

Temperature Response of Whole-plant CO₂ Exchange Rates of Three Magnolia Cultivars

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ADDITIONAL INDEX WORDS. *Magnolia grandiflora*, photosynthesis, respiration, Q₁₀, carbon use efficiency, net assimilation rate, heat tolerance

ABSTRACT. Temperature-response curves for photosynthesis and respiration are useful in predicting the ability of plants to perform under different environmental conditions. Whole crop CO₂ exchange rates of three magnolia (*Magnolia grandiflora* L.) cultivars ('MGTIG', 'Little Gem', and 'Claudia Wannamaker') were measured over a 25 °C temperature range. Plants were exposed to cool temperatures (13 °C day, 3 °C night) temperatures before the measurements. Net photosynthesis (P_{net}) of all three cultivars increased from 3 to 15 °C and decreased again at higher temperatures. 'MGTIG' had the highest and 'Little Gem' the lowest P_{net}, irrespective of temperature. The Q₁₀ (relative increase in the rate of a process with a 10 °C increase in temperature) for P_{net} of all three cultivars decreased over the entire temperature range. 'MGTIG' had the lowest Q₁₀ at low temperatures (1.4 at 8 °C), while 'Little Gem' had the lowest Q₁₀ for P_{net} at temperatures >17 °C and a negative Q₁₀ > 23 °C. This indicates a rapid decline in P_{net} of 'Little Gem' at high temperatures. The decrease in P_{net} of all three cultivars at temperatures >15 °C was caused mainly by an exponential increase in dark respiration (R_{dark}) with increasing temperature. 'Little Gem' had a lower R_{dark} (per unit fresh mass) than 'MGTIG' or 'Claudia Wannamaker', but all three cultivars had a similar Q₁₀ (2.46). Gross photosynthesis (P_{gross}) was less sensitive to temperature than P_{net} and R_{dark}. The optimal temperature for P_{gross} of 'MGTIG' was lower (19 °C) than those of 'Little Gem' (21 °C) and 'Claudia Wannamaker' (22 °C). The Q₁₀ for P_{gross} decreased with increasing temperature, and was lower for 'MGTIG' than for 'Little Gem' and 'Claudia Wannamaker'. All three cultivars had the same optimal temperature (11 °C) for net assimilation rate (NAR), and NAR was not very sensitive to temperature changes from 3 to 17 °C. This indicates that the plants were well-adapted to their environmental conditions. The results suggest that respiration rate may limit magnolia growth when temperatures get high in winter time.

Perennial plants experience a wide range of environmental conditions. Their natural range often is limited by their ability to tolerate temperature extremes. Laboratory studies of plant responses to temperature can help predict the environmental conditions under which a species or cultivar will perform well. CO₂ exchange rate is a good indicator of plant performance, because photosynthesis and respiration are responsible for almost all dry matter changes in plants. Temperature response curves of CO₂ exchange rate can be used to predict the growth of plants over a wide range of temperatures and have been used to assess the heat tolerance of plants (Ranney and Peet, 1994; Ranney and Ruter, 1997). An understanding of the effects of temperature on net photosynthesis (P_{net}) and dark respiration (R_{dark}) is also important for plant growth models, which can be used to predict the adaptability of crops to different environments (Higgins et al., 1992).

Effects of temperature on CO₂ exchange are most commonly measured on individual leaves (Higgins et al., 1992; Larigauderie and Körner, 1995; Martindale and Leegood, 1997; Ranney and Peet, 1994; Ranney and Ruter, 1997) or fruit (Marcelis and Baan Hofman-Eijer, 1995; Ogawa and Takano, 1997; Pavel and DeJong, 1993; Whitfield, 1992). It seems likely that the temperature response may differ among leaves in a canopy, due to such factors as developmental stage, exposure to light, or nutritional status of the leaves. To draw meaningful conclusions from single-leaf photosynthesis measurements, similar leaves have to be selected from different plants and these leaves are not necessarily representative for the entire plant. Whole-plant CO₂ exchange mea-

surements provide an integral measurement of the entire plant, thus giving a more representative indication of whole-plant response to temperature. Whole-plant CO₂ exchange of *Alstroemeria* was measured by Leonardos et al. (1994) over a temperature range from 10 to 35 °C. They found that dark respiration (R_{dark}) increased exponentially with temperature, while net photosynthesis (P_{net}) reached a maximum at 20 °C.

Experimental error in CO₂ exchange measurements can be reduced by measuring several plants together, instead of individual plants. We describe a technique to measure CO₂ exchange-temperature response curves of multiple groups of plants or canopies simultaneously. The system is fully automated and can operate unattended, thus simplifying data collection. We also discuss different methods to estimate the Q₁₀ for R_{dark}. Magnolia was used as a model species, because it is an important evergreen landscape tree in the Southeastern US and its performance is greatly affected by temperature (Martin et al., 1991).

