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Relationship between stem CO_2 efflux and stem temperature at different measuring depths in *Pinus massoniana* trees

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ABSTRACT

The response of stem CO_2 efflux to temperature is crucial in predicting the carbon cycle in forest ecosystems under future scenarios. However, the relationship between stem CO_2 efflux and stem temperature at different measuring depths is not well understood. In this study we measured stem CO_2 efflux and stem temperature at different depths in six *Pinus massoniana* trees for 2 days. We found a strong diel hysteresis between stem CO_2 efflux and stem temperature. The diel hysteresis varied with increasing depth from a counterclockwise direction at a depth of 0 cm to a clockwise direction at depth of 7 cm. The effects of the high resistance to radial diffusion and sap flux on stem CO_2 efflux may contribute to the diel hysteresis. The results also showed that the Q_{10} values of stem CO_2 efflux increased from 1.51 at a depth of 0 cm to approximately 2.22 at a depth of 7 cm, indicating that the depth for stem temperature measurement plays a pivotal role in estimating the temperature sensitivity of stem CO_2 efflux. Moreover, we found that 3 cm deep was the appropriate depth for stem temperature measurement, because of the highest R^2 (0.96) for the efflux–temperature curve and nearly no hysteresis between stem CO_2 efflux and temperature in our study. Therefore, consideration of the stem temperature measurement depth is necessary to understand the response of stem CO_2 efflux to temperature and accurately fit the Q_{10} value of stem CO_2 efflux. However, this generalization must be examined under other conditions such as different seasons or other tree species.

1. Introduction

The CO_2 efflux from the stem surface has been estimated as 9–33% of total ecosystem respiration in forests [1–4], and therefore plays a critical role in the carbon cycle of forest ecosystems [5–7]. Stem temperature is considered as the most important factor controlling stem CO_2 efflux. However, many scholars have found a diel hysteresis, i.e. different stem CO_2 effluxes measured at the same temperature at different times, and lag time varies from 10 min to several hours [8–11]. Many explanations have been offered for the hysteresis between stem CO_2 efflux and stem temperature. One possible cause of hysteresis is the transport of CO_2 in xylem sap. Given the high solubility of CO_2 in water, a part of this gas is dissolved in the xylem sap, and transported by the transpiration stream [12–13]. Gansert and Burgdorf [14] observed the daytime depression of stem CO_2 efflux compared to the predicated value based on an exponential model from nighttime data in *Betula pendula* trees. However, Zhu et al. [15] demonstrated that the occurrence of sap flux results in the daytime increase of stem CO_2 efflux in *Schima superba* trees. Maier and Clinton [16] artificially reduced sap flux by progressively removing the tree canopy, but did not observe any effect of sap flux on stem CO_2 efflux in loblolly pine trees. The high resistance of trees to radial diffusion is another possible explanation to hysteresis [17]. A counterclockwise or clockwise hysteresis typically occurs when stem CO_2 efflux is plotted against stem temperature at shallow layers, particularly against air temperature [8,11]. However, little information is available about the relationship between stem CO_2 efflux and stem temperature at different measuring depths.

To predict the response of stem CO_2 efflux to global warming, an important parameter, Q_{10}, which represents the temperature sensitivity of stem CO_2 efflux, has been applied to certain models [1,7,9]. Minor changes in the Q_{10} value significantly affect the response of stem CO_2 efflux to temperature, further the estimates of the carbon budget. Previous studies have found that the Q_{10} values of stem CO_2 efflux are affected by temperature [18] and substrate availability [19]. Some researchers also confirmed that Q_{10} values change with the seasonal variation [20–22]. However, most studies only used the temperature at a single depth when fitting the Q_{10} value. This limitation inevitably results in errors in Q_{10} values, because the amplitude and phase of the stem temperature will change with increasing depth. Some studies have

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compared the Q_{10} values among different sites [9,23], species [23–25], or climate zones [20]. However, these studies did not consider the potential effect of temperature measurement depth on the Q_{10} values. The depths of the stem temperature measuring points varied across different studies from 0.3 cm to 3 cm (Table S1). Some researchers only point out to measure the temperature of the cambial zone (Table S1). Whether the depth of stem temperature measuring point causes a significant variation in Q_{10} (Table S1) remains unclear. Therefore, we must understand the controlling factors of the Q_{10} values, and explore the response of the Q_{10} values of stem CO_2 efflux to the depth of stem temperature measuring point to improve the accuracy of process-based models of the carbon cycle in forests.

