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The dependence of respiration on photosynthetic substrate supply and temperature: integrating leaf, soil and ecosystem measurements

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Abstract

Interactions between photosynthetic substrate supply and temperature in determining the rate of three respiration components (leaf, belowground and ecosystem respiration) were investigated within three environmentally controlled, *Populus deltoides* forest bays at Biosphere 2, Arizona. Over 2 months, the atmospheric CO_2 concentration and air temperature were manipulated to test the following hypotheses: (1) the responses of the three respiration components to changes in the rate of photosynthesis would differ both in speed and magnitude; (2) the temperature sensitivity of leaf and belowground respiration would increase in response to a rise in substrate availability; and, (3) at the ecosystem level, the ratio of respiration to photosynthesis would be conserved despite week-to-week changes in temperature. All three respiration rates responded to the CO_2 concentration-induced changes in photosynthesis. However, the proportional change in the rate of leaf respiration was more than twice that of belowground respiration and, when photosynthesis was reduced, was also more rapid. The results suggest that aboveground respiration plays a key role in the overall response of ecosystem respiration to short-term changes in canopy photosynthesis. The short-term temperature sensitivity of leaf respiration, measured within a single night, was found to be affected more by developmental conditions than photosynthetic substrate availability, as the Q_{10} was lower in leaves that developed at high CO_2, irrespective of substrate availability. However, the temperature sensitivity of belowground respiration, calculated between periods of differing air temperature, appeared to be positively correlated with photosynthetic substrate availability. At the ecosystem level, respiration and photosynthesis were positively correlated but the relationship was affected by temperature; for a given rate of daytime photosynthesis, the rate of respiration the following night was greater at 25 than 20 °C. This result suggests that net ecosystem exchange did not acclimate to temperature changes lasting up to 3 weeks. Overall, the results of this study demonstrate that the three respiration terms differ in their dependence on photosynthesis and that, short- and medium-term changes in temperature may affect net carbon storage in terrestrial ecosystems.

Keywords: belowground respiration, ecosystem respiration, ecosystem warming, elevated CO_2, leaf respiration, photosynthesis, *Populus deltoides*, Q_{10}, soil respiration, substrate availability

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Introduction

Only approximately 45% of the CO_2 released by man's activities has ended up in the atmosphere and it is believed that increased photosynthesis in terrestrial

ecosystems has absorbed a large proportion of the remaining emissions (Houghton *et al*., 1998; IPCC, 2001). In addition, terrestrial ecosystems have large stores of carbon, especially in soils, which are potentially vulnerable to temperature changes (Cox *et al*., 2000; Bellamy *et al*., 2005). Understanding whether terrestrial ecosystems will continue to absorb carbon via photosynthesis, or start to release carbon via temperature-mediated increases in respiration, is of critical importance in determining the rate of global warming over coming decades. Fundamental to achieving such an understanding, is determining the extent to which ecosystem respiration fluxes are dependent on carbon input from photosynthesis and/or dependent on the surrounding temperature.

There is growing evidence of a strong linkage between plant respiration and photosynthesis, not only in individual leaves (Dewar *et al*., 1999; Loveys *et al*., 2003), but also in roots (Fitter *et al*., 1998) and whole plants (Gifford, 1995). For example, rates of night-time leaf respiration have been shown to be highly dependent on total photosynthesis the previous day, demonstrating a rapid link between photosynthesis and leaf respiration (Whitehead *et al*., 2004). Also, the ratio of respiration to photosynthesis is often conserved across species and environmental gradients, both in individual leaves (Loveys *et al*., 2003) and whole plants (Gifford, 2003). In addition, strong links between photosynthesis and leaf respiration have previously been demonstrated in the experimental facility chosen for this study (Griffin *et al*., 2002; Turnbull *et al*., 2004). However, growth under elevated CO_2, while increasing photosynthesis, does not always result in large increases in leaf respiration (Griffin *et al*., 2001b; Davey *et al*., 2004; Gonzalez-Meler *et al*., 2004). This suggests that, at least at the leaf level, the ratio of photosynthesis to respiration is not always constant and may be altered as atmospheric CO_2 concentrations increase.

There is also increasing evidence for the dependence of belowground respiration on recent photosynthesis. Tree-girdling studies (Högberg *et al*., 2001; Bhupinderpal-Singh *et al*., 2003), shading and clipping experiments (Craine *et al*., 1999), isotopic studies (Kuzyakov & Cheng, 2001; Ekblad *et al*., 2005) and correlations between respiration and photosynthesis among different forest sites (Janssens *et al*., 2001), have all been cited as evidence for primary productivity being the main driver of belowground respiration. However, doubts remain as to the extent to which primary productivity controls above- and belowground respiratory CO_2 release and the speed of the link between respiration and photosynthesis.

If a respiration term responds strongly and rapidly to a change in photosynthesis then it might be expected that abiotic factors, such as temperature, may have less of a role to play in controlling its rate in the longer term. Conversely, in the case of a weak and slow response, the opposite may be true. Attempts have been made to use natural $\delta^{13}C$ variation caused by fluctuations in the air relative humidity to calculate the speed of link between photosynthesis and belowground respiration (Ekblad & Högberg, 2001; Barbour *et al*., 2005; Ekblad *et al*., 2005); such studies have suggested that the rate of photosynthesis over the previous 1–6 days is important in determining the rate of belowground respiration. However, these results are purely correlative as photosynthesis was not directly manipulated, and differences in the responses to increasing and decreasing photosynthesis have not been compared. Also, little attempt has been made to investigate whether above- or belowground respiration dominates the response of ecosystem respiration to short-term fluctuations in the rate of photosynthesis. The relative importance of photosynthesis in controlling the rates of leaf, belowground and ecosystem respiration and the degree to which these fluxes are buffered against short-term changes in photosynthesis requires further study.

The relationship between substrate provision by photosynthesis and the temperature sensitivity of the different respiration fluxes is also poorly understood. One hypothesis is that the temperature response of respiration will be dependent on substrate availability especially at high temperatures (Atkin & Tjoelker, 2003). In support of this, the addition of exogenous substrates to the roots of two *Plantago* species increased the temperature sensitivity of respiration (Covey-Crump *et al*., 2002). Therefore, respiration may become more temperature sensitive if photosynthetic activity increases in an elevated CO_2 world. However, Griffin *et al*. (2002) found a negative relationship between substrate availability and the temperature sensitivity of respiration when comparing leaves from different heights in a canopy. Moreover, below ground, the short-term temperature sensitivity of root-free soil respiration has been found to be insensitive to changes in substrate availability in an incubation study (Fang *et al*., 2005). Therefore, the hypothesis that increased substrate availability will increase the temperature sensitivity of respiration requires further testing at the leaf, the belowground system and the ecosystem level.