Materials and Methods

PLANT MATERIAL. 'Claudia Wannamaker', 'MGTIG' (also known as 'GreenBack'), and 'Little Gem' magnolia cuttings were propagated from cuttings in the fall of 1996 in 3.8-L containers filled with a peat-based growing mix. These three cultivars were chosen because of their different growth habit. 'MGTIG' is a relatively new, fast growing cultivar, 'Claudia Wannamaker' has an intermediate growth rate, while 'Little Gem' is a relatively slow growing cultivar. Cuttings were placed in a polyethylene covered cold-frame and grown until 6 or 13 Feb. 1998, when CO₂ exchange measurements were started. Average maximum and minimum temperatures inside the cold-frame during the 2-week period before the measurements were 13 and 3 °C, respectively. Plants were fertilized twice weekly with a 20N–8.7P–16.6K

Received for publication 27 July 1998. Accepted for publication 4 Jan. 1999. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

water-soluble fertilizer solution, containing N at a concentration of 200 mg·L⁻¹, from May until September. Plants were watered as needed. Average leaf areas of the plants were 565, 531, and 578 cm², while shoot fresh mass averaged 30, 39, and 31 g for 'Claudia Wannamaker', 'MGTIG', and 'Little Gem', respectively.

DATA COLLECTION. CO₂ exchange data of groups of whole magnolias was collected using a multichamber, semicontinuous CO₂ exchange system. Ambient air was blown into acrylic gas-exchange chambers (3.2 × 5 × 6 dm³) and air flow into the chambers was measured with mass flow meters (GFM37-32, Aalborg Instruments and Controls, Monsey, N.Y.). The CO₂ concentration of the incoming air was measured with an infrared gas analyzer (IRGA) (SBA-1, PP-systems, Haverhill, Mass.). The difference in the CO₂ concentration of the air entering and exiting the chamber was measured with an IRGA in differential mode (LI-6251, LI-COR, Lincoln, Neb.). Air flow to the differential IRGA was controlled by opening and closing solenoid valves. The solenoid valves were controlled by a SDM-CD16AC relay module and CR10T datalogger (Campbell Sci., Logan, Utah). Whole-chamber CO₂ exchange (μmol·s⁻¹) was calculated as the product of mass flow (mol·s⁻¹) and the difference in CO₂ concentration of the air entering and exiting the chamber (μmol·mol⁻¹). Every chamber was measured for 30 s, once every 10 min. There was a 30 s delay in data collection after solenoids were switched to measure the next chamber, to assure that all air from the previous gas exchange chamber was purged from the tubing. The data from the 30 s measuring period was automatically collected, averaged, and stored by the datalogger.

Four plants of a cultivar were enclosed in each acrylic gas exchange chamber and eight chambers were placed in larger growth chambers (model E-15, Conviron, Asheville, N.C.). Errors in the measurements due to zero drift of the differential IRGA were corrected by subtracting the CO₂ exchange rates of empty gas exchange chambers from the measured CO₂ exchange rate of the plants. Temperature in the gas exchange chambers was measured with shielded, aspirated, type T thermocouples connected to a thermocouple multiplexer (Model AM25T, Campbell Sci.). To measure photosynthesis across a temperature range, the growth chamber was programmed for eight different temperatures (-3 to 25 °C) in 4 °C steps. The temperature series was started immediately after the plants were placed in the chamber and every temperature was maintained for 3 h. Temperature inside the gas exchange chambers was higher than that in the growth chamber, because of heat output from the incandescent and fluorescent lights and ranged from 3 to 28 °C. Photosynthetic photon flux density was 440 μmol·m⁻²·s⁻¹ at the top of the plant canopies. Relative humidity in the gas exchange chambers was measured with humidity probes (HTO-45R, Rotronic, Huntington, N.Y.), and decreased from 87% to 63% with increasing temperature. We made no attempt to maintain a constant vapor pressure deficit at the different measurement temperatures, because vapor pressure deficit under natural conditions normally increases with increasing temperature. CO₂ concentrations in the gas exchange chambers ranged from 345 to 380 μmol·mol⁻¹ during the P_{net} measurements.

Respiration was measured during the following 24-h period, using the same plants. The growth chambers were programmed to decrease the temperature from 29 to 1 °C in 4 °C steps. Without the radiative heating by the lights, temperatures inside the gas exchange chambers were close to the growth chamber set points. Relative humidity during the R_{dark} measurements ranged from 97% at 3 °C to 56% at 28 °C and CO₂ concentrations were between 390 and 435 μmol·mol⁻¹.

Leaf area and shoot fresh mass were measured immediately after the conclusion of the R_{dark} measurements. To correct for differences in plant size among the groups of plants, P_{net} was calculated per unit leaf area, while R_{dark} was expressed per unit shoot fresh mass, unless otherwise mentioned. Since only eight groups of plants could be measured simultaneously, the experiment was replicated in consecutive weeks. This resulted in a total of 16 groups of magnolia plants (5 replications for 'Claudia Wannamaker' and 'Little Gem', 6 replications for 'MGTIG').

