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Temperature dependence of coastal wetland ecosystem respiration confounded by tidal activities: a temporal perspective

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Abstract

Variations of temperature and hydrological conditions result in the fluctuation of ecosystem respiration (ER). Temperature sensitivity is widely used to describe ER-temperature relationship, but hydrological condition with similar dynamics as temper-

- ature could cause confounding effect. Many researchers have made comparisons between long-term and short-term models to show the confounding effect. However, how temperature sensitivity is confounded by hydrological condition in different time scales remains unknown. In this study, data from two coastal wetland sites were used. By comparing the variations of temperature and tidal influence at three time scales (monthly, scales and half yearly), we found that: (1) the covariation of temperature and other
- seasonal and half-yearly), we found that: (1) the co-variation of temperature and other environmental factors accounted for the long-term confounding effect, and (2) the small variances of temperature in short time scale explained the short-term confounding effect. As a result of the long-term confounding effect, greater system errors were introduced in long-term model than short-term did. As the temperature sensitivity derived
- from long-term "ignored" the alternation of main driving factor of ER, temperature influence on ER was overestimated while the tidal influence was underestimated. Tidal activities had great influences on ER when the variances of temperature were small. If short-term model without tidal effect was applied, short-term confounding effect was inevitable. Compared to the long-term model (half-yearly), short-term model (monthly without tidal effect) performed better that helped reduce the long-term confounding effect. and intervention a memory factor like tide would further reduce the
- effect, and integrating a proper secondary factor like tide would further reduce the short-term confounding effect.

1 Introduction

Temperature and hydrological conditions are considered as the two most important regulating factors of ecosystem respiration (ER) (Bubier et al., 2003; Griffis et al., 2004), and the former is often regarded as the dominant factor, especially in those areas with



sufficient water. Most of the respiration variations can be described by the exponential functions with an independent variable, i.e. temperature (Lafleur et al., 2005; Tang et al., 2008). A constant temperature sensitivity (i.e. Q_{10}) on yearly or seasonal scale is widely used, while this may ignore the influence of other factors in "finer" time scales (Janssens and Pilegaard, 2003; Reichstein et al., 2005; Fierer et al., 2006).

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Hydrological condition is assumed as the active factor when environment is far from the optimum condition, for example too dry or too wet (Qi et al., 2002; Reichstein et al., 2003). It is often regarded as the secondary factor to mediate ER by changing the temperature-respiration relationship. The high temperature in summer makes hydrological condition behave as a limiting factor of respiration, and the lower temperature in winter makes itself the limit factor (Flanagan and Johnson, 2005), which implies that ecosystem respiration may also experience alternation of main driving factor.

There are numerous evidences that Q_{10} is affected by hydrological condition. In most ecosystems, soil moisture and Q_{10} are positively correlated (Xu and Qi, 2001; Qi et al.,

- ¹⁵ 2002; Reichstein et al., 2002; Flanagan and Johnson, 2005; Maseyk et al., 2008), as the increasing soil moisture relieves the water depression. But DeForest et al. (2006) reported a converse correlation between soil moisture and Q_{10} in an oak-dominated forest, where the respiration level and Q_{10} in growing season were lower in wetter year. It is common in wetland that rising water level has a significant negative effect on res-
- piration (DeBusk and Reddy, 2003; Hirota et al., 2007; Juszczak et al., 2012), as it reduces the available soil oxygen concentration. In some cases, the oxygen concentration is even near zero in near surface layer (Lafleur et al., 2005). Therefore, drought in wetlands tends to induce rising of respiration level and temperature sensitivity (Savage and Davidson, 2001; Bubier et al., 2003; Phillips et al., 2010).
- In some ecosystems, the hydrological condition has the similar seasonal dynamics as temperature. It makes difficult to distinguish between temperature and hydrological influence on respiration (Davidson et al., 2006). The confounding effect caused by this co-variation would lead to under- or overestimates of annual temperature sensitivity, and thereby the temperature sensitivities derived from long-term models may not



be reliable. To quantify the difference between long- and short-term derived temperature sensitivities affected by confounding effect, Reichstein et al. (2005) tested several lengths of sub-period, and found that a window size of 15-days turned out to be a good choice. Janssens and Pilegaard (2003) also noticed this problem, but they found that even within 4- to 7-days the respiration response of temperature was still confounded by soil moisture.

