Night Temperature has a Minimal Effect on Respiration and Growth in Rapidly Growing Plants

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INTRODUCTION

There is a consensus that average global temperatures have warmed significantly in the last 100 years, and that this trend will continue, raising average global temperatures by 1–6 °C in the next 100 years (Sarmiento and Quere, 1996; Hansen et al., 1999). Much of this increase is the result of night temperatures rising faster than day temperatures due to less radiant heat loss because of increased cloudiness (Alward et al., 1999). It is therefore important to understand the influence of both day and night-time warming on the carbon balance of plants, and thus on the carbon balance of the planet.

Plants have evolved in an environment that has cooler nights than days, but the impact of cool nights on carbon gain is not clear. In single leaves of cottonwood trees (Populus deltoides), the maximum potential photosynthetic rate increased for single, mid-canopy-level leaves after a single warmer night, which was attributed to less carbohydrate-induced feedback inhibition of photosynthesis (Turnbull et al., 2002). McCree and Amthor (1982) found that a constant 20 °C day/night temperature slightly increased growth rate of a community of white clover (Trifolium repens) when compared to a community grown in 30 °C days and 10 °C nights. They suggested that the warm day temperature caused excess substrate use, while night respiration rates were not low enough to offset the daytime carbon loss.

Unfortunately, many conclusions about growth and respiration are based on measurements of single leaves, leaf disks or mature plant parts (Crawford and Huxter 1977; Labate and Leegood 1989; Bunce 1991; Roberts et al. 1992; Alexander et al., 1995; Maier et al., 1998). However, leaves typically have a photosynthetic rate that is 10–20 times their respiration rate (Björkman, 1981), and the photosynthetic rate of whole plants is four times their respiration rate (Gifford, 1994). If leaf mass is 30–70 % of total plant mass, 70–85 % of total respiration occurs in roots, stems and meristems. Therefore, even if a leaf was selected that represented the rest of the leaves, respiration rates derived from this leaf would poorly represent the whole plant.

Rarely, whole plants are measured, but even then the respiration measurements are done for only a few hours (Tjoelker et al., 1999). Teskey and Will (1999) and Percival et al. (1996) observed a lower temperature sensitivity for whole plants than for leaves, but Griffin et al. (2002) argue that temperature sensitivity should increase in whole plants.
because they would be less carbohydrate-limited than single leaves during measurement at warm temperatures.

Classically, a functional model of respiration assigns the energy derived in respiration to a ‘growth’ component and a ‘maintenance’ component. While this model is only a functional model and the biochemistry to derive the energy in respiration for these components is the same, this model still provides one of the best ways to explain and model respiration. The theory behind this model has been supported in recent reviews (Amthor, 2000; Cannell and Thornley, 2000; Thornley and Cannell, 2000). The growth respiration coefficient (or efficiency of biosynthesis) has long been considered temperature insensitive (Penning de Vries et al., 1974), and maintenance respiration is considered temperature dependent (McCree, 1974). This is not to say that growth respiration is temperature insensitive; growth may increase with temperature and, as a result, growth respiration may increase. However, the cost of that growth is believed to remain constant, whereas the cost of the maintenance changes with temperature.

Short-term studies on mature plant tissues typically indicate a respiratory $Q_{10}$ of at least 2, which indicates that respiration doubles for every 10 °C rise in temperature (Burton et al., 1996; Bustan and Goldschmidt, 1998; Lomander et al., 1998). Ecological models and eco-physiological models assign the temperature-sensitive component only to the maintenance (or analogous) term, so that the total respiratory $Q_{10}$ is less than 2, but there is a lack of whole-plant measurements performed in long-term studies to validate these ecological models. Still, reported $Q_{10}$ values range from 1-2 to 4-0, and no mechanistic explanation for the variance is demonstrated (Larigauderie and Körner 1995; Boone et al., 1998; Chapman and Thurlow, 1998; Neven, 1998; Urmeneta et al., 1998; Nielsen et al., 1999; Quinlan and Lighton, 1999). Further confusing matters are researchers ‘correcting’ for temperature differences in their studies by assuming a $Q_{10}$ of 2 for total respiration to calculate a basal respiration rate at a common temperature (Pearman et al., 1981; Wullschleger et al., 1992; Wullschleger and Norby, 1992; Witowski, 1997), which can mislead overall conclusions about the role of temperature on respiration.