In the present study, stem CO_2 efflux and stem temperature at different depths were measured in a Masson's pine (*Pinus massoniana* Lamb.) plantation. The objectives of this study are to: (1) explore the relationship between stem CO_2 efflux and stem temperature at different depths, and (2) analyze the effect of the depth of stem temperature measuring point on Q_{10} of stem CO_2 efflux.

2. Materials and methods

2.1. Site description

The study site is located in the Jigongshan National Nature Reserve (114°01′–06′E, 31°46′–52′N), Henan Province in central China. This region is characterized by a monsoon climate. The mean annual temperature is 15.2 °C, and ranges from 2.0 °C in January to 27.5 °C in July. The mean annual precipitation is 1120 mm with nearly half of the total precipitation occurring in summer. The experiment was carried out in a *Pinus massoniana* plantation that was planted in 1980. A 30 m × 30 m plot was established in this plantation in August 2008. The stand density is 589 trees ha^{-1}, and mean diameter at breast height (DBH) is 25.7 ± 2.3 cm. The main understory vegetation includes *Quercus dentata*, *Rhus chinensis*, *Forsythia suspensa*, and *Carex stenophylla*. Moreover, the soil has an average organic C content of 27.5 ± 2.2 g/kg, a total N content of 1.5 ± 0.1 g/kg, and a pH of 5.1 ± 0.3.

2.2. Stem CO_2 efflux and stem temperature measurements

Six trees in the plantation were randomly selected for stem CO_2 efflux measurements. The characteristics of the six sample trees are presented in Table 1. The horizontally oriented soil chamber technique was used in the stem CO_2 efflux measurements [26–27]. A custom-built polyvinyl chloride (PVC) collar was attached to the stem surface to connect the stem and the soil CO_2 efflux chamber (Li-cor 6400-09 unit). The two ends of the opaque PVC collar were cut to match the approximate curvature of the stem and the Li-cor 6400-09 unit. The collar was then attached to the eastern side of the stem at a height of 1.3 m by using a silicone sealant, and was left in the same location throughout the study period. The Li-cor 6400-09 unit was held in place with bungee cords during the measurement, and a gas leakage test was conducted before each measurement was taken. Stem CO_2 efflux was continuously measured every 1 h to 2 h from May 6 to 8, 2009. A hole was also drilled approximately 5 cm below the PVC collar and into the stem at a depth of 7 cm to measure stem temperature from the stem surface to the aforementioned depth. During measurements of stem CO_2 efflux, stem temperatures at different depths were simultaneously measured by using a temperature probe connected to the Li-cor 6400-09 unit. Stem temperature was recorded when it became constant. The temperature measured at a specific stem depth is the total of the temperature gradient along the probe because the temperature probe is made of metal and conducts heat. The hole was sealed with a tape between measurements to reduce biases. The difference in stem temperatures at different depths was obvious. It took 7 min to 8 min to take measurements of stem CO_2 efflux and stem temperature at different depths in a single tree; thus, one round of measurements for the six sample trees took 1 h to 2 h with 34 rounds over 2 days.

Table 1
Diameter at breast height (DBH), tree height, and crown area of the examined six *Pinus massoniana* trees in the study site.

No.	DBH (cm)	Height (m)	Crown area (m^2)
Tree 1	31.4	23.4	6.81
Tree 2	14.8	16.2	3.78
Tree 3	20.9	20.1	5.13
Tree 4	17.0	17.5	3.96
Tree 5	23.9	21.1	5.41
Tree 6	29.6	23.8	5.78
Mean	22.9	20.4	5.14

2.3. Data analysis

Stem CO_2 efflux was expressed based on the stem surface area enclosed by the opaque PVC collar. The stem surface area was calculated according to the report of Yang et al. [27]. The response of stem CO_2 efflux to stem temperature at various depths was expressed by the following exponential equation [28]:

$$E_S = \alpha \times e^{\beta T} \tag{1}$$

where E_S is the measured stem CO_2 efflux, T is the stem temperature, and α and β are the regression coefficients calculated by nonlinear regression analysis according to the available database.

