Modelling the diurnal and seasonal dynamics of soil CO$_2$ exchange in a semiarid ecosystem with high plant-interspace heterogeneity

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Abstract

In this study we investigated i) the roles of different C-flux components in regulating soil CO$_2$ exchanges ($F_S$) in a dryland ecosystem of high plant-interspace heterogeneity, and ii) plant-interspace differences in the C flux components. A process-based approach was used to model the diurnal and seasonal dynamics of $F_S$, which considered simultaneously the CO$_2$ production, transport and surface exchanges (e.g. biocrust photosynthesis, respiration and photodegradation). The model was parameterized and validated with multivariate data measured during year 2013-2014 in a semiarid shrubland ecosystem in Yanchi, northwestern China. The model explained reasonably well the $F_S$ dynamics measured from a non-crusted and two lichen-crusted plots during a two-year period. The model simulation showed that, soil rewetting could enhance CO$_2$ dissolution and delay the emission of CO$_2$ produced from root-zone. In addition, an ineligible fraction of respired CO$_2$ might be removed from soil volumes under respiration chambers by lateral water flow and root uptake. During rewetting, the lichen-crusted soil could shift temporally from net CO$_2$ source to sink, due to the photosynthesis of lichens and restricted CO$_2$ emissions from subsoil. The presence of plant cover could decrease the root-zone CO$_2$ production and biocrust C sequestration, but increase the temperature sensitivities of these fluxes. On the other hand, the sensitivities of root-zone emissions to water content were decreased by canopy, which may be due to the advection of water flows from the interspace. To conclude, the complexity and plant-interspace heterogeneities of soil C processes should be carefully considered to extrapolate findings from chamber to ecosystem scales, and to predict the ecosystem responses to climate change and extreme climatic events. Our model can serve as a useful tool to simulate the soil CO$_2$ efflux dynamics in dryland ecosystems.
Keyword: ecosystem modelling; heterogeneity; inorganic carbon; semiarid shrub ecosystem; biocrust

1. Introduction

The CO₂ exchange between soil and atmosphere constitutes a major C loss from terrestrial ecosystems (Raich et al., 2002; Giardina et al., 2014). It also plays an important role in the feedbacks between global carbon cycle and climate change (Rustad et al., 2000; Giardina et al., 2014; Karhu et al., 2014). Arid and semiarid (dryland) ecosystems cover over 40% of land surface and contribute notably to inter-annual variations of terrestrial C sink (Poulter et al., 2014). However, the contribution of soil CO₂ flux (Fₛ) from those ecosystems to the global C budget is less-studied (Castillo-Monroy et al., 2011; Gao et al., 2012; Jia et al., 2014). The temperature dependency of biological CO₂ production (i.e. autotrophic respiration and heterotrophic respiration) serves a conventional basis for Fₛ modelling in many terrestrial ecosystems (Raich and Tufekciogul, 2000; Ryan, 2005; Song et al., 2015). Soil CO₂ flux of dryland ecosystems is also widely interpreted using temperature-response functions modified by other environmental constraints, e.g. soil water content, abundances of substrates and microbial activities (Curiel Yuste et al., 2007; Wang et al., 2014a, 2014b, 2015).

Although many empirical studies have explained the dynamics of soil CO₂ flux in specified space-time, their lack of mechanistic descriptions represents a major difficulty in extrapolation under changing environmental conditions (Fan et al., 2015). Soil CO₂ flux is a “bulk” exchange that comprises two main sets of processes, i.e. the CO₂ production and transport (Fang and Moncrieff, 1999; Fan et al., 2015). Hence, models considering only autotrophic and heterotrophic respiration often fail to account for the observed Fₛ dynamics (Austin and Vivanco, 2006). Gas transport processes are important mechanisms regulating the magnitude and hysteretic feature of soil CO₂ efflux (Ma et al., 2013). A substantial fraction of respired CO₂ may be transported to atmosphere via xylem, and may not be measured by techniques like soil repARATION chambers (Bloemen et al., 2013; 2016). During wet periods, soil CO₂ efflux could decrease significantly by water clogging of soil pores, which restricts the diffusion of O₂ and CO₂ gases (Šimunek and Suarez, 1993; Fang and Moncrieff, 1999). In dryland soils of high salinity/alkalinity, CO₂ transport and water cycle are tightly coupled, as large inorganic C fluxes can be driven solely by dissolution and infiltration of CO₂ and carbonates (Buysse et al., 2013; Ma et al., 2013; Fa et al., 2014). Such inorganic transport may not only introduce fluctuations to hourly or diurnal soil CO₂ efflux (e.g. Emmerich, 2003; Xie et al., 2009; Buysse et al., 2013), it may also to terrestrial CO₂ sinks at much broader spatiotemporal scales (Schlesinger, 2009; Li et al., 2015).

Key processes contributing to CO₂ production in dryland soils also extend beyond autotrophic respiration and heterotrophic respiration. Although biocrust organisms (lichens, mosses, bacteria, fungi and microfauna) inhabit in the top few centimetres of the soil profile, they constitute up to 70% of biomes in interspace areas (Belnap, 2003). These communities are able to uptake C from the
atmosphere (Belnap, 2003; Castillo-Monroy et al., 2011; Maestre et al., 2013), leading to largely
greater concentration of organic matter in the crusted layer than the soil underneath (Ciais et al., 2013).
Although crust organisms could be inactive under stresses (e.g. drought, Green and Proctor, 2016),
their photosynthetic potential could be large (Zaady et al., 2000; Lange, 2003), even comparable to
temperate forests with closed canopies (e.g. Zaady et al., 2000). The net C uptake by biocrust is
highly sensitive to stresses like droughts, thermal extremes and excessive ultraviolet radiation
(Pointing and Belnap, 2012). Such variations can readily alter the crusted soils between considerable
CO$_2$ sinks and sources within a few hours (e.g. Bowling et al., 2011; Feng et al., 2014). In addition,
the accumulation of debris from crust and canopy fuels photodegradation, which represents an
important abiotic C loss in arid conditions beside the biotic decomposition (e.g. Austin and Vivanco,
2006; Throop et al., 2009). Photodegradation is likely to dominate the mineralization during dry
daytime periods, when radiation is strong and microbial activities are prohibited by low moisture
content and high temperature (e.g. Gliksman et al., 2016). On an annual basis, photodegradation could
consume more than 10% of soil organic matter (SOM) at surface (e.g. Austin and Vivanco, 2006;
Henry et al., 2008; Brandt et al., 2010), even for the substrates (e.g. lignin) that are difficult to degrade
via biotic pathways (Henry et al., 2008).

The influences of multiple C processes (i.e. autotrophic and heterotrophic respiration, net C uptake
by biocrust, inorganic C fluxes and photodegradation) on soil CO$_2$ exchange are highly overlapped
and tightly related to the water-energy processes. In dryland ecosystems, patchy vegetation and large
fractions of interspace are common features (Domingo et al., 2000), and the water-thermal conditions
can vary considerably from plant cover to interspace even within a few meters (Rodríguez-Iturbe et al.,
2001; Caylor et al., 2008; Ma et al., 2011). The water-energy dynamics at the different surfaces are
linked by multiple advection processes both above- and below-ground (Gong et al., 2016). Due to the
complexity of water-energy processes, there may exist possibly high non-linearity of water-thermal
responses to the climatic variability (e.g. Phillips et al., 2011; Barron-Gafford et al., 2013). This will
also complicate the C responses and consequently affect the relationships between the CO$_2$ fluxes and
environmental controls (e.g. Jarvis et al., 2007; Song et al., 2015).

Global climate change is expected to increase annual mean air temperature considerably and alter
precipitation regimes (Donat et al., 2016). Understanding the response of dryland ecosystems to such
changes requires mechanistic models that integrate the multiple biotic and abiotic mechanisms in soil
C cycling. So far, only a few models have coupled the biotic CO$_2$ production with the transport of gas
and heat (Šimunek and Suarez, 1993; Fang and Moncrieff, 1999; Phillips et al., 2011; Ma et al., 2013;
Fan et al., 2015). Nevertheless, none of those models has described the heterogeneous water-energy
processes in soil-vegetation-atmosphere continuum (SPAC), or the unconventional C fluxes such as
net C uptake by biocrust and photodegradation despite the importance of these processes in arid and
semiarid environments. Perhaps, models by Porada et al. (2013) and Kinast et al. (2016) represent the
few existing works in this sense. However, both the models focus on the patterns at the regional-scale with very simplified ecosystem processes.

