植物生态学报 2007，31(4)695～710
Journal of Plant Ecology (Chinese Version)

RETHINKING ACCLIMATION OF GROWTH AND MAINTENANCE RESPIRATION OF TOMATO IN ELEVATED CO_2：EFFECTS OF A SUDDEN CHANGE IN LIGHT AT DIFFERENT TEMPERATURES

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Abstract ***Aims*** Changes in light and temperature are among the most common and most profound environmental perturbations. The independent effects of light and temperature on photosynthesis and respiration are well studied in single leaves, but are less well studied in whole plants. The short and long term influence of light and temperature on carbon use efficiency is also poorly understood, and is commonly modeled to remain constant over a wide range of conditions. We sought to determine the primary effects of changing light at two growth temperatures on photosynthesis, respiration, and their balance, as defined by carbon use efficiency.

Methods We separated respiration into growth and maintenance components using whole-canopy gas-exchange in an elevated CO_2 environment in a controlled environment, and supplemented that information with tissue analysis.

Important findings Decreases in light level decreased carbon use efficiency through a reduction in the maintenance coefficient, increased the growth coefficient, and reduced partitioning of N in protein. Growth temperature did not significantly affect either maintenance or growth respiration coefficients, suggesting that long-term temperature responses can differ greatly from short-term observations.

Key words environmental acclimation, canopy, whole plant, R:P ratio, tomato, carbon use efficiency

Plants experience changes in light and temperature over the course of a single day and growing season. How species acclimate to these changes helps define their ecological niches, optimal growth ranges, ability to withstand climate change, and agricultural utility. For example, cold tolerance is often selected for field crops in colder growing climates, but may not be an important trait in areas where low temperature is non-limiting (Rife & Zeinali, 2003). Similarly, low-light plants such as African violets (*Saintpaulia ionantha*) are preferred ornamental species for houseplants because they thrive in indoor environments (Faust & Heins, 1994), whereas some ornamental grasses need much higher light to grow well (Fausey *et al.*, 2005).

Photosynthesis and respiration, which determine biomass gain, are both influenced by light and temperature. Temperature affects photosynthetic efficiency or quantum yield, and light affects both photosynthetic rate and quantum yield. Photosynthesis is much better understood than plant respiration. Respiration has long been reported to increase exponentially in warmer temperatures, while light either decreases respiration through photoinhibition (Atkin *et al.*, 2000; Sharp *et al.*, 1984) or stimulates respiration by increasing the carbohydrate supply (Azcón-Bieto & Osmond, 1983; Moser *et al.*, 1982).

Respiration is classically divided into growth and maintenance fractions (McCree, 1974), with different processes falling under either growth or maintenance depending on authors' definitions of each (see Amthor,

Received：2007-02-12 Accepted：2007-03-03

Foundation item：Supported by the National Aeronautics and Space Administration Advanced Life Support Program and the National Aeronautics and Space Administration Graduate Student Research Program.

We thank Justin Robinson and Emily Mills at Utah State University for technical assistance. Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by the USDA, and does not imply its approval to the exclusion of other products or vendors that also may be suitable

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2000 for complete discussion of different assumptions concerning growth and maintenance respiration). Growth respiration is typically assumed to be dependent on the type of biomass being synthesized and growth rate, and maintenance respiration is influenced by temperature, chemical composition, and plant size. Literature values for maintenance respiration are usually below 5% of existing biomass per day (Adu-Bredu *et al.*, 1996; Lavigne & Ryan, 1997; Ryan *et al.*, 1995), while growth respiration is in the range of 0.13 to 0.43 mol CO_2 respired per mol carbon in the new biomass, depending on the plant composition (Amthor, 2000). Both maintenance and growth coefficients have been reported to acclimate to changes in environment (Bunce & Ziska, 1996; Quigg & Beardall, 2003; van Iersel, 2006), but are often modeled as constants.

Carbon use efficiency (*CUE*) is a calculated term that describes the relationship between photosynthesis and respiration, and can be thought of as the efficiency of carbohydrate conversion into plant biomass. It is the ratio of the carbon gained during a 24-h period (net photosynthesis minus night-time respiration, or daily carbon gained (*DCG*)) to carbon fixed during the day (gross photosynthesis (P_{gross})). Because it is a ratio, it is less sensitive to environmental fluctuations than either *DCG* or P_{gross} individually, yet it provides insight into how efficient the plant is at converting the carbon fixed during the day into dry matter.

Models often include considerable detail describing environmental influences on photosynthesis and respiration, but they typically have little or no description on the effect of environment on *CUE*. In fact, limited variation in *CUE* is recommended as an "unforced outcome of mechanistic models" (Cannell & Thornley, 2000). Dewar *et al.* (1998) attempted to provide a mechanistic model describing carbon and light use efficiencies at the whole leaf and plant level. In their model, constant *CUE* was the result of stored reserves and available material for growth and respiration being approximately balanced over several days when compared to steady-state environments with the same average light environment. The pool of carbohydrate available for growth and respiration is typically large enough to negate small, temporary changes (changes on the order of seconds to minutes) in the environment and the result is constant *CUE*.

Variations in temperature were not modeled by Dewar *et al.* (1998) but have been tested previously (Frantz *et al.*, 2004a). In those studies, *CUE* increased when night temperature decreased. The resulting change in *CUE* was caused by a one-time temperature change for the duration of the study possibly causing the pools of carbohydrate available for growth and respiration to be permanently altered, thereby resulting in a new *CUE* value. van Iersel (2003) showed that *CUE* can be expressed as a function of the relative growth rate and growth and maintenance respiration coefficients. This function showed that *CUE* decreases with decreasing relative growth rate, unless there is a simultaneous decrease in the maintenance and/or growth coefficients.

In another study (Frantz & Bugbee, 2005), reduced light decreased *CUE* by as much as 80% of pre-treatment values. *CUE* eventually returned to or near pre-treatment levels, depending on the species tested. Using the Dewar *et al.* (1998) model to explain the results, carbohydrate pools presumably adapted to new steady-state levels thereby allowing *CUE* to return to steady levels, providing that all respiration needs were met in the new, lower light environment. The Dewar *et al.* (1998) model was constructed assuming non-limiting conditions and if those conditions are not met (i.e. lower light), the new supply of carbohydrate may not meet the demand (i.e. maintaining existing biomass) and *CUE* may adjust to a lower level. The interactive effects of light and temperature on *CUE* have not been studied.

We sought to determine the influence of light on the growth, photosynthesis, respiration, and *CUE* of tomato plants grown at two temperatures. We wanted to evaluate why there may be a change in *CUE* in response to a change in light and how rapidly *CUE* adjusts back to pre-treatment levels or a new steady-state level at different growth temperatures. Furthermore, interactions between light and temperature may be evident because of the co-dependence of photosynthesis and respiration on these parameters. We also wanted to examine the growth, and subsequent acclimation to environmental change from a more mechanistic standpoint, so we separated respiration into growth and maintenance fractions. These measurements provide insight into the shortcomings of models as well as the processes that are the basis for those models.

1 Materials and Methods

1.1 Plant growth environment

Dwarf tomato plants (*Solanum lycopersicon* cv. Micro-Tina) were germinated and transplanted after 5 days into a 10-chamber gas-exchange system at a density of 85 plants·m^{-2} (Fig. 1). High densities were used to obtain rapid canopy closure. This open gas-exchange system has been described previously (van Iersel & Bugbee, 2000).

CO_2-gas-exchange of each chamber was monitored for 15 s per chamber every 10 min. Each chamber was 0.5 m × 0.4 m × 0.9 m (length × width × height) and fully enclosed a hydroponic tub. Five chambers were maintained at 20 ℃ day and night and five were maintained at 30 ℃ day and night. Chamber temperature was controlled to within ± 0.2 ℃ of the set point with a chilled water coil and small heaters. Root-zone temperature was maintained at the same temperature as the shoot. The air flow rate through the chamber was continuous at 20 L per minute. Hydroponic solution was bubbled with the same air as that used in the canopy.

Fig. 1 The ten-chamber gas-exchange system

There are five chambers on each side, each chamber has independent temperature control and a separate hydroponic system. The chambers are housed inside a walk-in growth chamber illuminated by water-filtered high pressure sodium lamps. Reflective Mylar was wrapped around each chamber and raised as the canopy grew to minimize side-lighting

CO_2 was controlled to within ± 2% of the set point of 1 200 $\mu mol \cdot mol^{-1}$. CO_2 was elevated for three reasons：1) to ensure that photosynthesis would be light-limited rather than CO_2-limited；2) to partially close stomates and thus minimize any effect of vapor pressure deficit differences between chambers on photosynthesis；and 3) to minimize temperature effects on photorespiration. The temperature responses most likely would be smaller if the plants were carbohydrate limited by ambient CO_2 (See **Discussion** for applicability of data to ambient CO_2 environments).

