Temperature Effects on Photosynthesis, Growth Respiration, and Maintenance Respiration of Marigold

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Abstract

Marigolds *(Tagetes patula)* were grown from seed to flowering at either 20 or 30 °C, and the CO_2 exchange rate of the plants was measured throughout the 60-day growing period. Plants grew faster at 30 than at 20 °C, because of higher whole-plant photosynthesis (P_{net}) from 5 to 40 days after seeding. The maintenance respiration coefficient (r_m) was lower at 20 than at 30 °C (Q_{10} = 1.3), while the growth respiration coefficient was not affected by temperature (0.51 $g \cdot g^{-1}$). The ratio of maintenance respiration to total respiration increased throughout plant development and reached 43 and 55% at 20 and 30 °C, respectively. Carbon use efficiency (CUE) of the plants increased during germination, and then decreased throughout the remainder of the growing period. This decrease in CUE was the result of a decrease in relative growth rate (RGR). Plants grown at 20 °C had a higher CUE than those at 30 °C from 40 to 51 days after seeding, which was the result of a lower RGR and higher r_m at 30 °C. Although plants grown at 20 °C had equal or higher CUE, a lower r_m, and less dark respiration (R_{dark}), their growth was less than that of plants at 30 °C, suggesting that whole-plant P_{net} is a more important determinant of growth than CUE, r_m, or R_{dark}.

INTRODUCTION

Temperature greatly affects the carbon exchange rate and growth of plants. However, the exact method by which it effects growth is not always clear, because temperature affects both photosynthesis and respiration. Respiration, in turn, can be divided into two separate processes, i.e., growth respiration (R_g) and maintenance respiration (R_m). Because differences in plant size and growth rate make it difficult to make direct, meaningful comparisons of R_g and R_m among different treatments, R_g is commonly expressed as the growth respiration coefficient (r_g) × growth rate, while R_m is expressed as the maintenance respiration coefficient (r_m) × plant size. Maintenance respiration (and r_m) is considered to be highly sensitive to temperature, mainly due to increased protein turnover and membrane leakage at higher temperatures (Hesketh et al., 1980). On the other hand, r_g will only be affected by temperature, if temperature affects the chemical composition of the plants or the biochemical pathways by which the plant compounds are synthesized (Penning de Vries et al., 1989).

Much of the previous research on temperature effects on R_g and R_m has looked at short-term effects of temperature changes. However, long-term effects may be different from short-term effects, since the isozyme composition of plants can change in response to the environmental conditions. If plants adapt to higher temperatures by producing enzymes with a lower turnover rate, long-term effects of temperature on R_m are likely to be less than short-term effects. The objective of this research project was to quantify the effect of temperature on photosynthesis and respiratory processes of marigold, throughout plant development. We hypothesized that temperature would increase r_m (although less than normally seen in short-term studies), but not r_g.

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MATERIALS AND METHODS

Growing Conditions and CO_2 Exchange Measurements

Plants were grown in 50×25×5 cm^3 trays (6.3 L), filled with a 50/50% (v/v) mixture of fine sand and perlite. The growing medium was watered thoroughly with nutrient solution before seeding each flat with 36 seeds of marigold 'Queen Sophia'. These trays subsequently were enclosed in CO_2 exchange chambers (van Iersel and Bugbee, 2000), which were placed inside two growth chambers (four CO_2 exchange chambers per growth chamber). The growth chambers were programmed for a 14 hour light period and had a photosynthetic photon flux of 410 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the surface of the growing medium, which resulted in a total daily photon flux of 20.7 $mol \cdot m^{-2}$.

The plants were subirrigated as needed with a nutrient solution made from a complete, water-soluble fertilizer (Peters' 15-5-15 CalMag, The Scotts Co., Marysville, Ohio, USA) dissolved in deionized water with a concentration of 100 $mg \cdot L^{-1}$ N.

The CO_2 exchange rate of whole trays of plants was measured every 10 minutes for 60 days, using a multi-chamber, semi-continuous CO_2 exchange system (van Iersel and Bugbee, 2000).