The different lengths of sub-period represent different time scales. A hydrological factor that has different short-term and long-term dynamics from temperature could be a good material to study alternation of driving factor across time scales. Compared to other ecosystems, coastal wetland is affected by a special periodical hydrological condition, i.e., tide. The intruded tidal water not only aggravates the oxygen insufficiency, but also barricades diffusion of carbon dioxide. Guo et al. (2009) found that the tidal activity had a significant impact on net CO₂ flux of coastal wetland ecosystem on 15-days period, which was similar to the periodicity of the tidal cycle. As tide do not co-vary with temperature, it would be convenient to separate the influence of tide from temperature.

In this paper, we used continuous flux data to investigate the relative importances of temperature and tide on ER along different time scales and tried to answer the following questions: (1) what is alternation of respiration driving factor in different time scales and associated reasons? (2) What "details" are ignored by an annual constant Q_{10} and how? (3) Are temperature sensitivities derived from short-term really better than long-term?

2 Materials and methods

2.1 Study sites

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Our study area is located in the eastern coast of Chongming Island (Fig. 1). The climate is subtropical monsoon, and annual precipitation was 800–900 mm in 2005–2007. The mean temperature and relative humidity in three years were 16.5 °C and 77.7 %. Proper





temperature range and ample rainfall creates a long growing season. The dominant species are *Phragmites australis*, *Scirpus mariqueter* and *Spartina alterniflora*. *S. alterniflora* has the longest growing period from March to November, while *S. mariqueter* and *P. australis* grow from April to September and from April to October, respectively. In our study area, apring baging in carly April (DOX 01, 05) and and a in mid, lung (DOX).

our study area, spring begins in early April (DOY 91–95) and ends in mid-June (DOY 199–203), while autumn begins in late September (DOY 290–294) and ends in late November (DOY 351–355).

Tidal pattern of this area is mixed semi-diurnal tide, which means that there are two high tides and low tides each day with different heights. There are three observation sites in the area, but only two (CMW1 and CMW3) were chosen for the following analysis because CMW1 (31°31′0.0″ N, 121°57′38.6″ E) and CMW3 (31°31′0.8″ N, 121°58′18.0″ E) locate along the elevation gradient (Fig. 1). Both sites experience in-undation by seawater at spring tide.

Both sites were equipped with same instruments. CO₂ flux was measured at 5m ¹⁵ above ground by eddy covariance method. A three-axis sonic anemometer (CSAT3, Campbell, USA) measured high-frequency (10 Hz) wind velocity and sonic temperature, while an open path infrared gas analyzer (Li-7500, Li-COR, USA) measured CO₂ and H₂O density at the same frequency. The air temperature probes were mounted at 1.6 m, 2.7 m and 4.8 m above ground. A CSC616 was installed to observe 5cm deep volume water content (VWC) of soil.

2.2 Ecosystem respiration (ER) data handling

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 CO_2 fluxes were computed from 30-min covariance of wind velocity and CO_2 density. We discarded the half-hour data which were measured during rain. To avoid the potential bias introduced by gap-filled algorithm, only quality controlled flux data was used in following analysis.

Nighttime flux data were assumed to equal ER. To obtain continuous nighttime data rather than break them into two parts, we set the beginning of a day at 12:00 a.m. For example, DOY 1 begins at 1 January 12:00 a.m. and ends at 2 January 12:00 a.m.



Solar elevation angles were used to separate the daytime and nighttime. Considering the effect of twilight, we defined nighttime as the period when solar elevation angle was less than -6° . The solar elevation angles were compute by the standard method. All the nighttime flux less than zero was deleted.