The pH of the hydroponic solution was maintained between 4 and 5 to eliminate CO_2 dissolved in solution (Monje & Bugbee, 1998). The nutrient solution contained 7.0 $mmol \cdot L^{-1}$ N (as nitrate), 1.25 $mmol \cdot L^{-1}$ P, 3.2 $mmol \cdot L^{-1}$ K, 2 $mmol \cdot L^{-1}$ Ca, 1.5 $mmol \cdot L^{-1}$ Mg, 1.5 $mmol \cdot L^{-1}$ S, 11.5 $\mu mol \cdot L^{-1}$ Fe, 9 $\mu mol \cdot L^{-1}$ Mn, 4 $\mu mol \cdot L^{-1}$ Zn, 40 $\mu mol \cdot L^{-1}$ B, 4 $\mu mol \cdot L^{-1}$ Cu, and 0.1 $\mu mol \cdot L^{-1}$ Mo. Relative humidity was maintained between 60% and 85%, but average differences in humidity among treatments were less than this range on a given day. Photosynthetic photon flux density (*PPFD*) was provided by water-cooled high pressure sodium lamps that initially provided 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (± 5%) for all chambers until canopy closure. The photoperiod was 16-h, which provided a daily integrated *PPFD* of 17.3 $mol \cdot m^{-2} \cdot d^{-1}$. Light treatments were control (300 $\mu mol \cdot m^{-2} \cdot s^{-1}$), low *PPFD* (80 $\mu mol \cdot m^{-2} \cdot s^{-1}$；4.6 $mol \cdot m^{-2} \cdot d^{-1}$), and high *PPFD* (600 $\mu mol \cdot m^{-2} \cdot s^{-1}$；34.6 $mol \cdot m^{-2} \cdot d^{-1}$).

Light treatments began 2 days after canopies closed, which occurred 16 days after transplanting for the canopies at 30 ℃ and 24 days after transplanting for the canopies at 20 ℃. Canopy closure was determined when less than 3% of the ground area was visible from directly overhead. Shade was applied with neutral-density window screen (10-mesh) on the top of the chambers. This screen reduced *PPFD* by 50% with each layer. Additional opaque black plastic was used for the low light treatments. *PPFD* was measured twice weekly with a line-quantum sensor (Model LQSV-ELEC, Apogee Instruments, Inc., Logan, UT, USA) that averaged *PPFD* across the top of the canopy. Shading material was adjusted at those times to maintain the set point *PPFD*. Treatments continued for 20 days after applying the shade. Side lighting was minimized by wrapping each chamber in reflective Mylar, which was raised daily so that the top of the Mylar was level with the top of the canopy.

Gas exchange systems are difficult to calibrate and are usually only tested by zeroing one or more chambers with different flow rates of air and by ensuring the gas analyzer to be used has been properly zeroed and spanned. We zeroed each chamber, calibrated the gas analyzers, and finally calibrated the entire system by slowly reacting 4 $mol \cdot L^{-1}$ HNO_3 with a known mass of dried $CaCO_3$. This caused CO_2 to be evolved, which was measured with the gas analyzers. This continued until the reaction was complete and the total moles of CO_2 evolved were compared to the initial moles of C in the $CaCO_3$. This process was repeated until the molar amount of CO_2 evolved from the reaction equaled that which was initially placed into the chamber (100% ± 2%) by finding and repairing leaks in the different sections of the system.

1.2 Calculations

In all cases in this study, the units of area refer to the ground area rather than the leaf area of the canopy. Using the measured CO_2 exchange rates of the net photosynthesis in the light period (P_{net}, mol $C \cdot m^{-2} \cdot d^{-1}$) and night-time respiration (R_n, mol $C \cdot m^{-2} \cdot night^{-1}$；night is the night period following the photosynthesis period, which together make up one 24-h period), *DCG* can

be calculated as:

$$DCG = P_{net} - R_n \quad (1)$$

P_{gross} is a calculated term that incorporates both the net C fixed (P_{net}) and the C that is simultaneously being respired. Since day-time respiration (R_d) can not be measured directly, P_{gross} is calculated as the sum of P_{net} and some percentage of night-time respiration rate. Different studies have indicated that R_d can remain high during the day due to higher carbohydrate content during the day (Azcón-Bieto & Osmond, 1983), or can be lower due to some type of light-inhibition of respiration (Atkin *et al.*, 2000; Sharp *et al.*, 1984). We have taken the common approach to assume that R_d is occurring at the same rate as R_n. R_d would then be defined as:

$$R_n \times (\text{time in light})/(\text{time in darkness}) \quad (2)$$

So, for a 16-h photoperiod, $R_d = R_n \times 2$. In these equations, respiration assumes a positive value (i.e. mass respired). P_{gross} can be calculated as:

$$P_{gross} = P_{net} + R_d \quad (3)$$

CUE is the ratio of carbon gained per day to total carbon fixed, or:

$$CUE = DCG/P_{gross} \quad (4)$$

Sensitivity analysis of *CUE* to the assumption of R_d being equal to R_n to calculate P_{gross} indicates that R_d can be as much as 50% higher or lower than R_n and change *CUE* by only 0.08 or 12% (assuming a *CUE* of 0.65, a typical value). Therefore, the assumption of constant day and night respiration rate has little impact on the calculated value of *CUE*.

Canopy quantum yield (*CQY*) was calculated for each canopy after canopy closure. *PPFD* incident upon the canopies was measured and 95% of that was assumed to be absorbed (Klassen *et al.*, 2003). P_{gross} for the light period (mol $C \cdot m^{-2} \cdot d^{-1}$) was then divided by total photons absorbed (mol photons $\cdot m^{-2} \cdot d^{-1}$) to give *CQY* (mol C fixed per mol photons absorbed). Data from each canopy were averaged for the 20-day post *PPFD* treatment period.

1.3 Plant tissue analysis

Upon harvesting, tomatoes were separated into leaves, stems, roots, and fruits. Tissue was weighed and dried in a forced-air oven at 80 ℃ for 72 h. The dried biomass was subsequently weighed, ground, and subsampled for analysis. Samples (0.2 g) were analyzed for percent C, H, and N (LECO C-H-N analyzer, LECO Corp., St. Joseph, MI, USA) and 1.0 g samples were used for elemental analysis with inductively coupled plasma optical emission spectroscopy (Thermo Corp. Model Iris-Advantage; Utah State Plant and Soils Analysis Laboratory, USA). Nitrate was analyzed with a 0.2 g sample placed in a 50 ml solution of 0.05 mol $\cdot L^{-1}$ $Al_2(SO_4)_3$ solution. The tissue and solution were shaken four times during the 1-h extraction period. The solution was measured with a NO_3^- selective and a reference electrode (model 930700 and model 900200 Thermo Orion, Beverly, MA, USA). The readings were then converted from volts to NO_3^--N from a previously-determined calibration curve. Reduced N was calculated as total N minus NO_3^--N.

1.4 Growth and maintenance estimates

A two-component model was used to separate respiration into growth and maintenance portions (Hesketh *et al.*, 1971). The divisions between growth and maintenance processes are somewhat arbitrary given that there is no biochemical distinction between ATP pools for growth or maintenance. In this study, we used the assumptions behind the growth-and-maintenance-respiration paradigm, which is the theoretical framework that is most useful for analysis of data to explain how respiration is divided into different fractions (Amthor, 2000). The two-component model is based on the classic respiration model made popular by McCree (1974) where respiration is a function of size of biomass and new growth:

$$R_{tot} = cW + mG \quad (5)$$

Where R_{tot} is total respiration in 24-h, c is the amount of carbohydrate needed for maintenance per unit of existing biomass W (maintenance respiration coefficient; mmol C $\cdot$ mol^{-1} C $\cdot d^{-1}$ or mg glucose $\cdot g^{-1}$ biomass $\cdot d^{-1}$), m is the amount of carbohydrate needed to produce one unit of new biomass (growth respiration coefficient; mol $C_{resp} \cdot$ mol^{-1} C_{growth} or g glucose $\cdot g^{-1}$ new growth), and G is daily growth (*DCG* from above; also calculated in g biomass using the carbon content of the biomass). Thus, cW is the maintenance respiration and mG is the growth respiration. If both sides are divided by W:

$$R_{tot}/W = cW/W + mG/W \quad (6)$$

The equation is equivalent to:

$$\text{Specific respiration} = c + m \times RGR \quad (7)$$

Or, assuming that c and m are constant, specific respiration is a linear function of relative growth rate (*RGR*). Using CO_2 gas exchange from seedlings of whole canopies to final harvest permitted an estimation of specific respiration and *RGR* throughout canopy growth. In this study, *RGR* was calculated as *DCG* divided by the estimated plant biomass defined as the cumulative carbon gain (*CCG*, running total of all *DCG*). The initial dry mass of the seedlings was assumed to be negligible. Specific respiration was calculated as:

$$(R_n + R_d)/CCG \quad (8)$$

Only the data after the shade treatments began were used for growth and maintenance estimates.