Amthor (2000) suggested that low temperature sensitivity in long-term measurements may be due to acclimation. Low $Q_{10}$ values might be evidence for acclimation (Arnone and Körner, 1997). There is, however, great species variability in how much acclimation occurs. Larigauderie and Körner (1995) found that some species acclimated to some degree (long-term acclimation ratio, LTR$_{10}$ = 1.0–1.5), but others had LTR$_{10}$ of between 2 to 5.5 indicating little to no acclimation. Root respiration was observed to acclimate in how much acclimation occurs. Larigauderie and Körner (1995); Boone et al., 1998). The growth respiration coefficient (or efficiency of biosynthesis) has long been considered temperature insensitive (Penning de Vries et al., 1974), and maintenance respiration is considered temperature dependent (McCree, 1974). This is not to say that growth respiration is temperature insensitive; growth may increase with temperature and, as a result, growth respiration may increase. However, the cost of that growth is believed to remain constant, whereas the cost of the maintenance changes with temperature.

Materials and methods

Experimental set-up and design

Three studies were conducted to compare night-temperature effects across three crops: lettuce (Lactuca sativa ‘Grand Rapids’), tomato (Lycopersicum esculentum ‘Red Robin’) and soybean (Glycine max ‘Hoyt’). These species were chosen to compare the temperature sensitivity of two starch accumulators (soybean and tomato) to a sucrose accumulator (lettuce). Seedlings were transplanted 4–7 d after imbibition into a ten-chamber, computer-controlled gas-exchange system (Fig. 1). Temperature within each chamber was controlled with a chilled water coil and small heaters. System details have been described previously (van Iersel and Bugbee, 2000).

Often, CO$_2$ gas exchange systems are difficult to calibrate and are usually only tested with no plant material in a chamber. They are usually zeroed before measurement, ensuring that the gas analyser to be used has been properly zeroed and spanned. We zeroed each chamber, calibrated the gas analysers, and finally calibrated the entire system by slowly reacting dilute acid with a known mass of dried CaCO$_3$. This caused CO$_2$ to be evolved, which was measured with the gas analysers. The total moles of CO$_2$ evolved was then compared to the initial moles of C in the CaCO$_3$. This was repeated until the molar amount of CO$_2$ evolved from the reaction equalled that which was initially placed into the chamber (100 ± 2 %) by repairing leaks in the system.

Lettuce and tomato were grown at a constant 25 °C, and soybeans were grown at a constant 20 °C until canopy closure. Daytime temperatures remained at these temperatures for the duration of the trial. The night temperatures were changed on Day 16 for lettuce and tomato and Day 17 for soybean. On that day (Day 1 after treatment on Fig. 3; there is no treatment Day 0), the night temperature set points were adjusted across a 17 °C range from 17 to 34 °C. Temperature treatments were maintained for 13 d until harvest on Day 29 for lettuce, for 20 d until Day 36 for tomato, and for 15 d until Day 34 for soybeans. Treatments extended into flowering for tomato and soybeans. Control plants had constant day/night temperature. Temperatures were measured with an aspirated, type-E (0.5 mm diameter, 24-AWG) thermocouple, and were maintained within ±0.2 °C of the set point. Groups of whole plants or plant communities were studied and arranged at the following...
densities: lettuce at 106 plants m$^{-2}$, tomato at 80 plants m$^{-2}$, and soybean at 35 plants m$^{-2}$.

