

Direct and Acclimatory Responses of Dark Respiration and Translocation to Temperature

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- **Background and Aims** Accounting for the acclimation of respiration of plants to temperature remains a major problem in analysis of carbon balances of plants and ecosystems. Translocation of carbohydrates out of leaves in the dark requires energy from respiration. In this study relationships between the responses of leaf respiration and translocation to temperature are examined.
- **Methods** Direct and acclimatory responses to temperature of respiration and translocation in the dark were investigated in mature leaves of soybean and amaranth. In some cases translocation from leaves was prevented by heat-girdling the phloem in the leaf petiole, or photosynthesis during the previous day was altered.
- **Key Results** In both species short-term increases in temperature early in the dark period led to exponential increases in rates of respiration. However, respiration rates decreased toward the end of the dark period at higher temperatures. Stopping translocation largely prevented this decrease in respiration, suggesting that the decrease in respiration was due to low availability of substrates. In soybean, translocation also increased with temperature, and both respiration and translocation fully acclimated to temperature. In amaranth, translocation in the dark was independent of temperature, and respiration did not acclimate to temperature. Respiration and translocation rates both decreased with lower photosynthesis during the previous day in the two species.
- **Conclusions** Substrate supply limited total night-time respiration in both species at high temperatures and following days with low photosynthesis. This resulted in an apparent acclimation of respiration to high temperatures within one night in both species. However, after long-term exposure to different temperatures there was no evidence that lack of substrates limited respiration in either species. In amaranth, respiration did not limit translocation rates over the temperature range of 20–35 °C.

Key words: Temperature, acclimation, respiration, translocation, soybean, amaranth.

INTRODUCTION

Concern over the rising concentration of carbon dioxide in the atmosphere has stimulated interest in understanding the global carbon cycle, and there remains considerable uncertainty about the temperature dependence of ecosystem respiration (e.g. Van Dijk and Dolman, 2004). Respiration by autotrophs is a large component of ecosystem respiration. Modelling work by Wythers *et al.* (2005) and King *et al.* (2006) showed that variation in the Q_{10} of respiration with temperature, and the acclimation of respiration to temperature, as occurs in many plants, would have substantial effects on the carbon balance of ecosystems. Thermal acclimation of respiration refers to changes in rate with a change in temperature being partly or fully reversed upon long-term exposure to that temperature. The existence of ecotypic variation in the response of respiration to temperature was demonstrated by some of the first ecophysiological measurements made with infrared CO₂ analysers (Mooney and Billings, 1961), and ecotypic variation in acclimation potential has been known for over 30 years (Billings *et al.*, 1971). However, causes of acclimation of respiration to temperature remain uncertain, and acclimation is often difficult to reconcile with the ‘growth and maintenance model’ of respiration, which remains the basis of many ecosystem carbon models (Amthor, 2000; Thornley and

Cannel, 2000). Amthor (2000) and Thornley and Cannel (2000) suggested that progress may be made by considering specific components of respiration in specific tissues. The present study focuses on respiration of mature leaves in combination with one of the processes dependent on that respiration, the translocation of the products of photosynthesis out of the leaf during the dark.

Many of the causes of acclimation of respiration of mature leaves to temperature suggested in the literature relate directly or indirectly to the availability of carbohydrates. For example, the idea that increased respiration after prolonged exposure to low temperatures might be the result of an increase in the alternative pathway of respiration (Gonzalez-Meler *et al.*, 1999) was based on the concept of the alternative pathway as an overflow system to deal with excess carbohydrates or to prevent the production of reactive oxygen species (Fiorani *et al.*, 2005). Similarly, the idea that acclimation of respiration to temperature reflects changes in leaf nitrogen content (Tjoelker *et al.*, 1999) and maximum photosynthetic capacity (Loveys *et al.*, 2003) relates to the fact that variation in maximum photosynthetic capacity with growth temperature results from changes in the availability of carbohydrates to developing leaves (Bunce, 1983, 1991). More generally, increased temperature is thought to increase sink activity (the use of photosynthates in other parts of the plant) more than source activity (photosynthesis), thus reducing