1.5 Experimental design and statistics

The shade treatments were arranged as an incomplete block design with one block at 20 ℃ and the other at 30

℃. Both blocks contained a single control chamber (intermediate *PPFD*), two low *PPFD*, and two high *PPFD* treatments. Each chamber contained 17 plants, but was considered one experimental unit. The respiration coefficients were analyzed using linear regression (Proc GLM in SAS; SAS Institute, Cary, NC, USA). Because growth and maintenance coefficients and their interactions are not independent from one another, a backward selection procedure was used starting with the model:

Maintenance or growth respiration coefficients = V + (X × temperature) × (Y × *PPFD*) + (Z × temperature × *PPFD*) (9)

V is the estimated respiration coefficient at 0 ℃ and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ *PPFD*. If X, Y and/or Z (X, Y and Z are statistical parameters used to test each term) were significant, then temperature, *PPFD*, or the interactions of the two parameters significantly affected the respiration coefficient, respectively. In the selection procedure, the non-significant parameters were removed one at a time from the model beginning with the parameter with the highest p-value. This process was continued until only parameters with significant p-values ($p < 0.05$) remained. Because this approach is using the general linear regression model to determine differences due to light and temperature, replicates at any given environmental setting (including that of the control) are not necessary (Neter *et al*., 1996).

The carbon, nitrogen, nitrate, and reduced N values were analyzed again under the General Linear Model (Statistix version 8.1, Analytical Software, Tallahassee, FL, USA) using the main effects of *PPFD* and temperature and an interaction term. This method uses similar regression procedures as the Proc GLM described above and can therefore be used with unbalanced designs and lack of replicates at any given environmental setting. Canopy quantum yield was tested with a 2-way ANOVA repeated measures because the same plants were measured on multiple days.

Treatment effects on *CUE* were expressed as a percent of their initial value, then normalized to the control in the following manner:

(post-treatment$_{CUE}$ day$_b$/pre-treatment$_{CUE}$ value)/(post-treatment$_{control\ CUE}$ day$_b$/pre-treatment value$_{control\ CUE}$) × 100 (%) (10)

Where "post-treatment$_{CUE}$" indicates the post-treatment value of *CUE* on that post-treatment day indicated by "day$_b$", "pre-treatment$_{CUE}$ value" is the value of *CUE* on the day before the light was changed, "post-treatment$_{control\ CUE}$ day$_b$" is the post-treatment value of *CUE* for the control on day$_b$, and "pre-treatment value$_{control\ CUE}$" is the pre-treatment value of *CUE* for the control the day before treatments began. This data normalization results in determining the light effects through time relative to the treatment plants in the numerator, and the effects through time relative to the control in the denominator.

For *CUE* recovery, the simplest linear regression equations were selected that provided the best fit based on r^2 values and plots of residual values. To determine original estimates of maintenance and growth coefficients, first order linear regression was used as explained above in the relationship between specific respiration and relative growth rate.

2 Results

2.1 Early growth and flowering

Photosynthesis and respiration rates were similar within temperature treatments prior to *PPFD* treatments (Fig. 2A, 2B). Daily carbon gain (*DCG*) was also similar in the chambers before *PPFD* was changed (Fig. 3A, 3D). There were large differences in the rate of leaf area development between the two temperature treatments. As a result, the number of days required for canopy closure and subsequent *PPFD* treatment initiation differed between temperatures. The 30 ℃ treatment reached canopy closure on day 16, while the 20 ℃ treatment reached canopy closure on day 24. The different temperatures also caused different development rates with the 30 ℃ treatment requiring only about 25 days for all canopies to initiate flowering while the 20 ℃ canopies required about 35 days to first flower.

2.2 After *PPFD* treatment: 30 ℃

Net photosynthetic rate decreased from 0.74 to 0.12 $mol \cdot m^{-2} \cdot d^{-1}$ (84% reduction) the initial day after reducing the *PPFD* from 300 to 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (73% shade) (Fig. 2A). Net photosynthesis rate increased from 0.74 to 1.47 $mol \cdot m^{-2} \cdot d^{-1}$ (93% increase) the initial day after increasing *PPFD* from 300 to 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (100% increase). On subsequent days, photosynthetic rate slightly increased in the shaded canopies, and slightly decreased in the high light treatment. Respiration rate decreased from 0.11 $mol \cdot m^{-2} \cdot night^{-1}$ to 0.055 $mol \cdot m^{-2} \cdot night^{-1}$ (50% reduction) (expressed here as a positive value, shown as a negative carbon exchange rate in Fig. 2A) the initial day after reducing the *PPFD* from 300 to 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 2A). Respiration rate increased from 0.11 to 0.17 $mol \cdot m^{-2} \cdot night^{-1}$ (52% increase) the initial day after increasing *PPFD* from 300 to 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

After the change in *PPFD*, *DCG* approximately doubled in the 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatment while it decreased by about 75% in the 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatments (Fig. 3A). *CCG* increased at three distinct rates following the change in *PPFD* with the lowest *PPFD* increasing *CCG* at the lowest rate and the highest *PPFD* increasing *CCG* the most (Fig. 3B). *RGR* decreased over

time in all treatments, but differed distinctly among the three *PPFD* treatments (Fig. 3C). When *PPFD* was changed, the *RGR* increased in the 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatment on that day by about 60%, and then declined exponentially on subsequent days. The *RGR* of the 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatment decreased at the start of the *PPFD* treatment and remained low throughout the remainder of the trial.

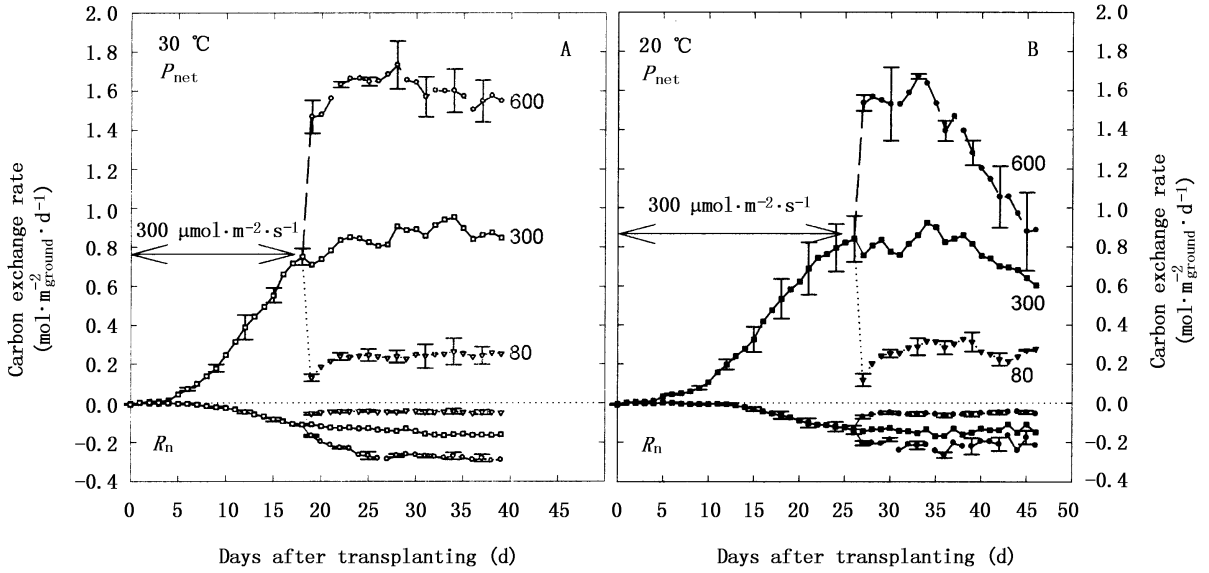

Fig. 2 Carbon exchange rates including day-time net photosynthesis (P_{net}) or night-time respiration (R_n) of tomato plants at 30 ℃ (A) and 20 ℃ (B) Photosynthetic photon flux density (*PPFD*) was changed from 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ on day 19 for the 30 ℃ canopies and on day 27 for the 20 ℃ treatment to 80, 300, or 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Open symbols are for 30 ℃ treatment and closed symbols indicate 20 ℃ treatment. Circles are 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$, squares are for 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and inverted triangles represent 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ *PPFD* treatments. Error bars represent the standard deviation

