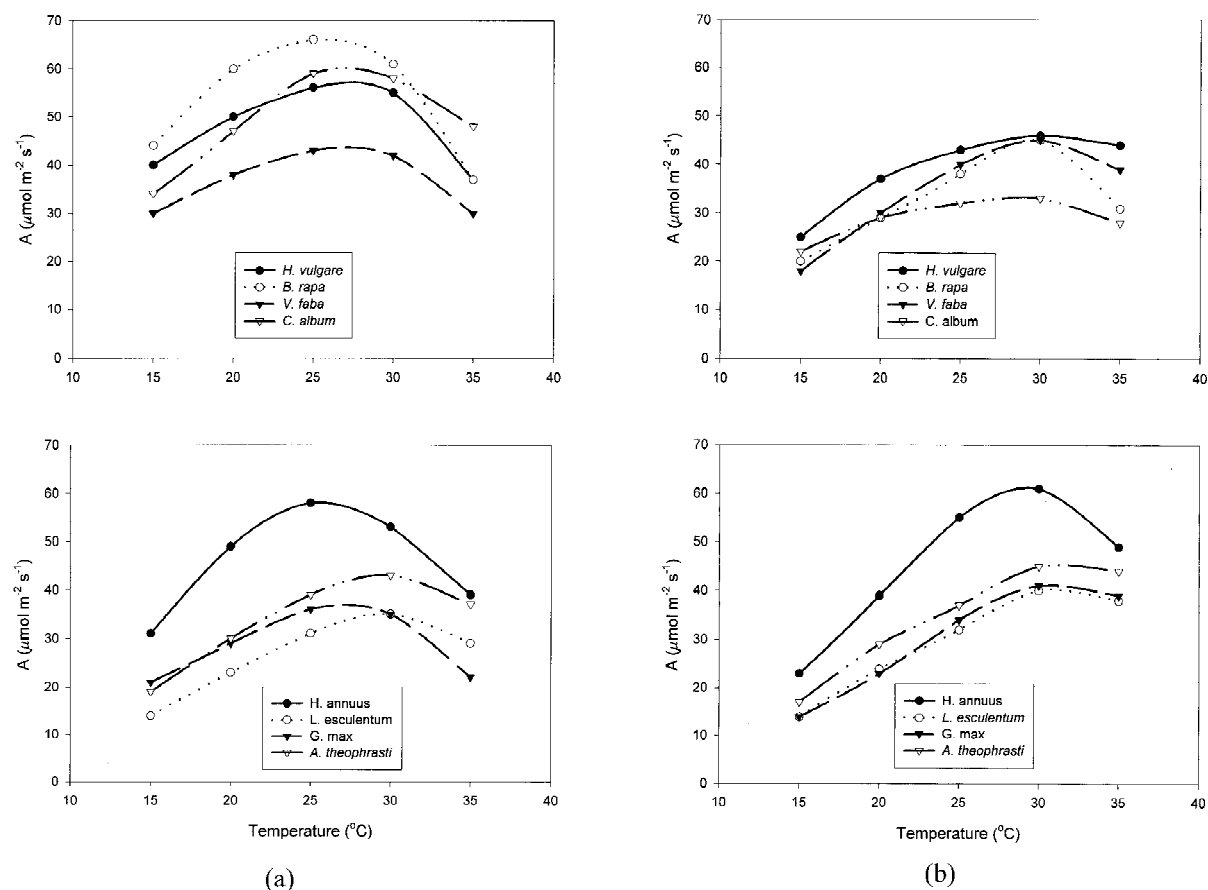Stomatal conductance measured at an external [CO_2] of 350 μmol mol^{-1} increased approximately

Figure 3. The temperature dependence of the carbon dioxide assimilation rate (A) at the highest measurement substomatal [CO_2] (C_i) for eight species grown at 15 °C (A) or at 25 °C (B). Each point represents a mean of 3 measurements on different leaves.