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carbohydrate availability for respiration, and low temperature would reduce sink activity more than photosynthesis, increasing the supply of substrates for respiration (Dewar *et al.*, 1999). However, direct relationships between rates of respiration and measured concentrations of carbohydrates have often not been clear in studies of acclimation of respiration to temperature (e.g. Mullen and Koller, 1988; Atkin *et al.*, 2001). It is uncertain how commonly leaf respiration rates are substrate-limited, and the identity of limiting substrates has not been established (Azcon-Bieto and Osmond, 1983). Because respiration is required for the translocation of carbohydrates out of leaves, in addition to using carbohydrates as its primary substrate, complex relationships between respiration rates and carbohydrate levels can be envisaged, if respiration is not always substrate-limited.

In the growth and maintenance model of respiration, respiration consists of two components, respiration required for the synthesis of new tissue, and respiration required for the maintenance of existing tissue. Growth respiration is proportional to relative growth rate, but the proportionality has been found to be independent of temperature (McCree and Amthor, 1982). Maintenance respiration is proportional to mass, but the proportionality coefficient increases with temperature (McCree and Amthor, 1982). The overall response of respiration to growth temperature depends substantially on how relative growth rate responds to temperature. In the case of roots, the observed acclimation of respiration to temperature was reasonably consistent with the growth and maintenance model of respiration, in that in genotypes in which relative growth rate was more constant across growth temperatures, respiration responded less to growth temperature, i.e. there was more acclimation of respiration to temperature (Kurimoto *et al.*, 2004). However, in mature leaves, there would be no growth respiration, and a consistent increase in respiration with growth temperature would be expected. Thus, acclimation of mature leaf respiration to growth temperature would be difficult to reconcile with the growth and maintenance model of respiration, unless it reflected changes in leaf mass or protein content. Another possibility is that respiration associated with translocation is a large fraction of the respiration of mature leaves, and that a decrease in translocation with increasing growth temperature could account for acclimation of respiration to temperature. How increased temperature might decrease translocation is unclear, unless translocation became limited by the availability of carbohydrates. In this situation, evidence for acclimation of respiration to temperature might depend on whether respiration was measured early or late in the dark period.

In order to examine the possible involvement of changes in translocation in the acclimation of leaf respiration to temperature, respiration and translocation were measured over the whole night in mature leaves of two species subjected to short- and long-term changes in temperature.

MATERIALS AND METHODS

Soybean (*Glycine max* L. Merr. 'Clark') and amaranth (*Amaranthus hypochondriacus* L. 'Plainsman') were grown in controlled environment chambers with 16 h per

day of light at $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation from a mixture of high-pressure sodium and metal halide lamps. This plant material was chosen for having relatively little plant to plant variation and convenient leaf size. Soybean has C_3 photosynthetic metabolism, while amaranth has C_4 metabolism. C_3 and C_4 species were selected because they generally differ in the proportion of current photosynthesis translocated in the daytime (Grodzinski *et al.*, 1998). A 16-h day was used to increase the rate of translocation in the dark, which reduced the experimental error in estimating translocation rate (Bunce, 2004). Chamber $[\text{CO}_2]$ was maintained at $370 \pm 20 \mu\text{mol mol}^{-1}$ for 24 h per day. Plants were grown singly in 15-cm-diameter pots filled with vermiculite and flushed daily with a complete nutrient solution containing 14.5 mm nitrogen. For most experiments, which examined responses to single nights at altered temperatures, plants were grown from seeding at 25°C . These experiments were conducted on soybean plants 17 d after planting, a few days after full area expansion of the first trifoliolate leaf, and on amaranth plants 16 d after planting, a few days after full area expansion of the fourth main stem leaf. In other experiments examining long-term responses to growth temperature, plants were grown entirely at 20 or at 30°C , and experiments were conducted at the same leaf developmental stages as when plants were grown at 25°C .