2.3 After *PPFD* treatment: 20 ℃

Net photosynthetic rate decreased from 0.72 to 0.12 $mol \cdot m^{-2} \cdot d^{-1}$ (or 83%) the initial day after reducing the *PPFD* from 300 to 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (73% shade) (Fig. 2B). Photosynthesis rate increased from 0.85 to 1.39 $mol \cdot m^{-2} \cdot d^{-1}$ (or 63%) the initial day after increasing *PPFD* from 300 to 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (100% increase). On subsequent days (after day 35), photosynthetic rate slightly increased in the shaded canopies, and gradually decreased in the elevated light treatments. Respiration rate decreased from 0.12 to 0.071 $mol \cdot m^{-2} \cdot night^{-1}$ (or 41%) the initial day after reducing the *PPFD* from 300 to 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 2B). Respiration increased from 0.14 to 0.18 $mol \cdot m^{-2} \cdot night^{-1}$ (or 32%) the initial day after increasing *PPFD* from 300 to 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$. On subsequent days, respiration rate continued to decrease in the shaded canopies, and continued to increase slightly in the canopies receiving high light.

After the change in *PPFD*, *DCG* approximately doubled in the 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatment, but it was cut by about 90% in the 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatments (Fig. 3D). In the 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatment, *DCG* began to decline a week after *PPFD* was increased, perhaps due to heavier fruit load on that treatment compared to others, which shaded the canopy as fruit developed near the top of the canopy. *CCG* in the 20 ℃ treatments increased in a similar manner as in the 30 ℃ treatments, with the *CCG* in the highest *PPFD* increasing at a higher rate than the control or lowest *PPFD* treatments (Fig. 3E). Like the 30 ℃ plants, *RGR* decreased over time in all *PPFD* treatments (Fig. 3F). Upon changing *PPFD*, the *RGR* in the 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatment increased on that day by about 40%, and then declined exponentially on subsequent days. The *RGR* of the 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatment decreased upon *PPFD* treatment initiation and remained low throughout the remainder of the trial, similar to that of the 30 ℃, 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatment.

2.4 After *PPFD* treatment: canopy quantum yield

There was a significant difference in *CQY* among *PPFD* levels ($p < 0.000\ 1$) with the lowest light resulting in the highest *CQY*, while the highest *PPFD* resulted in the lowest *CQY* (Fig. 4). Growth temperature also had a significant effect on *CQY* ($p = 0.004\ 5$) with warmer temperatures having higher efficiencies. This response has been observed before in elevated CO_2 due to the reduction in photorespiration but increase in electron

transport (Farquar *et al.*, 1980; Frantz *et al.*, 2004b). There was also a significant interaction between *PPFD* and growth temperature ($p < 0.000\ 1$) with a larger decrease in *CQY* at 20 ℃ as light increased.

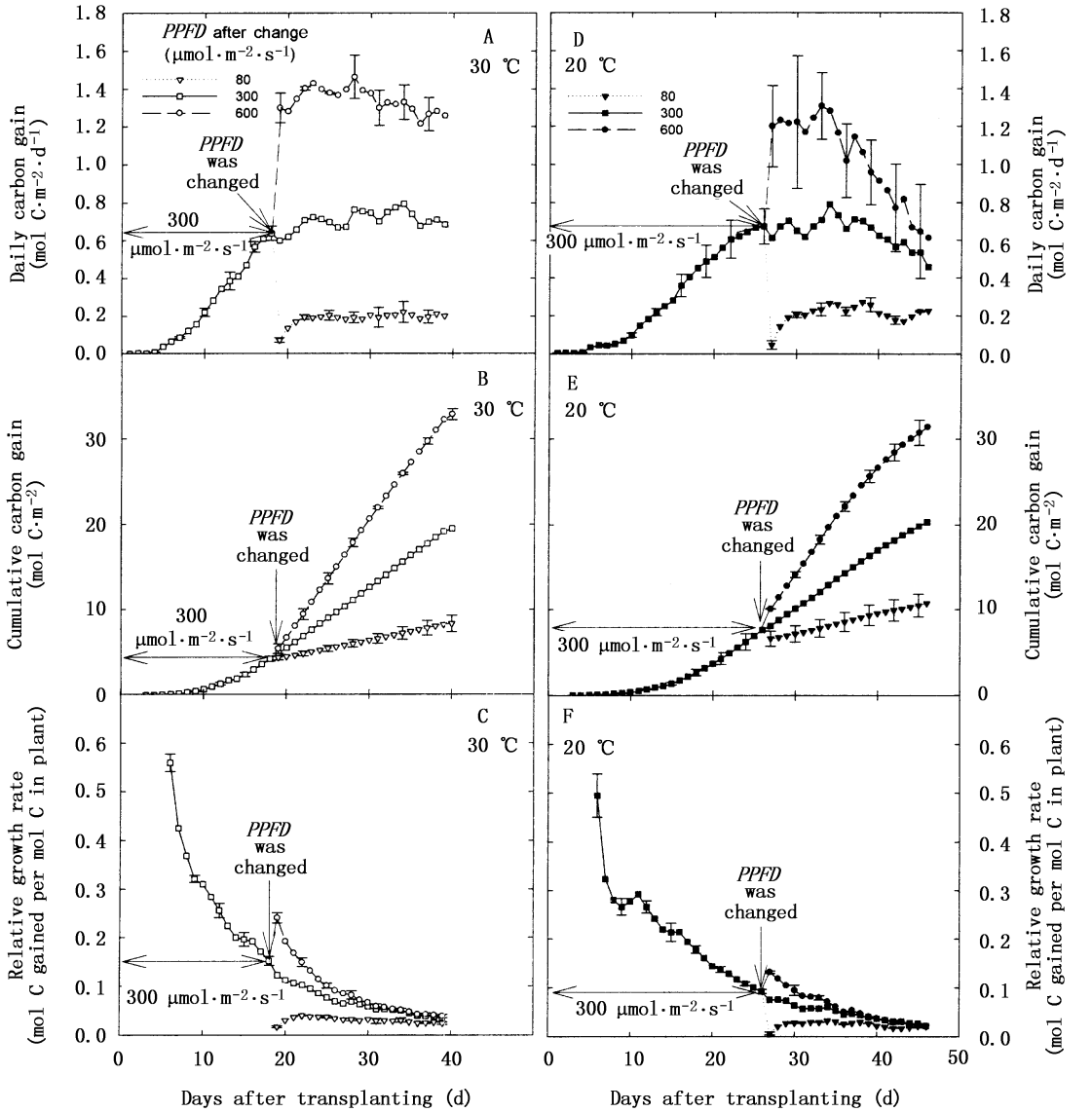

Fig.3 Daily carbon gain (A and D), cumulative carbon gain (B and E) and relative growth rates (C and F) before and after light treatments were started
Photosynthetic photon flux density (*PPFD*) was changed from 300 μmol·m^{-2}·s^{-1} on day 19 for the 30 ℃ canopies and on day 27 for the 20 ℃ treatment to 80, 300, or 600 μmol·m^{-2}·s^{-1}. Open symbols are for 30 ℃ treatment and closed symbols indicate 20 ℃ treatment. Circles are 600 μmol·m^{-2}·s^{-1}, squares are for 300 μmol·m^{-2}·s^{-1}, and inverted triangles represent 80 μmol·m^{-2}·s^{-1} *PPFD* treatments. Error bars represent the standard deviation

2.5 After *PPFD* treatment: yield

Shoot, root, and fruit mass was slightly lower in the 30 ℃ than in the 20 ℃ treatments (Table 1). However, the 20 ℃ treatments grew for a longer period of time than the 30 ℃ treatments. Fruit set was heavier in the 20 ℃ treatment and high light, which, due to the fruit located at the top and above the leaves of the canopy, decreased the photosynthetic rate gradually from 33 days until the end of the experiment in the high light treatment at this temperature.

The final mass can be predicted by using the *CCG* for each chamber. By multiplying *CCG* (mol C·m^{-2}) by 12 g·mol^{-1} for carbon, and dividing this by the measured carbon content (see **2.8 Tissue analysis** later in this section), the final mass can be estimated, and then compared to the actual mass. If the gas exchange measurements were accurate, the slope should be close to 1 with a high correlation. The actual slope for the regression was 1.01 with an r^2 of 0.949, indicating the CO_2 gas-exchange was accurate (Fig. 5).