In terms of feedbacks to climate change it is the balance between respiration and photosynthesis that is most important. In the short term, plant respiration is considered to be more temperature sensitive than photosynthesis (Dewar *et al*., 1999). This has led to the popularly voiced notion that net primary productivity (NPP) may be reduced if global temperatures rise. However, plant respiration often acclimates to changing temperature regimes (Atkin & Tjoelker, 2003; Atkin *et al*., 2005), and this response may be mediated passively, through changes in substrate supply, or actively,

through changes in the enzymatic capacity of a cell. The latter often requires development of new tissue at the new temperature (Loveys *et al*., 2003; Armstrong *et al*., 2006). In some cases acclimation can result in the ratio between plant respiration and photosynthesis being maintained (Gifford, 1995; Gunderson *et al*., 2000; Loveys *et al*., 2003). Most studies of thermal acclimation have been conducted at the level of the leaf (Larigauderie & Körner, 1995; Tjoelker *et al*., 1999a, b; Atkin *et al*., 2000; Loveys *et al*., 2003), or the root (Covey-Crump *et al*., 2002; Loveys *et al*., 2003) and it is not known whether total ecosystem respiration (TER) will acclimate to maintain the balance between respiration and photosynthesis. At the ecosystem level, the response of soil respiration to changes in temperature may alter the balance between respiration and photosynthesis as there is little evidence for the active acclimation of microbial respiration in response to soil warming (Kirschbaum, 2004). Rather, the transient nature of soil temperature responses can be explained primarily by changes in substrate availability.

In this study, we investigated how photosynthetic substrate supply and temperature interact to determine the rate of respiration in poplar stands at the level of the leaf, the belowground system and the ecosystem. We tested the following hypotheses: (1) the responses of leaf, belowground and ecosystem respiration to changes in the rate of photosynthesis would differ both in their speed and magnitude; (2) increasing substrate provision by photosynthesis would increase the temperature sensitivity of the leaf and belowground respiration; and, (3) over the course of a few weeks, the ratio of respiration to photosynthesis, measured at the ecosystem level, would not be significantly altered by a 5 °C temperature transition. To test these hypotheses, we used the Intensive Forestry Biome (IFB) at Biosphere 2, Oracle, Arizona, USA. This facility provided the unique capability of allowing the atmospheric CO_2 concentrations and air temperatures in three large bays to be manipulated over the course of just a few hours. In addition, net ecosystem exchange (NEE) could be monitored without the need for turbulent air conditions (Barron-Gafford *et al*., 2005), which gave the facility a major advantage over eddy covariance techniques. By combining chamber measurements and NEE data with the experimental manipulations, hypotheses could be tested directly rather than relying on natural environmental fluctuations.

Materials and methods

Experimental Site

The IFB at Biosphere 2 consisted of three large bays (41 m × 18 m × 14 m) named after their relative positions (east, centre and west). Each of the bays had a soil area of ~550 m^2 and, as the soils were 1 m deep, a soil volume of 550 m^3. Within these bays, stands of eastern cottonwood trees (*Populus deltoides* Bartr.) were established at different atmospheric CO_2 concentrations for 4 years. During this time the east bay was held at 400 ppm, the central bay at 800 ppm and the west bay at 1200 ppm. For the duration of this study, there were 25 trees present in the east and west bays and 22 present in the centre bay (Barron-Gafford *et al*., 2005). The mean tree height in the east bay was 5.8 m but trees were on average 7.2 and 7.4 m tall in the centre and west bays, respectively. Although it would have been ideal to have had identical plant masses in the different bays (particularly when comparing *absolute* changes in ecosystem CO_2 flux), it was still possible to compare *relative* changes in ecosystem CO_2 flux brought about by changes in canopy photosynthesis. The soil was a mixture of 60% base soil and 40% organic matter and was texturally classified as a silt loam, with a ~28% sand, ~54% silt and ~17% clay content (Murthy *et al*., 2003; Barron-Gafford *et al*., 2005). The soils had an organic C content of 2.2–2.5% (Murthy *et al*., 2003) and there was evidence of soil C losses over the 4 years (Barron-Gafford *et al*., 2005). This may have been because all leaf litter was removed from the bays each month for inclusion in aboveground biomass measurements. Litter removal also resulted in the depletion of nutrients in the soil, especially in the upper 25 cm (Barron-Gafford *et al*., 2005).

Measurements were made on replicate trees and soil collars within these bays. While these measurements do not represent truly independent replicates, there is no more pseudo-replication in this study than in a study using replicate plants within a growth cabinet or controlled environment room. However, at the ecosystem level, fluxes were clearly not replicated. The unique opportunities that this facility provided in terms of the control of environmental conditions and the number of different flux measurements possible, justify the approach taken.

Treatments

Ecosystem CO_2 exchange was measured for 2 months during September and October 2003, while leaf and belowground respiration measurements took place during the 4 weeks between 15 September and 14 October. The atmospheric CO_2 concentration and temperature manipulations during this time are summarized in Fig. 1. Between these two dates there were five controlled night-time rain events which occurred on 15 September, 22 September, 29 September, 5 October

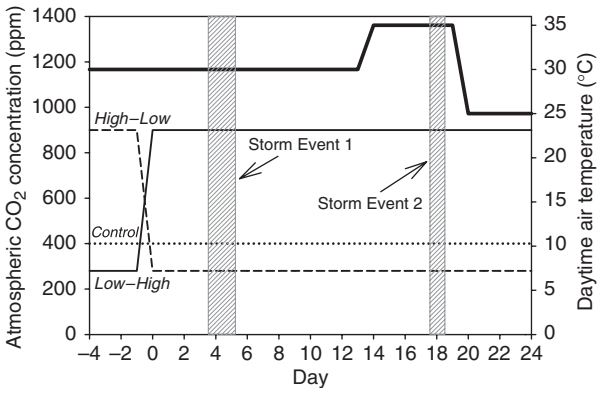

Fig. 1 The atmospheric CO_2 concentration and the air temperature maintained in the different bays over the 4 weeks between 15 September (day 4) and 14 October (day 25) during which time the leaf and belowground respiration measurements were made. The manipulation of the atmospheric CO_2 concentration in the *high–low* (– – – –), *control* (· · ·) and *low–high* (—) bays is displayed on the left-hand *y*-axis while the daytime air temperature (—) in the three bays is shown on the right-hand *y* axis. The days affected by the two storm events are enclosed in grey hashed boxes.

and 11 October. These were used to split these 4 weeks into five periods.

On the 3rd of September, 2 weeks before the start of leaf and belowground measurements, the atmospheric CO_2 concentrations in the three bays were reduced from the pretreatment levels. The reduction in the CO_2 concentrations was carried out to maximize the differences in the photosynthetic activity within the bays while working within a range of past and future atmosphere CO_2 concentrations. The concentration during daylight hours in the east bay was reduced from 400 to 280 ppm. This concentration represented preindustrial CO_2 levels and was applied in order to reduce photosynthesis and maximize the chances of respiration being substrate limited. The concentration in the central bay was reduced from 800 to 400 ppm to represent a level roughly equal to the current day atmospheric CO_2 concentration. In the west bay, the atmospheric concentration was reduced from 1200 to 900 ppm (a CO_2 concentration many model scenarios predict may be reached towards the end of this century; IPCC, 2001). On 19 September, the CO_2 concentrations in the east and west bays were then increased and decreased, respectively, with the east bay moving to 900 ppm and the west bay to 280 ppm (Fig. 1). These concentrations were then maintained until the end of leaf and belowground measurements on 15 October when they reverted back to 400 ppm in the east, 800 ppm in the centre and 1200 ppm in the west bay. Ecosystem exchange measurements were continued throughout. In the context of the leaf and belowground respiration measurements, the east bay will be referred to as the *low–high* bay, the centre bay as the *control* bay and the west bay as the *high–low* bay. In the following text and figures the date of the CO_2 concentration change, 19 October, will be referred to as day 0 with all other dates being numbered from this point.