Since whole plants, including the containers, were enclosed in the gas exchange chambers, CO₂ exchange rates include growing medium and root respiration. Since root respiration is part of the whole-plant metabolism, this should be included in whole-plant CO₂ exchange measurements. Respiration by microorganisms in the root zone consists of two separate processes, respiration of organic compounds leaking from plant roots and microbial breakdown of organic matter in the growing medium. Respiration resulting from the breakdown of organic products leaking from plant roots into the soil or growing medium should be included in whole-plant net CO₂ exchange measurements. The carbon in these compounds was originally fixed in the photosynthetic process, but they are no longer available for plant growth after they leak from the roots. This leakage represents a net loss of carbon from the plants, and thus has to be accounted for in whole-plant carbon exchange measurements. This can be done by including root-zone respiration in whole-plant carbon exchange measurements.

Breakdown of organic matter in the growing medium by microorganisms could cause errors in whole-plant CO₂ exchange estimates, since this is independent of the metabolism of the plant. However, respiration caused by the breakdown of organic matter in a peat-based growing mix normally is negligible compared to whole-plant photosynthesis (<1%; Bugbee and van Iersel, unpublished results), and thus has a minimal effect on measurements of whole-plant CO₂ exchange rates, unless small plants are grown in large containers. Whole-plant CO₂ exchange measurements, including the root zone, are a good measure of plant growth. In a previous experiment, it has been shown that there is a close correlation (r² = 0.998) between the total measured carbon accumulation and dry mass of the plants (van Iersel and Bugbee, 1997).

DATA ANALYSIS. To allow the temperature and CO₂ exchange rate of the plants in the gas exchange chambers to stabilize after changing the growth chamber temperature, the first 2 h of data at a specific temperature were not used for further analysis. Temperature response curves were constructed by averaging the data from the last hour of measurements at every temperature.

Temperature coefficients (Q₁₀) for dark respiration were determined by fitting an exponential function to the data:

$$R_{\text{dark}} = R_0 \cdot Q_{10}^{(T/10)} \quad [1]$$

where R₀ is R_{dark} at 0 °C (μmol·g⁻¹·s⁻¹), Q₁₀ is the relative increase in R_{dark} with a 10 °C increase in temperature, and T is the temperature (°C).

Since P_{net} reaches a maximum at a certain temperature and decreases as temperature increases further, a third order polynomial was fitted to the P_{net} data and this curve was used to determine the Q₁₀ for P_{net} at 1 °C increments. The Q₁₀ at temperature T was determined as the calculated P_{net} at T + 5 °C divided by P_{net} at T - 5 °C.

A temperature response curve for gross photosynthesis (P_{gross}, Fig. 1A) was estimated as the sum of the response curves for P_{net} and R_{dark} (both expressed per unit leaf area), assuming that respiration rates in the light and dark are the same. Q₁₀ for P_{gross} was

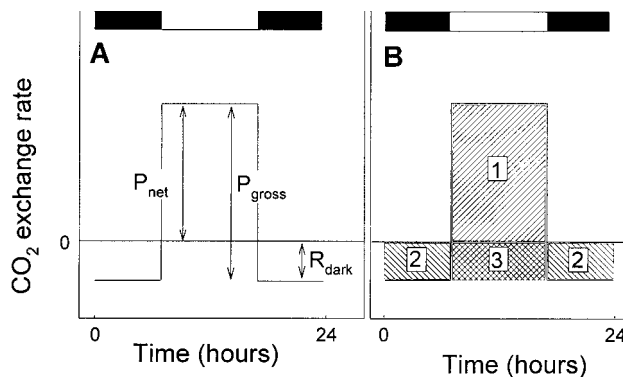


Fig. 1. A schematic representation of whole-plant CO_2 exchange of whole plants during a 24-h period with constant temperature. Net photosynthetic and dark respiration rate measurements were used to estimate gross photosynthetic rate (A). Daily carbon accumulation of plants (area 1 – area 2) and total gross photosynthesis during the light period (area 1 + area 3) were calculated (B). These values were then used to estimate carbon use efficiency [(area 1 – area 2)/(area 1 + area 3)] and net assimilation rate [(area 1 – area 2)/leaf area]. Carbon use efficiency and net assimilation rate were determined based on the assumption of constant temperature, 13 h of darkness, and 11 h of light. The bars in the top of the diagrams indicate periods of light (open bar) and dark (closed).

calculated using the same method as used for P_{net} . Carbon use efficiency (CUE) of the plants at different temperatures was estimated as if the plants were exposed to a constant temperature and light intensity throughout the day, with an 11-h light period and a 13-h dark period (close to the natural day length at the time of the experiment). Total daily photon flux during this hypothetical day was $17.4 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, which is normal for winter time in the southern US. Carbon use efficiency, the fraction of the carbohydrates formed by P_{gross} that is incorporated into new dry matter, was calculated as (Fig. 1B):

$$\text{CUE} = (P_{\text{net}} \cdot 11 - R_{\text{dark}} \cdot 13) / (P_{\text{gross}} \cdot 11) \quad [2]$$

where P_{net} , R_{dark} , and P_{gross} are all expressed on a leaf area basis.