- As we focus on daily ER change in the study, averages of daily nighttime flux data and corresponding standard error were calculated. As the result of quality control, reject rates were highly variable from day to day. For the reliability of averages, each day must include at least five validated values. There were extremely high values of validated flux in winter. Those values were low enough to pass annual outlier test, but unreasonably high compared to the rest observation data in the same day. As one value like that
- would greatly change the average, we excluded diel flux averages whose standard errors were 1.25 times bigger than average values.

2.3 Stratifying by tidal effect

As lack of field records of tidal elevation, tide tables from the nearest tidal station (Heng-

- ¹⁵ sha station) were used. Tidal elevations were also integrated into diel value by extracting the maximum value of each night. Each day would be marked according to their distances to the nearest spring tide (DST). Because the ER does not correlate with tidal height directly, DST was used to analysis the ER variation in spring-neap tidal cycle. In a 15-days cycle, the day with maximum tidal elevation would be marked as
- 0, and the rest days were marked from -7 to 7 according to their distances to nearest spring tide. Some tidal cycles were longer than 15 days, and all the distances longer than 8 days would be marked as -7 or 7.

Because ER was not synchronous with tidal elevation, a tidal effect index (TEI) was proposed for further analysis. TEI was derived from the regression between ER and

DST to simulate the tidal effect on ER. The index was an asymmetric-sine curve and the range was set from 0 to 1. The maximum value was set at -3 and -4 for CMW1 and CMW3, respectively, and the minimum value was set at 1 for both sites (Fig. 2).



2.4 ANOVA and error assessment

We supposed that the tide (TEI) was a downward regulatory factor to ER in coastal wetland. Based on the exponential function between temperature and ER, a correction parameter J_{TEI} was used to reflect the effect of tide (Eq. 1). Air temperature (T_a)

s was chosen as the argument, as it is more sensible than soil temperature, and could explain more variances of ER (Reichstein et al., 2005). ε is the error caused by other environmental factors.

$$\mathsf{ER} = J_{\mathsf{TEI}} R_0 e^{k \cdot T_{\mathsf{a}}} \varepsilon$$

TEI was calculated from the observations of ER and DST in early summer, when the temperature was relatively constant (range from 26.5 to 27.5 °C). Considering the effect of tide on ER may be smaller in other time, a parameter *s* was used to adjust the range of TEI into [*s*, 1]. The parameter *s* also could be seen as an index of tidal effect and a larger *s* relates to a smaller tidal effect. If *s* equals 1, it means tide have no effect on ER.

¹⁵ $J_{\text{TEI}} = \text{TEI} \cdot (1 - s) + s$

 R_0 , k and s are fitted parameters in Eq. (1). Q_{10} was calculated from k by Eq. (3).

$$Q_{10} = e^{10 \cdot k}$$
(3)

The logistic form of Eq. (1) was used for ANOVA. Relative Error was used to assess the regression.

²⁰
$$\ln(\text{ER}) = \ln(R_0) + kT_a + \ln(J_{\text{TEI}}) + \ln(\varepsilon)$$

Considering that TEI was a 15-days periodic factor and the possible failure caused by insufficient data, three lengths of window, 1-, 3- or 6-months were selected to stand for three time scales, monthly, seasonal and half-yearly. Each month was separated



(1)

(2)

(4)



by lunar calendar, and followed the cycles of the moon, containing 29 or 30 days. To prevent the over-fitting of model, the results whose residual freedom degree was less than 3 were removed. The ratio between sum square (SS_{Factor}) of each factor and total sum square (SS_{Total}) is used to illustrate the relative contributions (C_{Factor}) of temperature and tide (Eqs. 5 and 6).

$$C_{T_{a}} = SS_{T_{a}}/SS_{Total}$$

$$C_{\text{Tide}} = SS_{J_{\text{TEI}}} / SS_{\text{Total}}$$

The total contribution in one time scale was calculated by the mean of C_{Factor} .