Table 1. Photosynthetic carbon dioxide assimilation rates (A) at a carbon dioxide concentration of 1000 μmol mol^{-1} at 15 °C relative to rates at the optimum temperature, for leaves of eight species grown at two temperatures. *Brassica rapa*, *Chenopodium album*, *Hordeum vulgare* and *Vicia faba* were considered 'cool climate' species, and the other species were considered 'warm climate' species

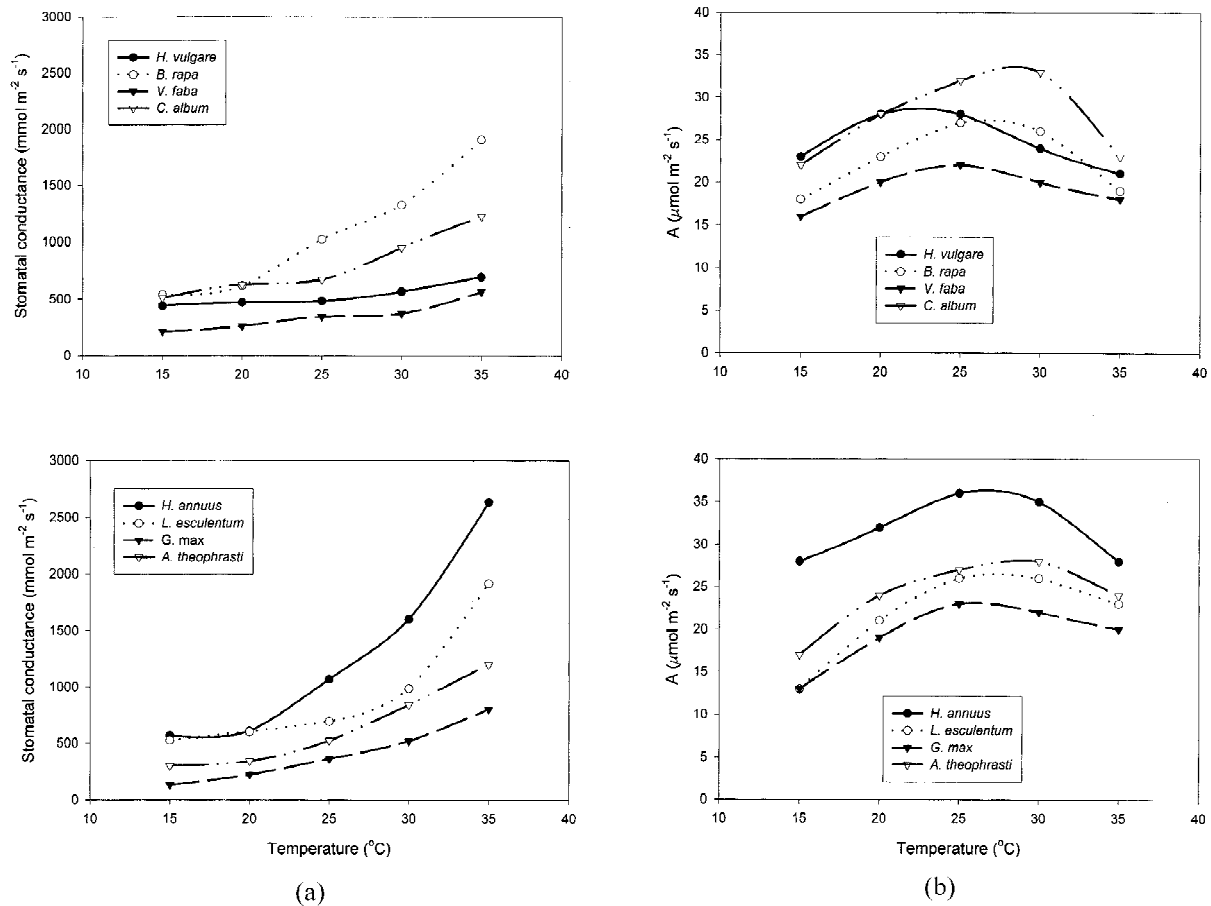| Species	A at 15 °C / A at optimum temperature	
	15 °C Growth	25 °C Growth
Brassica rapa	0.66	0.45
Chenopodium album	0.57	0.69
Hordeum vulgare	0.67	0.53
Vicia faba	0.70	0.41
Abutilon theophrasti	0.43	0.38
Glycine max	0.56	0.33
Helianthus annuus	0.55	0.37
Lycopersicon esculentum	0.38	0.33
Mean of cool climate species	0.66	0.50
Mean of warm climate species	0.48	0.35