Initially, the air temperature in each bay was maintained at 30 °C during the day and 25 °C at night (Fig. 1). To investigate whether changes in temperature altered the rates of the different respiration terms and the balance between photosynthesis and respiration at the ecosystem level, air temperature manipulations were carried out. From day 14, 3 October, the air temperature was increased to 35 °C in the day and 30 °C at night (35 °C period) before it was dropped on day 20, 9 October, to 25 °C during the day and 20 °C at night and maintained at this level for the rest of the month (25 °C period).

During this study, two tropical storms passed through Arizona. The first occurred on days 4 and 5, September 23–24, and the second on day 18, October 7, during the 35 °C treatment (Fig. 1). On both occasions, these storm events reduced the light intensity in the three bays by ~75% and therefore provided an opportunity to study the effects of a short-term change in the rate of photosynthesis on the three respiration terms.

Leaf measurements

Every 1–2 days, between 09:00 and 12:00 hours, light-saturated photosynthesis (A_{sat}) was measured on three leaves in the lower canopy in each bay using a portable infra-red gas analyser (model Li-Cor 6400, Li-Cor, Lincoln, NE, USA) at the ambient CO_2 concentration and with the light intensity inside the leaf cuvette set to 1500 μmol photons $m^{-2} s^{-1}$. The location of these measurements meant that these leaves were partially shaded.

Between each rain event (during each ~6 day period), the leaf respiration rate at the ambient stand temperature was measured on three nights (between 20:00 and 01:00 hours). Dark respiration was measured on the same leaves as were used for photosynthetic measurement during the day, using the Li-Cor 6400, with each leaf being measured two to three times during the 5 h (values shown represent the mean of the multiple measurements). Measurements did not commence until at least 1 h after darkness fell to avoid postillumination transients (Azcon-Bieto & Osmond, 1983; Atkin *et al*., 1998).

The rapid air temperature control possible in the IFB allowed the temperature of the entire canopy to be manipulated during the course of an evening. We could thus assess the effect of short-term changes in canopy

temperature on leaf metabolism (and therefore establish the short-term Q_{10} values of leaf respiration). On one night during each ~6 day period, between 20:00 and 22:00 hours, the respiration rate of each leaf was measured at a temperature 2 °C below the normal night-time temperature. The air temperature was then raised 6 °C and a further cycle of leaf respiration measurements carried out between 22:00 and 12:00 hours.

After the respiration measurements were completed, leaves were harvested and then submerged in liquid nitrogen before being stored at −80 °C. Subsequently they were freeze-dried under vacuum, ground and then the ethanol-soluble sugar fraction was analyzed enzymatically for glucose, fructose and sucrose, using an assay kit (Sigma, St Louis, MO, USA; see Loveys *et al*., 2003).

Belowground respiration measurements

A portable infrared gas analyser (model Li-Cor 6200, Li-Cor) was used to make measurements of belowground respiration at six long established, 10 cm diameter collars in each bay. The collars selected were approximately 1 m away from the trunk of the nearest tree. Measurements were made at each collar up to four times a day between 12:00 and 24:00 hours and the soil temperature at 3, 6 and 15 cm depths was recorded each time using the Li-Cor 6200's soil temperature probe.

Ecosystem flux measurements

The rates of CO_2 exchange in each bay were recorded and averaged every 15 min using an infrared gas analyser (model Li-Cor 6262, Li-Cor) connected to a datalogger. Corrections were applied to account for leaks and the CO_2 injected into the bays to maintain the required atmospheric CO_2 concentrations (Barron-Gafford *et al*., 2005). It was not possible to measure ecosystem respiration throughout the entire night as the bays were flushed with air to allow the CO_2 concentrations to be brought back down to the daytime targets. Therefore, night-time ecosystem respiration measurements were restricted to between 20:00 and 24:00 hours.

Soil incubations

Four trees were selected in each of the three bays. A 15 cm deep soil core was taken 1 m away from each tree using a corer with a diameter of 8 cm. The soil samples where then sieved through a 5 mm mesh and any remaining roots were removed with forceps. Each sample was then split into four ~270 g subsamples. Three were placed in 1.4 L containers with airtight seals (Lock&Lock®, New South Wales, Australia) and incubated at 20, 25 and 30 °C in incubators set to a humidity of 95% and a CO_2 concentration of 400 ppm. The final subsample was dried in an oven at 100 °C overnight and its moisture content calculated. These data were used to correct the moisture content in all of the incubated samples to 20%. The samples were watered each day to maintain a constant weight.

To calculate the rate of CO_2 production from the soils, the containers were closed for 3 h after 2, 5, 9 and 12 days of incubation. Gas samples were taken at time 0 and then again after 3 h. These samples were then injected into a rheodyne gas sampling valve fitted with a 1 mL sample loop inserted into the sample line of an infrared gas analyser (model Li-Cor 6400, Li-Cor) set to full CO_2 scrub. The heights of the peaks produced by each sample were logged and CO_2 concentrations calculated against 391 ppm standards. Headspace volumes were calculated and fluxes expressed as micrograms of C per gram dry mass of soil per hour ($\mu g\,C\,g\,DM^{-1}\,h^{-1}$). Soil samples were removed from each bay on four occasions and the same incubation procedure used each time. The results presented represent the mean of the four 12-day incubations for each tree in each bay.

Data Analysis

The fluxes were expressed per m^2 of leaf for the leaf photosynthesis and respiration measurements, per m^2 of soil for the belowground respiration measurements and per m^2 of the total bay area for the ecosystem photosynthesis and respiration measurements.

To standardize the effects of increasing vs. decreasing CO_2 concentrations, the responses of light-saturated photosynthesis, stand-level photosynthesis and the three different respiration terms were expressed in the following way:

$$(\text{high } [CO_2] \text{ rate} - \text{low } [CO_2] \text{ rate})/\text{high}[CO_2] \text{ rate}.$$

We have termed this parameter the 'ratio of change'.

Measurements were not made on days immediately following a rain event as fluxes were found to be greatly reduced. The rate of belowground respiration in the *control* bay was highly variable over the course of the experiment and the changes did not correlate with any of the variables that were measured. This pattern was also observed in the ecosystem exchange data, demonstrating that it was not just occurring at the soil collars. This variation prevented these collars being included in the CO_2 and temperature response analyses. Also, one collar in the *low–high* bay was not included in the analysis as water from the rain events failed to drain from inside this collar and thus diffusion may have been affected by high soil moisture. In the *low–high* bay, a large proportion of the daytime ecosystem