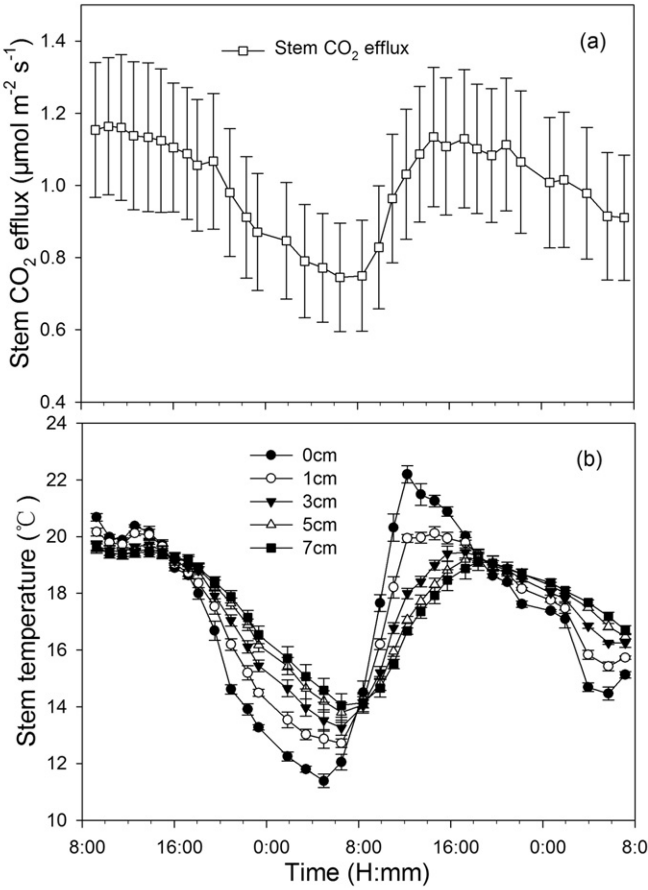

Fig. 1. Diel courses of the mean stem CO_2 efflux (a) and stem temperature (b) at different depths from the stem surface (0 cm) up to a depth of 7 cm of the examined six *P. massoniana* trees. Values are mean ± SE for n = 6.

The Q_{10} value was calculated as follows [28]:

$$Q_{10} = e^{10\beta} \tag{2}$$

where Q_{10} represents the temperature sensitivity of stem CO_2 efflux, and β represents the regression coefficient obtained from Eq. (1).

Q_{10} values also were estimated based on daytime and nighttime data. The differences between daytime and nighttime Q_{10} values were analyzed by one-way ANOVA. The residual stem CO_2 efflux (ΔE), the difference between the observed CO_2 efflux (E_S) and the predicted CO_2 efflux (E_P) based on the nighttime data, was also estimated at various depths.

3. Results

Stem CO_2 efflux and stem temperature were measured continuously for 2 days. The stem CO_2 efflux of the *P. massoniana* changed diurnally, typically reaching the highest value in the afternoon and the lowest in early morning (Fig. 1a). The mean stem CO_2 efflux of the six tree samples over 2 days was 1.01 ± 0.02 μmol m^{-2} s^{-1}, with minimum and maximum values of 0.74 μmol m^{-2} s^{-1} and 1.16 μmol m^{-2} s^{-1}, respectively. The greater variation in the stem CO_2 efflux among the six tree samples ranged from 0.48 μmol m^{-2} s^{-1} to 1.70 μmol m^{-2} s^{-1}.