Treatments

Temperature inside the gas exchange chambers was measured every 2 seconds with type-T thermocouples. Based on these temperature measurements, a datalogger controlled a 200-W heater in each chamber. Temperature set points in the gas exchange chambers were 20 or 30 °C and were kept constant throughout the entire experiment. The average temperature was within 0.2 °C of the set point, with short-term fluctuations of approximately 0.5 °C.

Calculated Parameters and Statistical Analysis

The CO_2 exchange measurements resulted in direct measurement of net photosynthesis and dark respiration (P_{net} and R_{dark}, $mol \cdot plant^{-1} \cdot s^{-1}$). These values were used to calculate daily carbon gain (DCG, a measure of growth rate; $mol \cdot plant^{-1} \cdot day^{-1}$), carbon use efficiency (CUE, the amount of carbon incorporated into the plant divided by the amount of carbon fixed in gross photosynthesis; $mol \cdot mol^{-1}$), and cumulative carbon gain (CCG, a measure of plant size; $mol \cdot plant^{-1}$) according to van Iersel and Bugbee (2000). Relative growth rate (RGR, $mol \cdot mol^{-1} \cdot day^{-1}$) was calculated as:

$$RGR = DCG/CCG \qquad [1].$$

To minimize the effect of the C present in the seeds, which contained approximately 0.063 mmol/plant, data with a CCG < 6.3 mmol/plant were not used for further analyses.
Growth and maintenance respiration coefficients at 20 and 30 °C were estimated using linear regression, using data from all eight CO_2 exchange chambers:

$$R_d = x_0 \times DCG + x_1 \times DCG \times T + x_2 \times CCG + x_3 \times CCG \times T \qquad [2],$$

where R_d = daily respiration ($mol \cdot day^{-1}$), T = temperature, and x_0 ... x_3 are regression coefficients.

RESULTS AND DISCUSSION

CO_2 Exchange Rate and Plant Growth

Plants grown at 30 °C germinated faster and had higher photosynthetic rates from 5 until 40 days after seeding than plants grown at 20 °C (Fig.1). During the latter part of the experiment, P_{net} remained higher in the 30 than in the 20 °C treatment, but these differences were no longer statistically significant. In the 30 °C treatment, P_{net} reached is maximum value after 32 days, while it took 44 days at 20 °C. Presumably, at his stage the crop had reached canopy closure and almost all the available light was intercepted by the foliage. The subsequent small decrease in P_{net} may have been caused by the continuing increase in R_{dark} (Fig. 1), as well as by interception of some of the light by flowers, thus reducing the amount of light available for photosynthesis.

Growth and Maintenance Respiration

Regression analysis, using Eq. 2, indicated that there was no temperature effect on r_g (0.487 ± 0.008 mol·mol^{-1}, mean ± SE). Since r_g more commonly is expressed in grams of glucose per gram of dry matter, it was converted based on the carbon content of the plants (42% C) and that of glucose (40%), and found to be 0.51 g·g^{-1}, resulting in a glucose requirement (glucose needed to produce 1 g of dry matter) of 1.56 g·g^{-1}. This estimate is slightly higher than the commonly used values of 1.39 and 1.45 g·g^{-1} for leaves and stems of non-leguminous species, respectively (Penning de Vries et al., 1989), but similar to estimates for sorghum [*Sorghum bicolor* (L.) Moench] plants (1.54 g·g^{-1}, Amthor et al., 1994), and leaves of yellow-poplar (*Liriodendron tulipifera* L.) (1.46 g·g^{-1}, Wullschleger et al., 1997). A glucose requirement of 1.56 g·g^{-1} yields a conversion efficiency of 0.64 g·g^{-1}, within the normal range of 0.6 to 0.8 g·g^{-1} (McCree, 1982).