Table 1 Average yield ($g \cdot m^{-2}$) of tomato leaf, stem, root, and fruit in the different treatments. Standard deviation is shown after averages for 80 and 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ light treatments ($n = 2$ for those photosynthetic photon flux density (*PPFD*) treatments; $n = 1$ for 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ *PPFD* treatment)

PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	20 ℃			30 ℃		
	Shoot	Root	Fruit	Shoot	Root	Fruit
80	271.6 ± 34.5	42.3 ± 8.3	5.0 ± 2.9	210.2 ± 15.3	25.9 ± 2.6	0.2 ± 0.3
300	598.1	73.2	0.9	549.9	59.3	10.4
600	799.1 ± 13.8	121.3 ± 1.3	36.2 ± 24.7	785.7 ± 3.6	85.7 ± 1.2	38.3 ± 9.2

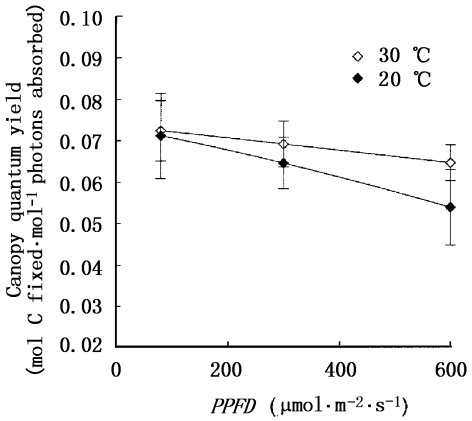

Fig. 4 Average canopy quantum yields (*CQY*) for 20 days after different light treatments were imposed at 30 ℃ or 20 ℃ growth temperatures

There were significant differences in *CQY* at the different light and temperature treatments, as well as a significant interaction between photosynthetic photon flux density (*PPFD*) and growth temperature ($p < 0.000\ 1$). Error bars represent ± 1 standard deviation

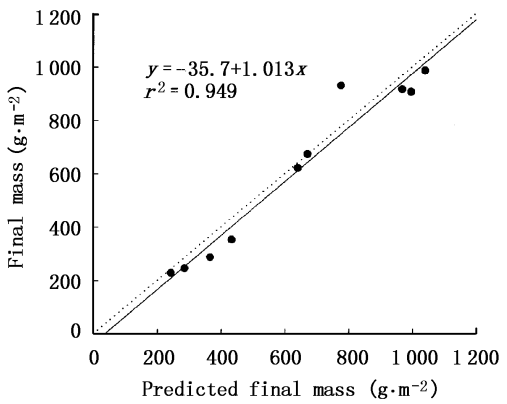

Fig. 5 Correlation between predicted and actual final mass in each gas exchange chamber

The predicted value was determined by using the cumulative carbon gain ($mol\ C \cdot m^{-2}$) multiplied by the molecular weight of carbon ($12\ g \cdot mol^{-1}$) divided by the average carbon fraction for each chamber (determined by C-H-N analysis; see **Materials and Methods**). Dotted line indicates the ideal 1:1 correlation and solid line indicates the regression line

2.6 Carbon use efficiency

The *CUE* increased from 0.65 to 0.72 $mol \cdot mol^{-1}$ on the first day after increasing *PPFD* in the 30 ℃ treatment (Fig. 6A) and from 0.64 to 0.68 $mol \cdot mol^{-1}$ in the 20 ℃ treatment (Fig. 6B). Acclimation at the two temperatures was different, with the *CUE* in the 30 ℃ treatment declining exponentially to completely acclimate after about 10 days compared to normalized, pre-treatment value (Fig. 7A). A best fit regression for the *CUE* at 20 ℃ and a *PPFD* of 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ indicated a significant linear decrease throughout the 20 day period ($p < 0.001$; $r^2 = 0.68$). Our analysis does not eliminate the possibility of an exponential decrease with a low slope. The different light treatments at both 30 ℃ and 20 ℃ were maintained for 20 days, so it is not known if the decrease in *CUE* is asymptotic or remains linear beyond 20 days after the initiation of the different light treatments.

The *CUE* decreased from 0.65 to 0.31 $mol \cdot mol^{-1}$ on the first day after shading for the 30 ℃ treatment (Fig. 6A) and from 0.64 to 0.18 $mol \cdot mol^{-1}$ for the 20 ℃ treatment (Fig. 6B). At both temperatures, *CUE* recovered completely after about 10 days, with most recovery occurring after the first three days of shade (Fig. 7B).

2.7 Growth and maintenance respiration

Fig. 8 shows strong correlations between relative growth rate and specific respiration for plants in each chamber ($p < 0.001$, $0.52 < r^2 < 0.99$). The figures are separated based on chamber temperatures to facilitate comparisons among *PPFD* levels.

The growth coefficient increased with decreasing *PPFD*, while the maintenance coefficient decreased with lower *PPFD* (Fig. 9A, 9B). There was no effect of temperature on growth or maintenance coefficients. Shade treatments had low *RGR*s, so the distance the line must extrapolate to the *y*-axis is a larger fraction of the total line, which may result in less accurate estimates of the growth and maintenance coefficients. The correlations in the low *PPFD* treatments were still highly significant ($p < 0.001$) with the r^2 ranging between 0.52 to 0.79 with an average of 0.69.

Growth respiration stayed almost constant in the 30 ℃ growth temperature regardless of the *PPFD* (Fig. 10A). On the other hand, growth respiration decreased in the 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ *PPFD* and 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatments during the 20 days of treatment at a growth temperature of 20 ℃. Maintenance respiration increased steadily after the *PPFD* treatments were imposed for both

growth temperatures (Fig. 10B). In fact, maintenance respiration accounted for the majority of total respiration in the 600 μmol·m^{-2}·s^{-1} *PPFD* treatment after 16 treatment days.

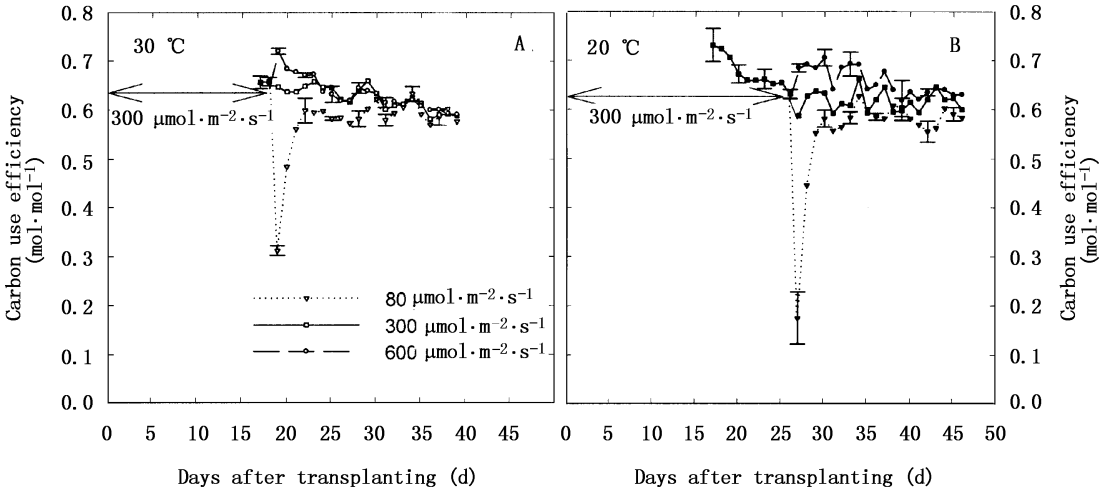

Fig.6 Carbon use efficiency (*CUE*, mol C respired·mol^{-1} C in plant) before and after photosynthetic photon flux density (*PPFD*) change with plants grown at both 30 ℃ (A) and 20 ℃ (B)

Open symbols represent the 30 ℃ treatment and closed symbols represent the 20 ℃ treatment. Circles are 600 μmol·m^{-2}·s^{-1}, squares are for 300 μmol·m^{-2}·s^{-1}, and inverted triangles represent 80 μmol·m^{-2}·s^{-1} *PPFD* treatments. Error bars represent ± 1 standard deviation of the mean for that day. Due to instability in photosynthesis and/or respiration measurements relative to each other when plants were small, only *CUE* data is shown from a few days immediately prior to the beginning of the *PPFD* treatments