Net assimilation rate (NAR, $\text{mmol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) of the plants was calculated, because unlike P_{net} , P_{gross} , and CUE, it is a direct estimate of the growth rate of the plants (in moles of carbon per unit leaf area per day). As was the case with CUE, it was calculated based on an 11-h light and 13-h dark periods and constant temperature (Fig. 1B):

$$\text{NAR} = (11 \cdot P_{\text{net}} - 13 \cdot R_{\text{dark}}) \cdot 3.6 \quad [3]$$

where P_{net} and R_{dark} are expressed on a leaf area basis and 3.6 converts $\mu\text{mol}\cdot\text{s}^{-1}$ to $\text{mmol}\cdot\text{h}^{-1}$. Because P_{net} and R_{dark} were not measured at the exact same temperatures, CUE and NAR were calculated using the calculated temperature response curves.

Results and Discussion

There were large differences in P_{net} of the three cultivars (Fig. 2A). Irrespective of temperature, ‘MGTIG’ had the highest P_{net} followed by ‘Claudia Wannamaker’, while ‘Little Gem’ always had the lowest P_{net} . Despite the large differences in P_{net} among the cultivars, P_{net} of all three cultivars reached a maximum ($Q_{10} = 1$) at $\approx 15^\circ\text{C}$ (Fig. 2A and B). Although ‘MGTIG’ had the highest P_{net} at low temperatures, it was less responsive than the other two cultivars to an increase in temperature from 3 to 15°C (i.e., a lower Q_{10} , Fig. 2B). At temperatures $>15^\circ\text{C}$, P_{net} of ‘Little Gem’ decreased more rapidly than that of ‘MGTIG’ and ‘Claudia Wannamaker’. At 28°C , P_{net} of ‘Little Gem’ was 0, indicating that CO_2 consumption by P_{gross} and CO_2 evolution by respiration were equal. This type of photosyn-

thetic response to temperature is typical for many species (Higgins et al., 1992; Leonardos et al., 1994), with species-dependent differences in temperature above which P_{net} becomes negative (Higgins et al., 1992). The relatively low optimal temperature for P_{net} (15°C) of the plants in this study was caused by the cool growing temperature, since the optimal temperature for P_{net} of many species, including magnolia, increases with increasing temperature (Björkman et al., 1980; our unpublished results).

During these measurement, plants were exposed to 24 h of continuous light, followed by 24 h of darkness. Feedback inhibition of photosynthesis and a lack of substrates for respiration can affect P_{net} and R_{dark} (Amthor, 1994; Sharkey, 1994). However, preliminary data (not shown) indicated that exposing plants to 24 h of light before the start of the measurements did not affect the response of P_{net} to temperature. Dark respiration responses to temperature remained unchanged even after 48 h of darkness before the start of the measurements. This indicates that possible effects of feedback inhibition of P_{net} and substrate limitation of R_{dark} are negligible compared to temperature effects.