10 3 Result

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3.1 Variation of ER and environmental factors

ER exhibited significant changes between winter and summer in 2005–2007. Respiration level was low in winter, slightly higher above zero. The peak value in summer can reach $12 \,\mu$ molm⁻² s⁻¹. The observations of two sites showed similar patterns. The respiration level in CMW1 was slightly higher than that in CMW3.

The measurements of air temperature were very close in two sites. Obvious correlation existed between ER and air temperature. Due to the high moisture content in soil, the VWC in both sites was near 1 in winter and early spring. It was about 0.6–0.7 in middle summer, significantly lower than that in winter. The seasonal dynamics of VWC was similar with air temperature.

3.2 Variation of ER in tidal cycle while temperature is relatively constant

Periodic dynamics of ER was observed during spring-neap tidal cycles (Fig. 2). Early summer observations (DOY 200–230) were used to demonstrate the relationship between ER and DST, as the temperature during that time was relatively stable (range



(5)

(6)



from 26.5 to 27.5 °C). Four and three days before the spring tide (DST equals -3 and -4), ER reached its maximum value in CMW1 (average 9.65 µmolm⁻²s⁻¹) and CMW3 (average 8.59 µmolm⁻²s⁻¹) respectively. There were clear decreases in both sites in following days and reached their minimum values one day after spring tide (DST equals 1) 3.86 µmolm⁻²s⁻¹ in CMW1 and 2.75 µmolm⁻²s⁻¹ in CMW3. There was an obvious hysteresis between ER and DST, and it was also the reason why we did not use DST to explore the tidal effect.

3.3 Relative contributions along time scale

In monthly scale, temperature explained 0–81.1 % variations of observed ER and varied from month to month. The proportion of tidal influence was 0–78.8 %. Temperature was the dominant factor in later winter–early spring (February to May) and autumn (September to November), while tide had greater influence in summer (June, July and August) (Fig. 3).

In seasonal scale, the relative contribution showed similar dynamics as monthly

scale. But relative contribution of temperature (C_{T_a}) in each window was greater than the mean value of corresponding windows in monthly scale (Fig. 3). In half-yearly scale, temperature explained 78.8–93.1% and 51.9–76.1% variations

of observed ER in CMW1 and CMW3 separately, while tidal activity only explained 0.3–1.1% (Fig. 3). The mean relative contributions of temperature in half-yearly scale
(85.3% for CMW1, 78.9% for CMW3) were much higher than that in seasonal scale (64.9% for CMW1, 44.0% for CMW3) and monthly scale (51.2% for CMW1, 37.1%)

for CMW3). The influences of temperature on ER increased with time scale, while the tidal effect decreased.

3.4 Factors that affect the relative contribution

The variances of T_a in three time scales were different. The vertical dashed-lines in Fig. 4 show boundaries of three time scales. The dotted-curves show the boundaries





of $\ln Q_{10}$. As the time scale goes larger, the range of Q_{10} becomes narrower. Four colors were used to stratify C_{T_a} levels. In monthly scale, most of red and orange dots $(C_{T_a}$ larger than 0.5) are located in the right side (the second vertical dashed-line), while the correspondent $\ln Q_{10}$ values are typically larger than 1. Green and blue dots tend to have low temperature variances or low Q_{10} values. Thus, the magnitude of C_{T_a} was determined both by T_a variance and Q_{10} is helf variable to difference the difference of the d

determined both by T_a variance and Q_{10} . In half-yearly scale, the difference between Q_{10} was much smaller, but the large variances of T_a keep the C_{T_a} at relatively high level (mostly larger than 0.5) (Fig. 4). Therefore the increases of C_{T_a} across different time scales was mainly caused by the increasing variation of T_a (Figs. 3 and 4).

It is worth to note that when the temperature variance is low (usually less than 0.2), the Q_{10} value may not be reliable. For example, Q_{10} of blue dot marked by an arrow is 66.7. It is an unreasonable high value. But if we integrated the month average temperature (17.4 °C) and the corresponded R_0 (4.88 × 10⁻³ µmolm⁻² s⁻¹) into Eq. (1) (set *s* as 1, no tidal effect), a reasonable ER (7.28 µmolm⁻² s⁻¹) would be produced. Apparently, this error was not caused by observation data but by the improper function between

temperature and ER.