Relative humidity was maintained between 60 and 80 %, but varied much less among the chambers for any given day because the daytime environments were similar (data not shown). A photosynthetic photon flux (PPF) of 600 $\mu$mol m$^{-2}$ s$^{-1}$ ($\pm$5 % among chambers) was provided by water-filtered, high-pressure sodium lamps. The photoperiod was 16 h for lettuce and tomato, and 12 h for soybeans. Reflective material was wrapped around each chamber and was adjusted daily to the top of the canopy to minimize side lighting (Fig. 1). CO$_2$ was controlled at 1200 $\mu$mol mol$^{-1}$ for the duration of all the studies. These studies were conducted at elevated CO$_2$ for three reasons: (1) to increase photosynthesis and thus help ensure that the plants did not become carbohydrate-limited at the higher temperatures; (2) to minimize the effect that vapour pressure deficit differences would have on photosynthesis if there were differences between chambers on a given day; and (3) to minimize possible temperature effects on photorespiration. Temperature responses most likely would be smaller if the plants were carbohydrate-limited by ambient CO$_2$. Separate hydroponic systems were enclosed in each chamber so that root respiration was included with the shoot. Hydroponic solution was bubbled with the same air as that used for the shoot environment.

Manual adjustment of pH on a daily basis resulted in a one pH unit day-to-day range. The pKa of carbonate is 6-2, which means that 50 % of the carbon dissolved in the water is in the carbonate form and 50 % is CO$_2$. pH changes around pH 6 cause significant fluxes in and out of the nutrient solution. For this reason, the pH of the hydroponic solution was maintained between 4 and 5, which forces between 90 and 99 % of the CO$_2$ out of solution. Previous studies indicate that healthy plants can be grown in pH of 4-0 (Monje and Bugbee, 1998).

**Plant tissue analysis**

Upon harvesting, plants were separated into shoots and roots (lettuce and tomato), or leaves, stems and roots (soybean). Tissue was weighed and dried at 80 °C for 72 h. Dry biomass was subsequently weighed, ground and sampled for analysis. Samples weighing 0-2 g were analysed for percent C, H and N with a LECO analyser (Model 1000; LECO Corporation, St Joseph, MI, USA) and samples of 1-0 g were used for analysis of other nutrients (ICP-ES analysis, Utah State University Plant and Soil Analysis Laboratory). Nitrate was analysed with a 0-2 g sample placed in a 50 mL solution of 0-05 M Al$_2$(SO$_4$)$_3$. The tissue and solution were shaken four times during the 1 h extraction period. The solution was measured with a NO$_3^-$- selective electrode and an associated reference electrode (Models 930700 and 900200; Thermo Orion, Beverly, MA, USA). The readings were then converted from volts to NO$_3^-$-N from a previous calibration curve. Assimilated N was calculated by subtracting NO$_3^-$-N from total N.

**Calculations**

Carbon use efficiency (CUE) is a calculated term that measures how efficiently plants can incorporate the carbon fixed during the day into biomass gain. It is used instead of ‘percent respiration’ ($100 \times$ night respiration/net photosyn-
thesis) because it incorporates differences in photoperiod automatically, whereas calculating a ratio of night respiration to net photosynthesis does not. While meaningful conclusions about a given species in a set of environmental conditions can be made, a ratio of night respiration to net photosynthesis precludes useful comparisons to be made across species and environmental conditions. Finally, CUE is an efficiency parameter that can easily fit within models. Using \( P_{\text{net}} \) (net photosynthesis, mol C m\(^{-2}\) d\(^{-1}\) based on ground area) and \( R_n \) (night-time respiration, mol C m\(^{-2}\) night\(^{-1}\) based on ground area), daily carbon gain (DCG) can be calculated as:

\[
\text{DCG} = P_{\text{net}} - R_n
\]

Cumulative carbon gain (CCG) is the running total of DCG.

\( P_{\text{gross}} \) is a calculated term that reflects the net C fixed (\( P_{\text{net}} \)) and the amount of C that is simultaneously being respired. Because daytime respiration (\( R_d \)) can not be measured directly, \( P_{\text{gross}} \) is expressed as the sum of \( P_{\text{net}} \) and some percentage of \( R_n \). Some studies have indicated that \( R_d \) in leaves can be higher during the day due to their higher daytime carbohydrate content (Azcon-Bieto et al., 1983; Azcon-Bieto and Osmond, 1983). Other studies indicate daytime \( R_d \) is lower due to light-inhibition of respiration (Sharp et al., 1984; Wang et al., 2001). Monje and Bugbee (1996) found that root respiration, at a constant temperature, is increased in the day presumably due to increased carbohydrate supply. The common approach for whole plants is to assume that the rate of \( R_d \) and \( R_n \) (\( \mu\text{mol} \text{ m}^{-2} \text{ s}^{-1} \) based on ground area) are equal when temperatures are constant. In a 12 h photoperiod, \( R_d \) (mol C m\(^{-2}\) d\(^{-1}\), ground area) then equals \( R_n \). In a 16 h light/8 h dark photoperiod, \( R_d = R_n \times 2 \). In these equations, respiration assumes a positive value (i.e. mass respired). \( P_{\text{gross}} \) (mol C m\(^{-2}\) d\(^{-1}\), ground area) can, therefore, be calculated as:

