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

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Abstract

- *Background and Aims* Carbon gain depends on efficient photosynthesis and adequate respiration. The effect of temperature on photosynthetic efficiency is well understood. In contrast, the temperature response of respiration is based almost entirely on short-term (hours) measurements in mature organisms to develop Q_{10} values for maintenance and whole-plant respiration. These Q_{10} values are then used to extrapolate across whole life cycles to predict the influence of temperature on plant growth.
- *Methods* In this study, night temperature in young, rapidly growing plant communities was altered from 17 to 34 °C for up to 20 days. The day temperature was maintained at 25 °C. CO_2 gas-exchange was continuously monitored in 10 separate chambers to quantify the effect of night-temperature on respiration, photosynthesis, and the efficiency of carbon gain (carbon use efficiency).
- *Key Results* Respiration increased only 20 to 46% for each 10 °C rise in temperature (total respiratory Q_{10} of between 1.2 to about 1.5). This change resulted in only a 2 to 12% change in carbon use efficiency, and there was no effect on cumulative carbon gain or dry mass. No acclimation of respiration was observed after 20 days of treatment.
- *Conclusions* These findings indicate that whole-plant respiration of rapidly growing plants has a small sensitivity to temperature, and that sensitivity does not change among the species tested, even after 20 days of treatment. Finally, our results support respiration models that separate respiration into growth and maintenance components.

Key words

Latuca sativa, *Lycopersicum esculentum*, *Glycine max*, carbon use efficiency, R:P ratio, whole

canopy CO_2 gas-exchange, hydroponics, Q_{10}, respiration, night temperature

Introduction

There is a general 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 to 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 from 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 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 due to improved carbon balance 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 day-time carbon loss.

Unfortunately, many conclusions about the effects of whole plant respiration are based on measurements of single leaves, leaf disks, or mature plant parts (Alexander *et al.*,1995; Crawford and Huxter 1977; Bunce 1991; Roberts *et al.* 1992; Labate and Leegood 1989; Maier *et al.*, 1998). Leaves poorly represent whole-plant respiration because the measurements do not include roots, stems, flowers, or meristems. For example, leaves typically have a photosynthetic rate that is 10 to 20 times their respiration rate (Björkman, 1981). Whole plants typically have a photosynthetic rate that is 4 times their respiration rate (Gifford, 1994). If leaf mass is 30 to 70% of total plant mass, 70 to 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). Tesky and Will (1999) and Percival *et al.* (1996) observed a lower temperature sensitivity for whole plants than for leaves, but they attributed this to their choice of species rather than a fundamental physiological mechanism. However, 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. Even single plants can be misleading because side lighting of single plants illuminates lower leaves and increases carbohydrate supply, complicating extrapolation to plant communities. Collectively, these studies make it difficult to predict the effect of night temperature on the growth of plant communities.

In addition to measuring respiration rates, it is important to measure whole-plant respiratory efficiency and carbon conservation. A widely used parameter for this is the ratio of net carbon gain (net photosynthesis - dark respiration) in a 24-h period to the total carbon fixed during the light period (P_{gross}) (Amthor, 1989). This ratio, called carbon use efficiency (CUE), is a measure of the efficiency of incorporation of fixed carbon into new biomass. The term integrates all growth and respiratory processes in a plant during a 24-h period. Carbon use efficiency should be sensitive to temperature and growth rate because it incorporates growth and respiration components.

Given that carbon partitioning to roots, leaves, stems, and seeds varies dramatically among species and from germination to harvest, it is surprising that some studies have found that CUE changes little during a plant's life cycle. Gifford (1994) reported an average CUE (calculated from his R:P ratio) of 0.58 to 0.60 (58 to 60%) for several species and sizes of plants across a wide range of environments, although it is important to note that no environmental conditions were specifically mentioned in this study. Monje and Bugbee (1998) found a CUE for wheat (*Triticum aestivum* L.) communities of 0.59 to 0.61 except for the first and final week of the life cycle. Dewar *et al.* (1998) modeled CUE of mature communities and suggested it should be constant because stored reserves should buffer short-term changes in substrate availability.

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). McCree (1974) described the growth portion as a function of daily photosynthesis and the maintenance portion as a function of existing biomass. Growth and maintenance occur simultaneously in growing plants. Since most of the respiration is used for growth in a rapidly growing plant, they should be relatively less temperature sensitive than an older plant with a larger maintenance requirement. It was recently proposed that CUE can be described by changes in growth and maintenance respiration in addition to relative growth rate (van Iersel, 2003).

Based on measurements of mature tissue, there is general acceptance that respiration rises exponentially with temperature. 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 2.0. There is a lack of whole-plant measurements performed in long term studies investigating the effect of temperature on respiration, so there is a shortage of data to validate these ecological models.

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 (Lomander *et al.*, 1998; Burton *et al.,* 1996; Bustan and Goldschmidt, 1998). Unfortunately, this temperature correction term is widely used to correct total respiration measurements for differences in temperature without understanding that the Q_{10} should only apply to the maintenance respiration term, as it does in the ecological models of Ryan *et al.* (1995) and Heuvelink (1995). For example, Witowski (1997) corrects for temperature differences in their study by assuming a Q_{10} of 2 to calculate a basal respiration rate at a common temperature. This technique is repeated in many other studies (Pearman *et al.*, 1981; Wullschleger *et al.*, 1992; Wullschleger and Norby, 1992), which can mislead overall conclusions about the role of temperature on respiration.