Stem temperature followed a diel pattern similar to that of stem CO_2 efflux, and typically increased during the day and decreased at night. The mean stem surface (0 cm) temperature was 17.45 °C. The minimum

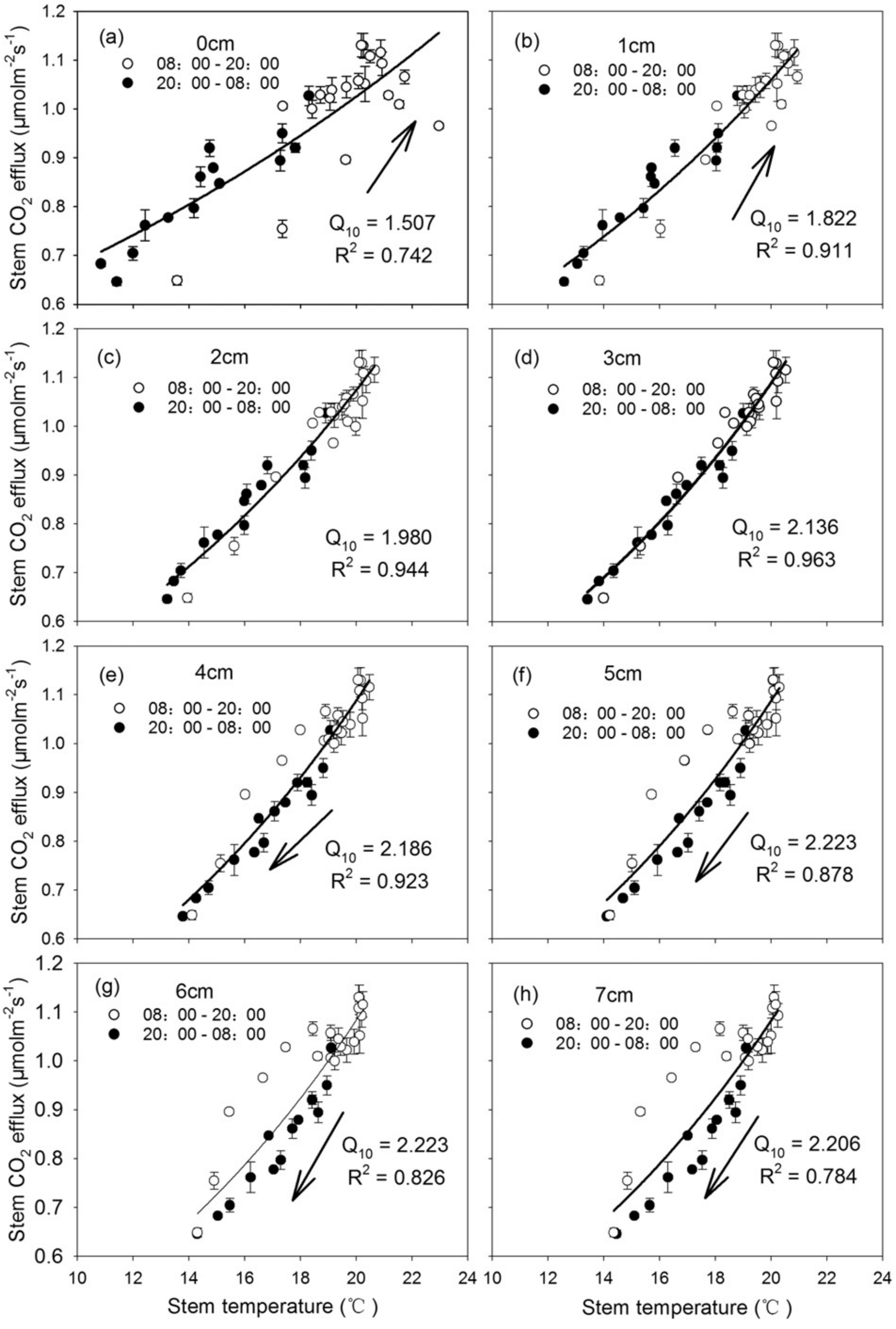

Fig. 2. Example of the dependence of stem CO_2 efflux (μmol m^{-2} s^{-1}) on the stem temperature (°C) at different depths from the stem surface (0 cm) to a depth of 7 cm. The open circle represents the data from 8:00 to 20:00, whereas the filled circle represents the data from 20:00 to 8:00 of the next day. The arrows indicate rotational direction over time. The solid curve represents a non-linear least squares fit between stem CO_2 efflux and stem temperature at different depths.