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With the definition of s (tidal effect index), smaller s corresponded to higher tidal contribution. The same range of s corresponded to smaller relative contribution in half-yearly scale than monthly, which implied tidal effect decreased with time scale (Fig. 5).

20 3.5 Regression assessment

The relative errors of long-term model were higher than short-term ones (half-yearly vs. monthly, Fig. 6 bottom vs. top and middle). The relative error median of each month in long-term model was not always close to zero, which indicates there were system errors in long-term model. Respiration level was underestimated in spring and overestimated in winter (Fig. 6 bottom).

Short-term models (Fig. 6 top and middle) had much smaller system (distance between medians and zero) and random errors (the length of whisker) than long-term model. The median distribution (system error) of long-term model is [-0.34, 0.44]





(α = 0.05), short-term model with tidal effect is [-0.069, 0.11] (α = 0.05) and the without one is [-0.071, 0.14] (α = 0.05). The distribution of whisker length (random error) of long-term model is [0.36, 2.02] (α = 0.05), short-term model with and without tidal effect is [0.38, 1.52] (α = 0.05) and [0.50, 1.77] (α = 0.05) respectively.

⁵ The short-term model with tidal effect (Fig. 6 top) performed better than the without one, with smaller relative errors, especially in summer when tide had strong influence on ER (Fig. 6 top vs. middle). The AIC of models with tidal effect was also significantly smaller (p < 0.05) than the without ones.

4 Discussion

10 4.1 Long-term or short-term model

Long-term temperature sensitivity could work well in the ecosystems where factors are constant except temperature. For example, Tang et al. (2008) reported that longterm Q_{10} was suitable to estimate annual total carbon flux in an old growth forest. Two lessons of this research could be learned: (1) Q_{10} s were used to describe the responses of component respiration (soil, debris, stem and leaf) to temperature, but sampling frequency of those measurements was only 3–4 weeks once. Those exponential models are not suitable to simulate the short-term respiration variation, though enough for estimating annual value. (2) Evenly distribution of precipitation held a stable water condition and reduced the seasonal variation. Thus, high R^2 is not a solid proof for long-term temperature sensitivity, as co-variation of environmental factors helps

build the high R^2 values of long-term models.

Our results showed that relative contribution (alternation of R^2) of temperature increased with time scale. A long-term Q_{10} is not only a temperature sensitivity parameter, but also a coefficient including the information of other factors that co-vary with temperature on yearly scale (Yuste et al., 2004). The declining of tidal influences is the re-

²⁵ perature on yearly scale (Yuste et al., 2004). The declining of tidal influences is the result of this co-variation (Fig. 5). Although tidal activity did not co-vary with temperature,





the dynamics of *s* (tidal influence index) had a close relationship with seasonal variations of VWC and biomass, which were similar to the seasonal variation of temperature (not shown). We could conclude that reliability of long-term temperature sensitivity was overall overestimated.

- ⁵ Recently, it is becoming controversial that whether short-term Q_{10} s would provide more precise results. DeForest et al. (2006) showed that summer respiration was underestimated and winter respiration was overestimated by annual model. In comparison, winter respiration was underestimated and spring respiration was overestimated in our study. Short-term temperature sensitivity did reduce the relative errors (Fig. 6).
- ¹⁰ Reichstein et al. (2005) compared the temperature sensitivities derived from long-term (annual) and short-term (mainly 7- and 15-days) data, and concluded that short-term Q_{10} reduced the confounding effect of other factors. Janssens and Pilegaard (2003) believed that short-term Q_{10} derived from 4- to 7-days was still confounded by other factors. The different definitions of these two "confounding effects" are important to un-
- ¹⁵ derstand this disparity. The "confounding effect" in the former research refers to passive or active response of ER to temperature in seasonal scale, while "confounding effect" in latter research means the co-variation of temperature and other factors in the very 4- to 7-days long sub-period. Thus, there are two kinds of confounding effect: the longterm one and the short-term one. An annual or seasonal constant model would "ignore"
- the variation of temperature sensitivity. In comparison, short-term model reduces long-term confounding effect and both system and random errors (Fig. 6 top and middle vs. bottom).