Amthor (2000) suggested that respiration may be less temperature sensitive during the long term, which might 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 or LTR_{10} = 1.0 to 1.5), but others had LTR_{10} of between 2 to 5.5 indicating little to no acclimation. Low Q_{10} values do not necessarily indicate acclimation. Tjoelker *et al.* (2001) conclude that plants acclimate because Q_{10} decreases as the measurement temperature increases. However, Q_{10} is an empirically derived relationship between temperature and respiration, and the relationship is not perfectly exponential. Because the relationship is slightly less than exponential, there will be a lower Q_{10} calculated at the higher temperatures and a higher Q_{10} calculated for the cooler temperatures.

We examined both the short-term (days) and long-term (weeks) effects of temperature on respiration, net photosynthesis, and CUE of plant communities. We minimized the effect of temperature on photosynthesis by maintaining a constant daytime temperature, and we grew the plants at elevated CO_2 to increase carbohydrate supply for respiration. We also minimized the effect of temperature on leaf expansion by imposing temperature treatments when canopies were uniform. We hypothesized that changing night temperature would exert a strong influence on night respiration and that change would result in differences in photosynthetic rates on the following day (Turnbull *et al.*, 2002). Furthermore, we hypothesized that altered night respiration would change CUE, but that both respiration and CUE would acclimate to their pre-treatment levels in a few days.

Materials and Methods

Experimental Setup and Design

Three studies were conducted to compare night-temperature effects across three crops: lettuce (*Latuca 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 four to seven days after imbibition into a 10-chamber, computer-controlled gas-exchange system (Figure 1). Temperature within each chamber was controlled with a chilled water coil and small heaters. System details procedures were described previously (van Iersel and Bugbee, 2000)

Each chamber was calibrated in the following manner: A known mass of dried $CaCO_3$ was placed within a chamber and reacted slowly with 4M HNO_3. This caused CO_2 to be evolved and was measured with the gas analyzers. This continued until the reaction was complete and the total moles of CO_2 evolved was 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 equaled that which was initially placed into the chamber (100% ± 2%) by adjusting the span of the flow meters.

Lettuce and tomato were grown at 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. 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}.

Night temperatures were controlled across a 17 °C range from 17 to 34 °C. Temperature treatments were maintained for 13 days until harvest on Day 29 for lettuce, for 20 days until Day 36 for tomato, and for 15 days until Day 34 for soybeans. Treatments extended into flowering for tomato and soybeans. Control plants had constant day/night temperature. All days are after transplanting.

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 µmol m^{-2} s^{-1} (±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 (Figure 1). CO_2 was controlled at 1200 µmol 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 insure that the plants did not become carbohydrate limited at the higher temperatures, 2) to minimize the effect that vapor 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 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).

Calculations

Carbon use efficiency 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 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 it is an efficiency parameter that can easily fit within models. Using P_{net} (net photosynthesis, mol C m_{ground}^{-2} d^{-1}) and R_n (night-time respiration, mol C m_{ground}^{-2} $night^{-1}$), daily carbon gain (DCG) can be calculated as:

$$DCG = P_{net} - R_n$$

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

P_{gross} is a calculated term that reflects the net C fixed (P_{net}) and the amount of C that is simultaneously being respired. Because day-time respiration (R_d) can not be measured directly, P_{gross} is expressed as the sum of P_{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 (µmol m_{ground}^{-2} s^{-1}) are equal when temperatures are constant. In a 12-h photoperiod, R_d (mol C m_{ground}^{-2} d^{-1}) then equals R_n. In a 16-h light / 8-h dark photoperiod, $R_d = R_n * 2$. In these equations, respiration assumes a positive value (i.e., mass respired). P_{gross}

(mol C m_{ground}^{-2} d^{-1}) can, therefore, be calculated as:

$$P_{gross} = P_{net} + R_d$$

Plants were grown in constant day/night temperatures until treatments were applied. Treatment effects were expressed as a percent of their initial value, then normalized to the control in the following manner:

$$(\text{post-treatment}_a\ \text{day}_b\ /\ \text{pre-treatment}_a\ \text{value}) \div$$
$$(\text{post-treatment}_{control}\ \text{day}_b\ /\ \text{pre-treatment value}_{control}) \times 100(\%)$$

where post-treatment$_a$ indicates the post-treatment value of parameter a (i.e., CUE, P_{net}, Rdark), day$_b$ indicates the day after treatment, pre-treatment$_a$ value is the value of the parameter of interest on the day before treatments began, post-treatment$_{control}$ day$_b$ is the post-treatment value of the parameter of interest on the same post-treatment day, and pre-treatment value$_{control}$ is the pre-treatment value of the parameter of interest the day before treatments began. Temperature effects through time are measured in the numerator, and the effects relative to the control and through time are accounted for by normalizing to the denominator. Finally, the Y-intercept was adjusted so that the regression lines at the control point passed through 100% on the Y-axis.

To compare our temperature sensitivities to the literature and to calculate the R_d from R_n to determine P_{gross}, Q_{10} values are reported. The R_n 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:

$$Q_{10} = e^{\frac{(R_n T - R_n \text{control})}{(T - \text{control } T / 10)}}$$

In this study, the temperature response was not obviously exponential, and so was explained statistically with linear regression.

Statistical analysis

A randomized block design was used with five treatments in each of two blocks, giving two replicates at each temperature. Occasionally, temperature control at the low or high treatments was not perfect. This caused us to use linear regression analysis and treat temperature as a continuous variable rather than as discrete treatments. Slopes of lines were compared to see if their slopes were equal using the test statistic ((slope a - slope b) - 0)/(variance of slope a) = $t_{\text{(degrees of freedom of slope a)}}$ (Neter *et al.*, 1996).

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 analyzed for percent C, H, and N with a LECO analyzer 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 analyzed 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). 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.