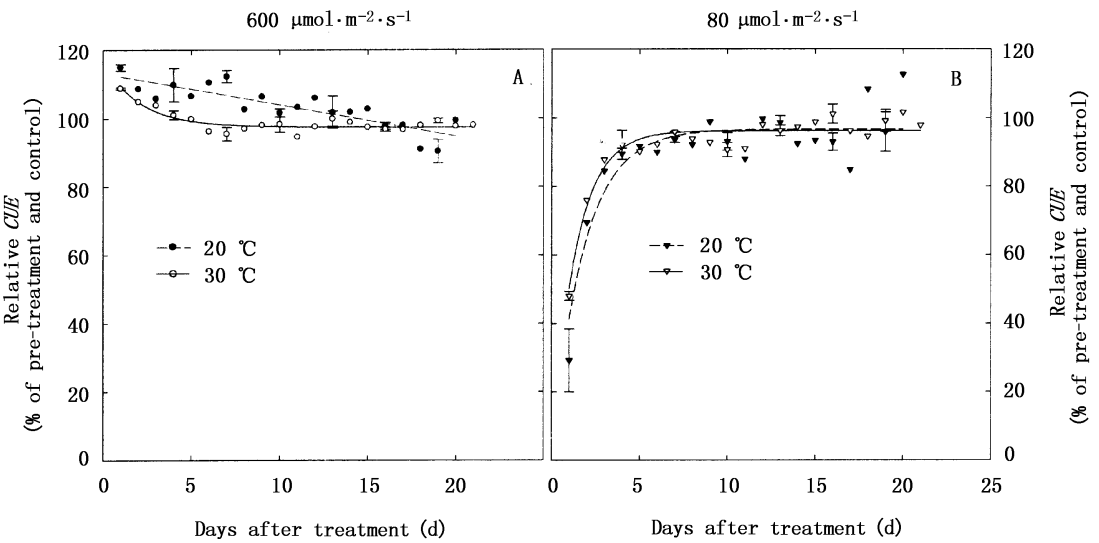

Fig.7 Change in carbon use efficiency (*CUE*) over time after increasing the photosynthetic photon flux density (*PPFD*) to 600 μmol·m^{-2}·s^{-1}(A) or decreasing the *PPFD* to 80 μmol·m^{-2}·s^{-1}(B)

The *CUE* of 20 ℃ canopies did not acclimate to 600 μmol·m^{-2}·s^{-1} in the same manner as those in 30 ℃ treatments, but *CUE* acclimated at both temperatures and returned to pre-treatment levels. The *CUE* of plants in the 80 μmol·m^{-2}·s^{-1} increased exponentially so that after 10 days, they were back to pre-treatment levels. Open symbols represent the 30 ℃ treatment and closed symbols represent the 20 ℃ treatment. Circles are 600 μmol·m^{-2}·s^{-1} and inverted triangles represent 80 μmol·m^{-2}·s^{-1} *PPFD* treatments. Error bars represent ± 1 standard deviation of the mean for that day

2.8 Tissue analysis

There were significant effects of both temperature and *PPFD* on leaf carbon concentration (Table 2; $p < 0.001$). Higher light and temperature led to higher C concentrations. There was also a significant interaction between *PPFD* and temperature on leaf carbon concentration ($p = 0.003$). Temperature-induced increases in leaf C concentrations were more pronounced at low light. Stem

and root C concentration also increased significantly with higher *PPFD*. Stem C concentration was not affected by growth temperature, but root C concentration was higher at 20 ℃ than at 30 ℃, the opposite of what was observed with leaf C concentration.

The nitrogen concentration of the leaves decreased with higher *PPFD*, and there was a significant light by temperature interaction, indicating that leaf N concentration decreased more with increasing *PPFD* at 20 ℃ than at 30 ℃. The nitrogen concentration in the stem was not influenced by either light or temperature. Nitrogen concentration was higher in 30 ℃ roots than in 20 ℃ roots. Leaf, stem, and root NO_3^- concentration decreased with additional *PPFD*. Reduced N decreased with increasing *PPFD* in the leaves, but remained about the same in the stem at the different *PPFD* and temperature treatments. At 20 ℃, reduced N increased with *PPFD* in the root, but remained unchanged at 30 ℃ growth temperature.

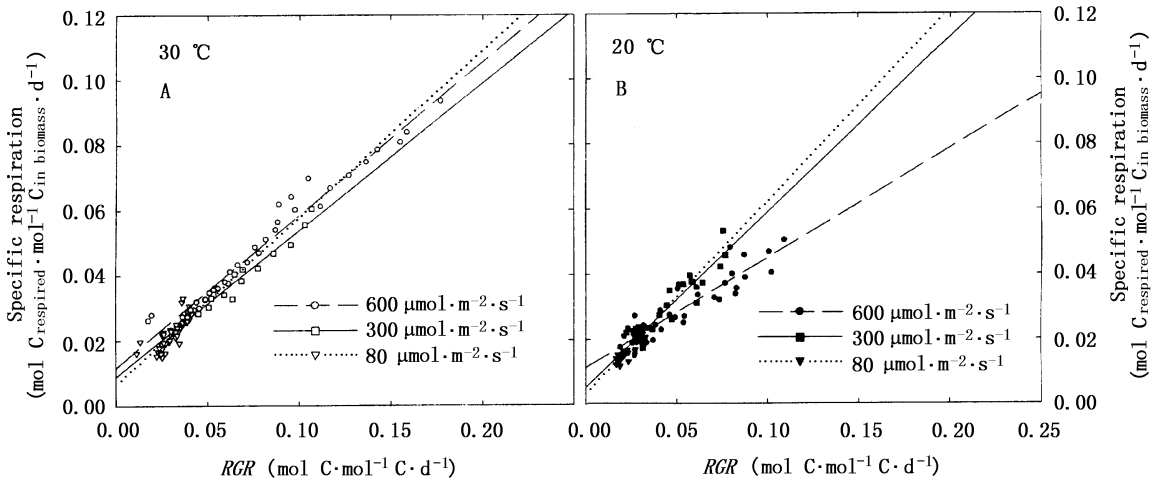

Fig. 8 Plots of relative growth rate (*RGR*) versus specific respiration, pooled for each photosynthetic photon flux density (*PPFD*) and temperature combination. (A) 30 ℃ treatment; (B) 20 ℃ treatment

The *y*-intercept provides an estimate of the maintenance respiration coefficient while the slope estimates the growth respiration coefficient. Individual chamber correlations were between $r^2 = 0.52$ to 0.99, with an average $r^2 = 0.82$. Open symbols represent the 30 ℃ treatment and closed symbols represent the 20 ℃ treatment. Circles are 600 μmol·m^{-2}·s^{-1}, squares are for 300 μmol·m^{-2}·s^{-1}, and inverted triangles represent 80 μmol·m^{-2}·s^{-1} *PPFD* treatments

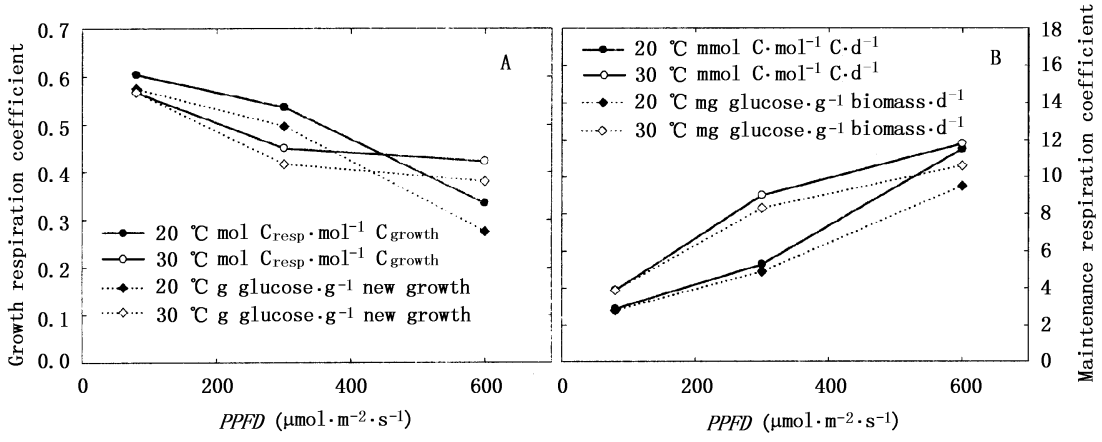

Fig. 9 Growth (A) and maintenance (B) respiration coefficients for tomato plants grown at different photosynthetic photon flux densities (*PPFD*) and temperatures

To facilitate comparisons with this study and other published reports, growth and maintenance estimates are reported in two different, commonly used units. There were no significant interactions between temperature and *PPFD* for either growth or maintenance respiration coefficients