Figure 4. The temperature dependence of stomatal conductance (A) and carbon dioxide assimilation rate (B) at the measurement $[CO_2]$ of 350 lmol mol^{-1} for eight species grown at 25 °C. Each point represents a mean of 3 measurements on different leaves.

exponentially with measurement temperature in all leaves (e.g. Figure 4a), while A under the same conditions decreased at the highest measurement temperature (e.g. Figure 4b). The temperature response of stomatal conductance was not substantially affected by growth temperature (not shown). Stomatal conductance at 35 °C averaged 2.5 times that at 15 °C for the cool climate species, and 4.3 times for the warm climate species, when averaged over both growth temperatures. This difference between groups was significant at $P = 0.05$, using a t-test.

Values of V_{Cmax} and J_{max} calculated for the 20 °C measurement temperature varied by factors of more than 2 across the species and growth temperatures and were positively correlated with each other (Figure 5), with an r^2 value of 0.60. When the regression was forced through the origin, the slope was:

$$J_{max} = 1.89^* V_{Cmax}$$

although the individual ratios of $J_{max} - V_{Cmax}$ ranged from about 1.2 to 2.6. The decrease in both J_{max} and V_{Cmax} with growth at warmer temperature for the cool climate species is evident in Figure 5. A two-way analysis of variance conducted on the ratio of $J_{max} - V_{Cmax}$ to compare cool vs. warm climate species and 15 vs. 25 °C growth temperatures indicated no significant differences between cool and warm climate species, nor between growth temperatures, and no significant interaction, at $P = 0.05$. There was no significant correlation ($r^2 = 0.07$) between the optimum temperature for A measured at 350 μmol mol^{-1}[CO_2] and the ratio of J_{max} to V_{Cmax} at 20 °C across species and growth temperatures.

Calculated values of V_{Cmax} increased with measurement temperature from 15 to 30 °C in all cases, and then increased, decreased or remained constant at 35 °C (Figure 6). Shapes of the curves from 15 to 30 °C
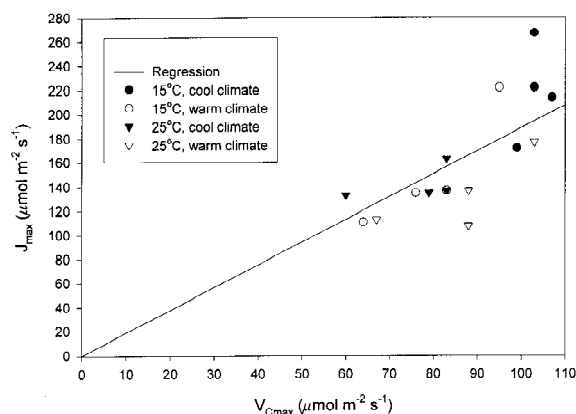
Figure 5. J_{max} and V_{Cmax} values at 20 °C for eight species grown at 15 °C and at 25 °C and the overall regression line forced through the origin. The slope of the regression is 1.89 and the r^2 is 0.60. Each point represents a mean of 3 measurements on different leaves.

ranged from convex to concave (Figure 6), depending on species and growth temperature.

Discussion

The plants used in this study had many of the features of photosynthetic acclimation to temperature which have been observed in other studies. These include smaller shifts in the optimum temperature of photosynthetic processes than in the growth temperature (e.g. Chabot and Billings 1972; Slatyer and Ferrar 1977; Sveinbjornsson and Oechel 1983), differences between plants adapted to different thermal regimes in the growth temperatures producing maximal photosynthetic capacity (e.g. Billings et al. 1971; Slatyer and Ferrar 1977) and the relatively minor role of stomatal acclimation in determining photosynthetic acclimation (e.g. Bjorkman et al. 1989). In the present study, it was determined that acclimation of photosynthesis to temperature involved changes in the absolute value and/or the temperature responses of both the initial slope of A vs. C_i and A at high C_i. How these parameters changed with growth temperature varied among species and between groups adapted to different temperatures. Although changes in the temperature dependence of J_{max} and V_{Cmax} are implied by these measurements, such changes are often not taken into account by those who use Farquhar-type photosynthesis models in crop or ecosystem modeling.