Results

Lettuce

Night respiration increased 2.0% per °C (Figure 2A, 3A). After 13 days 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 (Figure 2D). Net photosynthesis was not sensitive to night temperature (Figure 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 (Figure 3C). The sensitivity of CUE to temperature did not change during the 13 days of treatment based on comparison of slopes (P 0.35, df = 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 (Figure 4A), while root biomass decreased (Figure 4B). This caused the root fraction to decrease significantly with warmer temperatures (Figure 4D). Leaves were not separated from the stem. Nitrate in both shoots and roots increased with increasing temperature. 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 (Figure 2B and 3D). This caused the CUE to be slightly higher with cooler nights and lower with warmer nights (Figure 2E and 3F). After 20 days of temperature treatment, there was no difference in the sensitivity of CUE or respiration to altered night temperature (P = 0.48, df = 8). Net photosynthesis was not affected by the altered night temperatures (Figure 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 (Figure 4A to 4D). Leaves were not separated from the stem. There was no effect of night temperature on C and root NO_3^- but NO_3^- 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. 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 (Figure 2C and 3G). Carbon use efficiency changed after the night temperatures were changed because respiration changed (Figure 2F, 3I, and 3G). With no change in photosynthesis (Figure 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 (Figure 3G). No acclimation occurred after 15 days of treatment (P = 0.29, df = 8). 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 (Figure 4A), while root biomass decreased (Figure 4B). Stem increased significantly by the same absolute amount as the leaves decreased (Figure 4C). Together, these shifts caused the root fraction to decrease significantly with warmer temperatures (Figure 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. 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 (Figure 5A and 5B). Soybean respiration was significantly more sensitive than lettuce ($t = 6.34$, $df = 8$, $P < 0.001$), and had more CUE sensitivity than lettuce ($t = 2.91$, $df = 8$, $P < 0.025$), but all three species were much less sensitive than commonly believed. Lettuce respiration was significantly less sensitive than tomato ($t = 3.418$, $df = 8$, $P < 0.025$), and CUE was marginally significantly different ($t = 1.64$, $df = 8$, $P \sim 0.08$). 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).

Discussion

Current Paradigm: Respiration is always highly sensitive to temperature

Most formal models do an excellent job of separating growth and maintenance respiration and assigning the temperature sensitive portion only to the maintenance fraction so that the net result is a Q_{10} for total respiration much less than 2. Unfortunately, studies on the temperature sensitivity of respiration rarely divide respiration into its component parts and often assume a widely reported value of a Q_{10} of about 2 that is derived from short-term studies on mature plant parts (Ruter and Ingram, 1991; Witowski, 1997).

Values of Q_{10} for respiration in plants, animals, and microbes are reported from 1.2 to 4 (Urmeneta *et al.*, 1998; Neven, 1998; Boone *et al.*, 1998; Quinlan and Lighton, 1999; Lariguderie and Korner 1995; Chapman and Thurlow, 1998; Nielsen *et al.*, 1999). Some have speculated that the range in Q_{10} values is the result of acclimation to temperature, or simply a result of measurement temperature. However, much of the range in values is probably caused by differences in plant growth rate. If the growth coefficient for respiration is not temperature sensitive, and if a large fraction of the respiration is growth respiration, the temperature sensitivity for total respiration would be less than values obtained from mature, slow growing tissue. We studied rapidly growing plants, which should have had mostly growth respiration, and thus low Q_{10} values.

Studies that report low values for Q_{10} have all been done with growing organisms, which would result in a temperature-insensitive growth component included in the respiration measurements. 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 to 1.5). Urmenta *et al.* (1998) also showed that rapidly growing photosynthetic algae had low Q_{10} values (1.4 to 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 December. In this study, Q_{10} increased from about 1.6 in July (high growth) up to 2.7 in December.

Conversely, studies that include organisms with slower growth have larger Q_{10} values of about 2 to 2.5, regardless of the organism. When measuring dormant season stem and branch respiration, Maier *et al.* (1998) report a Q_{10} of 1.8 to 1.9. Interestingly, they later went on to calculate from their own measurements in this paper a basal respiration rate based on a Q_{10} for total respiration of 2. The Q_{10} for mature harvester ants (*Pogonomyrmex*) was about 2.3.

Neven (1998) provides yet another possibility to explain the ranges of measured Q_{10} values. In Neven (1998), Q_{10} values are compared that are derived in either multiple-organisms (moths) grown in constant temperatures (as in our present study) or single organism (moths) studies wherein the temperatures are changed rapidly over a similar range. It is stated 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. It is thus possible that one approach may over-estimate the response of respiration to temperature as much as the other approach under-estimates the response.

If we assume that the Q_{10} for maintenance respiration is between 2 and 2.2, maintenance and growth coefficients can be calculated. If all of the measured temperature sensitivity is due to maintenance respiration, the maintenance coefficient would be 0.03 to 0.04 mol C respired mol of in biomass^{-1} d^{-1}, which is a typical value (Amthor, 1989). If the remainder of the respiration is due to growth, the conversion efficiency (sometimes referred to as Y_g) would be 0.85 to 0.95 mol C in growth mol substrate^{-1}, which is a realistic value based on estimates of Penning de Vries *et al.* (1974). These calculations also indicate that 34 to 50% of the respiration is growth respiration, which is a reasonable value for these young plants (van Iersel and Seymour, 2000).

Since the biochemistry of respiration is the same regardless of the ultimate use of the energy made during respiration, 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 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 compositional changes 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. Future studies should examine both allocational shifts and potential compositional changes as possible responses to temperature rather than explaining any effect entirely with the growth and maintenance paradigm.