Dark respiration of all three cultivars increased exponentially

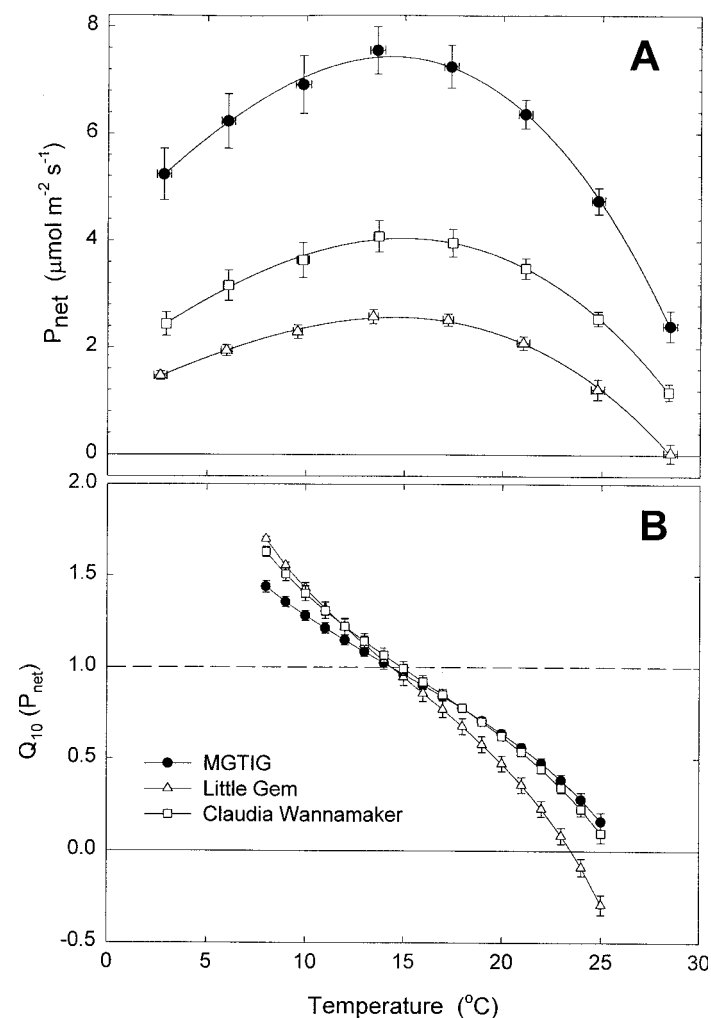


Fig. 2. Air temperature effects on the net photosynthesis of three magnolia cultivars. Net photosynthesis (A) was measured for 24 h, at eight different temperatures (3 h/temperature, increasing from 3 to 28°C). Data are the total CO_2 exchange rates of four whole plants, expressed on a leaf area basis. The Q_{10} of net photosynthesis (B) was estimated from a third order polynomial fitted to the net photosynthesis data. Error bars represent standard errors ($n = 5$ for ‘Claudia Wannamaker’ and ‘Little Gem’ and $n = 6$ for ‘MGTIG’).

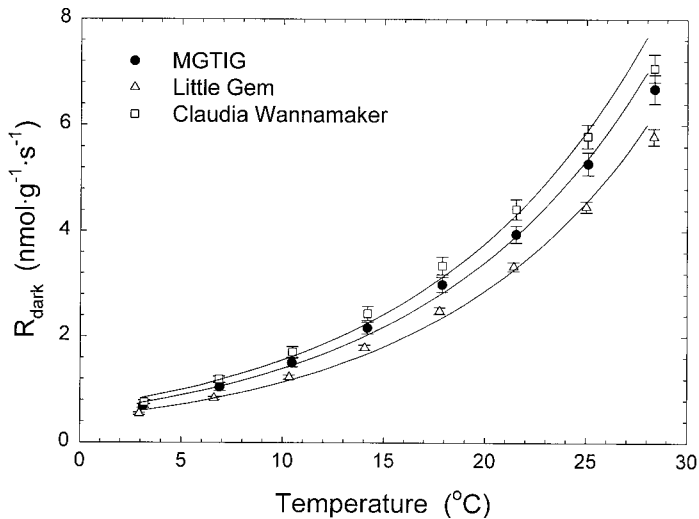


Fig. 3. Air temperature effects on the dark respiration of three magnolia cultivars. Dark respiration was measured for 24 h, at eight different temperatures (3 h/temperature, decreasing from 28 to 3 °C). Respiration data represent whole-plant respiration rates and are expressed per unit shoot fresh mass. The three cultivars had a similar Q_{10} (2.46). The lines represent best fit exponential models for the three cultivars. Error bars represent the standard error and bars not shown are within the limits of the symbol ($n = 5$ for 'Claudia Wannamaker' and 'Little Gem' and $n = 6$ for 'MGTIG').

with increasing temperature, but there were distinct differences among the cultivars (Fig. 3). 'Little Gem' had a lower R_{dark} than 'Claudia Wannamaker' and 'MGTIG', irrespective of temperature. All three cultivars had a similar Q_{10} (2.46), but R_0 of 'Little Gem' ($0.45 \text{ nmol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$) was significantly lower than that of 'MGTIG' ($0.57 \text{ nmol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$) and 'Claudia Wannamaker' ($0.64 \text{ nmol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$). Dark respiration rates of 'MGTIG' and 'Claudia Wannamaker' were not significantly different. A Q_{10} of 2.46 is within the normal range for R_{dark} . In a literature review, Larigauderie and Körner (1995) found that $\approx 40\%$ of the reported Q_{10} values for leaf R_{dark} are within the range of 2 to 2.5, with an average Q_{10} of 2.3.

The high r^2 (0.987 or higher) of the exponential curves fitted to the R_{dark} data indicates that the assumption of a constant Q_{10} for R_{dark} over the entire temperature range was realistic. Although it is possible to calculate a temperature-dependent Q_{10} (as was done for P_{net} and P_{gross}), using a second or third order polynomial model may produce unrealistic results at low temperature. Polynomial functions predict an increase in R_{dark} as the temperature drops below the inflection point of the curve, which introduces anomalies in the calculated Q_{10} (Higgins et al., 1992, our unpublished results). Another approach that has been used to estimate Q_{10} for R_{dark} , is by fitting the Arrhenius equation to the data (Johnson and Thornley, 1985):