stem surface temperature (11.39 °C) occurred at approximately 05:00, whereas the maximum value (22.19 °C) occurred at approximately 12:00. The diel variation of stem temperature decreased with increasing depth (Fig. 1b). The mean, maximum, and minimum stem temperatures at a depth of 3 cm were 17.57, 19.71, and 13.26 °C, respectively. A relatively small range of 14.05 °C to 19.66 °C was observed at a depth of 7 cm. However, the mean stem temperature at this depth remained similar to stem surface temperature. The lag time between stem temperature at various depths and stem surface temperature increased with increasing depth. For example, the lag time of the maximum temperature at a depth of 1 cm was approximately 2 h, whereas the corresponding value at a depth of 7 cm was approximately 6 h.

Plotting stem CO_2 efflux against stem temperature at various depths showed that the direction of elliptical rotation changed from counterclockwise at a depth of 0 cm to clockwise at a depth of 7 cm (Fig. 2). At the surface layers, stem CO_2 efflux is higher at night than that during the day at a given temperature, particularly at a depth of 0 cm. Therefore, stem CO_2 efflux exhibited hysteresis by following a counterclockwise time course, thus indicating that the stem CO_2 efflux lagged temperature. However, hysteresis was not apparent with increasing depths, and it even disappeared at a depth of 3 cm. A clockwise hysteresis was observed as depth increases, thus indicating that temperature in deep layers lagged stem CO_2 efflux.

Stem CO_2 efflux was exponentially correlated with stem temperature, and most of its variations were explained by stem temperature at different depths across the six *P. massoniana* samples, with the coefficient of determination (R^2) ranging from 0.48 to 0.97 (Fig. 3a). R^2 tended to increase with increasing depth until it reached a threshold, and then it declined, except for that in Tree 2 (Fig. 3a). For example, R^2 for Tree 5 increased from 0.74 at a depth of 0 cm to a peak of 0.96 at a depth of 3 cm, after which it declined to less than 0.80 at a depth of 7 cm (Figs. 2 and 3a). Apparent Q_{10} values increased with the increasing depth across all six *P. massoniana* samples because of the decrease in the amplitude of stem temperature with depth (Fig. 3b). For example, the Q_{10} value of the stem CO_2 efflux for Tree 5 increased from 1.51 at a depth of 0 cm to approximately 2.21 at a depth of 7 cm (Figs. 2 and 3b). However, the increasing trend of the Q_{10} value gradually slowed down as depth increases. The Q_{10} values of the samples increased by 0.63 at a depth of 0 cm to 3 cm, but increased by only 0.08 at a depth of 3 cm to 7 cm.

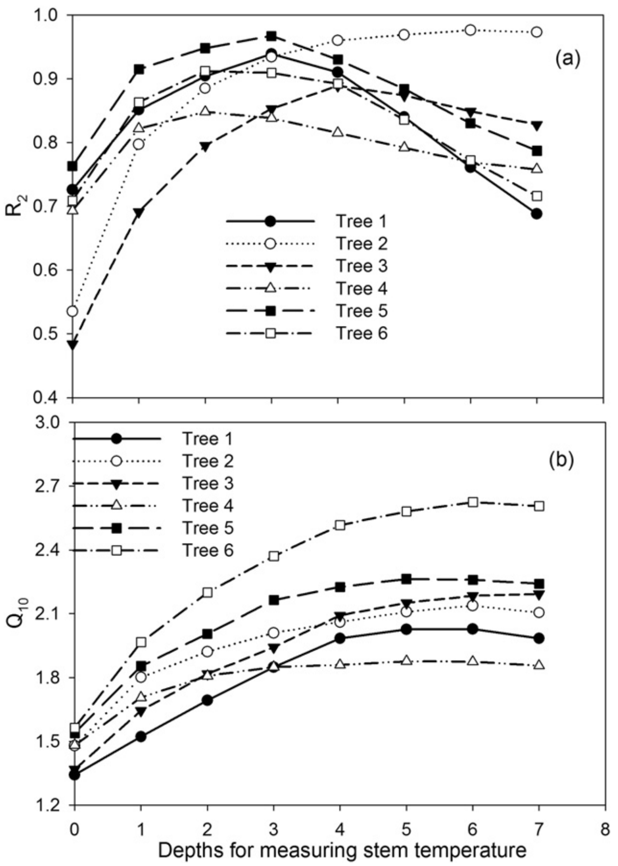

Fig. 3. The R^2 (a) and Q_{10} values of the dependence of the depth of stem temperature measuring point of the examined six *P. massoniana* trees.