Respiration rates, measured as net rates of CO_2 efflux in darkness, were determined by placing entire attached fourth leaves of amaranth or entire terminal leaflets of first trifoliolate leaves of soybeans in a water-jacketed cuvette containing a mixing fan. The plants and the cuvettes were in a darkened controlled environment chamber set to the temperature that leaf respiration was to be measured. Petioles passed through a groove in a side wall of the chamber and were sealed with caulk. A gas blending system provided an airstream to the cuvette with the same carbon dioxide and water vapour concentrations as the dark growth conditions at a flow rate determined by a mass flow meter. A portable photosynthesis system (CIRAS-1, PP Systems, Amesbury, MA, USA) recorded leaf temperatures, carbon dioxide concentrations and respiration rates. Airstreams were dried using magnesium perchlorate prior to entering the infrared carbon dioxide analyser. Leaf areas were measured with a photo-electric leaf area meter, and respiration rates expressed per unit of projected leaf area. In most cases respiration rates were measured on a single leaf every 10 min throughout the entire 8-h dark period. In some experiments sections of leaf petioles several centimetres below the leaf lamina were submerged in water at 70°C for 1 min just prior to insertion into the leaf cuvette. This was done in order to kill phloem tissue ('phloem girdling') and prevent translocation of material out of the leaf, while not disrupting xylem transport of water into the leaf. Tests showed that leaves with phloem girdling did not lose any dry mass over the dark period other than by respiration.

Short-term responses of respiration rate to temperature were determined by rapidly changing the temperature of water in the water-jackets of the cuvette, and determining respiration rates after temperatures and respiration rates had been stable for about 5 min at each new temperature.

These measurements were conducted on plants within 2 h of the beginning of the dark period, to avoid possible complications of substrate deficiency affecting respiration. Comparisons were made between responses for which the growth chamber temperature matched the leaf temperature, and for which the growth chamber temperature was kept constant at 25 °C.

Rates of translocation were calculated from changes in total dry mass over the whole dark period, obtained from destructive harvests on replicate leaves, and subtracting the loss in mass due to respiration. Translocation rates were expressed per unit of leaf area. For each estimate of translocation, leaf mass per unit area was measured at the beginning of the dark period on 8–10 leaves, and at the end of the dark period on 8–10 leaves of plants that had been in the same controlled environment chamber in which respiration was measured for the whole dark period. Change in the mean values of mass per unit of area over time was used as a single estimate of translocation plus respiration. The change in mass due to respiration was calculated from the respiration rate of the measured leaf, assuming the material respired was 40 % carbon.

In some experiments, effects of the amount of photosynthesis during the previous light period on respiration and translocation were examined. In these cases the radiation and/or the [CO₂] (in the case of soybean) during the previous 16-h light period were varied before measuring respiration and translocation during the dark period under the conditions of 25 °C air temperature, and 370 μmol mol⁻¹ [CO₂]. Photosynthetic rates were measured once per hour over the course of these days, using a CIRAS-1 portable photosynthesis system programmed to match the daytime conditions of light and [CO₂]. Photosynthesis was measured on three leaves at each time point.

For each treatment, three or four independent estimates of translocation were made, each based on 16–20 leaves, and three or four estimates of respiration were made, each based on a single leaf. Treatment effects were tested using analysis of variance, with $n = 3$ or 4, with multiple means separated using a Tukey's honestly significant difference (HSD) test. Tests were implemented using JMP v. 5 (SAS, Inc., Cary, NC, USA).