The aims of this study are: i) to investigate the roles of soil CO$_2$ components in regulating soil CO$_2$ effluxes in the studied ecosystem, and ii) to estimate the plant-interspace differences in the componental C processes. For these purposes, we developed a process-based model, which considered simultaneously the CO$_2$ production, transport and surface exchanges (e.g. biocrust photosynthesis, respiration and photodegradation). Based on the water-energy modelling of Gong et al. (2016), the model development focused on the CO$_2$ production and transportation in root-zone soil, and the C exchanges driven by surface processes, such as biocrust metabolism and photodegradation. The model was run at half-hourly time step to capture the responses of soil CO$_2$ effluxes to rain pulses and diurnal variations of radiation and thermal conditions. The model was parameterized and validated by multi-variant data measured during year 2013-2014 in a semiarid shrubland ecosystem in Yanchi, northwestern China. A series of sensitivity analysis were then carried to study the effects of stand-scale heterogeneities and the complexity of soil C processes in regulating the soil CO$_2$ exchanges in the dryland ecosystem.

2. Materials and methods

2.1 Model overview

The process-based model was build based on semiarid shrubland ecosystem located at the southern edge of the Mu Us desert (37°42'1" N, 107°13'7" E, 1560 m above sea level, Fig. 1a), Ningxia, China (see Wang et al., 2014a, 2015). The long-term mean temperature (1954–2004) is 8.1 °C, and the mean annual precipitation is 287 mm, most of which falls from July to September (Jia et al., 2014). The radiation and evaporation demand are high in this area, i.e. the annual incoming shortwave radiation is $1.4 \times 10^5$ J cm$^{-2}$ and the annual potential evaporation is 2024 mm. The vegetation is dominated by scattered crowns of *Artemisia ordosica* (Fig. 1b). The soil is highly alkaline (pH = 8.2). Biocrust (mainly lichens and algae) covers about 40% of interspace soil (Fig. 1c - 1e). The thickness of the crust layer was 0.5 – 2.5 cm (Gong et al., 2016).

In the modelling, the structure of ecosystem was considered as replications of “representative land units” (RLU, Fig. 1f; Gong et al., 2016), which comprises the area covered by shrubs and the surrounding soil (interspace). Vertically, the model simulates the C flows over the soil profile and the water-energy transport from the lower boundary of rooting zone to a reference height in the boundary atmosphere. Horizontally, the SPAC processes at plant cover and the surrounding interspace are differentiated but related via advection and diffusion flows, as driven by the gradients of temperature,
water potential and gas concentrations. The mineralization, uptake and transport of soil C and N are further regulated by water-energy conditions. 

Fig. 2 shows the framework of key processes and variables included in the F_s modelling. The model includes a set of sub-models, which describe: (i) CO₂ dissolution, transport and efflux; (ii) Autotrophic and heterotrophic CO₂ production in the soil profile; (iii) CO₂ uptake and emission by biocrust; (iv) Surface energy balance and soil temperature profile; and (v) Soil hydrology and water balance. These sub-models are linked by multiple feedbacks to represent the coupling of C, water, vapor and energy transportations in the ecosystem. Sub-models (iv) - (v) have been developed and described in details in our previous work (Gong et al. 2016), which focused on (i) introducing the plant-interspace heterogeneity into water-energy modelling, and (ii) investigating the influences of such heterogeneity on the ecosystem water-energy budgets for a dryland ecosystem. Gong et al. (2016) also validated the model in regard to the diurnal to seasonal dynamics of radiation balance, surface energy balance, soil temperature and moisture content in the footprint area of a eddy-covariance (EC) site (details of measurement see Jia et al., 2014). In this work, we therefore focused on the development of sub-models (i) – (iii) and their parameterization and validation by F_s measurements, based on automatic respiration chambers from crust-covered and non-crusted soils. Based on the validated model, we also analyzed the model sensitivities to stand parameters and plant-interspace heterogeneity and investigated the relative contribution of different flux components to F_s.

2.2 Modelling approaches

2.2.1 Submodel (i): CO₂ transport, dissolution and efflux

For soil fraction x (see Fig. 1f for RLU settings), CO₂ exchange (F_s, upward positive) was the sum of CO₂ exchange by biocrust (F_C), photodegradation (F_P) and the emission from soil under the biocrust layer (F_T):

\[ F_{Sx} = F_{Cx} + F_{Tx} + F_{P} \]  \hspace{1cm} (1)

where F_C is the net balance between biocrust photosynthesis (P_C) and respiration (R_C), and F_C = P_C – R_C (see Section 2.2.3). F_T was modelled based on the mass-balance functions developed by Fang and Moncrieff (1999), and combined major transport processes in both gaseous and liquid phases. To account for the plant-interspace heterogeneity, we expanded the original one-dimensional function to the two-dimensional space. For soil layer (x, i) and time step t, the CO₂ concentration and C flows were calculated as follows:

\[ \frac{\partial \bar{C}_{xi}}{\partial t} = \frac{\partial}{\partial z} \left( F_{dg}^v + F_{dg}^h + F_{dw}^v + F_{dw}^h \right) + \frac{\partial}{\partial h} \left( F_{dh}^v + F_{dh}^h + F_{dh}^v + F_{dh}^h \right) + S_{x,i} \]  \hspace{1cm} (2)
where superscripts \( v \) and \( h \) denote the vertical and horizontal directions, respectively (see also in Gong et al., 2016); \( C \) is the total CO\(_2\) content; \( F_{dg} \) and \( F_{dw} \) are the CO\(_2\) flows due to diffusion/dispersion via the gaseous and liquid phases; \( F_{ag} \) and \( F_{aw} \) are the flows in gaseous and liquid phases due to gas convection and water movement, and \( S \) is the net CO\(_2\) sink of the layer. The calculation schemes of \( F_{dg}, \ F_{dw}, \ F_{ag} \) and \( F_{aw} \) have been described in detail by Fang and Moncrieff (1999). \( F_T \) is the total exchange of gaseous CO\(_2\) between surface and topmost layer:

\[
F_{Tx} = F_{dgx,1}^v + F_{agx,1}^v + E_{sx,1}^s C_{wx,1} \tag{3}
\]

where \( E_{sx,1}^s \) is the soil evaporation at section \( x \) (see Eq. (17) in Gong et al., 2016); \( C_u \) is the equivalent CO\(_2\) concentrations in the solution of the topmost soil. For layer \((x, i)\), \( C_u \) is linked to the gaseous CO\(_2\) concentrations \((C_g)\):

\[
C_{x,i} = C_{gx,i}(V_{x,i} - \theta_{x,i}) + C_{wx,i}\theta_{x,i} \tag{4}
\]

where \( V \) is the total porosity; and \( \theta \) is soil water content.

\( C_g \) and \( C_w \) were further related via the dissolution-dissociation balance of CO\(_2\) in soil solution, following Fang and Moncrieff (1999) and Ma et al. (2013):

\[
\text{CO}_2(g) + H_2O(l) \rightleftharpoons H_2O(l) + \text{CO}_2^{aq} \quad K_H = P_C/\text{CO}_2^{aq} \tag{5}
\]

\[
\text{CO}_2(aq) + H_2O(l) \rightleftharpoons H_2\text{CO}_3 \quad K_0 = \text{CO}_2^{aq}/[H_2\text{CO}_3] \tag{6}
\]

\[
H_2\text{CO}_3 \rightleftharpoons [H^+] + [\text{HCO}_3^-] \quad K_1 = [H^+][\text{HCO}_3^-]/[H_2\text{CO}_3] \tag{7}
\]

\[
\text{HCO}_3^- \rightleftharpoons [H^+] + [\text{CO}_3^{2-}] \quad K_2 = [H^+][\text{CO}_3^{2-}]/[\text{HCO}_3^-] \tag{8}
\]

where \( P_C \) is the partial pressure of CO\(_2\) in pore air; \( K_H \) is Henry’s Law constant; \( K_0, K_1 \) and \( K_2 \) are equilibrium coefficients of dissolution, the first- and the second-order dissociation reaction for carbonic acid, respectively (for details see Fang and Moncrieff, 1999). The equilibrium \([H^+]\) was determined by the soil pH and the coefficients \( K_{H^+}, K_0, K_1 \) and \( K_2 \), which were functions of soil temperature in each soil layer (Fang and Moncrieff, 1999). \( C_w \) was calculated as the sum of \( \text{CO}_2^{aq}, \ H_2\text{CO}_3, \ \text{HCO}_3^- \) and \( \text{CO}_3^{2-} \).