The relationships between stem CO_2 efflux and temperature at various depths were analyzed based on daytime and nighttime data for all six samples. The R^2 of the fitting exponential function based on nighttime data was significantly higher than that based on daytime, except for that at a depth of 3 cm (Fig. 4). The predicted stem CO_2 efflux based on the measured nighttime data was also compared with the observed stem CO_2 efflux. The observed stem CO_2 efflux during the day was lower than the predicted stem CO_2 efflux at a depth of 0 cm (Fig. 5a). The residual stem CO_2 efflux at a depth of 3 cm was nearly zero, thus indicating that the observed CO_2 efflux was similar to the predicted value (Fig. 5b). An opposite pattern, i.e., a positive residual stem CO_2 efflux, was found at a depth of 7 cm (Fig. 5c).

4. Discussion

The typical diel counterclockwise hysteresis between stem CO_2 efflux and stem temperature in shallow layers as observed in this study (Fig. 2) has been reported previously [1,8,10,16,17]. Interestingly, the hysteresis disappeared as depth increased, and a clockwise hysteresis between stem CO_2 efflux and stem temperature was observed in deep layers (Fig. 2). Levy et al. [29] reported that at a given temperature stem CO_2 efflux is lower at night than that during the day (i.e. a clockwise hysteresis) at a given temperature.

High resistance to radial diffusion [17,30] is one of the possible reasons for diel hysteresis. Many scholars found that CO_2 concentration in the xylem varies between 3% and 20% [6,30–31], which is several magnitudes higher than the atmospheric CO_2 concentration of c. 0.04%. This finding suggests a high resistance to CO_2 radial diffusion from the xylem to the ambient air. Conifers, as reported in the present study, have higher resistance to radial gas diffusion because of few intercellular spaces, although the resistance to radial CO_2 diffusion was not quantify as reported by Steppe et al. [30]. Stem CO_2 efflux is the sum of CO_2 produced by the live cells (including inner bark, vascular cambium, and xylem) from various depths, which are exposed to different temperature regimes. Given the high resistance to radial diffusion and the

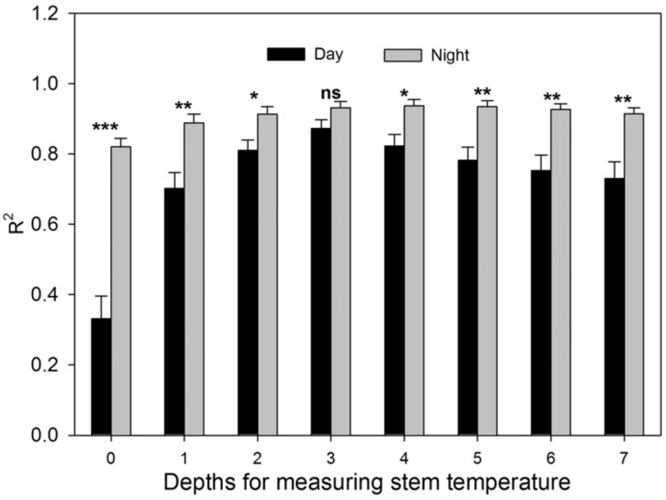

Fig. 4. The R^2 of stem CO_2 efflux to stem temperature based on daytime (black bars) and nighttime (gray bars) data of the six *P. massoniana* samples at different depths. $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$; ns, not significant ($P > 0.05$).

differences in heat energy gain and loss in the surface and deep layers, stem CO_2 efflux lags temperature in the surface layer, and vice versa in the deep layer, as indicated by the phenomenon of counterclockwise and clockwise hysteresis reported in the present study.