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 days 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 to 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 CO_2, so photorespiration at 30 °C would be significantly increased compared to 20 °C. This would decrease photosynthetic efficiency and reduce growth in the warmer day temperature treatment. They also used a 20 °C difference between day and night. This extreme change in temperature may have affected water relations, leaf expansion, and chilling injury in addition to respiration so the direct effect of night temperature on growth is not clear from their study.

In theory, respiration should be inadequate on cool nights and excessive on warm nights, but 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 P_{net}. Because the carbon flux in P_{net} is typically 4 to 5 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 P_{net} dominated the effect of the small, but statistically significant, differences in CUE on growth. If experimental error in P_{net} 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. Reflective skirts were wrapped around each chamber to minimize these side lighting issues and make the data more easily extrapolated to field conditions. 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 as these. For example, these chambers had a growing area of 0.17 m^2 (0.47 m× 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

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 reported respiratory acclimation or adaptation to changes in temperature, and some back to pre-treatment levels. For example, Illeperuma *et al.* (1998) report a sharp rise in respiration of harvested potato tubers upon transfer from 1 to 10 °C, but after about 7 days, 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 days. Gifford (1994) found that CUE returned to the pre-treatment level within four days. The initial change in CUE in our study was similar to Gifford (1994), but he altered both day and night temperature and grew his plants in ambient CO_2, so changes in photorespiration may have complicated the results.

Based on short-term measurements of detached plants, Tjoelker *et al.* (1999) concluded that a lower Q_{10} than that obtained from short-term measurements indicated acclimation to temperature. However, the temperature sensitivity in our study did not change during the entire treatment period (up to 20 days), so all of the acclimation would have had to occur during the first day. This seems unlikely.

Another possibility is that the low Q_{10} was due to substrate limitation; if there is no substrate to respire, then respiration can not increase with temperature. These plants were grown in 1200 μmol CO_2 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). If anything, the plants in this study should have been more sensitive to temperature than plants grown at ambient CO_2.

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 day-time respiration would need to decrease by 75% for CUE to remain the same. There was no effect of temperature on P_{net} so this should result in a 12% decrease in P_{gross}. 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 (Azcón-Bieto *et al.*, 1983; Azcón-Bieto *et al.*, 1983; Moser *et al.*, 1982; Monje and Bugbee, 1996). While a 75%

reduction in day-time respiration may be possible in single leaves, there is no evidence that this occurs on a whole plant level.

Dewar *et al.* (1998) developed a mechanistic model of CUE for mature leaves or canopies to explain why a constant daily CUE is often observed in many species and environmental conditions. In this model, stored reserves buffer short-term (minutes or hours) carbohydrate supply so brief environmental fluctuations do not affect CUE. The model was tested in variable light conditions, but variation in temperature was not modeled. The pool of carbohydrate available for growth and respiration is typically large enough to buffer temporary changes in photosynthesis, so daily CUE is constant. Furthermore, the synthesis of starch and proteins may be maintained in a steady state during these temporary fluctuations, so while the plant may grow more slowly in response to less light, it should have identical growth efficiency. That does not mean, however, that long-term CUE should also remain constant.

The plants in our study developed in one environment, which was suddenly changed for the duration of the study. The pools of carbohydrate available for growth and respiration may have been permanently altered, thereby resulting in a new CUE value. It is possible that the composition of new biomass (carbohydrate, lipids, proteins) was also affected by this change and, as a result, the CUE changed. We saw no evidence for this based on differences in C-fraction among treatments in leaves, stems, and roots. The two starch-accumulating species (tomato and soybean) were slightly more temperature sensitive than the sucrose accumulating species (lettuce).

Carbon use efficiency has been modeled to be a function of conversion efficiency (Y_g), the maintenance coefficient, and relative growth rate (RGR) (Thornley and Johnson, 2000), and this model was recently evaluated and supported in a case study with lettuce (van Iersel, 2003). According to this model, CUE should decrease as RGR decreases, assuming growth and maintenance respiration are constant. However, because the model uses a hyperbolic-type equation similar to the Michaelis-Menton enzyme kinetics equation, RGR can vary greatly without substantial change in CUE. Interestingly, Thornley and Cannell (2000) ignore the RGR:CUE relationship and state that one of the results from mechanistic analyses of respiration and growth should be a constant CUE. Furthermore, if growth and maintenance respiration play a role in determining CUE, if those requirements are not met (as in low CO2 or low light), CUE may decline, even with high relative growth rates.

Applicability to Ambient CO_2 Environments

We conducted these studies at elevated CO_2 to minimize the potential carbohydrate limitations to the temperature response. Some previous studies have suggested that elevated CO_2 inhibits respiration. For example, Amthor *et al.* (1992) initially reported a 20 to 30% reduction in dark respiration when CO_2 was doubled. However, no theoretical basis for the effect of CO_2 on dark respiration has been found. Recent studies indicated that the direct effect of CO_2 on dark respiration is statistically insignificant. Amthor (2000) used an improved gas exchange chamber and found that the apparent effect of CO_2 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 CO_2 concentration. Similarly, Burton *et al.* (1997) initially reported a significant inhibition of root respiration in elevated CO_2, but later re-did the tests and found that once leaks were sealed, no CO_2 effect was observed (Burton and Pregitzer, 2002). It is even questionable whether there is a long-term effect of elevated CO_2 on specific respiration rates. Monje and Bugbee (1998) compared specific respiration rates at high and low CO_2 (1200 vs. 400 μmol mol^{-1}) and found a small difference during the first 6 days of growth, but no difference during the remainder of the life cycle.