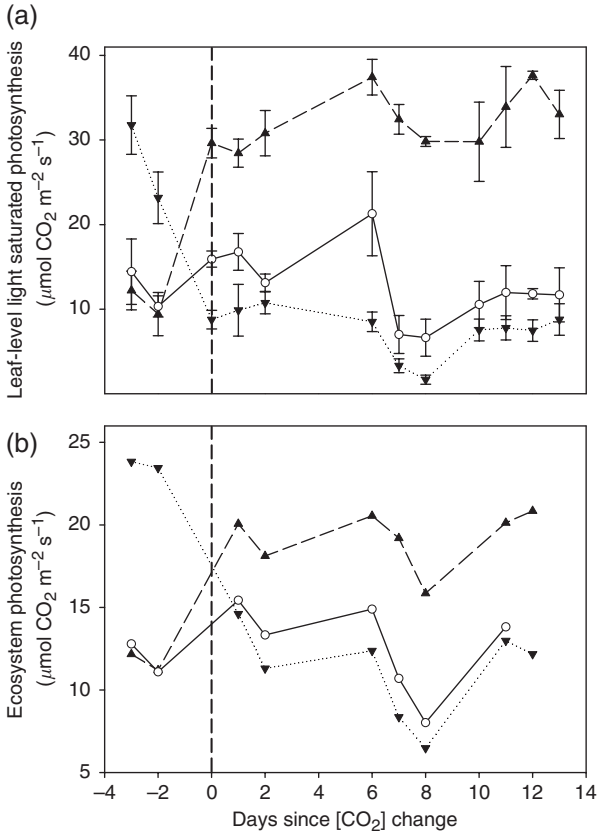

Fig. 2 The rate of (a) light-saturated photosynthesis (A_{sat}), measured on individual leaves with fluxes expressed per m^2 of leaf, between 9:00 and 12:00 hours, and (b) the daily maximal photosynthetic rate measured at the level of the ecosystem, with fluxes expressed per m^2 of total bay area, before and after the atmosphere CO_2 concentration changes (*low–high* bay –▲–, *control* bay —○—, *high–low* bay ···▼···). The dates shown represents the time during which air temperatures were maintained at 30 °C during the day and 25 °C at night. Days 4 and 5 were affected by the first storm event and were therefore not included in the figure. The CO_2 concentrations were changed on 19 September 2003. Error bars shown represent ±1SE ($n = 3$).

exchange data had to be discarded. Even with modelling and interpolation, a low confidence was associated with mean daytime exchange measurements from this bay. For this reason when between-bay comparisons were made, the maximum rate of photosynthesis observed in each bay was used, but not when the relationship between respiration and photosynthesis was investigated within the *control* or *high–low* bays. In the *high–low* and *control* bays, the mean difference between the maximum rate of ecosystem photosynthesis and the average rate measured between 10:00 and 14:00 hours was only ~18% and the rate of photosynthesis was relatively constant between these hours.

At the ecosystem level, the rate of photosynthesis was calculated by subtracting the night-time rate of respiration (measured between 20:00 and 12:00 hours) from the positive daytime flux. Ideally, such calculations should take into account light inhibition of leaf respiration (Atkin *et al*., 1998) and the effects of the reduced night temperature on the rate of respiration. However, belowground respiration correlated poorly with temperature over the course of a day and therefore applying a temperature function to respiration may have resulted in an overestimation of photosynthesis. Given the high photosynthetic rates exhibited by the poplar leaves (see Fig. 2), it is believed that light inhibition of leaf respiration was unlikely to have had a significant impact on estimates of daily photosynthesis.

Statistical analyses were carried out using SPSS 11 (SPSS Science, Birmingham, UK). ANOVAs and repeated measures ANOVAs were used to determine whether the atmospheric CO_2 concentration shifts significantly altered the rates of the different photosynthesis and respiration terms. One-sample *t*-tests were used to investigate whether the changes in the rate of leaf and belowground respiration were significantly different from 0. Independent sample *t*-tests were used to investigate the effect of changing the atmospheric CO_2 concentration on the overall ecosystem exchange between 12:00 and 24:00 hours in each bay with the days before and after the CO_2 concentration change considered as independent groups. Differences in the Q_{10}'s of leaf respiration between bays were analyzed using one-way ANOVAs. Linear regressions were used to investigate the relationship between the rate and temperature sensitivity of belowground respiration and the relationship between ecosystem photosynthesis and night-time ecosystem respiration. For the latter, the *F*-ratio method (Sokal & Rohlf, 1981) was used to investigate whether the relationship between ecosystem photosynthesis and night-time ecosystem respiration differed between nights with temperatures of 25 or 20 °C. To analyze whether the respiration rates of the cores taken from the different bays differed significantly, one-way ANOVAs within an incubation temperature were carried out.

Results

Atmospheric CO_2 concentration

The rate of photosynthesis, measured both at the leaf and ecosystem level, was significantly affected by altering the atmospheric CO_2 concentration (Fig. 2). The proportional change in the rate of photosynthesis was similar in both the increasing and decreasing CO_2 treatments (Table 1). However, light-saturated photosynthesis measured at the leaf level, appeared to be more responsive than stand-level photosynthesis.

All the respiration fluxes responded significantly to the changes in the rate of photosynthesis (Fig. 3). The responses can be considered both in terms of their magnitude and their speed. The proportional changes associated with each respiration term were similar in both the increasing and decreasing atmospheric CO_2 concentration treatments (Table 1). However, over the two weeks immediately after the CO_2 concentration manipulations, the proportional change in the rate of leaf respiration was over twice the magnitude of the belowground respiration response (Table 1; Fig. 3). Although the CO_2 concentration manipulations altered the rate of leaf respiration, only small and statistically insignificant changes in the leaf soluble sugar contents were observed with mean sugar contents varying between 116 and 129 mg g DM^{-1}.

The changes observed in the rate of ecosystem respiration were less than the changes in the rate of whole stand photosynthesis (Table 1). Also, decreasing the CO_2 concentration in the *high–low* bay significantly reduced the overall rate of CO_2 uptake within the ecosystem between 12:00 and 24:00 hours ($P = 0.024$). These results suggest that some of the additional carbon fixed at high atmospheric CO_2 concentrations may have been sequestered.

There were also differences in the time course of the response of the different respiration fluxes to the CO_2-induced changes in the rate of photosynthesis. This can be seen when the respiration responses were standardized by plotting them as a percentage of the maximum change observed over the 2 weeks immediately after the CO_2 concentrations were changed (Fig. 4). When the CO_2 concentration was decreased, while changes in the rates of photosynthesis were almost immediate (Fig. 2), the rate of belowground respiration was not significantly altered 7 days after the CO_2 change (Fig. 4b). In contrast, ecosystem respiration and leaf respiration responded much more rapidly. However, the same pattern was not observed in response to the increasing CO_2 concentration (Fig. 4a). Although ecosystem respiration did respond more rapidly than belowground respiration, the response of leaf respiration in the *low–high* bay was initially slow and variable (Fig. 4a). Belowground respiration responded more rapidly to the increasing CO_2 concentration in the *low–high* bay than to the decreasing CO_2 concentration in the *high–low* bay, while the opposite pattern was observed for leaf respiration (Fig. 4a and b).

Tropical storm events

To provide an insight into how a change in the light intensity affected the respiration terms investigated