As expected, r_m was lower at 20 (0.0090 ± 0.0004 mol·mol^{-1}·d^{-1}) than at 30 °C (0.0117 ± 0.0004 mol·mol^{-1}·d^{-1}), indicating that the Q_{10} for r_m was 1.3. Differences in R_m (calculated as $r_m \times$ CCG) between the two temperature treatments were larger than suggested by the differences in r_m, because plants grown at 30 °C not only had a higher r_m, but also were larger than those at 20 °C. Converting these estimates of r_m to the conventional units of grams of glucose per gram dry matter per day resulted in values of 9.4 and 12.2 mg·g·d^{-1} at 20 and 30 °C, respectively. Many previously reported values range from 0.003 to 0.050 g·g^{-1}·d^{-1} (Hesketh et al., 1980).

Initially, R_g accounted for most of the respiration (Fig. 2), but the importance of R_m increased throughout the growing period and R_m eventually (after 8 weeks) accounted for 43 and 55% of the total respiration at 20 and 30 °C, respectively.

Growth Rate, Relative Growth Rate, and Carbon Use Efficiency

Plants grown at 30 °C had a higher DCG (growth rate) than those grown at 20 °C (Fig. 3) during much of the growing period, but plants grown at 20 °C had a higher RGR. There was a decrease in RGR throughout the experiment, which is normal because of increased intra- and inter-plant competition for light.

Carbon use efficiency increased sharply during the early part of the growing period, and decreased thereafter. The low initial CUE was caused by respiration from the germinating seeds. Maximum CUE was reached when the seeds had germinated and all plants were photosynthesizing. The subsequent decrease in CUE was related to the decrease in RGR. Thornley and Johnson (1990) showed that $1/CUE = 1 + r_g + r_m/RGR$, and a decrease in RGR therefore results in a decrease in CUE, unless there are concomitant changes in r_g and/or r_m. The lower CUE from 40 to 51 days after seeding at 30 °C thus can be explained by the higher r_m and lower RGR at 30 than at 20 °C.

CONCLUSIONS

Marigolds grew faster at 30 than at 20 °C, because of higher whole-plant P_{net} during much of the growing period. Temperature had no effect on r_g, but r_m was lower at 20 than at 30 °C (Q_{10} = 1.3). The importance of R_m in the carbon balance of the plants increased during the growing period. Maintenance respiration increased from only 10% of total respiration shortly after germination to 43 (at 20 °C) and 55% (at 30 °C) of total respiration at the end of the growing period.

Despite the higher DCG at 30 °C during much of the growing period (day 5 to 40), plants at 20 °C had a higher RGR (from day 25 until harvest). Carbon use efficiency initially was low (0.3-0.4) because of respiration from germinating seeds, and increased until all seeds had germinated. There was a decrease in CUE throughout the remainder of the growing period, which was related to the concomitant decrease in RGR.

Plants grown at 20 °C had a higher CUE than those at 30 °C from day 40 until 51. This was the result of the higher RGR and lower r_m of plants grown at 20 °C. Even though plants grown at 20 °C respired less, had an equal or higher CUE, and had a lower r_m, plants at 30 °C grew faster during most of the experiment. This indicates that whole-plant P_{net} is a more important determinant of plant growth than CUE, R_{dark}, or r_m.