The existence of short-term confounding effect made short-term temperature sensitivity also takes the risk of unreliable. Thereby, both research (Janssens and Pilegaard,

²⁵ 2003; Reichstein et al., 2005) included a test of temperature range to ensure the reliability of Q_{10} . Our study supports their results that high variation of temperature is a resistant to short-term confounding effect, and tends to achieve higher relative contribution (Fig. 4). Short-term confounding effect in our research is slightly different from the one of Janssens and Pilegaard (2003), which is not caused by co-variation but by





the relatively constant temperature condition and the alternation of main driving factor. However, both can conclude that the true response of respiration to temperature was replaced by incorrect static parameters. Short-term models with tidal effect have smaller relative errors than without ones (Fig. 6 top vs. middle), and thus identifying the main driving factor can reduce the short-term confounding effect.

4.2 Tidal influence on ER

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Reichstein et al. (2003) proposed three types of water conditions: (1) ecosystems suffered in low water content; (2) ecosystems have a suitable moisture condition, and fluctuating of which is also near optimum condition; (3) ecosystems face high water content depression. Most of the wetlands belong to the third type. Increasing water level or soil moisture content would restrict the wetland respiration through suppressing the aerobic respiration (Juszczak et al., 2012). In coastal wetland, ER showed periodical variation during spring-neap tidal cycles (Guo et al., 2009). The activity of tide, namely the variation of water level has great influence on respiration.

Lafleur et al. (2005) reported an exception where the ER of a bog was not determined by water table depth. There are two reasons to explain the poor relationship: (1) ecosystem was too "wet" and WTD did not vary enough to exert influence on respiration or (2) WTD was too small that it did not have enough influence on surface soil layer where most of CO₂ were produced and released. This can also be used to explain hysteresis between DST and ER (Fig. 2).

Similarly, the hydrological condition was too "wet" for CMW1 and CMW3 in winter. Low temperature, short sunshine duration and deciduousness of plant weakened the evapotranspiration, and hence maintained the soil water content saturated, which is the reason for why tidal activity had tiny influence on ER in winter. Process was more complex in summer. The hysteresis between DST and ER indicated that tidal elevation was a "threshold"-limited factor. One proof is that ER dropped dramatically two or three days before the spring tide. It is the right time when the elevation of tide was high enough to show influence on ER. Because CMW3 has lower elevation than CMW1, the





declining in former site began one day earlier than the latter. In the following few days, ER was suppressed at a low level. Two or three days after spring tide, tidal elevation was too small to have impact on ER. Thus, ER "recovered" from water depression and reached its maximum 4 or 5 days after the neap tide.

5 5 Conclusions

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Temperature regulated the fluctuation of ER in most of the year. When the variations of temperature became smaller in summer, tidal activity replaced temperature as the main driving factor. However, this alternation was only found in monthly scale. The relative contributions of temperature increased with time scale, while the relative contributions of tide decreased.

Long-term model was still unreliable, though with very high R^2 , as the long-term constant temperature sensitivity was confounded by other factors that co-varied with temperature in seasonal or yearly scale. The long-term confounding effect could be introduced into long-term model by ignoring the alternation of main driving factor.