$$R_{\text{dark}} = A \cdot e^{-Ea/(R \cdot T)} \quad [4]$$

$$\ln(Q_{10}) = -10 \cdot Ea/(R \cdot T^2) \quad [5]$$

where A is a constant, Ea is the apparent activation energy of R_{dark} ($\text{J}\cdot\text{mol}^{-1}$), R is the universal gas constant ($8.31434 \text{ J}\cdot\text{mol}^{-1}\cdot\text{K}^{-1}$), and T is the absolute temperature (K). A problem with the use of the Arrhenius equation is that A and Ea are assumed to be temperature-independent, which may not be true (Johnson and Thornley, 1985). Using this approach, Leonardos et al. (1994) found that the Q_{10} for R_{dark} of whole *Alstroemeria* plants was ≈ 1.8 , but that it slowly decreased with increasing temperature. This reported decrease in the Q_{10} for R_{dark} with increasing temperature was an artifact of their method to calculate the Q_{10} , because use of the Arrhenius equation automatically results in a decreasing Q_{10} with

increasing temperature (see Eq. 5). To prevent this, we prefer to use a simple exponential regression, which results in a constant Q_{10} . If an exponential curve fits the respiration data well, this is the most direct and simple way to determine Q_{10} for R_{dark} . Since other data also indicates that a constant Q_{10} for R_{dark} is adequate to explain most of the variation (Higgins et al., 1992; Whitfield, 1992), this generally seems to be a satisfactory method. In cases where an exponential curve does not result in a good fit, it may be useful to fit a different curve, which will result in a temperature-dependent Q_{10} . Unfortunately, there appears to be no function with a strong biochemical or physiological justification to describe the relation between temperature and R_{dark} .

Although no direct measurements of P_{gross} were taken, it was estimated as the sum of P_{net} and R_{dark} . Gross photosynthesis showed similar trends as P_{net} , and the relative differences among the cultivars were similar (Fig. 4). 'MGTIG' had the highest P_{gross} , while P_{gross} of 'Little Gem' was lowest at every temperature. The optimal temperatures for P_{gross} were higher than for P_{net} (Figs. 2 and 4). 'MGTIG' had the lowest temperature optimum of the three cultivars (19 °C) and had the lowest Q_{10} for P_{gross} across the entire temperature range. The low Q_{10} of 'MGTIG' indicates that it was least responsive of the three cultivars to temperature changes at below-optimal temperatures, while 'MGTIG's' P_{gross} declined more rapidly than that of the other cultivars at above-optimal

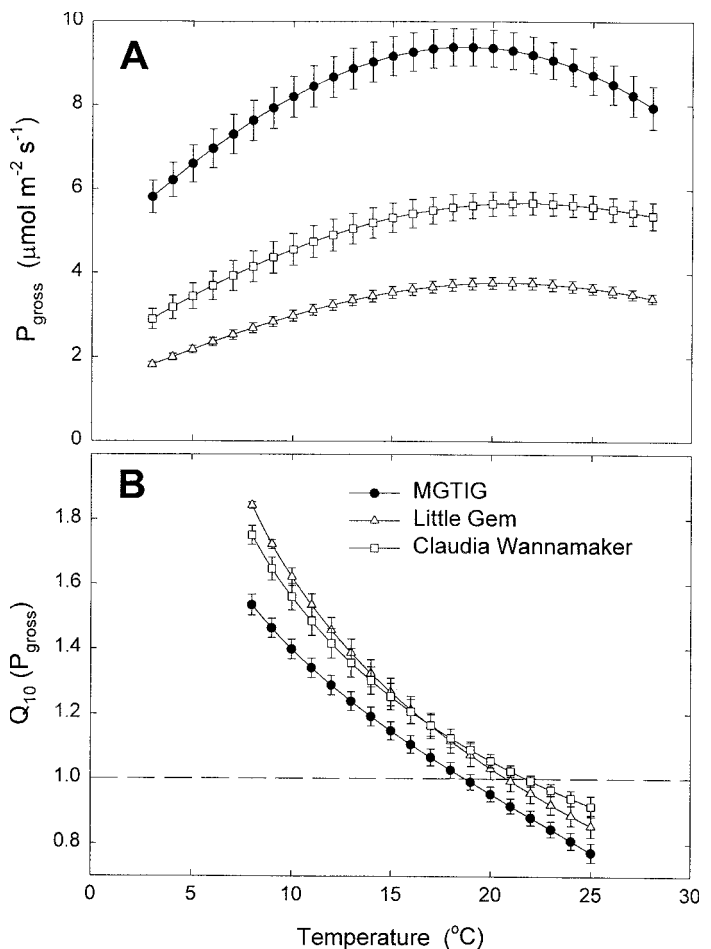


Fig. 4. Air temperature effects on the gross photosynthesis of three magnolia cultivars. Gross photosynthesis (A) was estimated as the sum of net photosynthesis and dark respiration, expressed on a leaf area basis. These results were used to estimate the Q_{10} for gross photosynthesis (B), using a third-order polynomial curve fitted to the estimated gross photosynthesis. Error bars represent the standard error and bars not shown are within the limits of the symbol ($n = 5$ for 'Claudia Wannamaker' and 'Little Gem' and 6 for 'MGTIG').