The temperature dependencies of J_{max} are closely parallel to the temperature dependencies of A at high C_i given in Figure 3. These curves are of the same

general shape as reported by others (cf. Leuning 1997, Figure 1), although some of the species examined here have a lower optimum temperature for J_{max} (e.g. 25 °C) than those reviewed by Leuning, and there are clear differences between species and growth temperatures in the steepness of the curves, as well as the optimum temperatures. Calculating the temperature dependence of V_{Cmax} from the initial slope of A vs. C_i requires assumptions about the temperature dependence of other kinetic parameters of Rubisco and the carbon cycle, such as the Michaelis constants for CO_2 and O_2, the relationship of O_2 to CO_2 flux in photorespiration (Wullschleger 1993) and the activation state of Rubisco. Assuming the kinteic parameters of Rubisco respond uniformly to temperature across species leads to apparent variation in the temperature dependence of V_{Cmax} in our data (Figure 6). However, it is possible that the temperature response of the kinetic parameters of Rubisco may not be uniform (cf. Bunce 1998), in which case the data in Figure 6 would not really represent the temperature dependence of potential carboxylation rate. The activity of fully activated Rubisco generally increases with temperature to at least 45 °C (e.g. Bjorkman et al. 1989; Devos et al. 1998), but the activation state of Rubisco may decrease at high temperature (e.g. Weiss 1981) and could cause the variation in the apparent temperature response of V_{Cmax}. Thus the patterns presented in Figure 6, while suitable for modeling the temperature response of photosynthesis, have an ambiguous biochemical interpretation at present. More practically, the non-uniform response of the initial slope of A vs. C_i to temperature found here at least implies that species and growth conditions affect the relative temperature sensitivities of carboxylation and other kinetic parameters of Rubisco or the carbon cycle sufficiently to affect the temperature response of photosynthesis.

Some studies have emphasized the tightness of the linear relationship between J_{max} and V_{Cmax} normalized to a constant temperature, suggesting that one could be estimated from the other (e.g. Leuning 1997; Raupach 1998). In this study, both the mean slope of the relationship and the correlation coefficient at 20 °C were less than for the data summarized by Leuning, and the ratio of $J_{max} - V_{Cmax}$ varied by more than a factor of 2 in our data. Thus there could be considerable error in assuming a constant relationship between J_{max} and V_{Cmax} for these species grown at a range of temperatures. The low correlation between the optimum temperature of photosynthesis at 350 μmol mol^{-1} [CO_2] and the ratio of J_{max} to V_{Cmax}
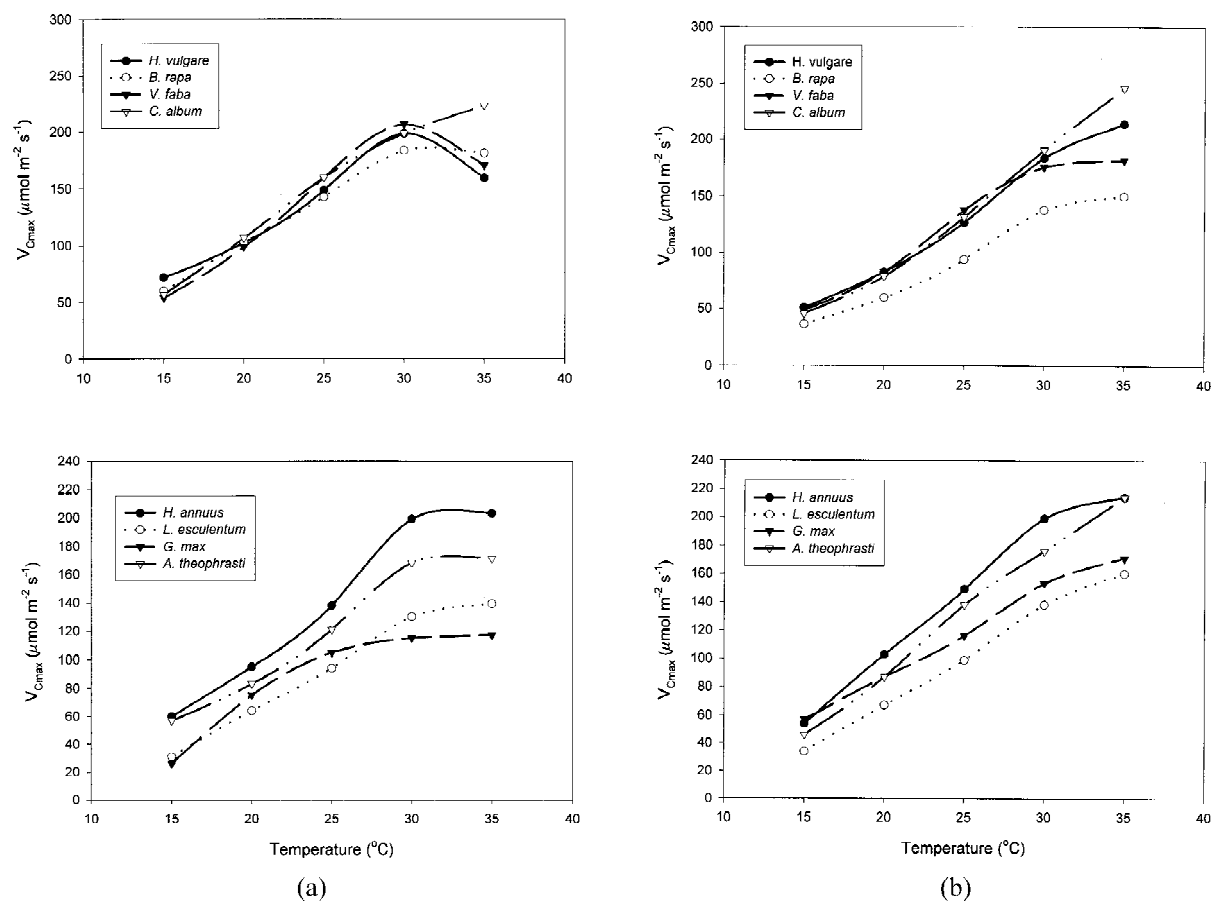
Figure 6. The temperature dependence of the V_{Cmax} for eight species grown at 15 °C (A) or at 25 °C (B). Each point represents a mean of 3 measurements on different leaves.