### 2.2.2 Submodel (ii): autotrophic and heterotrophic CO\(_2\) production along the soil profile

For soil layer \((x, i)\), \( S_{x,i} \) (Eq. 2) was calculated as the sum of autotrophic and heterotrophic CO\(_2\) production, and the dissolved CO\(_2\) removed with the water uptaken by roots:

\[
S_{x,i} = R_s x,i + R_a x,i - E_{x,i} C_{w,x,i} \tag{9}
\]

where \( E \) is the transpirative uptake of water (Gong et al., 2016); \( R_s \) is the CO\(_2\) production by heterotrophic SOM decomposition; \( R_a \) is the autotrophic respiration of the rhizosphere, which comprises maintenance respiration \((Rm)\) and growth respiration \((Rg)\):
\[ R_{ax,i} = Rm_{x,i} + Rg_{x,i} \]  

(10)

To simulate \( R_s \), we simplified the pool-type model of Gong et al. (2013, 2014), which was originated from Smith et al. (2010) for simulating coupled C and N cycling in organic soils. SOM pool in each soil layer was divided into debris \( (M_{deb}, \text{i.e. litters from roots and biocrust}) \), microbes \( (M_{mic}) \) and humus \( (M_{hum}) \), which are different in biochemical recalcitrance and N content. During decaying, mineralized masses transfer from \( M_{deb} \) and \( M_{mic} \) to more resistant form (i.e. \( M_{hum} \)), leading to a decrease in lability (e.g. Li et al., 1992). The mineralization of organic C followed first-order kinetics and was constrained by multiple environmental multipliers, including temperature, water content and oxygen content (Šimunek and Suarez, 1993; Fang and Moncrieff, 1999):

\[ m_{x,i}^r = M_{x,i}^r k_r f(T_{s,i}) f(\theta_{x,i}) f(O_{x,i}) dt \]  

(11)

where superscript \( r \) denotes the type of SOM pool \((r=1 \text{ for } M_{deb}, r=2 \text{ for } M_{mic}, \text{ and } r=3 \text{ for } M_{hum})\); \( m \) is mineralized SOM during time step \( dt \); \( k \) is the decomposition constant; \( dt \) is time step; \( f(T_{s,i}), f(\theta_{x,i}) \) and \( f(O_{x,i}) \) are multiplier terms regarding the temperature, water content and oxygen restrictions, respectively. \( f(O_{x,i}) \) was calculated following Šimunek and Suarez (1993). \( f(T_{s,i}) \) and \( f(\theta_{x,i}) \) were reparameterized with respect to the site-specific conditions of plants and soil (see section 2.4.3). The CO\(_2\) production from mineralization was further regulated by the N-starvation of microbes following Smith et al. (2010):

\[ R_{s_{x,i}} = r_E m_{x,i}^r \]  

(12)

where \( r_E \) is the gas production rate \((r_E \epsilon [0, 1])\), and \((1- r_E)\) is the proportion of organic matters passed to the downstream SOM pools. The evolution of each SOM pool was calculated as below:

\[ M_{x,i}^r = (1 - r_E) m_{x,i}^{r-1} - m_{x,i}^r + A_{x,i}^r dt \]  

(13)

where \( A \) is the SOM input rate \((A=0 \text{ for } M_{mic} \text{ and } M_{hum})\); superscript \( r-1 \) denotes the source SOM pools. \( R_{s_{x,i}} \) was calculated in a similar way to \( R_{s_{x,i}} \) (e.g. Chen et al., 1999; Fang and Moncrieff,1999). \( R_{g_{x,i}} \) was calculated as a fraction of photosynthetic assimilates, following Chen et al. (1999):

\[ R_{m_{x,i}} = M_{x,i}^R k_R f(T_{s,i}) f(\theta_{x,i}) f(O_{x,i}) dt \]  

(14)

\[ R_{g_{x,i}} = k_g P_g f r_{x,i} \]  

(15)

where \( M^R \) is the root biomass; \( k_R \) is the specific respiration rate of roots; \( k_g \) is the fraction of photosynthetic assimilate consumed by growth respiration; \( f r_{x,i} \) is the mass fraction of roots in soil layer \((x, i)\). \( P_g \) is the photosynthesis rate of plants. \( P_g \) was estimated using a modified Farquhar’s leaf biochemical model (see Chen et al., 1999). This model simulates photosynthesis based on biochemical parameters (i.e., the maximum carboxylation velocity, \( V_{\text{max}} \), and maximum rate of electron transport, \( J_{\text{max}} \)), foliage temperature \((T_c)\) and stomatal conductance \((g_s)\). The values of \( V_{\text{max}} \)
and $J_{\text{max}}$ were obtained from in situ measurements from the site (Jia et al., unpublished). $T_c$ and $g_s$ were given in the energy balance sub-model, which was detailed in Gong et al. (2016).

N content bonded in SOM mineralized and was added to soil layers simultaneously with decaying. The abundance of mineral N (i.e. $\text{NH}_4^+$ and $\text{NO}_3^-$) regulates the growth of microbial biomass and $r_E$ following Smith et al. (2010) and Gong et al. (2014). Key processes governing the dynamics of mineral N pools included nitrification-denitrification (Smith et al., 2010), solvent transport with water flows (Gong et al, 2014) and the N uptake by root system. However, the plant growth was not modelled in this work and therefore, $N_{\text{upt}}$ was calculated using the steady-state model of Yanai (1994), based on the transpiration rate, surface area of fine roots and the diffusion of solvents from pore space to root surface:

$$N_{\text{upt}} = 2\pi r_o L a C_o dt \quad (16)$$

where $r_o$ is the fine root diameter; $L$ is the root length, and $2\pi r_o L$ is the surface area of fine roots; $a$ is the nutrient absorbing power, which denotes the saturation degree of solute uptake system ($a \in [0, 1]$); $C_o$ is the concentration of solvents at the root surface, and is a function of bulk concentration of mineral N ($N_{\text{min}}$), inward radial velocity of water at the root surface ($v_o = E/(2\pi r_o L)$) and saturation absorbing power $a$. Further details for calculations of $a$ and $C_o$ can be found in work of Yanai (1994).

2.2.3 Submodel (iii): CO$_2$ exchange of biocrust and photodegradation

Biocrusts are vertically layered systems that comprise topcrust (or, bio-rich layer) and underlying subcrust (or, bio-poor layer), which are different in microstructure, microbial communities and C functioning (Garcia-Pichel et al., 2016; Raanan et al., 2016). Topcrust is usually few-millimetre thick, which allows the penetration of light and the development of photosynthetic microbes (Garcia-Pichel et al., 2016). On the other hand, the subcrust has little photosynthetic-activity. We here focused mainly on describing the C exchanges in the topcrust, but assumed the C processes in the subcrust were similar to those in the underneath soil. We developed the following functions to describe the C fixation and mass balance in the topcrust,

$$F_{Ct} = P_{Ct} - R_{Ct} \quad (17)$$

where $P_{Ct}$ is the bulk photosynthesis rate; and $R_{Ct}$ is the bulk respiration rate. $P_C$ and $R_C$ were further modelled as follows:

$$P_{Ct} = \frac{\alpha_C A_{\text{PAR}} P_{Cm}}{\alpha_C A_{\text{PAR}} + P_{Cm}} \quad (18)$$

$$R_{Ct} = M_{Ct} k_{cr} f_{RC}(T_{Ct}) f_{RC}(\theta_{Ct}) \quad (19)$$
where $\alpha_C$ is the apparent quantum yield, $P_{Cm}$ is the maximal rate of photosynthesis, and was a function of the moisture content ($\theta_{Ct}$) and temperature ($T_{Ct}$) in topcrust; $A_{PAR}$ is the photosynthetically active radiation (PAR); $M_C$ is the total C in the SOM of topcrust; $k_r$ is the respiration coefficient; $f(\theta_{Ct})$ and $f(T_{Ct})$ are water and temperature multipliers. Here, we assumed no photosynthesis in subcrust. The heterotrophic respiration ($R_{Cs}$) was calculated as was done for soil respiration (Eq. (11)) based on the C storages ($M_{s,i}$) and temperature and moisture content of crust layer (i.e. $T_{s,i}$ and $\theta_{s,i}$; see Eq. (29) and Eq. (14) in Gong et al., 2016).