Conclusions

Respiration had a much lower Q_{10} 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 days of treatment. Little acclimation was observed in C, nitrate, assimilated N, and K contents, and no trend was observed among tissues or species. Allocational 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.

Acknowledgments

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Table 1. Final dry mass (in 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. Data are the average of two groups of plants in separate chambers. Q_{10} was higher at cooler temperatures and lower in warmer temperatures. There was no effect of temperature on final dry mass in any species ($P>0.32$), nor on CCG after treatment initiation ($P>0.59$).

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

Table 2. Carbon, Nitrate, assimilated N, and K^+ for the three species in the different temperatures. Some of the samples for soybean were lost. Assimilated N is calculated by subtracting NO_3^- from total N. * indicates a quadratic fit.

	Night temperature	C			Nitrate			Assimilated N			K^+		
		shoot	root	stem	shoot	root	stem	shoot	root	stem	shoot	root	stem
			(%)			(%)			(%)			(%)	
Lettuce	18.2	40.2	39.8	--	0.55	0.10	--	1.8	2.6	--	5.7	2.9	--
	20	38.6	41.4	--	0.77	0.09	--	2.4	2.4	--	4.8	2.3	--
	25	38.2	40.8	--	0.95	0.22	--	2.3	2.5	--	5.0	2.9	--
	30	38.3	41.0	--	0.66	0.20	--	2.5	2.6	--	5.2	2.9	--
	31.3	39.6	40.2	--	0.67	0.43	--	2.5	2.4	--	4.9	3.7	--
	P-value	0.643	0.927	NA	0.029*	0.019	NA	0.132	0.788		0.458	0.142	NA
Tomato	18	37.0	40.7	--	0.45	0.10	--	2.1	2.3	--	4.4	4.7	--
	20	37.8	39.8	--	0.36	0.07	--	1.9	2.2	--	4.6	4.4	--
	25	37.6	39.3	--	0.38	0.09	--	2.0	2.1	--	4.6	4.4	--
	30	36.6	40.5	--	0.26	0.11	--	1.9	2.1	--	3.9	4.4	--
	31.5	36.7	40.5	--	0.17	0.12	--	2.2	2.1	--	5.3	3.3	--
	P-value	0.942	0.795	NA	0.006	0.529	NA	0.841	0.014		0.658	0.045	NA
Soybean	17	--	--	40.2	--	--	0.14	--	--	1.1	--	--	2.4
	20	41.1	--	--	0.22	--	--	3.2	--	--	2.4	--	--
	25	40.9	37.8	38.5	0.25	0.27	0.37	2.7	2.0	1.8	1.9	6.6	3.5
	30	39.9	38.1	40.1	0.40	0.27	0.27	3.1	2.2	1.3	2.6	5.5	3.0
	P-value	0.049	0.878	0.577	0.03	0.875	0.340	0.566	0.478	0.455	0.712	0.511	0.404

Figure Legends

Figure 1. The ten-chamber gas-exchange system. There are five chambers on each side of a walk-in growth chamber. Each chamber has a reflective skirt wrapped around the outside to minimize side lighting.

Figure 2. Net photosynthesis, night respiration, and carbon use efficiency for lettuce (A and D), tomato (B and E), and soybean (C and F). Data points are the average of two chambers for a given temperature. Carbon exchange rates are per m^2 of ground area. Temperature treatments were initiated on day 17 for lettuce and tomato, and day 18 for soybean.

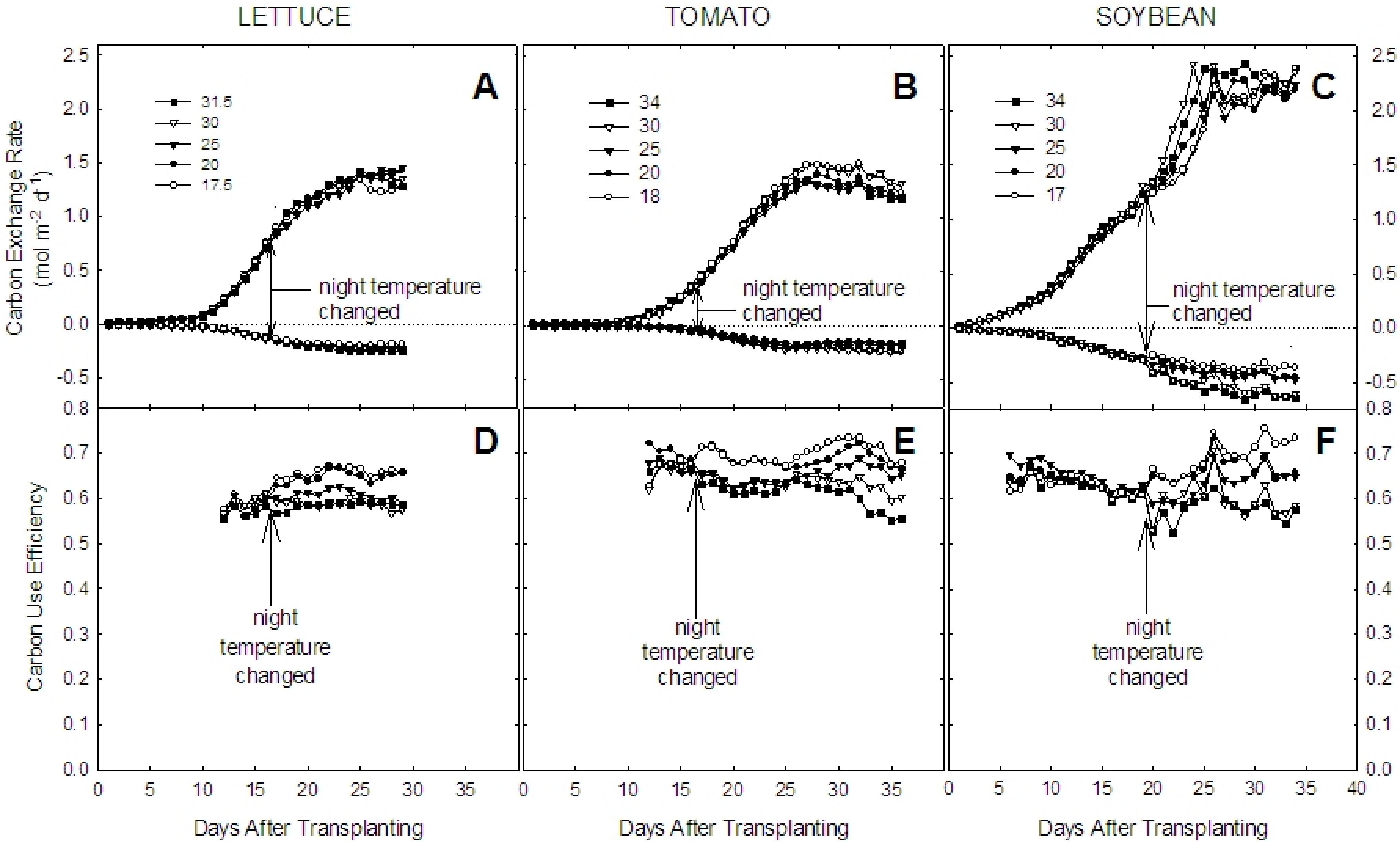
Figure 3. Effect of temperature on night respiration, photosynthesis, and carbon use efficiency for lettuce (A, B, C), tomato (D, E, F), and soybean (G, H, I). Data are shown relative to the control for the first and last day of treatment. The slopes between the first and last treatment day are not statistically different from one another within a species and parameter (lowest P value 0.29, df = 8), which indicates that there was no acclimation to temperature.