at 20 °C does not support the idea that variation in the relative values of normalized J_{max} and V_{Cmax} are a major source of variation in the optimum temperature of photosynthesis in normal air (Farquhar and Von Caemmerer 1982). Although variation in the relative values would by themselves shift the optimum temperature, differences in the temperature dependencies of J_{max} and V_{Cmax} were more important among the species examined here. Hikosaka et al. (1999) also found that growth temperature affected the temperature dependencies of RuBP carboxylation and regeneration in an evergreen tree.

The exponential increase in stomatal conductance continuing above the optimum temperature for photosynthesis agrees with some other studies in which water vapor pressure deficits were also kept low at high temperatures (e.g. Raschke 1970; Hall et al. 1976). This temperature response would tend to offset a decrease in conductance with the increasing water

vapor pressure which, in the field, would normally accompany high temperatures. It has been suggested that high stomatal conductance at high temperature would have the advantage of cooling leaves in hot environments (e.g. Lu et al. 1994; Fischer et al. 1998). This suggestion is reinforced by the relatively larger increase in stomatal conductance with temperature in the species adapted to warmer climates found in this study.

Apart from the degree to which the lowest measurement temperatures limited photosynthesis (Table 1), the clearest distinction between the groups of species adapted to cool or warm climates was in the direction of change in the absolute values of J_{max} and V_{Cmax} between the two growth temperatures. Although only two growth temperatures were examined here, the data indicate that the 'preferred' growth temperature, defined as the temperature producing leaves with highest photosynthetic capacity (Slatyer

and Ferrar 1977), was lower in the cool climate species than in the warm climate species. Adaptation of photosynthesis to climate was more consistently reflected in how the absolute values of J_{max} and V_{Cmax} responded to growth temperature than by variation in the temperature dependencies of J_{max} and V_{Cmax}. This may result from limited flexibility in the temperature dependencies of the underlying biochemical processes. Knowledge of how the absolute values and temperature dependencies of J_{max} and V_{Cmax} vary with growth temperature would improve the accuracy of photosynthesis models.

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