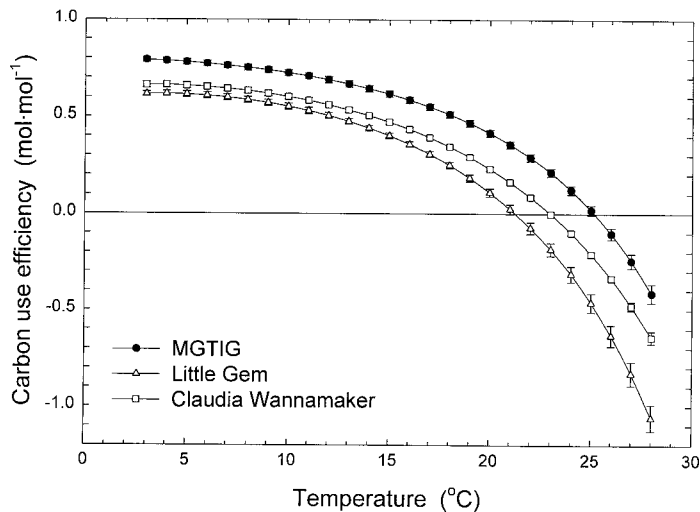


Fig. 5. The effect of temperature on the carbon use efficiency of three magnolia cultivars. Carbon use efficiency was calculated based on the assumption of constant temperature and an 11-h light and 13-h dark period. Carbon use efficiency is the fraction of total carbohydrates formed in gross photosynthesis, that is incorporated into plant material. Error bars represent the standard error and bars not shown are within the limits of the symbol ($n = 5$ for 'Claudia Wannamaker' and 'Little Gem' and $n = 6$ for 'MGTIG').

temperatures (a Q_{10} close to 1 indicates low sensitivity to changing temperatures).

Gross photosynthesis was less sensitive to changing temperatures than P_{net} (Figs. 2 and 4), because P_{net} was greatly affected by the exponentially increasing respiration with increasing temperature. This suggests that temperature effects on the growth of magnolia are mainly caused by effects on the respiration rate of the plants. Dark respiration of magnolia increases almost tenfold with a temperature increase from 3 to 28 °C, while P_{gross} increases only by a factor of 2 or less when the temperature increases from 3 °C to the optimal temperature (Figs. 3 and 4).

Although CO_2 exchange rates give an indication of the potential growth rate of plants, growth also depends on the efficiency with which plants convert carbohydrates into dry matter. There were large differences in CUE among the three cultivars (Fig. 5). Because differences in photosynthesis among cultivars were much larger than the differences in R_{dark} , differences in CUE reflect those in P_{net} and P_{gross} . 'MGTIG' had the highest CUE, followed by 'Claudia Wannamaker', and 'Little Gem' had the lowest CUE, regardless of temperature. Because of the exponentially increasing R_{dark} with increasing temperature, CUE of all three cultivars decreased with increasing temperature and eventually became negative. It is interesting to note that CUE of 'Little Gem' was negative at temperatures >21 °C, indicating that there was a net carbon loss from the plants at higher temperatures. The optimal temperature for P_{gross} was 21 °C, while P_{net} of 'Little Gem' was positive up to 28 °C. Carbon use efficiency of 'Claudia Wannamaker' and 'MGTIG' became negative at temperatures >23 and 25 °C, respectively. Reported CUE values range from -0.6 to 0.84 , with most of the CUEs between 0.4 and 0.8 (reviewed by Amthor, 1989). Unfortunately, most literature reports on CUE do not take into account the effect of temperature. The results of our study make it clear that CUE is extremely temperature sensitive and plants need to be grown under similar environmental conditions to make meaningful comparisons. In addition, CUE depends on the developmental stage and nutritional status of the plant (Amthor, 1989).

The negative CUE at relatively low temperatures clearly shows that P_{net} and P_{gross} are not necessarily good indicators of

plant growth rate. This explains the observation by Evans (1993) that leaf photosynthesis measurements are often poorly correlated with dry matter production and yield. To get a reliable measure of plant growth, it is essential that respiratory carbon losses are included in the estimate. It is important to note that these data do not imply that magnolias always have a net carbon loss when the temperature is higher than 21 to 25 °C. The temperature response curves of P_{net} , P_{gross} , and R_{dark} depend on the environmental conditions under which the plants were grown. Many plant species have higher optimal temperatures for photosynthesis, when they are grown under warmer conditions (Björkman et al., 1980), while R_{dark} at a given temperature decreases (Hurry et al., 1996; Pearcy, 1977; Rook, 1969; Tranquillini et al., 1986). This, combined with the longer day length during the summer months, will cause the CUE at high temperatures to be higher in summer than in winter time. Since this experiment was conducted in winter time and the plants were grown in a cold frame without heating, the plants were adapted to relatively cool temperatures. This explains the poor performance of the plants at temperatures that they would normally be exposed to during most of the growing season.