The large amount of CO_2 produced by the live tissues of the stem moved upward in the transpiration stream [6,11–12]. This effect is an important explanation for diel counterclockwise hysteresis. A strong negative correlation between stem CO_2 efflux and sap flux velocity was found in rimu (*Dacrydium cupressinum*) [31] and *B. pendula* [14]. The CO_2 transported by the transpiration stream from the soil or the lower part of the stem also contributes to stem CO_2 efflux [29,32–35] and results in a clockwise hysteresis response to temperature [15,29]. Sap flux velocity was not measured in our study. However, the result that the R^2 was significantly higher at night than during the day (Fig. 4) indirectly reflects that sap flux or other factors influence the relationship between stem CO_2 efflux and stem temperature. Therefore, we speculate that CO_2 transport in the xylem sap may reduce or increase stem CO_2 efflux during the day and partially contribute to the hysteresis in this study. However, Maier and Clinton [16] found that artificially manipulating sap flow does not influence counterclockwise hysteresis. They concluded that the negative correlation between stem CO_2 efflux and sap flux velocity may not represent a cause-and-effect relationship.

Woody tissue photosynthesis has been proposed as a factor that influences variation in stem CO_2 efflux under illumination [36–38]. A substantial amount of respired CO_2 in woody tissues or CO_2 transported in the transpiration stream can be assimilated by woody tissue