Figure 4. Effect of temperature on shoot (A), root (B), and stem (C) mass and root fraction (D). Lettuce shoot mass increased significantly with temperature, but soybean leaf mass decreased with temperature. Lettuce and soybean root mass decreased significantly with temperature, and soybean stem mass increased with temperature, likely because height increased with temperature. These changed caused the root fraction to decrease with temperature in both lettuce and soybean. Temperature did not influence any parameter in tomato.

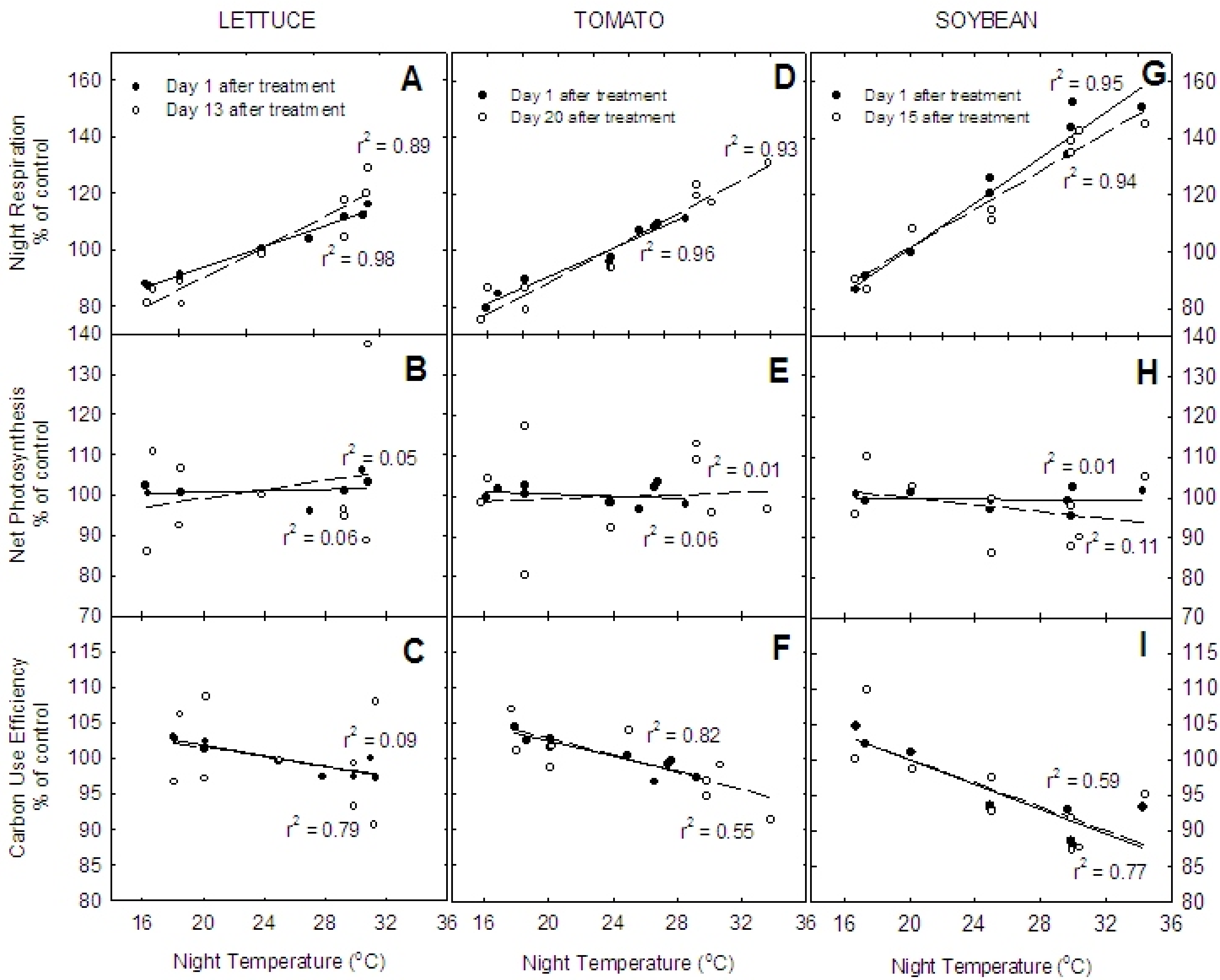
Figure 5. Effect of temperature on respiration (A) and carbon use efficiency (B) in lettuce, tomato, and soybean relative to the control. Soybean respiration was significantly more temperature sensitive than tomato ($t = 4.05$, $df = 8$, $P < 0.005$), and tomato respiration is significantly more sensitive than lettuce ($t = 3.418$, $df = 8$, $P < 0.025$). Soybean CUE was significantly more sensitive to temperature than tomato ($t = 2.04$, $df = 8$, $P < 0.05$), and tomato CUE was marginally more sensitive to temperature than lettuce ($t = 1.64$, $df = 8$, $P \sim 0.08$). Data

