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Leaf respiration is differentially affected by leaf vs. stand-level night-time warming

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Abstract

Plant respiration is an important physiological process in the global carbon cycle serving as a major carbon flux from the biosphere to the atmosphere. Respiration is sensitive to temperature providing a link between environmental variability, climate change and the global carbon cycle. We measured leaf respiration in *Populus deltoides* after manipulating the air temperature surrounding part of a single leaf, and compared this to the temperature response of the same leaves after manipulating the temperature of the stand. The short-term temperature response of respiration (Q_{10} – change in the respiration rate with a 10 °C increase in leaf temperature) was 1.7 when the leaf temperature was manipulated, but 2.1 when the stand-level temperature was changed. As a result, total night-time carbon release during the five-day experiment was 21% lower when using the Q_{10} estimates from the tradition leaf manipulation compared to the stand-level manipulation. We conclude that the temperature response of leaf respiration is related to whole plant carbon and energy demands, and that appropriate experimental procedures are required in examining respiratory CO_2 release under variable temperature conditions.

Keywords: Biosphere 2, *Populus deltoides*, Q_{10}, respiration, temperature

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Introduction

Plant respiration is highly sensitive to temperature with the temperature coefficient of the reaction or Q_{10} (change in the rate of a reaction with a 10 °C increase) varying between 1.4 and 4.0 (Azcón-Bieto & Osmond 1983). Accordingly, both short- and long-term variation in ambient air temperature can have profound effects on the carbon balance of natural ecosystems. Ecosystem modelers are well aware of the temperature response of respiration and draw from numerous gas-exchange measurements to parameterize their models (e.g. Foley 1994; Dewar *et al*. 1999; Melillo 1999). However, very little work has been done to verify that these leaf-level gas-exchange measurements are indicative of actual response to temperature fluctuations at the ecosystem scale. Until recently, experimentation at the proper spatial scale has been technically limited (Strain *et al*. 1991; Griffin *et al*. 1996).

It is predicted that global temperatures will increase 1–3.5 °C by the year 2100 (Hansen *et al*. 1988, 1999). Furthermore, global records reveal a warming trend that is more pronounced at night (Easterling *et al*. 1997; Alward *et al*. 1999; Hansen *et al*. 1999), stressing the importance of studying the effect of the minimum temperature as well as the diel temperature range. Warming could potentially increase the biological release of carbon to the atmosphere via plant respiration, which at the global scale currently accounts for as much as 60 GT C $year^{-1}$ (Amthor 1997). Ultimately, ecosystem function and carbon storage are affected as it is the relatively small difference between two large fluxes, net photosynthesis (~122 GT C $year^{-1}$) and total respiration

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(above and below ground ~120 GT C $year^{-1}$) that defines the primary productivity of ecosystems (Schimel 1995; Amthor 1997). Taken together, the predicted global warming and respiratory responses to temperature are compelling evidence of our need to be able to accurately quantify the interactions among temperature, plant respiration and ecosystem function.

Here we report the results of a stand-level warming experiment from the Biosphere 2 research facility in Oracle, Arizona. The two specific objectives of this communication are to illustrate the usefulness of large controlled-environment facilities for studying tree responses to climate change, and to test the hypothesis that leaf respiration would be more responsive to stand-level temperature fluctuations than to individual leaf-level manipulations. We took advantage of the technical innovations and size of the facility to regulate nighttime temperature of an intact stand of seventy, 4 m tall, one-year-old *Populus deltoides* trees. Both steady-state measurements of leaf respiration under the ambient temperature and short-term temperature-response curves were measured. The impacts of these results are considered by calculating the net effect on the total carbon exchange during the five nights of this experiment.

Materials and methods

Biosphere 2

Biosphere 2 covers 1.27 ha and is located 1200 m above sea level at 32.5 °N latitude in southern Arizona. This experiment was conducted in the 2000 m^2 forestry section, which is physically isolated from the remainder of Biosphere 2 and has independent climate and CO_2 control (Marino & Odum 1999). The total volume of this section, estimated by the injection of SF_6 as a trace gas, is 35222 m^3 (J. Van Haren, *pers. comm.*). The forestry section of Biosphere 2 has been further subdivided into three roughly equal bays with large plastic curtains. Each of the three bays is roughly 41 m long (in a north–south orientation) and 18 m wide, with a maximum height of 24 m. Each bay has three large air handlers, each capable of moving 566 m^3 min^{-1}. These air handlers provide both the primary means of air circulation and the temperature control. Within each bay, four additional fans help maintain the air circulation and break up the canopy boundary layer. The results presented in this communication are from the west bay which has an area of 543 m^2 and total air volume of 11 521 m^3.