\[
P_{\text{gross}} = P_{\text{net}} + R_d
\]

Carbon use efficiency can then be calculated as:

\[
\text{CUE} = \frac{\text{DCG}}{P_{\text{gross}}}
\]

Plants were grown in constant day/night temperatures until treatments were applied.

To compare our temperature sensitivities to the literature and to calculate the \( R_d \) from \( R_n \) to determine \( P_{\text{gross}} \), \( Q_{10} \) values were calculated for the first treatment night. The \( R_d \) of plants in different temperatures was used to calculate two \( Q_{10} \) values (one from control temperature to coolest temperature and one from the control temperature to the warmest temperature) using the temperature response function:

\[
Q_{10} = e^{\frac{\ln(R_nT) - \ln(R_{n\text{control}})}{(T - \text{control} T)/10}}
\]

where \( R_nT \) is the night respiration at temperature \( T \) and \( R_{n\text{control}} \) is the night respiration at the control temperature. An alternative method of \( Q_{10} \) calculation would be to calculate the slope of a respiration-to-temperature relation-

### Table 1. Final dry mass (g m\(^{-2}\) ground area), cumulative carbon gain (CCG) after treatment initiation, and respiration sensitivity to temperature, as measured by \( Q_{10} \) for each species

<table>
<thead>
<tr>
<th>Crop</th>
<th>Night temperature (C)</th>
<th>Final plant mass (g m(^{-2}))</th>
<th>CCG after treatment initiation (mol C m(^{-2}))</th>
<th>Sensitivity to temperature ( Q_{10} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lettuce</td>
<td>18.2</td>
<td>476.8</td>
<td>13.8</td>
<td>1.22 to 1.19</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>466.7</td>
<td>14.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>483.7</td>
<td>13.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>493.0</td>
<td>13.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>31.3</td>
<td>490.5</td>
<td>13.8</td>
<td></td>
</tr>
<tr>
<td>Tomato</td>
<td>18</td>
<td>768.3</td>
<td>22.8</td>
<td>1.38 to 1.34</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>730.8</td>
<td>20.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>740.0</td>
<td>21.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>784.1</td>
<td>23.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>31.5</td>
<td>751.6</td>
<td>22.4</td>
<td></td>
</tr>
<tr>
<td>Soybean</td>
<td>17</td>
<td>901.0</td>
<td>22.8</td>
<td>1.61 to 1.40</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>881.3</td>
<td>23.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>927.5</td>
<td>23.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>842.8</td>
<td>23.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>32</td>
<td>879.8</td>
<td>23.1</td>
<td></td>
</tr>
</tbody>
</table>

Data are the average of two groups of plants in separate chambers. \( Q_{10} \) was higher at cooler temperatures and vice versa. There was no effect of temperature on final dry mass in any species (\( P > 0.32 \)), nor on CCG after treatment initiation (\( P > 0.59 \)).

### Data analysis

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

\[
\left[ \frac{\text{post-treatment}_a \text{ day}_b/\text{pre-treatment}_a \text{ value}}{\text{post-treatment}_\text{control} \text{ day}_b/\text{pre-treatment value}_\text{control}} \right] \times 100
\]