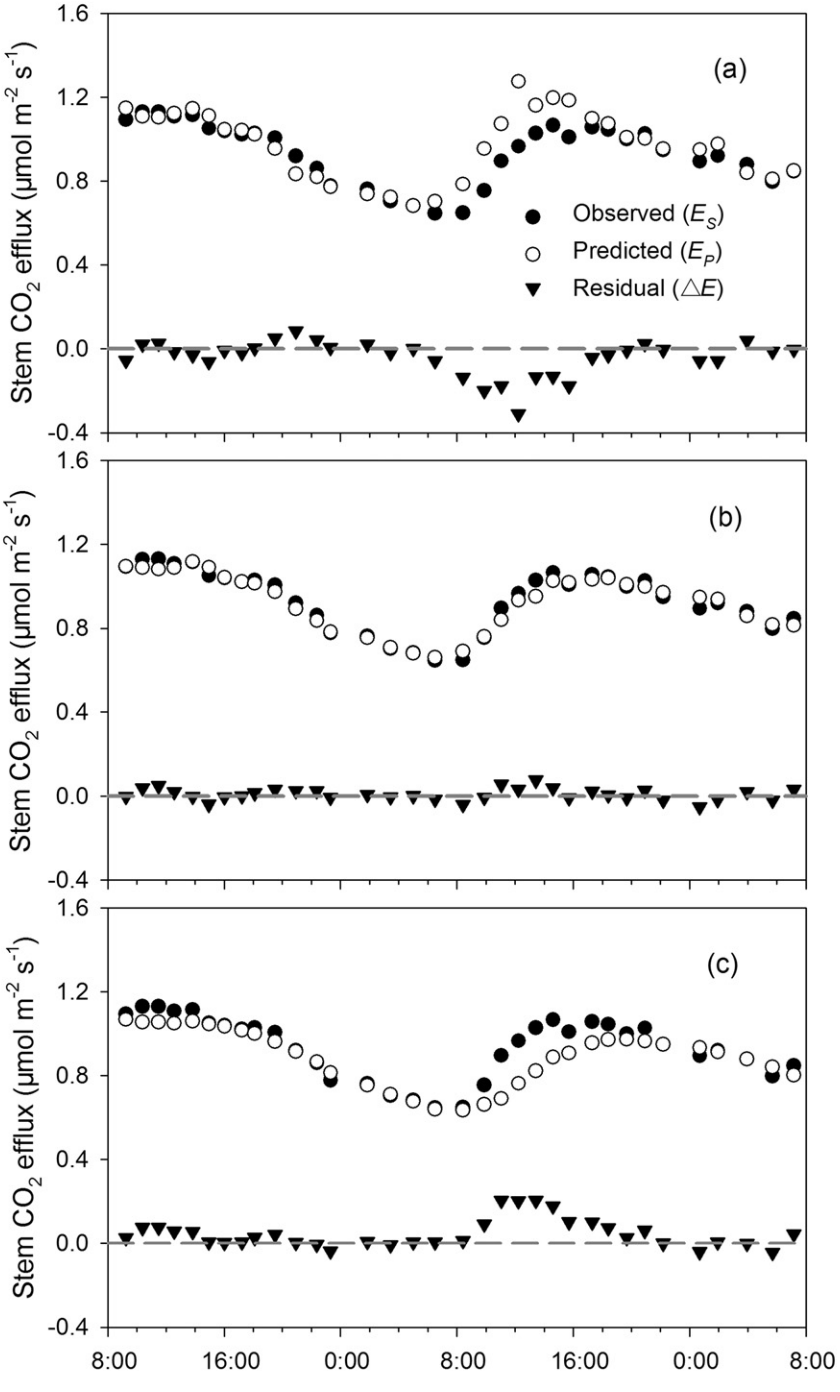

Fig. 5. Example of the observed (E_S), predicted (E_P) and residual (ΔE) stem CO_2 efflux at a depth of 0 cm (a), 3 cm (b), and 7 cm (c). The residual stem CO_2 efflux is the difference between E_S and E_P. The predicted stem CO_2 efflux (E_P) was estimated by using the temperature response curves derived from nighttime data.

photosynthesis [39–40]. This process may contribute to diel counterclockwise hysteresis. However, woody tissue photosynthesis is not likely the cause of hysteresis in our study. First, stem CO_2 efflux and stem temperature were measured in mature *P. massoniana* trees, and minimal or no chlorophyll was present in the sample section. Additionally, opaque chambers were also used to avoid woody tissue photosynthesis.

A single, more or less arbitrary, depth for measuring stem temperature was used to derive apparent Q_{10} values in previous studies [4,19,41–42]. In contrast, multiple temperature measurement depths were used in the present study. The results show that the depth of stem temperature measuring point influences the fitting Q_{10} of stem CO_2 efflux because the amplitude and phase of the stem temperature change with the increasing depth. The diel variation of stem temperature was gradually reduced with increasing depth (Fig. 1). This finding is in agreement with Fourier's law of heat conductance. Thus, apparent Q_{10} values will become increasingly large as depth increases. The apparent Q_{10} values increased from 1.51 at a depth of 0 cm to 2.21 at a depth of 7 cm (Fig. 2), thus indicating that different temperature measuring depths may be the cause of errors in determining Q_{10}. Moreover, temperatures at different depths were measured from the same hole, which partly reduced the difference in stem temperature at different depths because of faster heat conduction by air than by wood tissue. If the intrinsic temperature was used to fit the Q_{10} value, then the effect of temperature measurement depth would be more obvious.

For more accurate temperature sensitivity of stem CO_2 efflux, we must find the appropriate depth for stem temperature measurement. In our study, 3 cm deep was determined as the appropriate depth for measuring stem temperature because nearly no hysteresis between stem CO_2 efflux and temperature occurs at this depth. Moreover, the highest R^2 (0.96) for the efflux–temperature curve was found at this depth (Fig. 2). Stem temperature and CO_2 efflux courses at a depth of 3 cm were nearly synchronized. By contrast, stem temperature courses at other depths, particularly at a depth of 0 cm and 7 cm, must shift in time to synchronize stem temperature and CO_2 efflux and obtain the best goodness-of-fit. Therefore, we suggest that the apparent Q_{10} value is appropriate when the temperature measurement depth with the highest R^2 and lowest hysteresis is used.

5. Conclusion

Stem CO_2 efflux is a complex process, in which different sources of CO_2 are exposed to different temperature regimes. This study found the occurrence of two kinds of hysteresis between stem CO_2 efflux and stem temperature: counterclockwise hysteresis in surface layers and clockwise hysteresis in deep layers. High resistance to radial diffusion is the most important factor that explains the phenomenon of hysteresis. The effects of sap flux on stem CO_2 efflux may also partially contribute to the diel hysteresis. Moreover, the depth of temperature measurement influences the apparent Q_{10} values of stem CO_2 efflux. Therefore, the most suitable depth of stem temperature measuring point that corresponds to the measured stem CO_2 efflux is strongly recommended. However, given that our findings were based only on data from 2 days in spring, our conclusions should be examined under the conditions of other seasons or other tree species.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.chnaes.2016.05.001.

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