RESULTS

For plants grown at 25 °C, respiration averaged over the whole night increased with night temperature in both species (Fig. 1). However, at the higher temperatures, respiration rates were higher within the first 2 h of darkness than the average rates for the whole night (Fig. 1), and were also higher for the average rates for the whole night at the higher temperatures in leaves in which translocation was prevented by phloem girdling (Fig. 1). The same short-term responses of respiration to temperature occurred whether the rest of the plant was held at constant temperature or matched the leaf temperature (Fig. 1). Without phloem girdling, respiration rates measured at the end of the dark period were not significantly different for the night temperatures of 25, 30 and 35 °C in either species (Table 1). Phloem girdling prevented most or all of the

decrease in respiration rates at the end of the dark period in leaves at the higher temperatures (Table 1).

When the temperature was changed around whole plants of soybean, translocation rate increased with temperature (Fig. 2A), and there was a linear relationship between translocation rate and respiration rate (Fig. 2B). In amaranth, there was no significant effect of temperatures from 20 to 35 °C on translocation rate (Table 2). There was no significant change in translocation rate with change in respiration rate at the different temperatures in amaranth (Table 2).

Complete acclimation of both respiration and translocation to temperature occurred in soybean, as indicated by no significant differences in rates of either process when measured at the long-term growth temperatures of 20, 25 and 30 °C (Table 2). This result contrasts with differences for both processes over this range of temperature for plants grown at 25 °C and subjected to 20, 25 and 30 °C in the short term (Figs 1 and 2). Respiration rates at the end of the night were essentially the same as at the

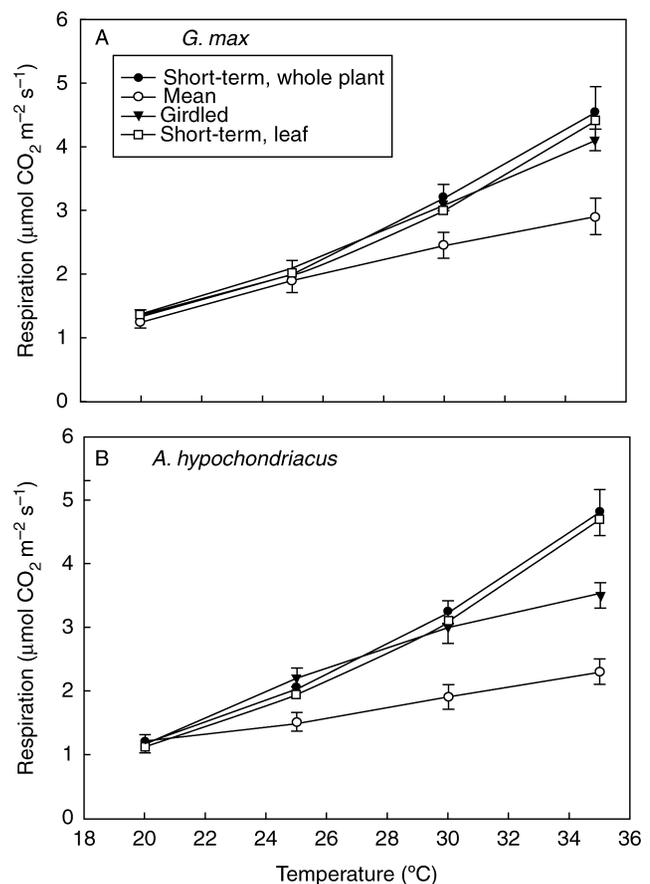


FIG. 1. Responses of respiration to temperature of leaves of (A) *Glycine max* and (B) *Amaranthus hypochondriacus*. Responses are given for short-term changes in temperature applied to the whole plant or just the measured leaf within 2 h of the beginning of the dark period, for the mean rate over the whole dark period, and mean values for the whole night for leaves in which the phloem was disrupted by heat girdling. Error bars are s.e. for $n = 3$ or 4. For clarity, error bars are not provided for the short-term responses for the leaf.