To consider different C losses and exchanges, and to calculate the C balance in topcrust and subcrust, respectively, we considered the following matters. $R_{Ct}$ includes the respirations from both autotrophic ($M_{CA}$) and heterotrophic ($M_{CH}$) pools. When autotrophic organisms die, SOMs pass from $M_{CA}$ to $M_{CH}$ and influence the turnover processes. A variety of topcrust organisms can reach into subcrust (e.g. through rhizines, Aguilar et al., 2009) and export litters there. When the surface is gradually covered by deposits, topcrust organisms tend to move upward and recolonize at the new surface (e.g. Garcia-Pichel and Pringault, 2001; Jia et al., 2008), leaving old materials buried into the subcrust (Felde et al., 2014). On the other hand, the debris left to soil surface are exposed to photodegradation. Based on above, the C balance in topcrust and subcrust was calculated as following, assuming the partitioning of respiration between autotrophic and heterotrophic pools was proportional to their fractions:

$$\begin{align*}
M_{Ct} &= M_{CA} + M_{CH} \\
\frac{dM_{CA}}{dt} &= P_{Ct} - R_{Ct} \frac{M_{CA}}{M_{Ct}} - k_m M_{CA} - k_b M_{CA} \\
\frac{dM_{CH}}{dt} &= k_m M_{CA} - R_{Ct} \frac{M_{CH}}{M_{Ct}} - k_b M_{CH} - F_p \\
\frac{dM_{Cs}}{dt} &= k_b M_{Ct} - R_{Cs}
\end{align*}$$

where $k_m$ is the rate of C transfer (e.g. mortality) from autotrophic pool to heterotrophic pool; $k_b$ is the rate of C transfer (e.g. burying) from topcrust to subcrust; $F_p$ is the loss of SOM due to photodegradation.

Photodegradation tends to decrease surface litter masses in a near linear fashion with the time of exposure (Austin and Vivanco 2006; Vanderbilt et al., 2008). Considering the diurnal and seasonal variations of radiation, $F_p$ was calculated as a function of surface SOM mass and solar radiation:

$$F_{p_x} = M_{surf} k_p Rad_x$$

where $Rad_x$ is the incident shortwave radiation at surface $x$ (Gong et al., 2016); $M_{surf}$ is the surface litter mass; and $k_p$ is the photodegradation coefficient.
2.3 Micrometeorological and soil CO$_2$ efflux measurements

Meteorological variables were measured every 10 seconds and aggregated to half-hourly resolution during 2013-2014. The factors measured included the incoming and outgoing irradiances (PAR-LITE, Kipp and Zonen, the Netherlands), PAR (PAR-LITE, Kipp and Zonen, the Netherlands), air temperature and relative humidity (HMP155A, Vaisala, Finland). Rainfall was measured with a tipping bucket rain gauge (TE525WS, Campbell Scientific Inc., USA) mounted at a nearby site (1 km away, see Wang et al., 2014a). The seasonal trends of the measured $T_a$ and $P$ can be found in Jia et al. (2016). No surface runoffs were observed at the site, indicating the horizontal redistribution of rainfall was mainly through subsurface flows.

Continuous measurements of $F_S$ were conducted using an automated soil respiration system (model LI-8100A fitted with a LI-8150 multiplexer, LI-COR, Nebraska, USA). The system was on a fixed sand dune of typical size (Wang et al., 2014a), which was located about 1.5 km south from the EC tower described in Gong et al (2016). Three collars (20.3 cm in diameter and 10 cm in height, of which 7 cm inserted into the soil) were installed on average at 3m spacing in March 2012. One collar (C1, see Fig. 1c) was set on a bare soil microsite with no presence of biocrust. Two other chambers (C2, see Fig. 1d and C3, see Fig. 1e) were set on lichen-crusted soils. $F_S$ was measured hourly from C1 and C2 by opaque chambers, whereas by transparent chamber from C3 to include the photosynthesis and photodegradation. Litters from the shrub canopies were cleared from the collars during weekly maintenance. Hourly $T_s$ and $\theta$ at 10 cm depth were measured outside each chamber using the 8150–203 soil temperature sensor and ECH2O soil moisture sensor (LI-COR, Nebraska, USA), respectively. Root biomass was sampled near each collar (within 0.5 m) in July 2012, using a soil corer (5 cm in diameter) to a depth of 25 cm. The samples were mixed and sieved sequentially through 1, 0.5 and 0.25 mm meshes, and the living roots were picked by hands. The comparison of the three micro-sites is shown in Table 1. Methods used in data processing and quality control have been described earlier in details (see Wang et al., 2014a, 2015). The quality control led to gaps of 10 - 13% in the $F_S$ dataset.

2.4 Model set-ups

2.4.1 Parameterization of vegetation and soil texture

The parameterization schemes supporting the simulations of energy balance and soil hydrology in sub-model (i) - (v) have been described previously in detail by Gong et al. (2016). As the water-energy budget is sensitive to vegetation (i.e. canopy size, density and leaf area) and soil hydraulic properties (see Gong et al., 2016), we hereby revalued these parameters for the $F_S$ site. Measurements based on four 5mx5m plots showed that the crown diameter $D$ (86 ± 40 cm) and height $H$ (47± 20 cm)
at this site were similar to those measured from the eddy-covariance (EC) footprint by Gong et al. (2016). However, the shrub density was 50% greater, leading to higher shrub coverage (42%), shorter spacing distance \( L \) (40.2 cm) and greater foliage area. On the other hand, the subsoil at the F5 site is sandy and much coarser than that at the EC footprint. Therefore, we collected 12 soil cores from 10 cm depth, and measured saturated water content \( (\theta_{sat}) \), bulk density and residual water content \( (\theta_r) \) from each sample. Then, the samples were saturated, and covered and drained by gravity. We measured the water content after 2-hour and 24-hour draining, which roughly represented the matrix capillary water content (10 kPa) and field capacity (33 kPa) (Armer, 2011). The shape parameters \( n \) and \( a_h \) (see Eq. (26) in Gong et al. 2016) for the water-retention function were estimated from these values (Table 2).

### 2.4.2 Parameterization of soil C and N pools

The sizes and quality of soil C pools were parameterized based on a set of previous studies. The total SOC in the root-zone soil (i.e. 60 cm depth, bulk density of 1.6 g cm\(^{-3}\)) was set to 1200 g m\(^{-2}\), based on the values reported from previous studies in Yanchi area (e.g. Qi et al., 2002; Chen and Duan, 2009; Zhang and Hou, 2012; Liu et al., 2015; Lai et al., 2016). The mass fraction of resistant SOM pool \( (M_{hum}) \) was set to 40 - 50 \% of total SOM, following work by Lai et al. (2016). The vertical distribution of the SOM pools was described following Shi et al. (2013). At the ecosystem level, the aboveground biomass was linearly related to the crown projection area \( (M^a = 0.2917 \pi(0.5D)^2, \text{see Zhang et al., 2008}) \). The total root biomass was then calculated as proportional to the aboveground biomass, using a root-shoot ratio of 0.47 \( (M^r = 0.47M^a, \text{Xiao et al., 2005}) \). The vertical profile of root biomass was parameterized as decreasing exponentially with depth, using the depth profile reported by Lai et al. (2016). On the horizontal direction, root biomass was set to decrease linearly with the distance from the centre of a shrub crown (Zhang et al., 2008). The N content was parameterized following the measurement of Wang et al. (2015).

Based on the above settings, the specific decomposition rate of debris was estimated from the litterbag experiment of Lai et al. (2016), which showed a 16% decrease in the mass of fine-root litters during a 7-month period of year 2013 at the Yanchi site. The photodegradation coefficient \( (k_p) \) was set to 0.23 yr\(^{-1}\), which was the mass-loss rate reported by Austin and Vivanco (2006). \( M_{surf} \) was set to 33\% of \( M_{CH} \) in topcrust, assuming the depth of light penetration was about 2 mm and C concentration was homogeneous in topcrust. The surface litter from canopy was not considered in this modelling, as the plant litters were cleaned from the collars during weekly maintenance. The specific respiration rate of roots \( (k_R) \), however, could be much greater during vegetative growing stage than other periods, e.g. at the defoliation stage (Fu et al., 2002; Wang et al., 2015). Here we linked \( k_R \) to the development of foliage in modelling using the approach of Curiel Yuste et al. (2004):

\[
k_R = k_{R0}(1 + n_RL_i/L_{max})
\]

(25)
where \( k_{\text{ROI}} \) is the “base” respiration rate (Table 2); \( L_l \) is the green leaf area, which is a function of Julian day (Gong et al., 2016); \( L_{\text{max}} \) is the maximum \( L_l \); \( n_R \) is the maximum percentage of variability and is set to 100%.