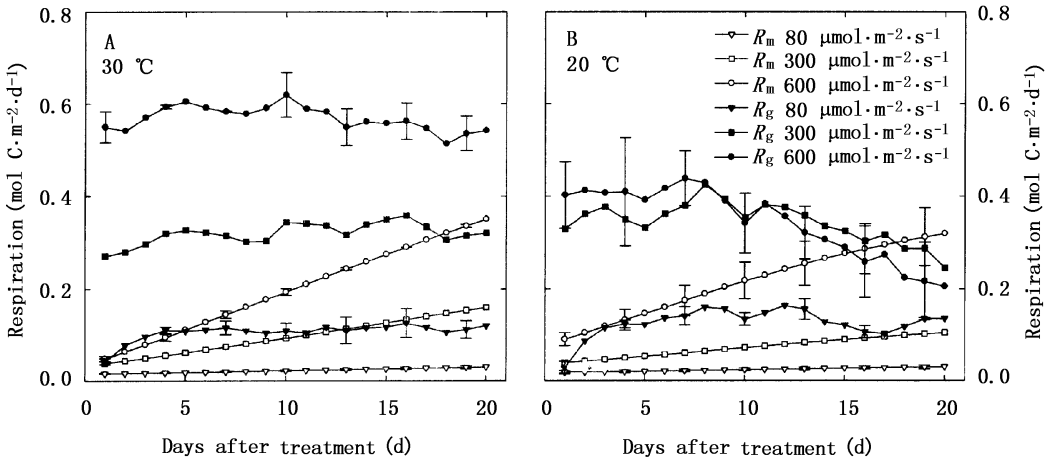

Fig. 10 Maintenance (R_m) and growth respiration (R_g) of tomatoes grown at both 30 ℃ (A) and 20 ℃ (B) and different light levels

Open symbols represent R_m and closed symbols represent R_g. Circles are 600 μmol·m^{-2}·s^{-1}, squares are for 300 μmol·m^{-2}·s^{-1}, and inverted triangles represent 80 μmol·m^{-2}·s^{-1} photosynthetic photon flux density (*PPFD*) treatments. Error bars represent ± 1 standard deviation of the mean for that day

Table 2 Average carbon, nitrogen, NO_3^-, and reduced N concentrations (g·kg^{-1}) in the different photosynthetic photon flux density (*PPFD*) and temperature treatments in leaf, stem, and root tissue

PPFD (μmol·m^{-2}·s^{-1})	Leaf			Stem			Root		
	80	300	600	80	300	600	80	300	600
20 ℃									
Carbon	319$^{c*\#}$	365$^{b*\#}$	375$^{b*\#}$	327^{b}	360^{ab}	388^{a}	354^{b*}	391^{a*}	395^{a*}
Nitrogen	66$^{a\#}$	45$^{bc\#}$	35$^{c\#}$	36	32	23	42^{b*}	44^{ab*}	41^{b*}
NO_3^-	27^{a}	13^{ab}	8^{b}	25$^{a\#}$	14$^{ab\#}$	6$^{b\#}$	19$^{a*\#}$	15$^{a*\#}$	8$^{b*\#}$
Reduced N	39^{ab}	32^{ab}	27^{b}	14	18	17	23$^{d*\#}$	29$^{b*\#}$	33$^{a*\#}$
30 ℃									
Carbon	382$^{b*\#}$	365$^{b*\#}$	403$^{a*\#}$	342^{ab}	351^{ab}	385^{a}	353^{b*}	365^{ab*}	385^{a*}
Nitrogen	60$^{a\#}$	52$^{ab\#}$	44$^{bc\#}$	34	34	29	45^{ab*}	47^{a*}	43^{ab*}
NO_3^-	19^{ab}	16^{ab}	9^{b}	20$^{ab\#}$	21$^{ab\#}$	13$^{ab\#}$	19$^{a*\#}$	19$^{a*\#}$	15$^{a*\#}$
Reduced N	41^{a}	37^{ab}	34^{ab}	14	14	16	26$^{c*\#}$	27$^{bc*\#}$	28$^{b*\#}$

Means followed by the same letter within each row indicate significant differences ($p < 0.05$) for that tissue type for the *PPFD* treatments, * indicates significant differences in means for that tissue type between the two temperature treatments and # indicates significant interactions between the temperature and *PPFD* for that tissue type

3 Discussion

3.1 Light and temperature effects on growth and maintenance respiration components

Models that separate respiration into growth and maintenance components commonly assume there is no effect of temperature on the growth coefficient but a strong effect on the maintenance coefficient (Heuvelink, 1995). This effect is usually described with a Q_{10} term of approximately 2.0 (Edwards & Hanson, 1996; McCullough & Hunt, 1993; Witowski, 1997). If these models are accurate, there should have been a doubling of the maintenance coefficient between the two temperature treatments in this study, but there was no effect of temperature. However, the plants in this study were exposed to constant temperatures, and thus had the opportunity to acclimate to that temperature. It is possible that temperature effects on the maintenance coefficient depend on how temperature treatments are imposed; plants may be able to acclimate to long-term temperature treatments. Conversely, a plant that is exposed to short-term temperature fluctuations (daily or hourly) cannot fully acclimate to a specific growing temperature. As a result, the maintenance coefficient of plants may be less sensitive to long-term than to short-term temperature changes. Most previous studies looked at how short-term temperature changes affect respiration, and the Q_{10} approach may be valid for such short-term effects. Models may need to reflect the

dynamic nature of a temperature response (i.e. Q_{10}) by scaling it to how often and severe a temperature fluctuation a plant or canopy experiences over the course of time (seconds, minutes, hours, or days) (van Iersel, 2006). Improved respiration models thus may need to incorporate a short-term sensitivity to temperature, while also accounting for acclimation to long-term changes in temperature.

Unlike the constant temperature treatments, *PPFD* changed drastically a single time during the trial. The regression model indicated that different *PPFD* levels affected maintenance and growth respiration coefficients. The growth coefficient decreased with increasing *PPFD*, suggesting the high *PPFD* plants synthesized simpler compounds, like sugars and starches, whereas the low *PPFD* treatments were synthesizing more complex compounds (Amthor, 1989). Low-*PPFD*-grown plants tend to synthesize more light-harvesting compounds, less storage compounds, and have less Rubisco (Zhao & Oosterhuis, 1998), which would result in higher growth coefficients, whereas tomatoes grown in high *PPFD* tend to accumulate starch in leaves (Goldschmidt & Huber, 1992; Yelle *et al*., 1989). These growth coefficients are consistent with those physiological changes as plants acclimate to low or high *PPFD*.

Generally, the more reduced a substance, the higher the C content, and the more costly that substance is for the plant to construct, and as a result, the growth coefficient is higher for more reduced, carbon-rich compounds (McDermitt & Loomis, 1980). Simple sugars (glucose, fructose, and mannose) have C contents of 400 $g \cdot kg^{-1}$ while starch or transportable sugars have slightly higher C content of about 420 to 444 $g \cdot kg^{-1}$. For example, cell wall material (cellulose, hemicellulose, and lignin) is similar to stored sugar whereas protein averages about 460 $g \cdot kg^{-1}$. Lipids have even more C due to their highly reduced nature, ranging from about 700 to 800 $g \cdot kg^{-1}$. The growth coefficients in this experiment are lower in high *PPFD* treatments and those treatments also have the higher C contents, which is the opposite of what one might expect. The 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ *PPFD* treatment had more reduced leaf N compared to the 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ or 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatments suggesting more protein in these treatments and therefore a higher growth coefficient. What is unknown is how much total mineral content there was in each of the treatments, which could dilute total C, thereby masking potential explanations for the discrepancy in growth and maintenance coefficients and C content.

There have been several attempts at correlating maintenance respiration requirements to N content or protein content (Dewar, 1996; Ryan *et al*., 1996). Reduced N content is a reflection of protein amount and therefore an indirect measure of amount of protein that would need to be maintained. As a result, it would be predicted that the higher the reduced N content, the higher the maintenance. In our study, reduced leaf N concentration decreased with increased light, which is opposite of what would be expected if N concentration predicts maintenance respiration, since the maintenance respiration coefficient increased with increased *PPFD*. Again, potential dilution of total N from different total mineral content should be considered.

The roots in the 20 ℃ treatment had more reduced N than the 30 ℃ treatment. Higher fractions of NO_3^--N may indicate a smaller requirement for maintenance respiration with maintenance being applied proportionally more towards maintaining ion gradients, a low maintenance cost requirement, rather than repair of functional proteins, a higher maintenance cost requirement (Thornley & Johnson, 2000). Although reduced N is an indicator of protein concentrations, not all proteins require the same amount of maintenance. We speculate that plants in the low-light treatments may have produced more biologically-inactive, storage proteins, reducing their maintenance respiration requirements. High light also increases protein turnover and repair (Telfer, 2005), which could account for the increased maintenance coefficient at high *PPFD*.