TABLE 1. Initial and final rates of respiration during the 8-h dark period in leaves of *Glycine max* and *Amaranthus hypochondriacus* grown and measured at different temperatures, and final rates of leaves in which the phloem in the leaf petiole had been girdled before the start of the dark period

Species	Temperature (°C)		Respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)		
	Growth	Measurement	Initial	Final	Girdled final
<i>G. max</i>	25	20	1.2 ^d	1.3 ^c	1.3 ^d
	25	25	1.8 ^c	2.1 ^a	2.2 ^c
	25	30	3.0 ^b	2.3 ^a	2.9 ^b
	25	35	4.2 ^a	2.3 ^a	3.9 ^a
	20	20	1.7 ^c	1.6 ^b	nd
	30	30	1.7 ^c	1.7 ^b	nd
	<i>A. hypochondriacus</i>	25	20	1.2 ^d	1.2 ^b
25		25	2.0 ^c	1.4 ^a	2.1 ^c
25		30	3.1 ^b	1.6 ^a	2.8 ^b
25		35	4.2 ^a	1.6 ^a	3.2 ^a
20		20	1.3 ^d	1.2 ^b	nd
30		30	2.1 ^c	1.5 ^a	nd

Within a column and species, values followed by different letters were significantly different at $P = 0.05$ by Tukey's HSD test. nd, not determined.

beginning of the night in soybean leaves exposed to 20 °C either for one night or continuously, and also in leaves exposed continuously to 30 °C (Table 1). In amaranth, there was no evidence of acclimation of respiration to temperature, because mean rates at 20 and 30 °C were the same for leaves grown at those temperatures as for plants that had been grown at 25 °C (Table 2). By the same criterion, there was also no evidence of acclimation of translocation to temperature but there was also no response of translocation to night temperature in this species when grown at 25 °C.

Respiration and translocation measured at 25 °C both varied with the mean rate of photosynthesis during the previous day in each species (Fig. 3), although to a smaller extent in soybean. When photosynthesis was altered by varying the daytime light and [CO₂] treatments, there was a linear relationship between translocation rate and respiration rate in soybean, but translocation was reduced only at the lowest rates of respiration in amaranth (Fig. 3).

DISCUSSION

It is conceivable that heat girdling of the petioles used in this study to prevent translocation might allow heat-shock signals to reach the leaves and affect respiration rates. However, it is unlikely that leaf respiration rates were affected in this way for two reasons. First, phloem girdling had no effect on respiration rates measured at 20 °C in either species or at 25 °C in soybean at any time during the 8-h night. Second, in cases where girdling did affect respiration rates, rates were not affected for several hours after girdling, i.e. not until rates of control leaves began to decrease over time, and rates of girdled leaves had smaller decreases in rate.

The contrast between the short-term responses of respiration to temperature and the responses of rates averaged over the whole night (Fig. 1), and the fact that phloem girdling largely eliminated the decrease in respiration during the night at high temperatures (Table 1) suggest that substrate availability limited respiration at the end of nights at the higher temperatures in both species. The probable limitation of respiration by lack of substrate caused respiration rates of leaves exposed to 30 and 35 °C for one night to reach the same rate at the end of the night as plants grown continuously at 25 °C. This produced the appearance of rapid acclimation of respiration to high temperatures.

However, this apparent rapid acclimation of respiration to high temperatures differed qualitatively from the longer-term