Biosphere 2 is subjected to the light regimes of a temperate desert region. The glass and metal structural components act as a neutral density filter for incoming solar radiation. Photon flux density (PFD) was more than 70% of outside incident, with mid-day levels exceeding 1600 μmol m^{-2} s^{-1} and mean daily PFD levels of approximately 15 mol m^{-2} day^{-1} in the winter and 25 mol m^{-2} day^{-1} in the summer. Virtually all UV radiation is blocked. During daylight hours, CO_2 control within each bay is maintained by adding pure CO_2 with a mass flow meter (Sierra Side-Track, Sierra Instruments Inc., Monterey, CA, USA) into the air handlers to mass balance for the carbon removed from the atmosphere by photosynthesis. Whenever respiratory CO_2 release exceeds photosynthetic carbon uptake, a variable speed fan introduces outside ambient air to maintain the target CO_2 partial pressure. The Biosphere 2 environmental control system is described elsewhere (Lin *et al*. 1998; Dempster 1999; Zabel *et al*. 1999)

Plant material

Cottonwood (*Populus deltoides* Bartr.) cuttings used in this experiment were obtained from Westvaco and came from a fibre production farm in Summerville, South Carolina. The clone (S7c8) is adapted to the lower Brazos River, Texas and is day neutral. The cuttings were kept in cold storage and then soaked in cold water for 24 h prior to planting. On May 20, 1998, a total of 282 cuttings were planted with 2 × 2 m spacing. Each cutting was approximately 50 cm long and 2 cm in diameter, and was placed in the ground such that approximately 20 cm was above the soil. The plantation was watered to field capacity with a combination of sprinklers and drip irrigation. No nutrients additions were made. During 1998, the average growth conditions were 28/15 °C (day/night) temperature, an average of 50/70%RH (day/night) and a CO_2 partial pressure of 37 Pa. In late November 1998, most of the leaves had senesced and the air temperature was lowered to 20/12 °C (day/night) to winter harden the buds. In January of 1999, the main stem of each tree was cut, leaving 30 cm above the soil and 8–10 buds. In March 1999, the ambient air temperature was increased to 25 °C and the trees re-sprouted. All trees were pruned to have a single leader in May 1999. By June 1, 1999, at the initiation of this experiment, the 77 trees growing in the west bay of the forestry section of Biosphere 2 were 3.9 ± 0.05 m tall and 27.6 ± 0.57 cm in diameter at the soil surface.

Gas-exchange

Leaf-level gas-exchange measurements were made with several cross-calibrated gas-exchange systems incorporating CO_2 control (Li-6400, Li-Cor Inc., Lincoln NE, USA). Environmental conditions within the cuvette were controlled to match the ambient conditions. Temperature-response curves were made by setting the cuvette temperature to three set points, bracketing the ambient

air temperature by 5 °C and recording the steady-state respiration rate as determined by maintaining a total coefficient of variation < 1% (measured as the variation in the CO_2, H_2O and flow rate over a 1-min period). Leaf and gas-exchange system temperature equilibration typically required 10–15 min. Measurements were made only after equilibration had taken place and a graph of respiration as a function of time was observably stable.

Experimental protocol

During the course of the 5-day experiment the night-time temperature was adjusted by 5 °C each night. On day one of the experiment (June 3, 1999) the temperature was maintained at its long-term set point of 28/15.5 °C (day/night). Respiration measurements were initiated no sooner than 2300 h, and thus were made during the most stable part of the night (Azcón-Bieto & Osmond 1983) on each of the five days of the experiment. The steady-state respiration rate of two leaves from the mid-canopy (~1.5 m) of six individual trees was measured under ambient environmental conditions. Following the completion of the respiration measurements, temperature-response curves were made by first reducing the temperature by 5 °C, then returning to the initial ambient set point and finally by increasing the temperature by 5 °C. On day two of the experiment, the daytime conditions remained at the long-term set point (28 °C) but the night-time temperature was set 5 °C lower. The respiration measurements described above were repeated. On day three of the experiment, the day and night temperatures were returned to the long-term set point and again the above measurements were repeated. The night-time temperature was increased by 5 °C compared to the long-term set point on day four of the experiment, and measurement protocol was repeated. On day five of the experiment, all conditions were again returned to the long-term set points and all measurements were repeated.