where ‘post-treatment\(_a\) day\(_b\)’ indicates the post-treatment value of a parameter (i.e. CUE, \( P_{\text{net}} \), \( R_n \)) on ‘day\(_b\)’, ‘pre-treatment\(_a\) value’ is the value of the parameter on the day before the night temperature was changed, ‘post-treatment\(_\text{control} \) day\(_b\)’ is the post-treatment value of the parameter for the control on day\(_b\), and ‘pre-treatment value\(_\text{control} \)’ is the pre-treatment value of the parameter for the control the day before treatments began. This data treatment results in determining the temperature effects through time relative to the treatment plants in the numerator, and the effects through time relative to the control in the denominator.
Normalized data were analysed with linear regression to determine the night temperature effects on each parameter for each day after treatment began. Slopes of lines on different days were compared to see if their slopes were equal using the test statistic \( \frac{(\text{slope } a \pm \text{slope } b)}{\text{variance of slope } a} = t(\text{d.f. of slope } a) \) (Neter et al., 1996). However, in the figures below, the \( Y \)-intercept was adjusted so that the regression lines at the control point passed through 100% on the \( Y \)-axis in order to facilitate visual comparisons for the Results and Discussion.

**RESULTS**

**Lettuce**

Night respiration increased 2.0% per °C (Figs 2A, 3A). After 13 d of treatment, the slopes did not differ significantly from one another, indicating no acclimation to temperature. The average CUE was 0.62 the day before treatments were imposed (Fig. 2D). Net photosynthesis was not sensitive to night temperature (Fig. 3B). The CUE values for the coolest night temperatures were about 2% higher than the control values and the warmest were about 2% lower than the control values for all days after treatments were applied (Fig. 3C). The sensitivity of CUE to temperature did not change during the 13 d of treatment based on comparison of slopes \( (P = 0.35, \text{d.f.} = 8) \). There was no difference in final dry mass or in CCG after treatments were imposed (Table 1). Lettuce shoot mass increased significantly with temperature (Fig. 4A), while root biomass decreased (Fig. 4B). This caused the root fraction to decrease significantly with warmer temperatures (Fig. 4D). Leaves were not separated from the stem. Nitrate in both shoots and roots increased with increasing temperature (Table 2). There was no effect of night temperature on C, assimilated N, or K fractions in the shoot or root (Table 2).

**Tomato**

Night respiration increased 2.7% per °C with warmer nights (Figs 2B and 3D). This caused the CUE to be slightly higher with cooler nights and lower with warmer nights (Figs 2E and 3F). After 20 d of temperature treatment, there was no difference in the sensitivity of CUE or respiration to altered night temperature \( (P = 0.48, \text{d.f.} = 8) \). Net photosynthesis was not affected by the altered night temperatures (Fig. 3E). There were no differences in the final dry mass of the treatments or in CCG after treatments began (Table 1). There was no effect of temperature on biomass partitioning for tomato (Fig. 4A–D). Leaves were not separated from the stem. There was no effect of night temperature on C and root NO\textsubscript{3}\textsuperscript{−}, but NO\textsubscript{3}\textsuperscript{−} decreased significantly in the shoot with increasing temperature.
Table 2). There was a significant effect of temperature on K in the root ($P = 0.045$), but not in the shoot (Table 2). There was a small, but statistically significant effect of temperature on assimilated N in the roots.

**Soybean**

Soybean was the most sensitive of the three crops studied. Respiration increased 4.0% per °C (Figs 2C and 3G). Carbon use efficiency changed after the night temperatures were changed because respiration changed (Figs 2F, 3I, G). With no change in photosynthesis (Fig. 3H), the decrease in respiration resulted in an increase of CUE of 3% relative to the control and a decrease of 12% relative to the control at the highest temperature (Fig. 3G). No acclimation occurred after 15 d of treatment ($P = 0.29$, d.f. = 8) (Fig. 3G). No differences in final dry mass were observed between treatments or in the CCG after treatments began (Table 1). Soybean leaf mass decreased significantly with temperature (Fig. 4A), while root biomass decreased (Fig. 4B). Stem biomass increased significantly by the same absolute amount as the leaves decreased (Fig. 4C). Together, these shifts caused the root fraction to decrease significantly with warmer temperatures (Fig. 4D). There was a significant effect of night temperature on C fraction of the leaves ($P = 0.049$), but not on stems or root (Table 2). Nitrate increased with temperature in shoots (Table 2). There was no effect of night temperature on assimilated N or K fractions in the shoot or root.