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Figures

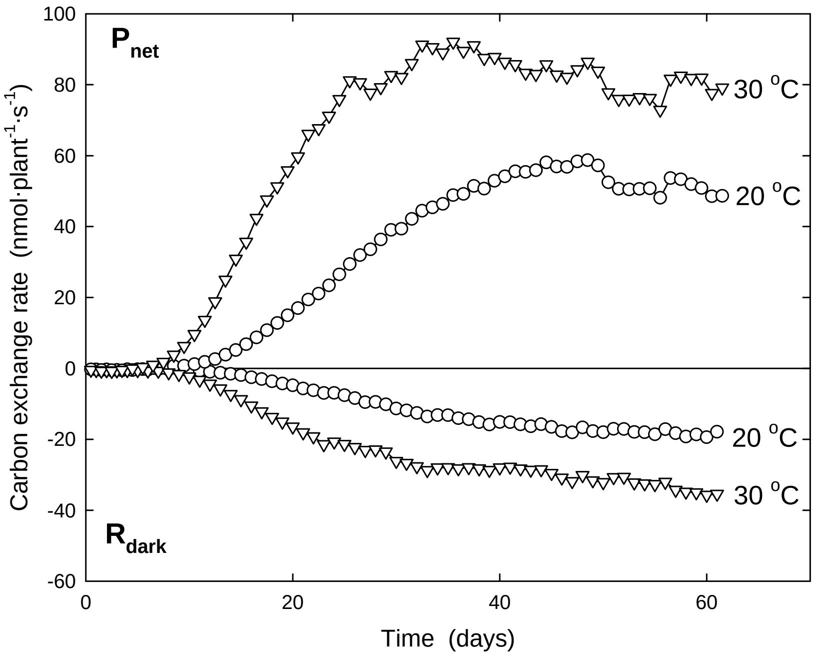

Fig. 1. Carbon exchange rates (net photosynthesis, P_{net} and dark respiration, R_{dark}) of marigolds grown from seed to flowering at 20 or 30 °C. Differences in P_{net} between the two treatments were statistically significant ($P < 0.05$) from day 5 to day 40, while differences in R_{dark} were significant throughout the entire experiment.

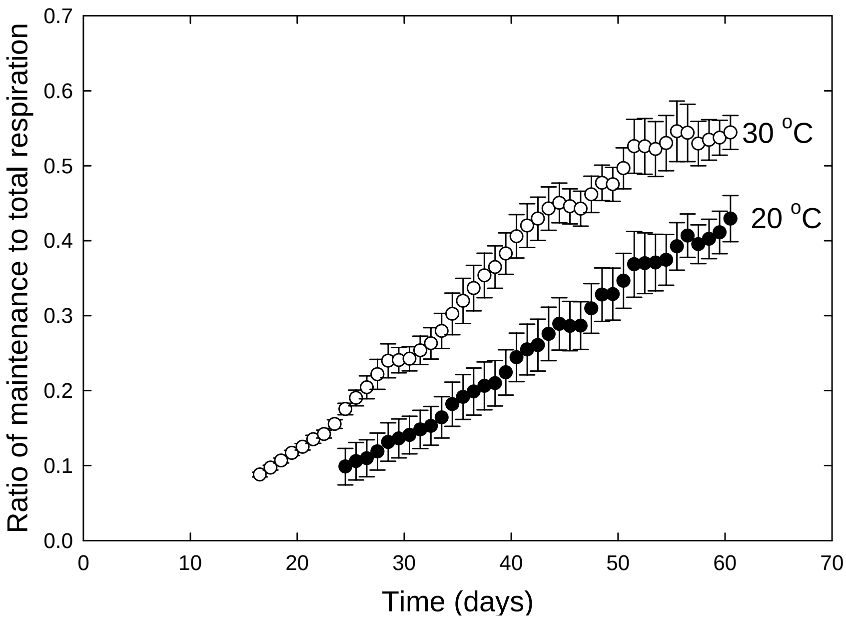

Fig. 2. Maintenance respiration of marigold as a fraction of total respiration. Plant size initially was too small to get reliable estimates of maintenance respiration. Error bars represent the standard error.