Temperature response

The response of leaf respiration to temperature was described with a simple Q_{10} (Salisbury & Ross 1985). However the exponential nature of the Q_{10} relationship results in the value changing depending on which 10 °C span it is described over. For this reason we used a modification of a basic Arrhenius equation previously described by Lloyd & Taylor (1994) and more recently by Turnbull *et al*. (2001):

$$R = \mathrm{R}_{10}\, e^{\left(\frac{\mathrm{E_o}}{R_g}*\left(\frac{1}{T_o}-\frac{1}{T_a}\right)\right)} \quad (1)$$

Where R is the respiration rate, R_{10} is the respiration rate at 10 °C (fitted), T_o is the absolute temperature at 10 °C (283 K), T_a is the measurement temperature of R (K), R_g is the ideal gas constant (8.314 J mol^{-1} K^{-1}) and E_o is the energy of activation, also a fitted variable (J $mole^{-1}$). This model was fitted using a nonlinear technique (NLIN procedure, SAS Inc., 1998).

Modelled carbon loss

The calculated temperature response (Equation 1 above) was used to predict the leaf respiration from the mean air temperature during the five nights of the experiment. The instantaneous rates were scaled to the stand-level by multiplying by the leaf area index (3.1 m^2 m^{-2}) and the total surface area covered by trees (220 m^2) in the west bay of the Biosphere 2 cottonwood plantation. Calculations were made on a 15-min time scale, and then were summed for the duration of the night-time period (2200 to 0600 h).

Statistical analysis

Analysis of variance for the respiration rates obtained using the two protocols described above was obtained using general linear models (GLM procedures, SAS Inc. 1998) and the means were compared using Tukey's test. All the tests of significance were made at the 0.01 level.

Results

The mean night-time temperature (10 pm to 6 am) on nights 1, 3 and 5 of the experiment was 15.3 ± 0.1 °C (Fig. 1). There were no significant differences between the three ambient nights. The cold night (night 2, target temperature of 10.5 °C) had a mean night-time temperature of 11.5 ± 0.2 °C and the warm night (night 4, target temperature of 20.5 °C) had a mean temperature of 19.7 ± 0.1 °C. No significant fluctuations were observed in soil temperature measured at either 50 or 80 cm from the surface (averaging 21.5 ± 0.01 °C at 50 cm depth and 20.9 ± 0.01 °C at 80 cm depth). The 20 cm measurements reflected changes in the air temperature, fluctuating between 19 and 24.5 °C with a 5 night average of 21.9 ± 0.1 °C (Fig. 1).

As the stand temperature was manipulated, leaf respiration increased by 104% from 0.7 ± 0.04 μmol m^{-2} s^{-1} at 10.5 °C to 1.4 ± 0.04 μmol m^{-2} s^{-1} at 20.5 °C (Fig. 2). This increase was significantly greater than the 69% increase in respiration from 0.6 ± 0.06 μmol m^{-2} s^{-1} at 10.5 °C to 1.0 ± 0.06 μmol m^{-2} s^{-1} at 20.5 °C estimated from the individual leaf-level response curves. As a result, the Q_{10} estimate from the stand-level manipulation was 2.1, while the Q_{10} from the independent leaf manipulation was 1.7, a difference of 24% (Table 1). Fitting Equation 1 to these data revealed that the E_o of the two estimates