**Differential temperature effects among species**

The effect of temperature on respiration and CUE differed among species (Fig. 5A, B). Soybean respiration was significantly more sensitive than lettuce ($t = 6.34$, d.f. = 8, $P < 0.001$), and had more CUE sensitivity than lettuce ($t =
2.91, d.f. = 8, P < 0.025), but all three species were much less sensitive than commonly believed. Lettuce respiration was significantly less sensitive than tomato (t = 3.418, d.f. = 8, P < 0.025) (Fig. 5A, 5B), and CUE was marginally significantly different (t = 1.64, d.f. = 8, P = 0.08). The average $Q_{10}$ for whole-plant respiration of lettuce was 1.20, tomato was 1.36, and soybean was 1.46, with lower $Q_{10}$ values for warmer temperatures (Table 1).
respiration would only be 12.8 µmol m⁻² s⁻¹ for a $Q_{10}$ for total respiration of only 1.28. Conversely, if growth respiration only accounts for 20% of total respiration, a $Q_{10}$ for total respiration of 1.82 would be predicted. This scenario is predicted by some current models, but there are no long-term studies with rapidly growing plant communities to validate these models. Unfortunately, studies on the temperature sensitivity of respiration rarely divide respiration into its component parts, and often assume a $Q_{10}$ of about 2 that is derived from short-term studies on mature plant parts to adjust measured respiration values back to a reference temperature (Ruter and Ingram, 1991; Witowski, 1997).

Some researchers have speculated that the range in $Q_{10}$ values is the result of acclimation to temperature, or simply a result of measurement temperature (Tjoelker et al., 2001). However, much of the range in values may be caused by differences in plant growth rate. Studies that report low values for $Q_{10}$ have often been done with growing organisms. When environmental conditions were conducive to rapid growth rates, Percival et al. (1996) showed that $Q_{10}$ values for respiration were very low (1.1–1.5). Urmeneta et al. (1998) also showed that rapidly growing photosynthetic algae had low $Q_{10}$ values (1.4–1.6). Perhaps the most convincing study to show an inverse relationship with growth rate and $Q_{10}$ values is from Ogawa and Takano (1997) as they tracked respiration sensitivity to temperature over the course of a growing season from mid-July through to December. In this study, $Q_{10}$ increased from about 1.6 in July (high growth) up to 2.7 in December.

Loveys et al. (2003) investigated the influence of relative growth rate on respiration rates by looking at a range of species with inherently high or low growth rates. They found no correlation between those species’ growth rates and single leaf and detached root-system respiration for those plants. Poorer et al. (1991) found strong relationships between inherent growth rates and respiration rates in roots. In that study, the authors separated respiration into growth, maintenance and ion uptake, and attributed the apparent differences in respiratory requirements to ion uptake of the different species.

Neven (1998) suggests that it is not the growth rate of the plant but the measurement techniques that determine, at least in part, the apparent temperature sensitivity of respiration. He states that stress on metabolism from rapid heating or cooling will increase the apparent $Q_{10}$ of respiration, whereas constant temperature models are poor estimators of variable temperature profiles because they lack the same stress. So by the nature of the measurement, short-term temperature ramping of tissue may over-estimate $Q_{10}$ through stress on the respiratory system, and constant temperature systems, as in our study, may underestimate the sensitivity because temperature stress to the respiratory system is low. This is analogous to differences in temperature sensitivity of respiration observed in plant material developed in a variable environment compared to that developed in a stable environment and switched to variable environments (see discussion in Atkin and Tjoelker, 2003). Plants exposed to variable environments have the capacity...
to deal with temperature stress more than plants developed in constant environments.

Current paradigm: respiration and CUE acclimate to temperature changes

Although both respiration and CUE were influenced by temperature, neither returned to pre-treatment levels after treatments began. Several studies have reported respiratory acclimation or adaptation to changes in temperature, and some back to pre-treatment levels. For example, Illeperuma et al. (1998) reported a sharp rise in respiration of harvested potato tubers upon transfer from 1 to 10 °C, but after about 7 d, respiration begins to decline. Bryla et al. (1997) showed that citrus root respiration increased sharply upon exposure to warm temperatures but completely returned to previous rates after only 4 d. Gifford (1995) found that CUE returned to the pre-treatment level within 4 d. The initial change in CUE in our study was similar to Gifford (1995), but he altered both day and night temperature and grew his plants in ambient CO₂, so changes in photosynthesis may have complicated the results.