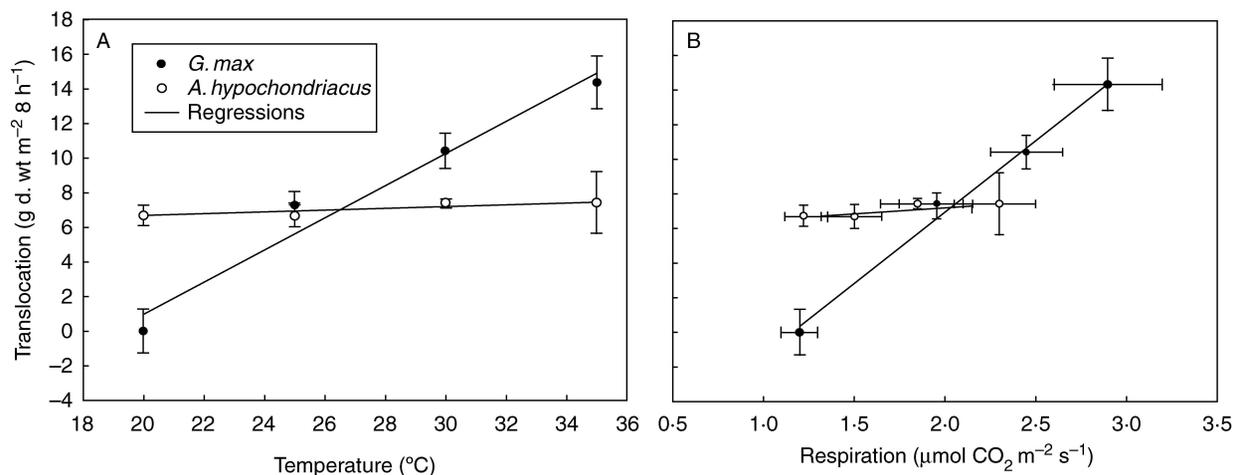


FIG. 2. (A) Responses of translocation rate over the whole dark period to temperature, and (B) relationships between translocation rate and mean respiration rate for the same temperature treatments, for leaves of *Glycine max* and *Amaranthus hypochondriacus*. In *G. max*, the linear regression of translocation rate on temperature had the equation: $\text{translocation} = -17.3 + 0.92 \times \text{temperature}$, with $r^2 = 0.96$, and the regression of translocation rate on respiration rate had the equation: $\text{translocation} = -9.6 + 8.3 \times \text{respiration}$, with $r^2 = 0.99$. Regressions for *A. hypochondriacus* were not significant. Error bars are s.e. for $n = 3$ or 4.

TABLE 2. Rates of translocation and respiration averaged over the whole 8-h night in leaves of *Glycine max* and *Amaranthus hypochondriacus* grown and measured at different temperatures

Species	Temperature (°C)		Translocation (g m ⁻² 8 h ⁻¹)	Respiration (μmol m ⁻² s ⁻¹)
	Growth	Measurement		
<i>G. max</i>	25	20	0.0 ^d	1.2 ^d
	25	25	7.3 ^c	1.9 ^c
	25	30	10.5 ^b	2.5 ^b
	25	35	14.3 ^a	2.9 ^a
	20	20	5.7 ^c	1.7 ^c
	30	30	5.9 ^c	1.7 ^c
<i>A. hypochondriacus</i>	25	20	6.7 ^a	1.2 ^d
	25	25	6.7 ^a	1.5 ^c
	25	30	7.4 ^a	1.9 ^b
	25	35	7.4 ^a	2.3 ^a
	20	20	6.8 ^a	1.3 ^d
	30	30	7.2 ^a	1.9 ^b

Within a column and species, values followed by different letters were significantly different at $P = 0.05$ by Tukey's HSD test.

responses of respiration to higher growth temperature in both species. In amaranth, this was shown by the fact that there was no long-term acclimation of respiration to higher temperatures (Table 2). In soybean, leaves of plants grown and measured at 30 °C had lower rates of respiration than did leaves of plants grown at 25 °C but measured at 30 °C even at the beginning of the dark period, and their respiration rates did not decrease during the night (Table 1). The lack of decrease in respiration rate during the night suggests that substrate availability did not limit the respiration rate of leaves acclimated to 30 °C. Thus, after long-term exposure to 30 °C, there was no evidence that lack of substrate availability directly limited respiration in soybean leaves. It is also likely that an increase in substrate availability did not directly cause the increase in respiration at 20 °C in soybean after long-term exposure to that temperature. This is because leaves of plants grown at 25 °C and measured at 20 °C showed no decrease in respiration through the night, which could be attributed to a lack of substrate, i.e. substrate availability apparently was never low enough to limit respiration.