### 2.4.3 Parameterization of soil CO\(_2\) production

Based on the empirical study of Wang et al. (2014a), the steady-state sensitivity of CO\(_2\) production to soil temperature and water content (i.e., \( f(Ts)f(\theta) \), Eq. (11)) can be described as a logistic-power function:

\[
f(Ts)f(\theta) = f(Ts, \theta) = \left(1 + \exp[\alpha(b - Ts)]\right)^{-1}(\theta/\theta_{\text{sat}})^c
\]

(26)

where \( a, b \) and \( c \) are empirical parameters. This function represents the long-term water-thermal sensitivity of CO\(_2\) production over the growing seasonal, yielding an apparent temperature sensitivity \( Q_{10} \) of 1.5 for the emitted CO\(_2\) (Wang et al. 2014a). However, this could underestimate the short-term sensitivities of CO\(_2\) production. The apparent \( Q_{10} \) could be much greater at the diurnal level than at the seasonal level (Wang et al., 2014a). In this work, we firstly calculated the “base” sensitivity using the long-term scheme (Eq. 26) with 1-day moving average of water-thermal conditions. Then the deviation of hourly sensitivity from “base” condition was adjusted by the short-term \( Q_{10} \):

\[
f(Ts)f(\theta) = f(Ts_{\text{short}}, \theta_{\text{short}}) + \left[f(Ts, \theta) - f(Ts_{\text{short}}, \theta_{\text{short}})\right]Q_{10}^{(Ts-Ts_{\text{short}})/10}
\]

(27)

\[
Q_{10} = \max \left[ Q_{10}(Ts_{\text{short}}), Q_{10}(\theta_{\text{short}}) \right]
\]

(28)

\[
Q_{10}(Ts_{\text{short}}) = -0.42Ts_{\text{short}} + 12.4
\]

(29)

\[
Q_{10}(\theta_{\text{short}}) = 18010 \theta_{\text{short}}^{3.721} + 1.604
\]

(30)

where \( Ts_{\text{short}} \) and \( \theta_{\text{short}} \) are the 1-day moving averages of \( Ts \) and \( \theta \), respectively; \( Q_{10}(Ts) \) and \( Q_{10}(\theta) \) are the adjustment functions for short-term apparent \( Q_{10} \), regarding the short-term \( Ts \) and \( \theta \).

Further non-linearity of soil respiration responses refers to the rain-pulse effect (or the “Birch effect”, Jarvis et al. 2007), that respiration pulses triggered by rewetting can be orders-of-magnitude greater than the value before rain event (Xu et al., 2004; Sponseller, 2007). Such response could be very rapid (e.g. within 1 hour to 1 day, Rey et al. 2005) and sensitive to even minor rainfalls. It also seems that the size and duration of a respiration pulse not only depend on the precipitation size, but also on the moisture conditions prior to the rainfall (Xu et al., 2004; Rey et al., 2005; Evans and Wallenstein, 2011). As numerical descriptions on such an effect remain unavailable at the moment, we simply multiplied Eq. (26) to a rain-pulse coefficient \( f_{\text{pulse}} \):

\[
f_{\text{pulse}} = \max[1, (\theta/\theta_{72h})^\gamma]
\]

(31)
where is the 3-day moving average of soil moisture content; \( n_p \) is a shape parameter and was set to 2 in this study. \( \theta_{72h} \) is the 72-hour moving average of \( \theta \). For tests on model sensitivities to different parameterization of \( f_{\text{pulse}} \) see section 2.5.3.

### 2.4.4 Parameterization of biocrust photosynthesis and respiration

In sub-model (iii), Equations (17) - (19) were parameterized based on the experiment of Feng et al. (2014). In the experiment, 50 lichen (topcrust) samples of 0.5-0.7 cm thickness (100% coverage, average C content of 1048 umol C cm\(^{-3} \)) were collected from a 20 m \( \times \) 20 m area. The samples were wetted and incubated under controlled \( T_{\text{Ct}} \) (i.e. 35°C, 27°C, 20°C, 15°C, and 10°C). These samples were divided into two groups to measure the net primary productivity (NPP) and dark respiration (Rd) separately. Gas exchange and light response curve for each crust sample were measured using LI-6400 infrared gas analyzer equipped with an LI-6400-17 chamber and an LI-6400-18 light source (LI-COR, Lincoln, NE, USA). Measurements were taken at ambient CO\(_2\) values of 385 ± 35 ppm.

Saturated topcrust samples were placed in a round tray and moved to the chamber. CO\(_2\) exchange was measured during the drying of samples, until the CO\(_2\) flux diminished. During drying, \( \theta_{\text{Ct}} \) was measured every 20 min. For more details see Feng et al. (2014).

Fitting measured Rd to \( T_{\text{Ct}} \) and \( \theta_{\text{Ct}} \) (see Fig. 3a) using Matlab\textsuperscript{\textregistered} (2012a) curve-fitting tool. The obtained multipliers in Eq. (19) are as following:

\[
f_{\text{RC}}(T_{\text{Ct}})f_{\text{RC}}(\theta_{\text{Ct}}) = Q_{\text{CT}} \left( \frac{T_{\text{Ct}} - 20}{10} \right)^{(-a_{\text{RC}} + b_{\text{RC}} \theta_{\text{Ct}} + c_{\text{RC}} \theta_{\text{Ct}}^2)}
\]

where \( Q_{\text{CT}}, a_{\text{RC}}, b_{\text{RC}}, c_{\text{RC}} \) are the fitted shape parameters (Table 2).

The parameterized Eq. (19) was then used to simulate the Rd for the NPP samples, based on the correspondent \( T_{\text{Ct}} \) and \( \theta_{\text{Ct}} \) of each measurement. \( P_{\text{Cm}} \) was determined by subtracting the simulated respiration rate from the NPP measured under light-saturated conditions. Then \( P_{\text{Cm}} \) was fitted to \( T_{\text{Ct}} \) and \( \theta_{\text{Ct}} \) in Matlab\textsuperscript{\textregistered} (2012a) curve-fitting tool using following equation (Fig. 3b):

\[
P_{\text{Cm}} = f_{\text{Pt}}(T_{\text{Ct}})f_{\text{PW}}(\theta_{\text{Ct}})
\]

\[
= (a_{\text{Pt}} + b_{\text{Pt}} T_{\text{Ct}} + c_{\text{Pt}} T_{\text{Ct}}^2 + d_{\text{Pt}} T_{\text{Ct}}^3)(-a_{\text{PW}} + b_{\text{PW}} \theta_{\text{Ct}} + c_{\text{PW}} \theta_{\text{Ct}}^2 + d_{\text{PW}} T_{\text{Ct}}^3)
\]

where \( a_{\text{Pt}}, b_{\text{Pt}}, c_{\text{Pt}}, d_{\text{Pt}}, a_{\text{PW}}, b_{\text{PW}}, c_{\text{PW}}, d_{\text{PW}} \) are fitted shape parameters (Table 2).

It should be addressed that \( T_{\text{Ct}} \) and \( \theta_{\text{Ct}} \) could change more rapidly than the mean conditions of the crust (i.e. \( T_{\text{s,1}} \) and \( \theta_{\text{s,1}} \)). In this work, \( T_{\text{Ct}} \) was calculated from the surface temperature (\( T_s \), see Eq. (13) in Gong et al., 2016) and \( T_{\text{s,1}} \) by linear interpolation. The calculation of \( \theta_{\text{Ct}} \), on the other hand, depended on the drying-rewetting cycle. During drying phases, \( \theta_{\text{Ct}} \) was interpolated linearly from \( \theta_{\text{s,1}} \).
and surface moisture content ($\theta_x$); whereas during wetting phases, the mass balance of water input $P$ and evaporation loss ($E'_{x,t}$, see Eq. (17) in Gong et al., 2016) was considered:

$$T_{x,t} = \frac{T_{x}Z_{x,t} + T_{x}Z_{x,t-1}}{Z_{x,t} + Z_{x,t-1}}$$  \hspace{1cm} (34)

$$\theta_{x,t} = \max\left(\frac{\theta_{x}Z_{x,t} + \theta_{x,t-1}Z_{x,t-1}}{Z_{x,t} + Z_{x,t-1}}, \theta_{x,t} + \frac{P - E'_{x,t}}{Z_{x,t}}\right)$$  \hspace{1cm} (35)

where $Z_{x,t}$ is the thickness of the biocrust; and $Z_{x}$ is the thickness of the topcrust. $\theta_x$ was calculated from the surface humidity and the water retention of the crust layer, using Eq. (25) – (26) by Gong et al. (2016).