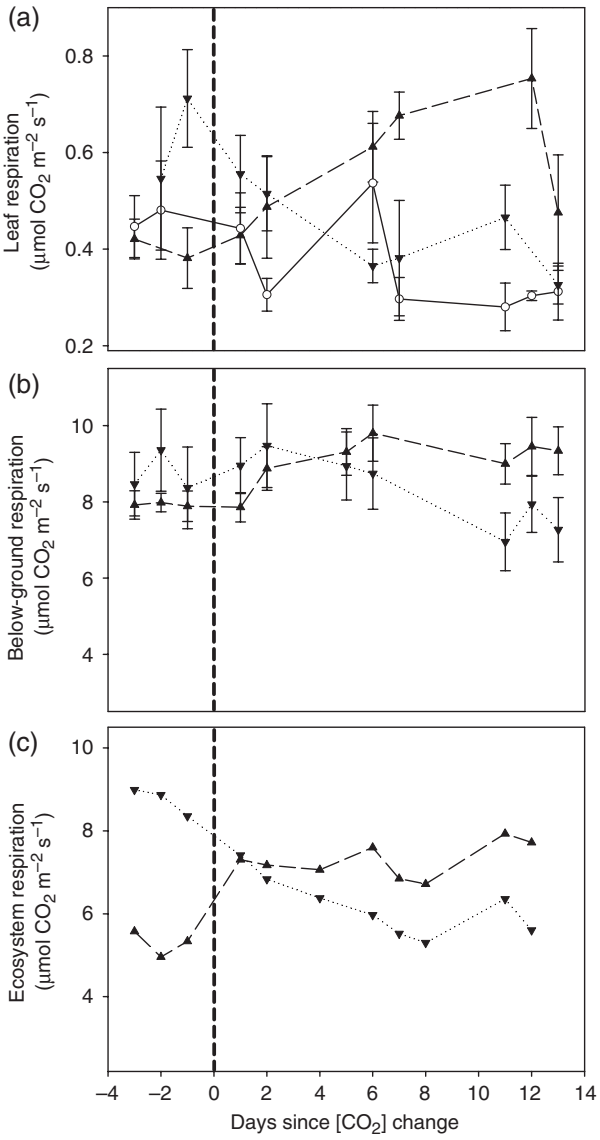

Fig. 3 The rates of (a) night-time leaf respiration, expressed per m^2 of leaf, measured between 20:00 and 24:00 hours, (b) average daily belowground respiration, expressed per m^2 of soil, measured between 12:00 and 24:00 hours and (c) night-time ecosystem respiration, expressed per m^2 of the total bay area, measured between 20:00 and 12:00 hours, before and after the atmosphere CO_2 concentration changes (*low–high* bay – –▲– –, *control* bay — ○ —, *high–low* bay ⋯ ▼ ⋯). The dates shown represents the time during which air temperatures were maintained at 30 °C during the day and 25 °C at night. Belowground respiration and ecosystem respiration were unstable in the *control* bay and not included in the figure (see 'Data Analysis'). Leaf respiration on days 4 and 5 was reduced by the first storm event and therefore these days were not included in the figure. The CO_2 concentrations were changed on 19 September 2003. Error bars shown represent ±1SE ($n = 3$ for leaf respiration, $n = 5$ for *low–high* belowground respiration, $n = 6$ for *high–low* belowground respiration).

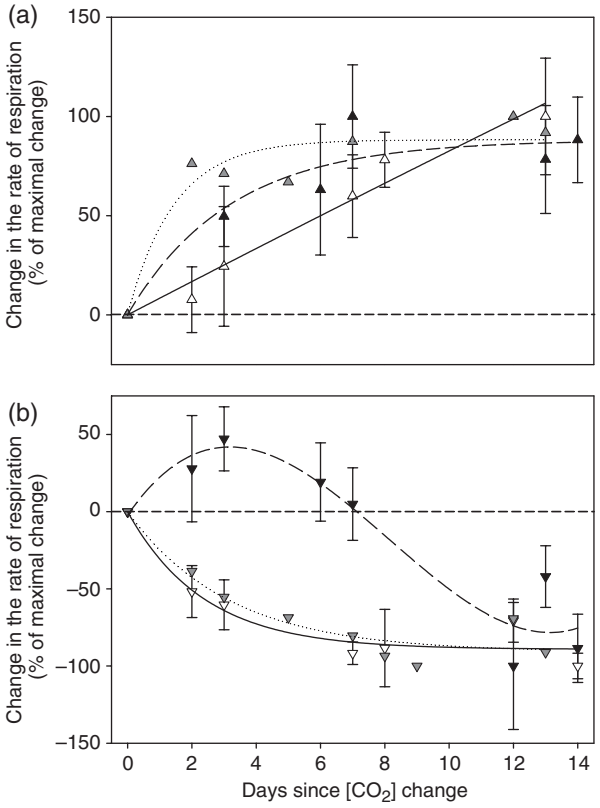

Fig. 4 The time course with which the different respiration fluxes responded to the changes in CO_2 concentration in (a) the *low–high* bay (belowground respiration −−▲−−, leaf respiration —△—, ecosystem respiration ···▲···) and (b) the *high–low* bay (belowground respiration —▼—, leaf respiration —∇—, ecosystem respiration ···▽···). The changes were normalized by expressing them as a percentage of the maximal change for each respiration response. The regression relationships that best fitted the measured changes were all exponential rises to a maximum except in case of leaf respiration *low–high* (the curve that best fitted this data was a linear relationship) and belowground respiration *high–low* (the curve that best fitted this data was a cubic relationship). Error bars on the leaf and belowground measurements represent ±1SE ($n = 3$ for leaf respiration, $n = 5$ for belowground respiration in (a), $n = 6$ for belowground respiration in (b)).

(i.e., ecosystem, belowground and leaf respiration), the responses to the two storm events were averaged. Although no significant reduction in the rate of belowground respiration was caused by the storm events, leaf respiration declined by on average ~40% (Table 2). In addition, belowground respiration rates on the 2 days immediately after each storm event were on average 5% higher than on the day immediately before each storm event. This demonstrates that the difference in the responses of leaf and belowground respiration was not due to a time delay in the response of belowground respiration.

The temperature response of the leaf and belowground respiration

The short-term Q_{10} of leaf respiration was substantially lower in the leaves that had developed at high CO_2 (*high–low* bay) than those that had developed at low CO_2 (Table 3). Shifting the CO_2 concentrations made no difference to this relationship, with the current CO_2 level apparently having no effect. After the CO_2 concentration change, the short-term Q_{10} of leaf respiration in the *high–low* bay remained lower than in the other two bays and this difference was statistically significant (Table 3, $P = 0.013$). The high standard deviation observed in the *low–high* bay before the CO_2 concentration switch probably reflects the fact that fluxes were very low and small measurement errors have major effects on the calculation of a Q_{10} (Table 3).

As it was not possible to calculate a short-term Q_{10} for belowground respiration over the course of a single day, the response of belowground respiration to changing the air temperature between the 35 and 25 °C periods was investigated (longer-term Q_{10}). Overall, belowground respiration in the *low–high* and *high–low* bays responded with a relatively low longer-term Q_{10} (overall average Q_{10}: 1.42, *low–high* bay Q_{10}: 1.47, *high–low* bay Q_{10}: 1.36). However, perhaps indicating a role of substrate availability, a positive relationship was observed between the rate of belowground respiration immediately before the temperature manipulations and the between-period, longer-term Q_{10} values (Fig. 5).

Over the course of a day, the rate of belowground respiration correlated poorly with soil temperature. On average, almost no change in the rate of belowground respiration was observed over the course of the day. For example, despite soil temperature at a depth of 3 cm changing by over 4 °C, a maximum change of less than 0.25 μmol $CO_2\,m^{-2}\,s^{-1}$ (less than 3%) in the rate of belowground respiration was observed in the *high–low* bay before the CO_2 concentration changes. Over the course of a day, the soil temperature at 15 cm generally changed by <1 °C.