3.2 Acclimation of carbon use efficiency: increased *PPFD*

The response of *CUE* to a change from 300 to 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was different at the two temperatures tested. Both showed an initial increase in *CUE* on the first day after increasing *PPFD*, and the 30 ℃ declined back to initial pre-treatment levels within a few days. At 20 ℃, *CUE* decreased linearly throughout the entire 20-d period. This may suggest differences in C mobilization or synthesis at different temperatures. The photosynthesis in the high light, 20 ℃ treatment declined rapidly after 8 days at high light, which may have been due to several different factors. First, flowers began to initiate in this treatment after changing the *PPFD*, and in this tomato cultivar, the majority of flowers appear above the canopy. These flowers shaded the canopy and as the flowers set fruit, further shading occurred. Starch accumulation also may have contributed to some feedback inhibition of photosynthesis if starch was synthesized and accumulated faster than carbohydrates were exported. Conversely, the

flowers in the 30℃ treatment did not set as many fruits, so there was less shading than in the 20 ℃ treatments, and the feedback inhibition was less because the elevated temperature either increased the rate of carbohydrate export from the leaves or decreased the rate of carbohydrate accumulation within the leaves as occurs in the seed of cereal crops at elevated temperatures (Bhullar & Jenner, 1986; Tashiro & Wardlaw, 1989).

3.3 Acclimation of carbon use efficiency: decreased *PPFD*

Reducing light levels from 300 to 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ resulted in similar changes in *CUE* at both temperatures; there was an initial decrease in *CUE* after decreasing the *PPFD*, but *CUE* recovered within 5 – 10 days, similar to the recovery time as previously reported (Frantz & Bugbee, 2005). Some of the acclimation could have been the result of *CQY* differences after shade was imposed. The low light plants had greater *CQY*, while the high *PPFD* treatments were less efficient photosynthetically. The large decrease in *CUE* on the initial day after shading indicated plants were temporarily less efficient at converting newly fixed carbon into dry matter after shading. The second day after starting the *PPFD* treatments, *CUE* greatly increased, back to within about 80% of its pre-treatment value. As before, we attribute the large initial change in *CUE* to a temporary imbalance, over a 24-h period, between supply of C (either from stored reserves or recently fixed C) and demand by respiration for C, permitting respiration to continue at a high rate; however, as those reserves are consumed, respiration decreases back into balance with the previous days' photosynthesis. This explanation fits the Dewar *et al*. (1998) explanation of steady *CUE* values under non-limiting conditions. The fact that there was no interactive effect of temperature and *PPFD* on *CUE* suggests that these stored reserves are consumed at roughly equal rates or are mobilized equally well at different temperatures when plants experience a shade stress.

3.4 Relationship of carbon use efficiency and respiration components

van Iersel (2003) described the relationship between *CUE*, *RGR*, and growth and maintenance respiration coefficients as:

$$1/CUE = 1 + m + c/RGR \quad (11)$$

Nemali & van Iersel (2004) further described the relationships between c and m, showing that *CUE* depends on the ratio of c and m during crop growth. This clearly illustrates that if *RGR* changes and *CUE* remains relatively stable, m, c, or both need to adjust. In the current study, *CUE* decreased from 0.68 $mol \cdot mol^{-1}$ to about 0.62 $mol \cdot mol^{-1}$ over the course of the experiment, depending on the treatment, while *RGR* decreased from a maximum of 0.15 to 0.01 $mol \cdot mol^{-1} \cdot d^{-1}$. In order for such a small relative supply of C to support a *CUE* of 0.62 $mol \cdot mol^{-1}$ or higher, c, m, or both needed to acclimate. This is precisely what happened with the maintenance coefficient at 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ being about half that at 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and only 20% of the 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatment. The growth coefficient increased in the low *PPFD* treatments, but the extent of increase was not enough to offset the gain in efficiency from reducing the maintenance coefficient thereby enabling *CUE* to remain relatively high, even in low *PPFD*.

Together, these data indicate that both growth and maintenance respiration coefficients respond to changes in light more so than to differences in growth temperature. Because respiration in general, and maintenance respiration in particular, have widely been reported to have a temperature response, we suggest that the temperature response is a function of not only the magnitude of temperature change, as is usually parameterized to be the only requirement in models, but also how often the change is incurred, and for what duration plants experience the change. If plants are exposed to changing temperatures gradually they may be able to acclimate, thus minimizing the temperature sensitivity of respiration; short-term changes in temperature on the other hand are much more likely to affect respiration. These data also indicate that *CUE* can change in response to the environment. However, as long as the plants acclimate to the new growing conditions, *CUE* may not be affected for prolonged periods.

3.5 Changes in tissue nutrient concentration

There was surprisingly little difference in N or NO_3^- concentrations between the two temperatures, except in root NO_3^- concentrations. Kafkafi (1990) reported an approximately 33% increase in leaf NO_3^- concentration in tomato as the temperature increased from 24 ℃ to 34 ℃ and a simultaneous 50% decrease in root NO_3^-. This was attributed to less NO_3^- transport from the root to the shoot in warmer conditions. This is consistent with our finding the root NO_3^- concentrations were higher at 30 ℃ than at 20 ℃.

The differences in carbon concentration at different *PPFD* levels may reflect the possible starch versus no starch accumulations in high versus low light. Tomatoes accumulate starch in leaves (Hocking & Steer, 1994), which would result in C concentrations closer to 400 $g \cdot kg^{-1}$ in that tissue (C is 40% of CH_2O). C content was

much lower than 400 $g \cdot kg^{-1}$ in the two lower *PPFD* treatments suggesting a dilution of C, possibly due to high total nutrients. A total nutrient analysis was not done in this study to confirm this hypothesis. Differences in C concentrations were found in leaves and roots, possibly reflecting how much and where starch was ultimately accumulating. There were slightly higher carbon concentrations in leaves grown at 30 ℃ than in leaves grown at 20 ℃, while there were higher carbon concentrations in roots of 20 ℃ plants than in 30 ℃ plants. There was no difference in stem carbon concentration at 20 ℃ and 30 ℃.

3.6 Applicability of results to ambient CO_2 environments

Since elevated CO_2 increases photosynthesis and carbohydrate supply, it is likely that *CUE* would have acclimated more slowly in ambient CO_2. Elevated CO_2 allows for greater C stores to meet pre-existing respiration demands (prior to *PPFD* treatment), and not force growth, maintenance, or both to acclimate as quickly to the sudden change in C supply in different *PPFD* and ambient CO_2. Nemali and van Iersel (2004) found that low light can depress *CUE* of begonia (*Begonia semperflorens-cultorum*) for several weeks in a non-enriched CO_2 environment, but we observed complete acclimation of tomato after only 12 days of low light and nearly complete acclimation in both high and low *PPFD* after only 2 days.

Some studies have suggested that elevated CO_2 inhibits respiration. However, no theoretical basis for a feedback effect of elevated CO_2 on dark respiration has been found, and recent studies indicated that the direct effect of elevated CO_2 up to 3-times ambient on dark respiration is statistically insignificant. Amthor *et al*. (2001) used an improved gas exchange chamber and found that the previously reported effect of CO_2 on respiration (Amthor *et al*., 1992) resulted from leaks in the original chamber. Indeed, using five different gas exchange measurement approaches, he consistently found that respiration was insensitive to short-term changes in CO_2 concentration. Similarly, Burton *et al*. (1996) initially reported a significant inhibition of root respiration in elevated CO_2, but later re-did tests and found that once leaks were sealed, no CO_2 effect was observed (Burton & Pregitzer, 2002).

4 Conclusions

Respiration, photosynthesis, and *CUE* changed dramatically with an increase or decrease in *PPFD*. However, *CUE* recovered after several days due to the acclimation of the maintenance respiration coefficient. The rate of recovery was not significantly faster at the warmer temperature. While the growth coefficient increased in low *PPFD* and decreased in high *PPFD*, the change in the maintenance coefficient was enough to offset these changes causing *CUE* to recover to pre-treatment levels for 20 days after *PPFD* treatments were imposed. Interestingly, growth and maintenance respiration were affected far more by *PPFD* and growth rate than by temperature. High *PPFD*, and the resulting rapid growth, appears to cause more rapid turnover of compounds and higher maintenance respiration than high temperature. Cumulatively, these data suggest that long-term temperature responses can differ greatly from short-term observations.

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