Absence of a direct effect of substrate availability on thermal acclimation of respiration does not rule out an indirect effect. This is often envisaged as an increase in substrate availability at low temperatures leading to increased protein content and photosynthetic capacity, and the reverse at high temperatures (Bunce, 1983). Such developmental changes are relatively slow, and complete acclimation can require synthesis of new leaves with different properties (Tjoelker *et al.*, 1999; Armstrong *et al.*, 2006). Our data for the thermal acclimation of respiration in soybean fit this pattern, as leaf photosynthetic capacity increased as temperature decreased over the experimental

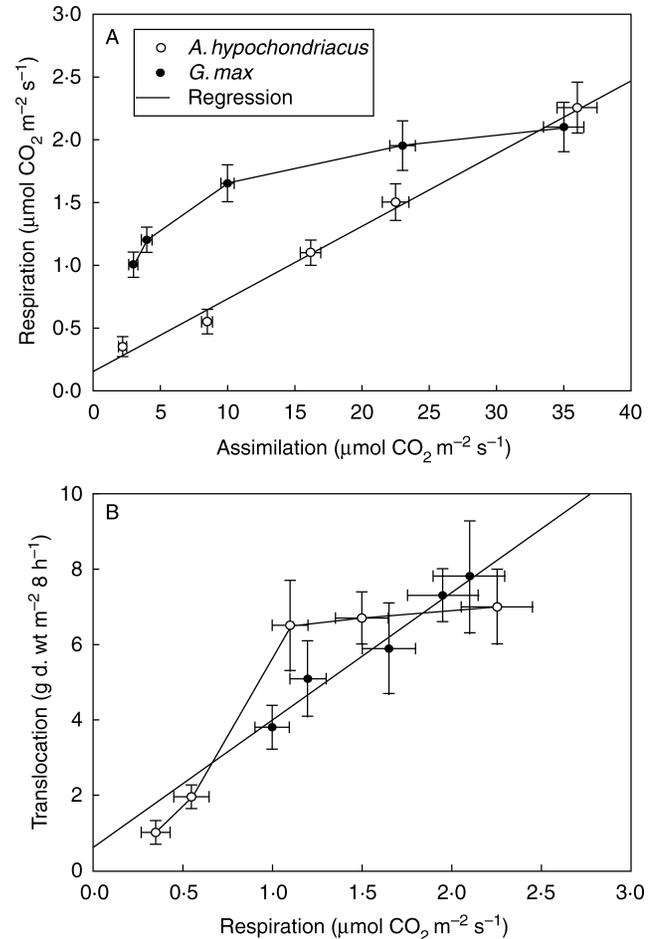


FIG. 3. Relationships between mean respiration rate over the whole dark period and mean photosynthetic assimilation rate of the previous day, and relationships between translocation rate and mean respiration rate for the same changes in assimilation rate, for leaves of *Glycine max* and *Amaranthus hypochondriacus*. In *A. hypochondriacus*, the linear regression of respiration on assimilation had the equation: respiration = $0.16 + 0.058 \times$ assimilation, with $r^2 = 0.99$. In *G. max*, the linear regression of translocation on respiration had the equation: translocation = $0.62 + 3.39 \times$ respiration, with $r^2 = 0.97$. Other lines are provided for clarity only. Error bars are s.e. for $n = 3$ or 4.

range used in the present study (Bunce, 1983). However, photosynthetic capacity also increased to a similar extent over this range of growth temperatures in amaranth (Bunce, 1983), but no acclimation of respiration occurred. This result contrasts with the correlation between the capacities of thermal acclimation of photosynthesis and respiration among *Plantago* species (Atkin *et al.*, 2006).