Laboratory incubation of the soils

Soil taken from all three bays and incubated in the laboratory responded to temperature with a Q_{10} of ~3 (3.02 ± 0.09). There were no significant differences in the Q_{10}'s between bays. In addition, there were relatively few significant differences between the three bays in terms of the rates of soil respiration. After 2 days of incubation, soil respiration was significantly higher in the historically high CO_2 (1200 ppm) bay than the historically low CO_2 (400 ppm) bay, both in the samples incubated at 25 and at 30 °C ($P = 0.024$ and $P = 0.021$,

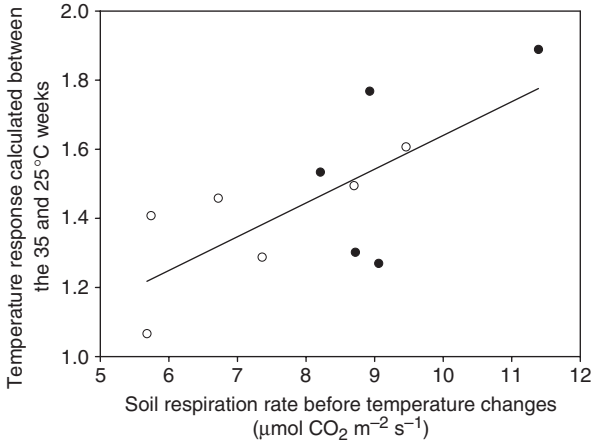

Fig. 5 The relationship between the average belowground respiration rate, measured during the final period at 30 °C, and the temperature response calculated between the average rates measured during the 35 and 25 °C periods. The temperature response is standardized to a 10 °C change in temperature based on the measured change in soil temperature between the two periods at each collar (i.e., is expressed as a between-period, longer-term Q_{10}). Only days 2, 3 and 4 after a rain event are included in the calculation. The figure includes collars from the *low–high* bay (•) and the *high–low* bay (○).

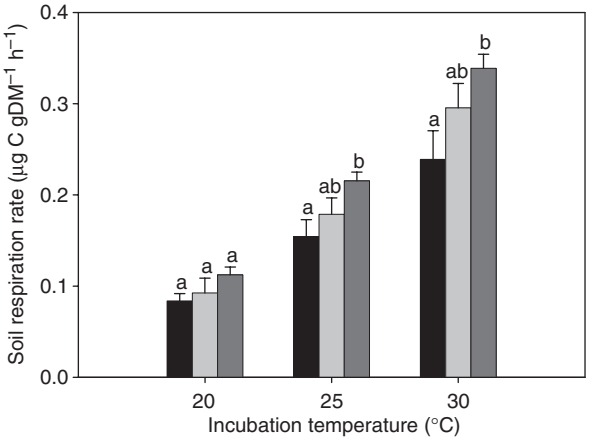

Fig. 6 The rates of root-free soil respiration in the samples removed from the three bays and incubated at the three different temperatures. These results represent the rate of respiration measured 2 days into the incubation. Bays are labeled by their historical CO_2 concentrations of 400 ppm (■), 800 ppm (■) and 1200 ppm (■). Within an incubation temperature, bars labeled with the same letter do not differ significantly. Error bars represent 1SE ($n = 4$).

respectively; Fig. 6). However, the difference between these two bays was not statistically significant after 5 days of incubation ($P > 0.05$).

Temperature effects on the relationship between respiration and photosynthesis at the ecosystem level

A strong positive correlation between the rate of ecosystem respiration measured during the night and the rate of photosynthesis the previous day was observed. This relationship was observed in both the *high–low* ($P < 0.001$) and *low–high* ($P < 0.001$) bays but was especially clear in the *high–low* bay (Fig. 7). However, the nature of this relationship was altered by temperature. For a specific rate of photosynthesis, the rate of ecosystem respiration was significantly higher during nights with a temperature of 25 °C as compared with nights with a temperature of 20 °C (*high–low* bay, *F*-ratio method: $F_{(2, 48)} = 14.20$, $P < 0.001$; Fig. 7).

Discussion

The dependence of respiration on photosynthesis

The rate of respiration. Altering the atmospheric CO_2 concentration in the two bays demonstrated that leaf, belowground and ecosystem respiration were all dependent on the recent rate of photosynthesis (Fig. 3). This result is in agreement with studies that have identified strong links between photosynthesis and leaf respiration (Gifford, 2003; Loveys *et al*., 2003; Whitehead *et al*., 2004) and photosynthesis and belowground respiration (Fitter *et al*., 1998; Craine *et al*., 1999; Ekblad *et al*., 2005). However, the proportional change in the rate of leaf respiration response was ~2.5 times that of the belowground respiration response (Table 1). Although it was not possible to make a direct statistical comparison between these two responses, such a large difference strongly implies that leaf respiration is more dependent on photosynthesis than belowground respiration. In addition, the relative responses of the leaf and belowground were very consistent in both the increasing and decreasing CO_2 concentration treatments (Table 1). It appears that, in the forest mesocosms at Biosphere 2, aboveground respiration plays a key role in the response of TER to short-term changes in the rate of photosynthesis.

As belowground respiration often contributes 70% of TER in forests (Janssens *et al*., 2001), it was expected that the response of ecosystem respiration would reflect the belowground response more than the leaf respiration response. However, this did not appear to be the case (Table 1). As leaf litter inputs were excluded in soils at Biosphere 2, belowground respiration may contribute less to TER than in a natural system. However, the rate of belowground respiration measured at the selected collars was actually higher than the rate of TER. The

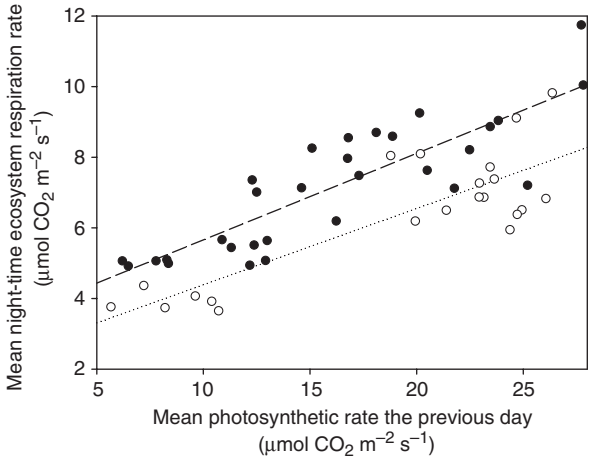

Fig. 7 The relationship between mean ecosystem level photosynthesis measured between 10:00 and 14:00 hours and the rate of ecosystem respiration, measured between 20:00 and 12:00 hours the following night in the *high–low* bay. Both fluxes are expressed per m^2 of total bay area. The figure shows all days between 1 September 2003 and 30 October 2003. However, it excludes the 6 day 35/30 °C period. The remaining data is split into nights with a temperature of 20 °C (··· ○ ···) and nights with a temperature of 25 °C (–– ● ––). Linear regressions were fitted to each data subset and there was a significant difference between the two regressions ($P < 0.001$).

Table 1 The effect of changing the atmospheric CO_2 concentration on the rates of whole stand photosynthesis measured between 10:00 and 14:00 hours, light-saturated photosynthesis (A_{sat}) measured between 09:00 and 12:00 hours, night-time ecosystem respiration measured between 20:00 and 24:00 hours, night-time leaf respiration measured between 20:00 and 24:00 hours and average daily belowground respiration measured between 12:00 and 24:00 hours

	Ratio of change				
	Photosynthesis		Respiration		
Treatment	Stand	A_{sat}	Ecosystem	Leaf	Belowground
Low–high	0.46	0.69	0.32	0.35	0.14
High–low	0.41	0.71	0.32	0.37	0.15

The changes are expressed as 'ratios of change' ((high $[CO_2]$ rate – low $[CO_2]$ rate)/high $[CO_2]$ rate) calculated between the rates measured on days −3 to 1 (just before the CO_2 concentration change) and the rates measured on days 11–13. These dates were 2, 3, and 4 days after a rain event.