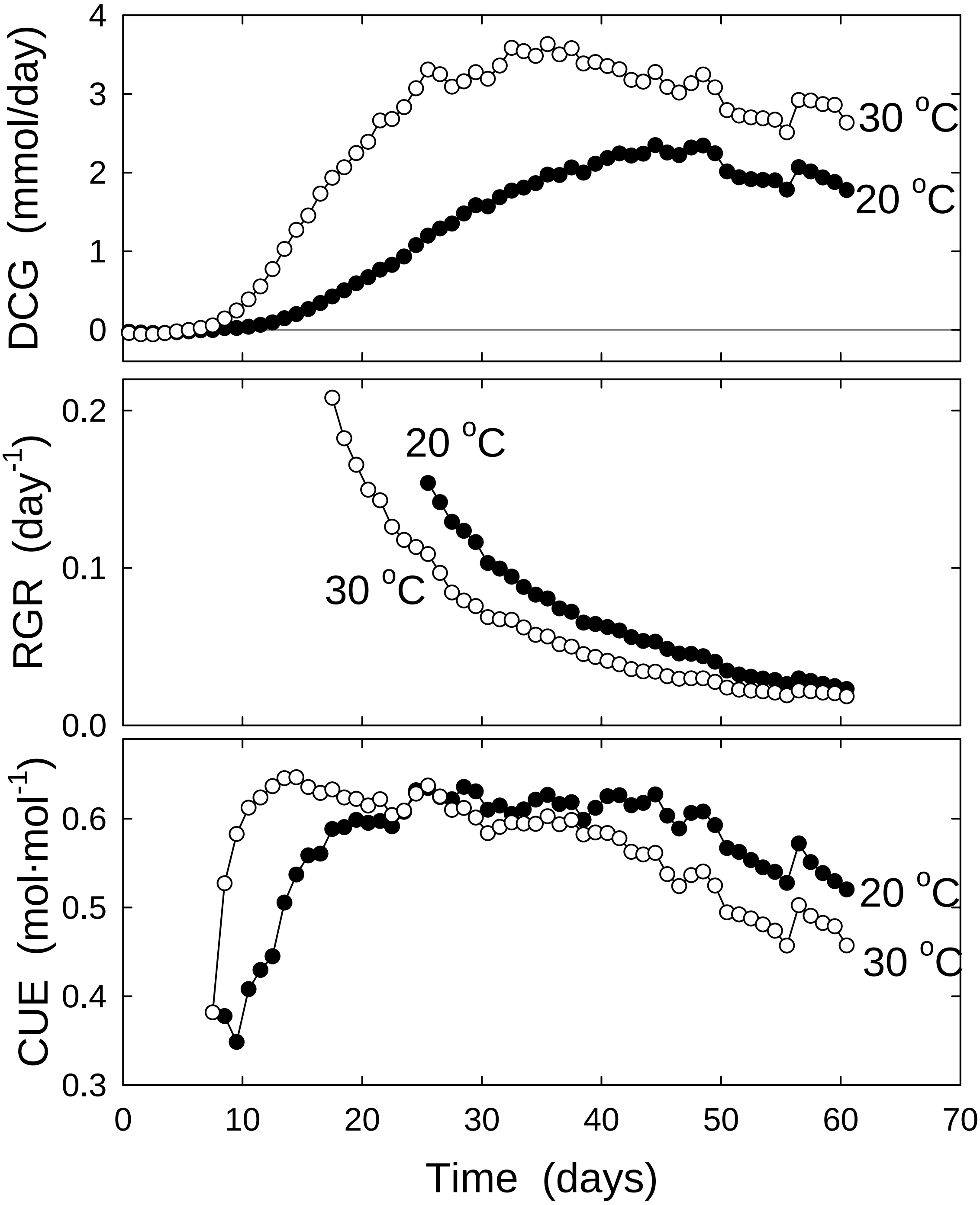

Fig. 3. Daily carbon gain (DCG), relative growth rate (RGR), and carbon use efficiency (CUE) of marigolds grown at 20 or 30 °C. Daily carbon gain was significantly ($P < 0.05$) higher at 30 than at 20 °C from day 5 until day 40. Relative growth rate was only calculated after DCG > 6.7 mmol/plant and always was significantly higher at 20 °C than at 30 °C. Carbon use efficiency was lower at 20 than at 30 °C at day 10 and higher from day 40 until day 51. The low CUE at the start of the growing period was caused by respiration from the germinating seeds. This also caused the DCG to be negative during the first 8 and 5 days at 20 and 30 °C, respectively.