are normalized to the control temperature (25 °C in lettuce and tomato, and 20 °C in soybean).

1

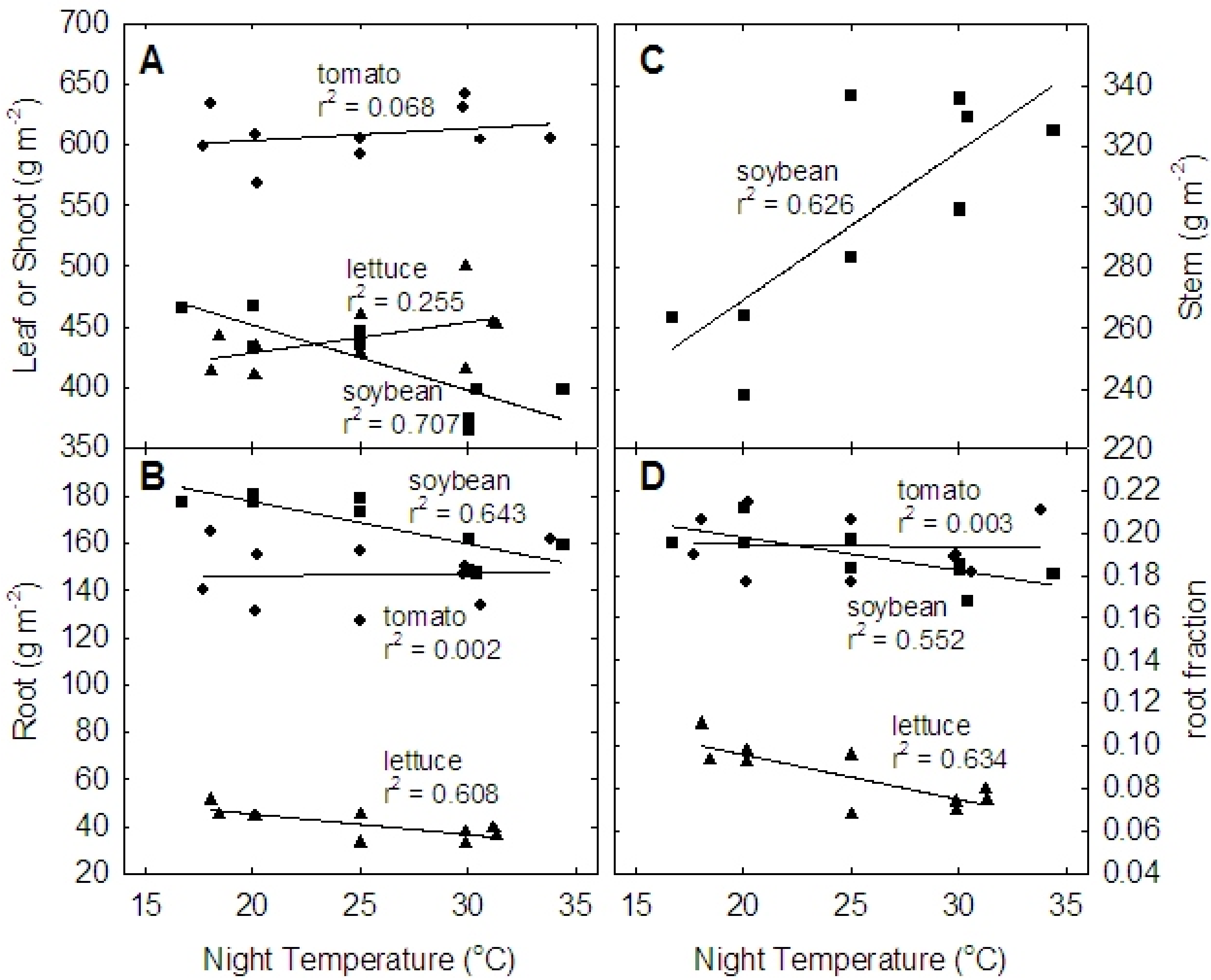

LETTUCE
TOMATO
SOYBEAN
Carbon Exchange Rate
(mol m-2 d-1)
Carbon Use Efficiency
A
B
C
D
E
F
31.5
30
25
20
17.5
34
30
25
20
18
34
30
25
20
17
night temperature changed
Days After Transplanting