- Short-term model had much smaller system and random errors and performed better. But if temperature variance was small, it still probably faced short-term confounding effect. The short-term confounding effect would magnify the relative error in short-term model, but integrating hydrologicalfactors (e.g. tide for coastal wetland) would help reduce the relative error.
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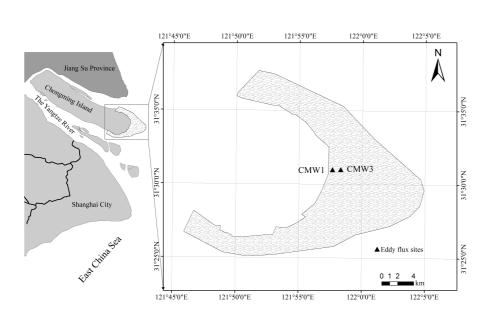


Fig. 1. Location of research sites.



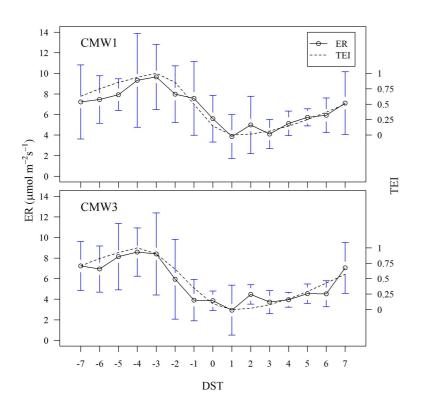
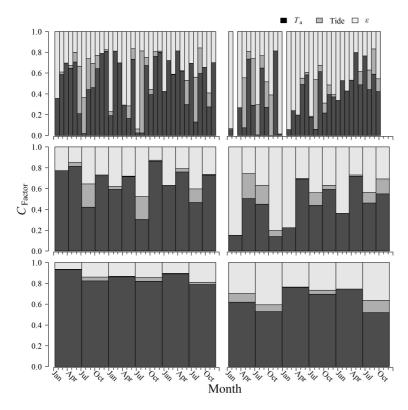
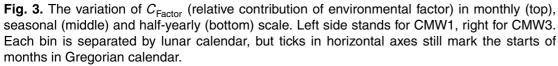


Fig. 2. The variation of ER (ecosystem respiration) during spring-neap tidal cycles. Solid line is ER, dashed line is the fitting line, TEI (tidal effect index). Top for CMW1, bottom for CMW3.











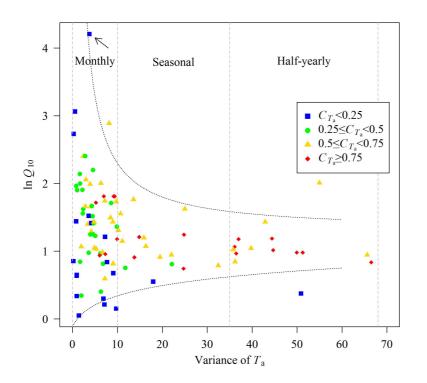


Fig. 4. The vertical dashed-lines show the typical range of variance of T_a (air temperature) of three temporal scales. The dotted-curves show the boundaries of Q_{10} distribution. Different colors represent different C_{T_a} (relative contribution of air temperature) level.



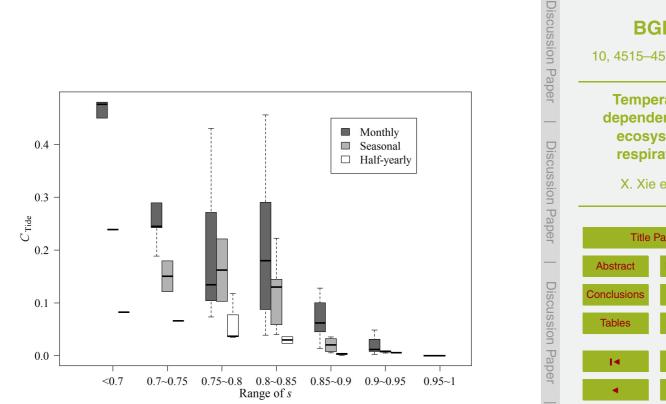


Fig. 5. C_{Tide} -*s* relationship in different temporal scales. Monthly scale has much higher C_{Tide} (relative contribution of tide) value than half-yearly while *s* (tidal effect index) less than 0.9.



Discussion Paper