Based on short-term measurements of detached plants, Tjoelker et al. (1999) concluded that a lower Q₁₀ than that obtained from short-term measurements indicated acclimatization to temperature. However, the temperature sensitivity in our study did not change during the entire treatment period (up to 20 d), so all of the acclimation would have had to occur during the first day. This seems unlikely.

Another possibility is that the low Q₁₀ was due to substrate limitation; if there is no substrate to respire, then respiration cannot increase with temperature. These plants were grown in 1200 μmol CO₂ mol⁻¹ with relatively high light (34.5 mol photons m⁻² d⁻¹). Previous studies done in similar environments indicated that these conditions provide an ample carbohydrate supply (Smart et al., 1994). The two starch-accumulating species (tomato and soybean) were slightly more temperature sensitive than the sucrose-accumulating species (lettuce). If anything, the plants in this study should have been more sensitive to temperature than plants grown at ambient CO₂. Loveys et al. (2003) report a negative correlation between substrate content and respiration rate, so clearly substrate availability is not the only determining factor for driving respiration.

It is unlikely that decreases in daytime respiration compensated for increases in night respiration. For example, the night respiration of soybean increased from 1.0 to 1.4 mol C m⁻² night⁻¹ when the night temperature was increased from 20 to 30 °C. The daytime respiration would need to decrease by 75 % for CUE to remain the same. There was no effect of temperature on Pₙₑᵗ so this should result in a 12 % decrease in Pₙₑₙₕ. Also, this type of change would indicate an uncoupling of temperature and respiration during the day as well as a decrease in respiration with an increase in carbohydrate supply, which is highly unlikely (Moser et al., 1982; Azcón-Bieto et al., 1983; Azcón-Bieto and Osmond, 1983; Monje and Bugbee, 1996). While a 75 % reduction in daytime respiration may be possible in single leaves, there is no evidence that this occurs on a whole-plant level.

Current paradigm: cool night temperatures improve growth

Since the biochemistry of respiration is the same regardless of the ultimate use of the energy made during respiration, some argue that the growth and maintenance model may not be sufficient to explain these results. Altered night temperature may shift C allocation between roots and shoots, or alter plant composition. These shifts could alter the energy requirements for growth respiration. Lettuce and soybean had slightly less root biomass and more shoot biomass with warmer temperatures, but this pattern was not observed in tomato. In spite of this shift, the temperature sensitivity remained the same for the duration of treatment.

There were no consistent patterns across species in biomass allocation between roots, shoots and stems. There was also no consistent pattern in C fraction, assimilated N or K fraction. Nitrate was significantly higher in warmer temperatures for lettuce roots, but some of this increase at the highest temperature is partly explained by dilution effects of K (i.e. low %N when %K is high). Carbon was partitioned more to lettuce shoots and less to roots as temperature increased. If root tissue was easier to make than shoot tissue, CUE would have slightly decreased with increasing temperature. However, both the C fraction and the assimilated N fraction of roots and shoots were similar so it is not clear that the energy required for synthesis of root and shoot tissue would be significantly different. Tomatoes accumulated less nitrate and had less assimilated N as the temperature increased, so the CUE should have increased slightly with increasing temperature.

Soybeans had more stem tissue and less leaf tissue at higher temperatures. Although the C fraction in soybean stems and leaves is similar, the assimilated N is higher in leaves, so leaf tissue would most likely be more difficult to synthesize. This suggests that the CUE of soybeans should slightly increase with increasing temperature.

Overall, it is unlikely that changes in allocation patterns or composition had a significant effect on the small temperature sensitivities. If there were allocation changes that were not measured, those changes did not influence the temperature sensitivity in the long term.