The best measure of the actual growth response of the plants to temperature may be NAR (Fig. 6). The differences among the three cultivars in P_{net} , P_{gross} , and CUE were also reflected in NAR. 'MGTIG' had the highest NAR, while 'Little Gem' had the lowest NAR over the temperature range from 3 to 27 °C. All three cultivars had a similar NAR at 28 °C. Interestingly, the optimal temperature for NAR of all three cultivars was 11 °C, indicating that the plants of all three cultivars were well-adapted to their growing conditions (average maximum and minimum temperatures were 13 and 3 °C during the 2 weeks before the measurements). Net assimilation rate also was not very responsive to temperature over the range that the plants would be likely to experience in winter time. Net assimilation rate varied by $<33\%$, when temperature increased from 3 to 17 °C. The increase in P_{net} over most of this temperature range was counteracted by the increasing R_{dark} and decreasing CUE, resulting in a relatively stable NAR. At temperatures over 17 °C, NAR of all three cultivars decreased rapidly. However, the plants were unlikely to

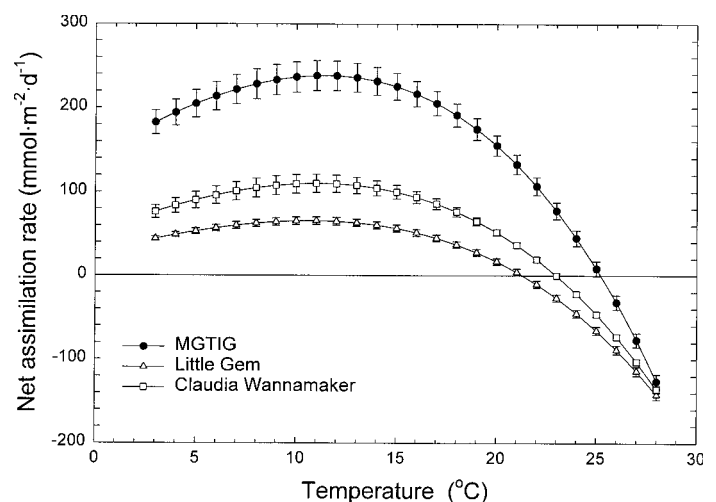


Fig. 6. The effects of temperature on the net assimilation rate of three magnolia cultivars. Net assimilation rate was calculated on the assumption of constant temperature and an 11-h light and 13-h dark period. Net assimilation rate is the amount of carbon the plants accumulate in one day, expressed per unit leaf area. Error bars represent the standard error and bars not shown are within the limits of the symbol ($n = 5$ for 'Claudia Wannamaker' and 'Little Gem' and $n = 6$ for 'MGTIG').

experience these higher temperatures for prolonged periods during the winter months and their low or even negative NAR at high temperatures may not have much practical significance. Since NAR is an actual estimate of the growth rate of the plants (per unit leaf area), this is probably the best measure to predict plant performance under different environmental conditions.

Conclusions

CO₂ exchange rates of magnolias are very sensitive to changes in temperature. Dark respiration rates of plants grown in winter time increased exponentially with increasing temperature ($Q_{10} = 2.46$), while P_{net} and P_{gross} reached maximum rates at ≈ 15 and 20 °C, respectively. There were large differences in photosynthesis among cultivars. 'MGTIG' had the highest P_{net} and P_{gross} at every temperature, while 'Little Gem' had the lowest P_{net} and P_{gross} . Dark respiration of 'Little Gem' also was lower than that of 'MGTIG' and 'Claudia Wannamaker'. These differences in CO₂ exchange rates also resulted in differences in CUE and NAR among cultivars. Carbon use efficiency of 'Little Gem' was lower than that of the other two cultivars and became negative at temperatures > 21 °C. The rapid decrease in CUE and P_{net} at temperatures > 18 °C was caused mainly by the exponential increase in R_{dark} . Gross photosynthesis was much less sensitive to temperature than R_{dark} . 'MGTIG' had the highest NAR of the three cultivars, while 'Little Gem' had the lowest NAR. The optimal temperature for NAR, and thus growth, was 11 °C for all three cultivars. The results suggest that high temperatures may inhibit magnolia growth in winter because of high respiration rates. However, the differences in R_{dark} among cultivars were much smaller than the differences in NAR and P_{gross} and do not appear to be a good selection criterion for heat tolerance. Actually, the cultivar with the lowest R_{dark} ('Little Gem') seemed to be most sensitive to high temperatures, because of its low P_{gross} . The data suggest that a high P_{gross} or NAR at high temperatures may be more useful than low R_{dark} in predicting magnolia performance at high temperatures.

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