### 2.4.5 Calculation of litter input to soil and SOC transport in biocrust

The litterfall added to each soil layer ($A_{x,t}^1$, Eq. (13)) were linked to the mortality of roots, which was calculated following Asaeda and Karunaratne (2000).

$$A_{x,t}^1 = k_{mo} Q_{mo} T_{x,t}^{\theta_{x,t} - 20} M_{x,t}^R$$  \hspace{1cm} (36)

where $k_{mo}$ is the optimal mortality rate at 20°C; $Q_{mo}$ is the temperature sensitivity parameter (Asaeda and Karunaratne, 2000). Similarly, we attributed the C transport rate ($A_{cm}$) from $M_{CA}$ to $M_{CH}$ mainly to the mortality of autotrophic organisms. We assumed that most mortality of crust organisms occurred during abrupt changes in wetness, as microbial communities may adapt slow moisture changes or remain inactive during drought (e.g. Roberson and Firestone, 1992; Reed et al., 2012; Coe et al., 2012; Garcia-Pichel et al., 2013; Maestre et al., 2013). Here, we introduced a water-content multiplier, $f_m(\theta_{x,t})$, to describe the impact of abrupt $\theta_{x,t}$ changes on $k_{mo}$:

$$A_{cm} = k_{mc} Q_{mo} T_{x,t}^{\theta_{x,t} - 20} f_m(\theta_{x,t}) M_{CA}$$  \hspace{1cm} (37)

$$f_m(\theta_{x,t}) = \max(0.01, 1 - \min(\theta_{x,t}, \theta_{CT}))/\max(\theta_{x,t}, \theta_{CT})$$  \hspace{1cm} (38)

where $k_{mc}$ is the optimal mortality rate at 20°C; $Q_{mo}$ is the temperature sensitivity parameter (Asaeda and Karunaratne, 2000); $\theta_{CT}$ is the forward 7-day moving average of $\theta_{x,t}$.

C transport from topcrust to subcrust was calculated as driven mainly by the sand deposition and burying of topcrust SOM. Assuming the C content in topcrust was homogeneous and the thickness $Z_{ct}$ was near-constant, the transport rate ($k_b$) was then proportional to the sand deposition rate:

$$k_b = \frac{k_{sand}}{\rho_{bulk}} Z_{ct}$$  \hspace{1cm} (39)

where $\rho_{bulk}$ is the bulk density of soil; $k_{sand}$ is the sand deposition rate in Yanchi area, which is a function of wind velocity (Li and Shirato, 2003);
2.5 Model validation and sensitivity analyses

2.5.1 Simulation set-ups

In the model simulations, soil depth was set to 67.5 cm to cover the rooting zone (Gong et al., 2016), including the crust layer (2.5 cm) and sandy subsoil (65 cm, stratified into 5 cm layers). Water content measured at 70 cm depth was used as the lower boundary condition for hydrological simulation (Jia et al., 2014). The calculation of soil temperature extended to 170 cm depth with no-flow boundary, regarding the probably strong heat exchange at the lower boundary of rooting zone (Gong et al., 2016). Zero-flow condition was set for the lower boundary of CO₂ and O₂ gases, whereas dissolved CO₂ was able to leech with seepage water. Based on presumed similarity of RLU structures, we assumed no-flux conditions for transports of water, heat, solvents and gases at outer boundary. In the simulation, we assumed instant gas transport via topcrust, whereas considered the CO₂ released by subcrust ($R_c$) was subject to the dissolving-transport processes. In this work, we aggregated the C processes in subcrust with those in soil profile. The initial ratio of $M_{CA} : M_{CH}$ was set to 2:3. The C concentration of organic matters was set to 50%.

The model run with half-hourly meteorological variables including the incoming shortwave radiation, incoming longwave radiation, PAR, $Ta$, relative humidity, wind speed and precipitation. Initial temperatures and soil moisture content for each soil layer were initialized following the work by Gong et al. (2016). Surface CO₂ concentration was set to 400 ppm. The initial gaseous CO₂ concentration was set to increase linearly with depth (5 ppm cm⁻¹). The initial CO₂ concentration in liquid form was then calculated based on Eq. (4) – Eq. (8). The initial content of mineral N content was set to 40 mg/g, which was within the range of the field observations. The two-dimensional transpirations of water, energy and gases along the soil profile were solved numerically using the Predict–Evaluate–Correct–Evaluate (PECE) method (Butcher, 2003). In order to avoid undesired numerical oscillations, the transport of water, energy and gases were calculated at 5-min sub steps.

2.5.2 Model validation

First, we validated the modelling of soil temperature and moisture content for the $F_s$ site (Test 0). The simulated hourly soil temperature and moisture content at 10 cm depth were compared to the measured values for each collar. The validation was based on the same meteorological data as used by Gong et al. (2016), who validated the model in regard to the diurnal to seasonal dynamics of radiation balance, surface energy balance, soil temperature and moisture content at the EC site.

The validity of the modelled $F_s$ was then examined in three separate tests. In Test 1, modelled $F_s$ was validated for non-crusted soils. In this case, $F_T$ in Eq. (1) was the only term affecting $F_s$ ($F_B=0$ and $F_F = 0$), and the crust influences on C-water exchanges were excluded. The biocrust-
related processes were considered in Test 2 and Test 3. Test 2 considered the dark respiration of biocrust \( \left( R_{C_b} \right) \), and set \( F_R = R_{C_b} \) and \( F_P = 0 \). Test 3 considered all the flux components \( \left( F_T, F_P \right. \) and \( \left. F_R \right) \). In these tests, different values of root biomass were assigned to the model regarding the different collar conditions (Table 1). In Test 1 – Test 3, half-hourly \( F_S \) were simulated and averaged to hourly values, and compared to those measured from the collar C1 – C3, respectively. Linear regressions were used to compare the modelled and measured values. The biases \( \left( \xi \right) \) of the simulated values were calculated by subtracting the measured values from the modelled ones. Gap values in the measurements were omitted in the validation and the bias analyses.

2.5.3 Simulating componental CO\textsubscript{2} fluxes and their parameter sensitivities

Using the validated model, we simulated the temporal trends of C flux components (i.e. \( P_{C_i}, R_{C_i}, F_P, \)
\( F_T, R_a \) and \( R_s \)) in Test 4, in order to find out how the different flux components may have contributed to the total efflux (Table 3). The simulation used the same model set-ups and climatic variables as Test 3. It should be noticed that, although the model was built as an abstract for ecosystem-level processes, the simulation set-ups and validation were performed at a point level corresponding to respiration chambers. Therefore, understanding the uncertainty sourced from parameterization could be helpful for future development and applications. In Gong et al. (2016), we have studied the sensitivities of modelled soil temperature and moisture content to the variations in soil texture, water retention properties, vegetation parameters and plant-interspace heterogeneities. In this study, we also tested the sensitivity of \( F_S \) and componental fluxes to the changes in a number of site-specific parameters (Table 4). These parameters included pH, nitrogen content, water-thermal conditions, root biomass, production and decomposability of litters, which are often key factors regulating soil C processes but likely to vary within and among ecosystems (see e.g. Ma et al., 2011; Gong et al., 2016; Wang et al., 2016). Furthermore, we tested the model sensitivities to several newly defined parameters (i.e. \( n_R, n_p \) and \( f_{\phi} \)), to understand their effects on model uncertainties. \( F_S \) and componental fluxes at interspace were simulated by varying single parameter value by 10% or 20%. The sensitivity of each tested flux was described by the difference \( \left( dF \right) \) in the annual flux rate simulated using manipulated parameter, as compared to the rate simulated under no-change conditions.