Current paradigm: cool night temperatures improve growth

Turnbull et al. (2002) reported increased maximum leaf photosynthetic rates following a single warm night. They attributed this effect to less carbohydrate-induced feedback inhibition of photosynthesis. They conclude by hinting that whole-plant carbon gain may increase with warmer night temperatures because of less feedback inhibition. We did not see any evidence after 20 d of warmer nights of increased photosynthesis on a whole plant community basis that would support their claims.

McCree and Amthor (1982) found that growth rate was improved by 15 % at a constant 20 °C compared with 30/10 °C day/night due to improved carbon balance. They attributed the growth improvement to excessive dark respiration during the day and only slightly reduced night-time respiration, but their studies were done at ambient CO₂,
gested that elevated CO2 inhibits respiration. For example, temperature response. Some previous studies have sug-
minimize the potential carbohydrate limitations to the theory. CO2 on dark respiration is statistically insigni®cant. Amthor
been found. Recent studies indicated that the direct effect of CO2 on dark respiration has not clear from their study.

Our studies do not indicate a statistically significant advantage of either warm or cool nights on final dry mass or on cumulative carbon gain after treatments were applied. There was a statistically significant effect of temperature on night respiration, as expected, but, surprisingly, there was no significant effect on Pnet. Because the carbon flux in Pnet is typically four to five times larger than dark respiration in growing plants, changes in dark respiration have only a small effect on CUE. The relatively small variation between replicate chambers in Pnet dominated the effect of the small, but statistically significant, differences in CUE on growth. If experimental error in Pnet was eliminated, the growth effects would have been determined by the night temperature effect on CUE, which was less than 0.5 % per °C in lettuce and tomatoes, and less than 1 % per °C in soybeans. These effects do suggest a small advantage of cool night temperatures that might be statistically significant in a study with many replicate chambers, but our data indicate that cool nights may not provide a large growth advantage (less than 1 % per °C).

One potential source of variation between chambers is variable side lighting that would have provided more or less light for a group of plants on any given day. Small differences in the height of the reflective curtain may have large effects in the amount of light a canopy receives, and therefore influence the amount of growth, especially in small canopies such as these. For example, these chambers had a growing area of 0.17 m2 (0.47 × 0.36 m). If the reflective curtain was only 1 cm lower than the height of the canopy, the effect is to increase the growing area by 10 % (Bugbee, 1994). This effect is larger than the effect of night temperature on CUE.

Applicability to ambient CO2 environments

These studies were conducted at elevated CO2 to minimize the potential carbohydrate limitations to the temperature response. Some previous studies have suggested that elevated CO2 inhibits respiration. For example, Amthor et al. (1992) initially reported a 20–30 % reduction in dark respiration when CO2 was doubled. However, no theoretical basis for the effect of CO2 on dark respiration has been found. Recent studies indicated that the direct effect of CO2 on dark respiration is statistically insignificant. Amthor (2000) used an improved gas exchange chamber and found that the apparent effect of CO2 on respiration resulted from leaks in the original chamber. Indeed, using five gas exchange measurement approaches, he consistently found that respiration was insensitive to short-term changes in CO2 concentration. Similarly, Burton et al. (1996) initially reported a significant inhibition of root respiration in elevated CO2, but later re-did the tests and found that once leaks were sealed, no CO2 effect was observed (Burton and Pregitzer, 2002).

CONCLUSIONS

Respiration had a much lower Q10 than is commonly reported. Whole-plant respiration is relatively insensitive to temperature in young plants because total respiration consists of a large fraction of growth respiration. In light of this, the present work validates models that divide respiration into a non-temperature-sensitive growth component and a temperature-sensitive component. No change in the sensitivity of respiration to temperature was observed even after 20 d of treatment. Little acclima-
tion was observed in C, nitrate, assimilated N and K contents, and no trend was observed among tissues or species. Alloca
tional shifts had minimal effects on the temperature sensitivity of respiration. Because respiration did not acclimate to temperature through time, CUE also did not acclimate. We believe this is the first long-term study to demonstrate continuously altered CUE as a result of environmental changes. Although cooler night temperature decreased respiration and slightly increased CUE, night temperature had a statistically and biologically insignificant effect on growth.

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LITERATURE CITED


production by respiration in darkened and illuminated wheat leaves. 