1

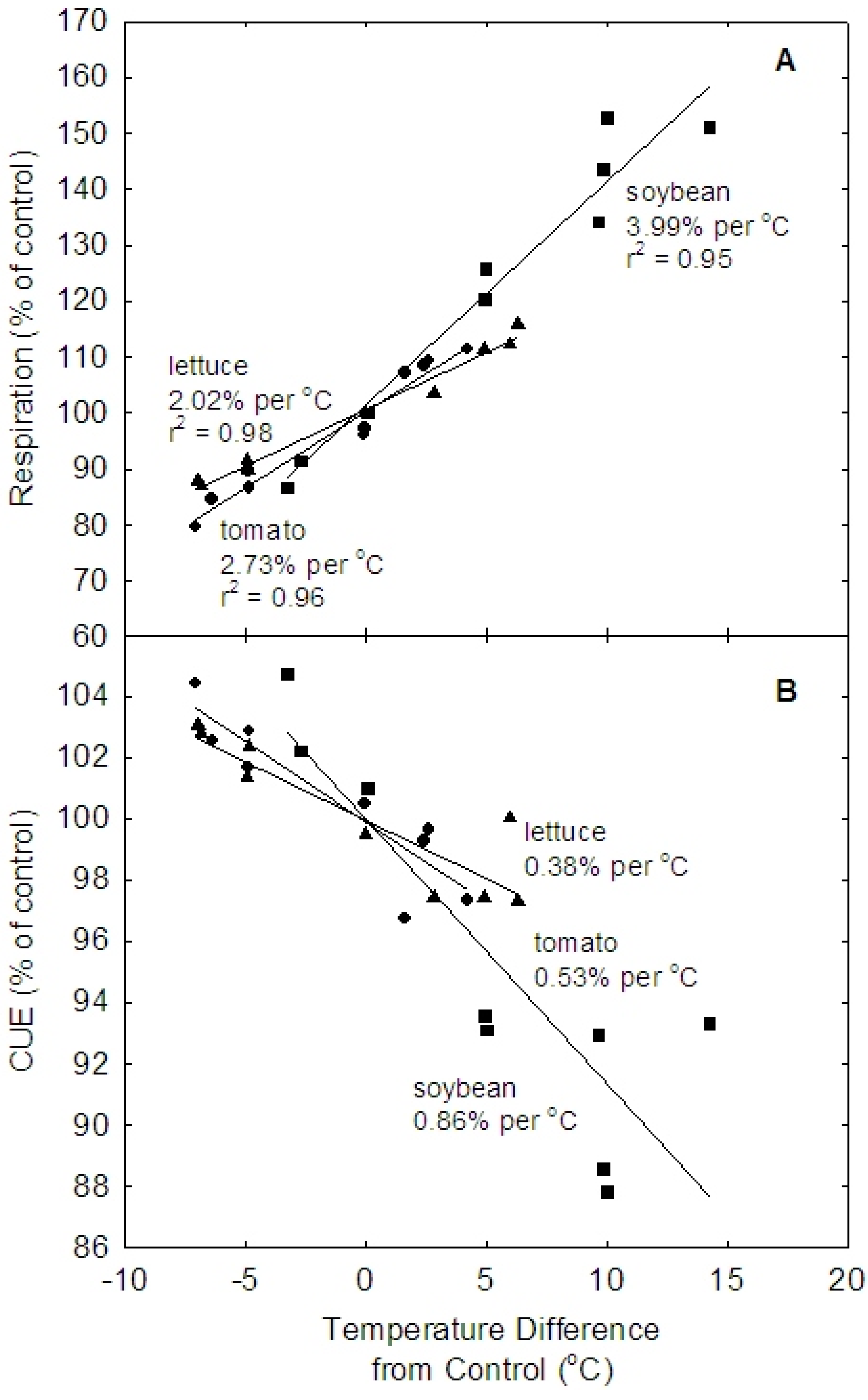


LETTUCE
TOMATO
SOYBEAN
A
Day 1 after treatment
Day 13 after treatment
r² = 0.89
r² = 0.98
D
Day 1 after treatment
Day 20 after treatment
r² = 0.93
r² = 0.96
G
Day 1 after treatment
Day 15 after treatment
r² = 0.95
r² = 0.94
Night Respiration
% of control
B
r² = 0.05
r² = 0.06
E
r² = 0.01
r² = 0.06
H
r² = 0.01
r² = 0.11
Net Photosynthesis
% of control
C
r² = 0.09
r² = 0.79
F
r² = 0.82
r² = 0.55
I
r² = 0.59
r² = 0.77
Carbon Use Efficiency
% of control
Night Temperature (°C)
Night Temperature (°C)
Night Temperature (°C)

1


A
B
C
D
tomato
r^2 = 0.068
lettuce
r^2 = 0.255
soybean
r^2 = 0.707
soybean
r^2 = 0.643
tomato
r^2 = 0.002
lettuce
r^2 = 0.608
soybean
r^2 = 0.626
tomato
r^2 = 0.003
soybean
r^2 = 0.552
lettuce
r^2 = 0.634
Leaf or Shoot (g m^{-2})
Root (g m^{-2})
Stem (g m^{-2})
root fraction
Night Temperature (°C)
Night Temperature (°C)
700
650
600
550
500
450
400
350
180
160
140
120
100
80
60
40
20
340
320
300
280
260
240
220
0.22
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
15
20
25
30
35
15
20
25
30
35

1


A
B
Respiration (% of control)
CUE (% of control)
soybean
3.99% per °C
r² = 0.95
lettuce
2.02% per °C
r² = 0.98
tomato
2.73% per °C
r² = 0.96
lettuce
0.38% per °C
tomato
0.53% per °C
soybean
0.86% per °C
Temperature Difference
from Control (°C)