2.5.4 Comparing model sensitivities between plant cover and interspace

In order to study the effects of plant-interspace heterogeneity on soil CO\textsubscript{2} efflux, Test 5 simulated annual \( F_S \) and componental fluxes at plant cover and compared the values to interspace. The simulation set-ups were almost same as those employed in Test 1-3; only exception was that same initial values of SOC storages \( \left( 650 \text{ gC m}^{-2} \right) \) and root biomass \( \left( 200 \text{ g m}^{-2} \right) \) were used for under-canopy and interspace areas for comparison purpose. Based on Test 4, we further compared the plant-interspace differences in the C-flux sensitivities to most important site-specific parameters, i.e. soil
temperature ($Ts$), water content ($\theta$) and root biomass ($M^r$) (see Section 3.2). The differences in parameter sensitivities were calculated by comparing the absolute values of sensitivities ($|dF|$; see section 2.5.3 and Table 4) from the area with plant cover to without (interspace).

3. Results

3.1 Model validity

Comparing to the EC site in previous work (Gong et al., 2016), the soil in this study is much coarser and the measured $\theta$ at 10 cm depth was constantly lower (Fig. 4), indicating the necessity of re-parameterization and validation of the water-energy algorithms. Figure 4a shows the modelled hourly $Ts$ and $\theta$ at 10 cm depth with the mean values measured from the F$_S$ site during year 2013. Based on the site-specific vegetation and soil texture parameters, our model explained 97% of the variations in the measured hourly $Ts$. The model underestimated the temperature mainly in summer time (i.e. day 150-250, Fig. 4a). The underestimation was more pronounced around the noontime in the diurnal cycle. As the water-content sensors may not accurately capture the moisture dynamics during freezing period, only the simulation during ice-free period were compared to measured data (Fig. 4b). During the ice-free period, the model explained 83% of the variations in the measured mean water contents at 10 cm depth. The biases in the modelled temperature and moisture content were less than the spatial variations observed in this area (e.g. Wang et al., 2015). Therefore, our model could be able to reproduce the time series for the measured water-energy fluxes at the site.

Our modelling reasonably reproduced the diurnal and seasonal fluctuations of $F_S$. The model explained 87 and 83% of the variations in the hourly $F_S$ measured on the non-crusted surface in year 2013 and 2014 (Fig. 5a). The root-mean-square errors (RMSE) were 0.43 umol m$^{-2}$ s$^{-1}$ and 0.29 umol m$^{-2}$ s$^{-1}$ respectively. The model mainly underestimated the daytime $F_S$ during the freezing seasons. During the ice-free periods, the model mainly overestimated the efflux in early springs. The biases in modelling largely showed a diurnal pattern (Fig. 5b), that $F_S$ was mainly underestimated in noon hours (i.e. from 10 a.m. to 3 p.m.) but slightly overestimated in the afternoon and evening. At the daily level, our model explained 94% of the variations in measured daily efflux during the two-year period (Fig. 5c).

Compared to the non-crusted soil (C1), the simulated $F_S$ for crusted surfaces (C2 and C3) showed greater deviations from measured data. At the hourly scale, our model explained 75% (year 2013) and 68% (year 2014) of variations in measured $F_S$ from C2 (Fig. 6a), and 68% (year 2013) and 61% (year 2014) of variations in measured $F_S$ from C3 (Fig. 6b). For the two-year period, RMSE of the modelled hourly $F_S$ were 0.25 umol m$^{-2}$ s$^{-1}$ and 0.35 umol m$^{-2}$ s$^{-1}$ for C2 and C3, respectively. The magnitudes of biases ($|\zeta|$) were generally greater during the rainfall period (i.e. from the start of raining to 24 hours after end of rainfall) than the inter-rainfall period (Fig. 7). The simulated $F_S$ for C2 showed similar diurnal pattern of biases as compared to C1, suggesting ineligible contributions of
biases in the simulated subsoil emissions. Introducing photosynthesis and photodegradation of biocrust to the system (C3) led to greater overestimations in $F_S$, and this was more obvious in the afternoon hours (i.e. from 12 a.m. to 6 p.m.) and during wetting period. Nevertheless, at the daily scale, the model explained 91% (C2, Fig. 5c) and 86% (C3, Fig. 5d) of the variations in the measured $F_S$ during the two-year period. There were no significant systematic deviations between the measured and the modelled daily values, as indicated by regression slopes close to 1 and intercepts close to 0 (Figs. 4 and 5).

The results above showed that, the model well described the seasonal variations of $F_S$ for both non-crusted and lichen-crusted soils. Moreover, the model was able to capture the strong variability of hourly/daily $F_S$ in wetting-drying cycles. Comparing to earlier statistic modelling by Wang et al. (2014a, 2014b), this model showed equality or improvement in performance. In this sense, we assume that our model has included the main mechanisms controlling the $F_S$ dynamics in the soil system, and could be used for further analysis on componental C processes and their parameter sensitivities.

3.2 Modelled C flux components of $F_S$

Test 4 showed that, $Rs$ was the main contributor to the root-zone CO$_2$ production, which accounted for a major source of effluxes ($F_S$). Our measurements showed large diurnal and seasonal variations in $F_S$ regardless the existence of crust covers (Fig. 5 and Fig. 6). Particularly, the $F_S$ dynamics depended strongly on rain events. Even at non-crusted soil (i.e. C1), $F_S$ dropped significantly from the pre-rainfall level even to near-zero, but rebound rapidly and peaked after rain stopped (Fig. 5a). This could relate to the mismatched trends of CO$_2$ production ($Rs + Ra$) and emission ($F_T$) from the rooting zone with respect to the wetting-drying cycles (Fig. 8a). Compared to CO$_2$ production, the responses of $F_T$ to rainfall were generally lagged and smoothed (see examples in Fig. 8b – 8d), irrespective of the size of rain events. In the simulation, soil rewetting increased CO$_2$ production rapidly but depressed $F_T$, which increased after rain ceased. In all the examples (Fig. 8b – 8d), $F_T$ exceeded $R_P$ within 48 hours after the ending of rain events. At the annual level, the total $R_P$ was larger during wetting period (i.e. raining days plus 1 day after rainfall) than the rest days of the year (i.e. drying period), whereas the total $F_T$ was greater during the drying period (Fig. 8e).

On the annual basis, CO$_2$ production ($Rs+Ra$) and emission ($F_T$) from root-zone soil were mismatched (Table 3), and the former was more than 15 % greater than latter. Such a gap was mainly due to the root uptake and transport of dissolved CO$_2$ (i.e. 36 gC m$^{-2}$ year$^{-1}$), whereas the loss of dissolved CO$_2$ via seepages or pore-mediated horizontal flows were limited (i.e. 7.4 gC m$^{-2}$ year$^{-1}$). The photosynthesis rate of topcrust was 31.1 gC m$^{-2}$ year$^{-1}$ at interspace. After rainfall, the C uptake by topcrust increased significantly, even turned the soil from net C source to sink during a few hours to one day (Fig. 6, Fig. 8). However, at annual scale, the C losses via respiration and photodegradation
accounted for 90% of the photosynthetic products, leading to a near-zero contribution of topcrust to $F_S$ during the two year period (i.e. < 5 gC m$^{-2}$ year$^{-1}$).

Analysis of parameter sensitivity showed that, the modelled $F_S$ and the component fluxes were more sensitive to ±2 °C in $T_S$ or ±10% in $\theta$, compared to the effects of ±10% or ±20% in the other parameters (Table 4). Varying $\theta$ by 10% produced greater impacts on the simulated $R_P$ and crust-related fluxes (i.e. $P_C$, $R_C$, and $F_P$), as compared to changing $T_S$ by ±2 °C. Increasing $\theta$ by 10% enhanced the simulated $P_C$ and $F_C$ by 41% and 28%, and doubled the net C sequestration ($F_C - F_P$) by topcrust. However, the contribution of such changes to annual $F_S$ was minor, and amounted for only 2.0% of the total efflux. Beside $T_S$ and $\theta$, the simulated efflux was also sensitive to changes in root biomass ($M^R$). Manipulating root biomass by ±10% changed the annual $F_T$ and $F_S$ by about 7%, and such effects were 100% greater than ±10% changes in $M_{tot}$ in soil. Adjustment of other parameters, e.g. $n_p$ (eq. (31)) and $f_m$ (eq. (38)), produced little influences on the modelled $F_S$ and the componential fluxes (Table 4). In addition, the model was robust to the adjustment of several crust-related parameters, i.e. $k_{unc}$, $M_C$, and $M_{C\text{\,H}}$. Hence, algorithms correspondent to those parameters could be simplified in future developments.