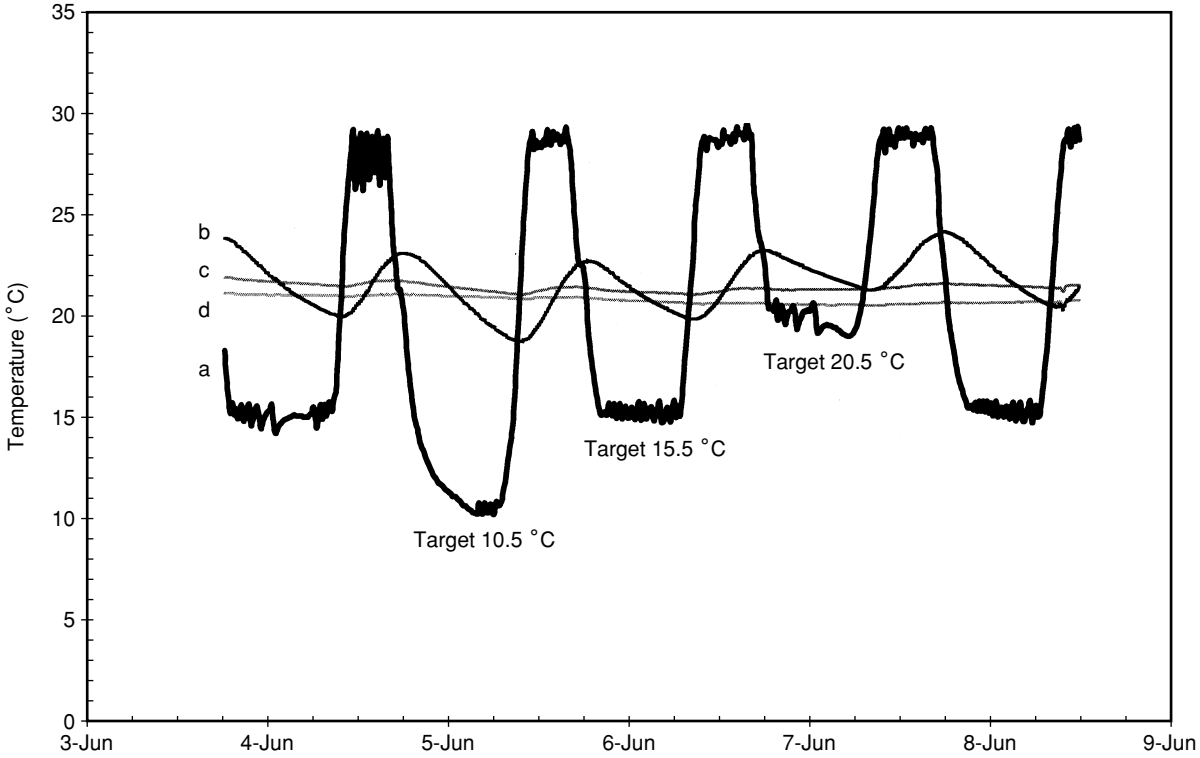

Fig. 1 Measured air (a) and soil temperature at 20 (b), 50 (c) and 80 (d) cm depth in the west bay of the cottonwood plantation of Biosphere 2 from June 3rd to June 8th 1999.