study of Barron-Gafford *et al*. (2005) also observed that belowground respiration was higher than TER. Given that the *low–high* and *high–low* bays contained 25 trees and that belowground respiration rates were measured 1 m away from the nearest tree, these rates were probably indicative of CO_2 production in 75–100 m^2 of soil. As mentioned above, each bay contained ~550 m^2 of soil, and therefore belowground respiration measurements made in this study were probably only representative of the rates occurring in <20% of the total soil area. In a previous study undertaken in the same macrocosms, soil respiration rates measured in areas in which roots were not present were only 2–3 $\mu mol\, CO_2\, m^{-2}\, s^{-1}$ (Barron-Gafford *et al*., 2005). Therefore the location of the belowground respiration measurements probably explains the high respiration rates. However, even if the mean contribution of belowground respiration to TER was lower than in natural systems, it would have had to only contribute ~20% of TER to account for the similarity of the leaf and ecosystem respiration responses (Table 1). A more likely explanation is that the leaves measured in this experiment were not representative of the entire canopy. Photosynthesis in the lower canopy may have been limited by light as well as atmospheric CO_2 concentration and therefore respiration in these leaves may have responded less than more illuminated leaves in the upper canopy. At Biosphere 2, it has been shown that *P. deltoides* leaves in the upper canopy have higher respiration rates than leaves lower down (Griffin *et al*., 2002). In addition, shading in the mid and lower canopy may explain why the response of light-saturated photosynthesis measured at the leaf level was greater than that of photosynthesis measured at the level of the entire stand (Table 1).

In summary, the results suggest that, in Biosphere 2 leaf respiration is more dependent on substrate supply from photosynthesis than is belowground respiration. By measuring leaves in the lower canopy and belowground respiration only 1 m from the nearest tree, overall leaf respiration responses may have been underestimated and overall belowground respiration responses overestimated. The dependence of aboveground respiration on the rate of photosynthesis probably places a strong constraint on its ability to respond positively to increasing temperatures in the long term. On the other hand, there may be potentially more role for abiotic factors, such as temperature, in controlling the rate of belowground respiration in the longer term.

Speed of the link between respiration and photosynthesis

When the rate of photosynthesis was declining, both in response to the CO_2 concentration manipulations and the two storm events, leaf respiration appeared to respond much more rapidly than belowground respiration (Fig. 4b and Table 2). Seven days after the CO_2

Table 2 The effect of the two storm events on the rates of the three respiration fluxes

	Low–high			*High–low*		
	Respiration rate			Respiration rate		
	Unshaded day	Shaded day	% change	Unshaded day	Shaded day	% change
Leaf	0.65 ± 0.10	0.40 ± 0.03	−41.78	0.44 ± 0.05	0.23 ± 005	−48.34
Ecosytem	7.98	7.69	−4.07	6.62	6.60	−0.31
Belowground	10.27	10.05	−0.00 ± 2.16	8.66	8.84	2.10 ± 1.40

Average rates of respiration ($\mu mol\, CO_2\, m^{-2}\, s^{-1}$) measured on the nonshaded days immediately before and after the storm event and the average rates on the shaded days are shown. These were then used to calculate a percentage change in the rate of respiration The effects of the two storm events in the *low–high* and *high–low* bays were averaged. The mean values and, where possible, ±1SE (leaf respiration $n = 3$, belowground respiration *low–high* $n = 5$, *high–low* $n = 6$) are shown.

concentration change, belowground respiration had not significantly declined in the *high–low* bay, while leaf respiration had declined by ~40% (Fig. 3) and stabilized (Fig. 4). In addition, the storm events reduced leaf respiration by ~40% but did not affect belowground respiration. These results contrast with a 27–37% drop in the rate of belowground respiration observed 5 days after girdling in an evergreen coniferous forest in Sweden (Högberg *et al*., 2001). The lack of agreement may have been caused by differences in the extent to which carbohydrate stores in the roots buffer respiration against short-term changes in photosynthesis. Alternatively, the ability of roots to demand substrates from shoots, even when photosynthesis is low (Farrar & Jones, 2000), may have been reduced due to the cutting of phloem tissue in the girdling experiment. Invasive experimental procedures, such as girdling, may introduce artefacts, which mask the true dependence of fluxes on photosynthesis in the short term.

Different patterns of gas exchange were observed when the CO_2 concentration was increased; here, belowground respiration responded more rapidly than did leaf respiration (Fig. 4a). The initial response of leaf respiration was highly variable so care should be taken not to overinterpret this result. Nevertheless, it is possible that in the short term leaf respiration was not limited by substrate supply and respiration rates did not increase until respiratory capacity increased (Atkin *et al*., 2005). Belowground respiration appeared to respond much more rapidly to increasing rather than decreasing rates of photosynthesis. Plant responses under elevated CO_2 may be limited by nutrient availability (Oren *et al*., 2001; Johnson, 2006; Reich *et al*., 2006), and nutrient depletion has been identified in these macrocosms (Barron-Gafford *et al*., 2005). Additional carbon fixed under elevated CO_2 may have been rapidly allocated below ground to roots, mycorrhizas and rhizosphere microorganisms to promote nutrient uptake and so increase respiration (Heath *et al*., 2005).

To our knowledge, no study has previously investigated the speed of the links between primary productivity and leaf, belowground and ecosystem respiration by manipulating photosynthesis in whole forest stands. Previous studies have suggested that the speed of the link between photosynthesis and respiration is likely to be rapid in leaves (Whitehead *et al*., 2004). Our data confirms that leaf respiration is dependent on photosynthesis over the previous 1–2 days (Fig. 4b and Table 2), but suggests that this may only be the case when photosynthetic rates are declining. Only broad estimates have been produced for the speed of the link between belowground respiration and photosynthesis. Isotopic studies have demonstrated that photosynthesis in the preceding 1–6 days has a major effect on belowground respiration (Ekblad & Högberg, 2001; Ekblad *et al*., 2005). Our study suggests that the speed of the response of belowground respiration to changes in photosynthesis differs between when photosynthesis was increasing compared with when it was decreasing.

Substrate availability and the temperature sensitivity of respiration

We hypothesized that the high CO_2 concentration would increase photosynthesis, and therefore the soluble sugar content of the leaves, which in turn would increase the short-term temperature sensitivity of leaf respiration. However, although the switches in atmospheric CO_2 concentration (Fig. 1) had a strong effect on the rate of leaf respiration (Fig. 2), they had no effect on the short-term temperature sensitivity of leaf respiration (Table 3). For our hypothesis to have been supported the enzymatic capacity and adenylate supply would have had to have been largely unaltered by the CO_2 treatments (Atkin & Tjoelker, 2003); in such cases,

Table 3 Short-term Q_{10} values of leaf respiration measured in the *low–high* and *high–low* bays before and after the atmospheric CO_2 concentration switch

Bay	Q_{10} before [CO_2] switch	Q_{10} after [CO_2] switch
Low–high	3.93 ± 1.74	3.31 ± 1.27
Control		3.12 ± 0.87
High—low	2.08 ± 0.08	1.94 ± 0.67

The short-term Q_{10} was only measured in the *control* bay after the atmospheric CO_2 concentration switch. Means ± 1 SD are shown.

increased substrate availability may increase the temperature sensitivity of leaf respiration. One reason for the lack of a leaf short-term Q_{10} response may be that substrate concentrations were not sufficiently altered to impact on the short-term Q_{10} of leaf respiration; alternatively, mitochondrial capacity may have changed in response to the alterations in the atmospheric CO_2 concentration (Griffin *et al*., 2001a) and resultant changes in respiratory capacity may have masked any substrate-induced changes in the temperature sensitivity of respiration.