In soybean, exposure of plants grown at 25 °C to 20 °C for one night completely eliminated translocation during that night. However, complete acclimation of translocation to 20 °C occurred. In winter wheat brief exposure to low temperature also nearly eliminated translocation, and acclimation to the low temperature partially restored it (Leonardos *et al.*, 2003). It is unclear whether the acclimation of translocation rate depends entirely on acclimation of respiration, which also occurred in both

soybean and wheat, or whether other processes are also involved.

It is puzzling why translocation in amaranth was insensitive to temperature. Turgeon (2006) suggested that there may be some cases in which active transport of carbohydrates between photosynthetic cells and the phloem is not required, in which case the temperature sensitivity might be lower than normal. However, Fisher and Evert (1982) showed that active transport of sugars into the phloem did occur in a different species of *Amaranthus*, so this explanation is unlikely. Furthermore, in our measurements of translocation, the rest of the plant was at the same temperature as the leaf in which respiration was measured. While the unloading of assimilates from phloem may be passive, their utilization would be expected to be highly temperature-sensitive. Regardless, there seemed to be no feedback from the rest of the plant affecting translocation as temperature varied. The constant rate of translocation over a range of temperatures in amaranth occurred despite large changes in respiration. Apparently translocation was not limited by energy supplied by respiration over the range of respiration rates that resulted from these temperature treatments.

Griffin *et al.* (2002) and Atkin *et al.* (2001) found a larger relative decrease in leaf respiration at low temperature when whole shoots were exposed to the low temperature than when only leaves were exposed to it. They suggested that cooling the shoot reduced translocation from leaves, further reducing their respiration rate. This effect did not occur in the species studied here. We thought that a decrease in leaf respiration with phloem girdling could be used to estimate the respiratory costs of translocation. However, in the species used in the present study, there was no time of night when phloem girdling decreased leaf respiration, so that approach did not work. Relationships between translocation and respiration have been used by others to estimate the respiratory costs of translocation (Bouma *et al.*, 1995; Noguchi *et al.*, 2001). However, the linear relationships between translocation and respiration found here in soybean are probably not appropriate for estimating the respiratory costs of translocation because the changes in respiration were probably not exclusively due to changes in translocation.

Respiration did not change with photosynthesis in the preceding light period except at extremely low values of photosynthesis in soybean (Fig. 3). This is consistent with the lack of changes in respiration due to cloudy days or elevated carbon dioxide in upper canopy leaves of soybean under field conditions (Bunce, 2005). The decrease in respiration at the end of the night only at temperatures above 25 °C in soybean is also consistent with the lack of change in respiration during the night in this species under field conditions (Bunce, 2005). The data presented here suggest that respiration in amaranth would be more susceptible to limitations caused by low photosynthesis or high night temperatures than in soybean (Fig. 3), but I am not aware of field measurements for amaranth. For translocation, by contrast, the present data indicate that effects of night temperature and prior photosynthesis are much more likely to affect translocation of photosynthetic products

out of source leaves in soybean than in amaranth (Fig. 3). In amaranth, extremely low previous photosynthesis reduced both respiration and translocation, but it is uncertain whether low respiration rates limited translocation, whether low translocation rates reduced respiration rates, or whether both processes were limited by availability of substrates. Differences between species in responses of translocation to environment may affect the time lags between responses of respiration of leaves and whole plants to environmental changes (Hartley *et al.*, 2006). Studies of other species would be required to determine whether the contrasting responses of soybean and amaranth are related to photosynthetic pathway.

In conclusion, comparing the direct and acclimatory responses of respiration and translocation to temperature proved a useful approach. It showed that apparent short-term acclimation of respiration to high temperatures probably resulted from low substrate availability, which did not occur after long-term treatment. It also showed that although respiration and translocation are fundamentally linked energetically, they still diverged in their responses to temperature and to previous photosynthesis, as well as differing dramatically in response between species.

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