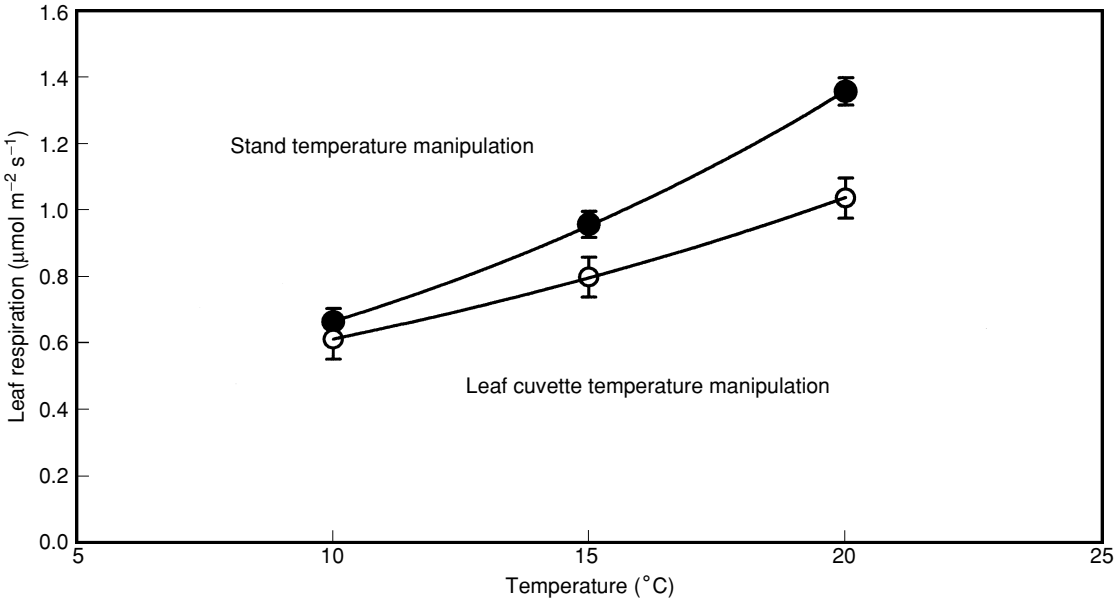

Fig. 2 Temperature response of respiration in the darkness measured under controlled-environment conditions. The open symbols are the mean leaf respiration estimated from temperature-response curves measured by manipulating the air temperature in a cuvette containing only a portion of an individual leaf while the temperature of the stand was maintained at a constant set point. Measurements were made each night of the five-night experiment and the average response is presented. The closed symbols are the estimated mean ambient leaf respiration rate measured over the course of the experiment with the cuvette temperature matching the stand air temperature. Values represent the mean of six replicate trees ($\pm$1 SE).

Table 1 Temperature response coefficients (R_{10}, the rate of respiration at 10 °C, E_o the energy of activation and Q_{10}, the change in the respiration rate when the air temperature was doubled from 10 to 20 °C) for *Populus deltoides* leaf respiration and modelled stand-level aboveground night-time carbon loss. Estimates were derived either by manipulating the ambient air temperature inside of Biosphere 2 on five sequential nights (Stand-level Manipulation), or by manipulating the air temperature in a cuvette containing only a portion of an individual leaf while the temperature of the ecosystem was maintained at a constant set point (Leaf-level Manipulation)

	Stand-level manipulation	Leaf-level manipulation
R_{10} (μmol m^{-2} s^{-1})	0.66 ± 0.04	0.61 ± 0.06
E_o (J mol^{-1} K^{-1})	49354	36347
Q_{10}	2.1	1.7
Simulated stand-level Respiratory carbon release		
10.5 °C night (mol C $stand^{-1}$ $night^{-1}$)	18.0	16.1
15.5 °C night (mol C $stand^{-1}$ $night^{-1}$)	23.6	19.6
20.5 °C night (mol C $stand^{-1}$ $night^{-1}$)	29.9	22.9
5 night total (mol C $stand^{-1}$ $night^{-1}$)	118.8	97.7

were also significantly different, increasing by 36% when comparing the stand manipulation to the leaf manipulation (Table 1).

Total night-time leaf carbon loss, estimated from the temperature response measured during the stand-level manipulation, averaged 23.6 ± 0.18 mol $stand^{-1}$ $night^{-1}$ when the ambient air temperature was maintained at the long-term mean of 15.5 °C (Table 1), and there were no significant differences between day 1, 3 and 5. Decreasing the night-time temperature to 10.5 °C reduced the total night-time leaf carbon loss by 24% to 18.0 mol $stand^{-1}$ $night^{-1}$, while increasing the temperature to 20.5 °C increased the total leaf carbon loss by 27% to 29.9 mol $stand^{-1}$ $night^{-1}$. These estimates of total leaf carbon loss were significantly higher than the estimates derived using the temperature response estimated from the leaf manipulations rather than the stand-level manipulations, and the differences between the estimates increased with temperature. For example at 10.5 °C the leaf manipulations resulted in a total leaf carbon loss of 16.1 mol $stand^{-1}$ $night^{-1}$, a value that was 12% lower than the estimate from the stand-level manipulation, while at 20.5 °C the estimate from the leaf manipulations, 22.9 mol $stand^{-1}$ $night^{-1}$, was 30% lower than the estimates from the stand-level manipulation (Table 1). Over the five nights of the experiment the total night-time leaf carbon loss estimated from the stand-level manipulation temperature response was 118.8 mol C $stand^{-1}$ $night^{-1}$, which was 22% higher than the 7.7 mol $stand^{-1}$ $night^{-1}$ estimated from the leaf manipulation temperature response (Table 1).