Both before and after the switches in atmospheric CO_2 concentration (Fig. 1), respiration in the leaves that developed at a CO_2 concentration of 1200 ppm was less temperature sensitive than respiration in the leaves that developed at 400 ppm (Table 3). In a study carried out on the same trees, Griffin *et al*. (2002) observed that the rate of leaf respiration increased with height in the canopy but became less temperature sensitive and a similar pattern was observed in a study of 18 deciduous tree species (Bolstad *et al*., 1999). When combined with our results, those of Griffin *et al*. (2002) suggest that, in *P. deltoides*, leaf development in conditions favorable for photosynthesis (high CO_2 or high irradiance) may have altered the phenotype of the leaves and resulted in leaf respiration becoming less sensitive to short-term changes in temperature. If this were to emerge as a general pattern, then it might be expected that plant respiration would become less, rather than more, temperature sensitive in a high CO_2 world. The mechanisms underlying this relationship require further investigation.

Unlike leaf respiration, the temperature sensitivity of belowground respiration could only be calculated between periods at different temperatures (longer-term Q_{10}) and not during a single day as no clear response of belowground respiration to within-day changes in soil temperatures was observed. This was probably due to the lack of a litter layer in this system which may have resulted in the most active soil layers at Biosphere 2 being deeper than in natural ecosystems; the soil temperature at a depth of 15 cm often changed by less than 1 °C during the course of a day. Overall, belowground respiration was relatively temperature insensitive (longer-term Q_{10} of 1.42). On average, root and rhizosphere respiration makes up ~50% of belowground respiration in forest ecosystems and this proportion may be even higher during the growing season (Hanson *et al*., 2000). At Biosphere 2, the removal of leaf litter may make belowground respiration even more dependent on root activity. This is emphasized by the large difference in the respiration rates measured in this study (7–10 μmol CO_2 m^{-2} s^{-1}) and the measurements of *in situ* root-free respiration rates (2–3 μmol CO_2 m^{-2} s^{-1}) made by Barron-Gafford *et al*. (2005). It appears that root and rhizosphere respiration may have contributed approximately 70% of total belowground respiration at the selected collars. Huang *et al*. (2005) demonstrated that root respiration may acclimate to a new soil temperature within 3 days which may explain the low longer-term Q_{10}'s observed. The low between-period temperature sensitivity of root respiration may also explain the difference between the long-term Q_{10}'s measured *in situ* and in the root-free soil incubation experiment (Q_{10} = 1.42 vs. Q_{10} = 3.02) and this demonstrates the dangers of applying temperature functions produced in laboratory incubation studies to intact systems. In addition, the carbohydrate content of these soils has been shown to be declining over time (Barron-Gafford *et al*., 2005) and substrate limitation in the rhizosphere may have reduced the temperature response of belowground respiration (Davidson *et al*., 2006). In the Biosphere 2 system, it appears that substrate availability limits the potential for root and rhizosphere respiration to respond positively to increasing temperatures. Overall, the low C content of the soils investigated in this experiment and the declining carbohydrate concentrations that have been observed (Barron-Gafford *et al*., 2005) suggest that this is a highly substrate limited system. Although the IFB may be indicative of conditions in forest plantations which have been established on agricultural land, it may not be appropriate to extrapolate the results presented here to all natural systems, especially those in which organically rich soils are present.

A positive correlation was observed between the rate and longer-term Q_{10} of belowground respiration (Fig. 5). The atmospheric CO_2 concentrations were switched before this relationship was observed. Therefore, this correlation was not simply caused by the differences in root biomass, as the pattern of belowground respiration was different before the shift. The relationship is more likely to have been caused by substrate input patterns controlling the ability of belowground respiration to sustain a positive temperature response between periods.

Relationship between respiration and photosynthesis at the ecosystem level: impacts of growth temperature

The IFB provided a unique opportunity to manipulate atmospheric CO_2 concentration and air temperature while monitoring total ecosystem exchange of a forest stand. To our knowledge no other study has been able to directly manipulate stand temperature and investigate the effect on the balance between ecosystem respiration and photosynthesis.

Measurements of stand level photosynthesis and ecosystem respiration were continued for 3 weeks following the reduction of air temperature to 25 °C in the day and 20 °C at night. It was hypothesized that the relationship between ecosystem respiration and photosynthesis would be relatively insensitive to changes in the temperature regime (Gifford, 1995; Dewar *et al*., 1999). However, for a given rate of daytime photosynthesis, the rate of respiration the following night was higher when the night-time bay temperature was 25 °C rather than 20 °C (Fig. 7). This agrees with the study by Turnbull *et al*. (2004) who noted that the rate of carbohydrate turnover in leaves increased with night-time air temperature. However, Turnbull *et al*. (2004) compared consecutive nights whereas the pattern in our study was apparent for a number of weeks. In contrast to our findings, other studies have observed that the relationship between canopy level respiration (Albrizio & Steduto, 2003) or NPP (Cheng *et al*., 2000) and photosynthesis is often conserved across a range of temperatures or photosynthetic rates.

There are a number of possible reasons for the ratio of photosynthesis to respiration, measured at the ecosystem level, not being maintained following the temperature transition. Three weeks may not have been long enough for maximum acclimation, as the development of new tissues had not occurred (Atkin & Tjoelker, 2003). Also, the measurements made in this study were made at the whole ecosystem rather than the plant level. In contrast to the belowground respiration measurements made 1 m from the nearest tree, given that there were only 25 trees present in the 550 m^2 of soil in each bay, the ecosystem exchange term would have also included bulk soil respiration in areas where root biomasses were low (Barron-Gafford *et al*., 2005). Soil respiration generally responds positively to increased temperature for a sustained period (Rustad *et al*., 2001; Kirschbaum, 2004; Eliasson *et al*., 2005) and the respiration of the incubated soil samples was highly temperature sensitive (Q_{10} of 3.02). Soil organic carbon has been found to be declining in this ecosystem (Trueman & Gonzalez-Meler, 2005) and the temperature transition may have affected the rate with which carbon was being lost from the soil system. In the IFB, the relatively low tree density and the lack of understory vegetation are not representative of most natural systems. Therefore these results are only indicative of the potential for the temperature response of belowground respiration, especially associated with soil organic matter turnover, to alter the balance between photosynthesis and respiration at the ecosystem level. Further investigation in more natural systems and longer-term measurements are required.

Conclusion

Our study has highlighted the major role that photosynthesis plays in determining the rates of leaf, belowground and ecosystem respiration. We have produced evidence to suggest that leaf respiration is more responsive than belowground respiration and may, in some conditions, dominate the response of ecosystem respiration to short-term changes in photosynthesis. These results also suggest that, in the long term, there may be a potentially greater role for temperature to play in regulating belowground rather than aboveground fluxes. In addition, highlighting previously unrecognized complexity, both leaf and belowground respiration appeared to respond differently to situations in which photosynthesis was either increasing or decreasing. At the leaf-level, no support was found for the hypothesis that increased photosynthesis would result in leaf respiration becoming more sensitive to short-term changes in temperature. Rather, it appears that development may play a key role in determining the temperature sensitivity of leaf respiration. However, below ground, a positive relationship was observed between the rate and longer-term temperature sensitivity of respiration, suggesting that substrate availability may, nevertheless, be important. While it was observed that photosynthesis plays a pivotal role in determining the rate of respiration, temperature altered the balance between photosynthesis and respiration at the ecosystem level, at least over the course of a number of weeks. Studies that investigate how the balance between respiration and photosynthesis at the whole ecosystem level changes with temperature in natural ecosystems are crucial for increasing our understanding of terrestrial C cycling.

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