Discussion

We were able to expose a cottonwood plantation containing 77 trees, each nearly 4 m tall, to a 10 °C night-time warming over the course of three days. As a result, we are able to compare respiratory response to temperature determined in two very different ways, and found an important distinction between these responses. When the temperature response was measured in a way most commonly used, i.e. by manipulating the air temperature in a cuvette that encloses only a small part of a single leaf while the remainder of the tree remains at a constant ambient air temperature, the temperature response was significantly lower than the response measured by increasing the air temperature of the entire tree. Our results are consistent with the findings of Atkin *et al*. (2000), who found the temperature response of *Eucalyptus pauciflora* is significantly larger ($Q_{10} = 2.6$ vs. 2.1) when the entire plant temperature is matched to the measurement temperature within the leaf cuvette rather than manipulating the cuvette temperature independently from the ambient air temperature. Our results extend their findings from small potted plants to large trees, rooted in a 120-cm deep model soil. Our experimental results also suggest the mechanistic response is a function of shoot, but not root temperature. Atkin *et al*. (2000) found no leaf level response to a 30 °C change in root temperature, and here we report a large observed difference in leaf respiration without a change in soil temperature. While additional research is needed to determine the mechanisms responsible for the differences we observed, it is logical to expect that soluble carbohydrate levels and source/sink relationships are involved (Atkin & Lambers 1998; Atkin *et al*. 2000). For example, if the sink activity of the entire tree is increased (during stand-level warming), it is logical to expect respiratory cost associated with phloem loading (e.g. Bouma *et al*. 1995) would increase the temperature response of leaf respiration above the estimate derived by leaf-level manipulations. Previous work on soybean showed that leaf vs. plant manipulation of the atmospheric CO_2 concentration can also differentially affect leaf physiology (Sims *et al*. 1998). The work of Sims *et al*. (1998) clearly demonstrates that photosynthetic acclimation to growth in elevated CO_2 has a whole-plant signal that is independent from the leaf signal, and the authors draw similar conclusions regarding the possible role of phloem loading.

The implications of our finding are that temperature fluctuations such as these, which are a common natural

phenomenon, result in considerably larger carbon losses than are currently modelled from data gathered by the more traditional leaf manipulation protocol. Our summation of the total carbon loss from the stand over the 5-day duration of this experiment shows a 21 mol or 250 g of carbon difference. Importantly, the magnitude of the effect increases with temperature, suggesting that further research needs to examine the potential implications of this observation in light of global warming trends, both observed and predicted (Hansen *et al*. 1988, 1999). These calculations assume all leaves in the canopy have a similar temperature response, and while this assumption is commonly made in vegetation models it is unlikely to the case (Griffin *et al*. 2001). Clearly further work is needed to address variation in respiration within the canopy directly. In order to stress the importance of these differences in the Q_{10} response we further calculate the effect of a 3.5 °C global warming on terrestrial carbon exchange by making several simplifying assumptions. If the global Q_{10} was 1.7 as we measured when only manipulating cuvette temperature, terrestrial plant respiratory carbon release would increase by nearly 20% to 72.2 GT C year^{-1}. If, however, the global Q_{10} were actually 2.1 as measured when whole-plant temperatures were increased in conjunction with cuvette temperatures, the same 3.5 °C warming would increase terrestrial plant respiratory carbon release by nearly 30% to 77.8 GT C year^{-1}. The difference between these two simple estimates is nearly 3 times larger than the current estimated missing carbon sink (Schimel 1995). While acclimation responses must be considered over longer periods of time relevant to global warming (Ryan 1991; Larigauderie & Körner 1995; Tjoelker *et al*. 2001), the implications of our findings for predicting the carbon sequestration potential of natural and managed ecosystems are substantial. Accordingly we concur with Atkin *et al*. (2000), that short-term leaf-level temperature-response curves may be a poor indicator of daily respiratory CO_2 release and therefore should be used only with caution. The development of a mechanistic understanding of these responses is critical for accurately modelling and predicting ecosystem carbon balance and is the subject of further experimentation currently underway at Biosphere 2.

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