3.3 Modelled plant-interspace differences in C flux components

At either plant-covered or interspace area, $R_S$ was a major contributor to root-zone CO$_2$ production and $F_T$ dominated the total effluxes (Table 3). The C loss at interspace was 14% faster than under-canopy on an annual basis, if root biomass and SOC were homogeneous at plant cover and interspace. The lower $F_S$ rate at plant cover mainly attribute to the lower CO$_2$ production ($R_T + R_d$) from subsoil. The C loss via seepage and root transport, which is the gap between subsoil CO$_2$ production and emission ($F_T$), was slightly higher under canopy (17%) than at interspace (15%). Comparing to interspace, the photosynthesis of biocrust ($P_C$) was 34% lower under canopy. This reduced the under-canopy $F_C$ by 42% in comparison with interspace. However, such a different was largely offset by the reduced photodegradation rate under canopy, leading to limited differences in net sequestration of topcrust between plant-interspace (i.e. by 1.4 gC m$^{-2}$ year$^{-1}$).

We further compared the flux sensitivities at plant cover and interspace to the changes in three most effective parameters (i.e. $T_S$, $\theta$ and $M^R$, see Table 5). For subsoil-mediated fluxes (i.e. $F_S$, $F_T$, $R_a$, $R_d$), the sensitivity values differed by less than 2% from plant cover to interspace. On the other hand, the sensitivities of crust-related fluxes (i.e. $P_C$, $F_C$, $F_P$) showed greater differences between plant cover and interspace. Comparing to interspace, $F_S$ and $F_T$ at plant-covered area were more sensitive to $T_S$ changes, but less sensitive to manipulations in $\theta$. On the other hand, the plant cover reduced the sensitivity of CO$_2$ effluxes to changes in root biomass. $P_C$, $F_C$, and $F_P$ were generally more sensitive to warming and $\theta$ manipulations at plant cover than interspace, except that plant cover decreased the
sensitivity of $F_p$ to -10% changes in $\theta$. Nevertheless, their contribution to the sensitivity of $F_S$ was marginal, due to the low flux rates of crusts.

4. Discussions

4.1 The roles of componential C processes in regulating soil CO$_2$ efflux

Our process-based model provided a useful tool to separate the multiple soil C processes and investigate their roles in regulating $F_S$ dynamics in dryland ecosystems. So far, efforts to quantify the soil C loss in terrestrial ecosystems have considered soil C efflux as a synonym of respired CO$_2$. However, based on this work, cautions must be taken when extrapolating the $F_S$ responses from the chamber to ecosystem scale and from short-term to long-term periods. Processes other than autotrophic and heterotrophic respiration could significantly modify the $F_S$ responses to climatic variability. Our simulation highlighted decoupled CO$_2$ production and emission during the wetting-drying cycle, as regulated by the CO$_2$ transport in soil profile. The simulated CO$_2$ production in soil profile were much greater than effluxes during rain pulses (e.g. Fig. 7). This indicated that, the low $F_S$ during rewetting was mainly due to the increase in CO$_2$ dissolution, instead of the reduced respiration rates by low O$_2$ supply (e.g. Fang and Moncrieff, 1999). This finding is further supported by the measurement of Maier et al. (2011), which showed that 40% of the respired CO$_2$ could be stored temporally in soil pore-space after rainfalls. The dissolved CO$_2$ then released gradually with the evaporation of pore water, leading to lagged responses of efflux as compared to respirations. Regarding that a major fraction of CO$_2$ was produced during the wetting periods (Fig. 5e), such a lagging effect should be carefully examined when analysing the climatic sensitivity of $F_S$. Our simulations showed that a considerable fraction of CO$_2$ produced could be removed by root uptake and leave the volume measured by the respiration chamber. Bloemen et al. (2016) showed that the CO$_2$ concentration in root xylems could be higher than in soil solutions. This implies that such a “missing source” might be even greater than the model estimation, although knowledge is still limited about the efficiency of the removal and the diffusion/release of CO$_2$ during the transport (Bloemen et al., 2016).

The contributions of biocrusts as C sink or source have remained largely unknown (Castillo-Monroy et al., 2011). This is mainly due to the difficulty to separate the CO$_2$ exchanges of crust organisms from the background respirations (Castillo-Monroy et al., 2011; Sancho et al., 2016). As demonstrated in our work (Fig. 5b – 5d), the photosynthesis of topcrust could be masked by background emission quickly (e.g. within 1 day) after rain events. The simulated $F_{Ct}$ was 31 g C m$^{-2}$ year$^{-1}$ at interspace. Considering a 30% coverage of lichens over the sampling area (Feng et al., 2014), the interspace-level NPP was 9.3 g C m$^{-2}$ year$^{-1}$. This value was largely greater than the lab-based estimation for the site (Feng et al., 2014). However, it was in range of the values reported from several other dryland ecosystems (i.e. 5.3 - 29 g C m$^{-2}$ year$^{-1}$, Sancho et al., 2016). Our simulations
also suggested that photodegradation might offset about 48 % of the CO$_2$ photosynthesized by biocrust. It could explain the much higher $F_S$ measured from the transparent chamber (C3) than the opaque chamber (C2) during dry daytime periods (e.g. Fig. 9). It should be also noticed that the litter from shrub canopy was not included in the measurement nor modelling. Also the interactions between photodegradation and biotic decaying were not considered either. Hence, the contribution of photodegradation to soil C balance could be greater than our estimation at the ecosystem level (see e.g. Gliksman et al., 2016). Although the contribution of surface exchanges were only marginal as compared to the annual CO$_2$ efflux, removing the biocrust processes would significantly reduce the model validity. For example, the goodness of fitting (i.e. $R^2$) in Test 3 dropped from 0.65 to 0.45 for the two-year period, if $F_C$ and $F_P$ were neglected. Therefore, delineating the gas exchange of biocrust could be helpful, in order to upscale the modelling of C balance from chamber to ecosystem level, where the distribution of crust cover may vary from one site to another.

4.2 Plant-interspace differences in soil C fluxes

Clumped distributions of foliage and biomass are critical features for the adaptation and functioning of vegetation in arid and semi-arid environments. Previous studies have mainly emphasized the shrub effects on ecohydrology (e.g. Rongo et al., 2006; Gong et al., 2016) and enrichment of sediments and nutrient, known as “resource island” effects (Reynolds et al., 1999; Rietkerk et al., 2004). Our simulations showed that the presence of shrub canopy also influenced the soil C exchanges. The presence of shrub cover affected the C functioning of biocrust mainly through shading, which reduced photosynthesis more than respiration and photodegradation. Comparing to the interspace, simulated annual $F_S$ was 13% lower under the canopy (Test 5). As we ruled out the plant-interspace differences in SOC and root biomass and the C-flux differences contributed by biocrusts were limited, such a decrease in plant-cover $F_S$ was probably due to the cooling effect of canopy (Gong et al., 2016). This effect was close to the modelled responses of $F_S$ to ± 2 °C in soil temperature or ± 10% in soil water content. As the density of roots and litter production are commonly larger under canopy than interspace (e.g. Zhang et al., 2008), the lower respiration rate under canopy tends to facilitate the accumulation of biomass and organic matters and feedback to functioning of “resource islands” during prolonged periods.

Our simulation further indicated considerable differences in the C-flux sensitivities between areas with plant cover and without. As the C processes and initial conditions were set to be homogeneous, those differences could mainly result from the different water-thermal conditions at plant cover and interspace. For example, the higher temperature sensitivities of $F_T$, $F_S$ and $F_C$ may relate to the cooling effect of canopy (see Gong et al., 2016), which may lead to a greater Q10 value for respiration estimations (i.e. eq. (27)). Moreover, the slower decomposition in under-canopy soil could also lead to the lower sensitivities of $F_T$ and $F_S$ to changes in root biomass and SOM contents. On the other hand,
water advection from interspace to plant cover, which may support over 30% of water loss from
under-canopy soils (Gong et al., 2016), could help to lower the $F_S$ sensitivity to water content changes
at plant cover. The increased water-thermal sensitivities of C exchanges of biocrust could be
explained by the less-stressful environment for crust organisms, e.g. higher moisture content but
lower radiation and temperature, although the photosynthesis of lichens ($P_C$) could be reduced by
shading (Table 3). Such heterogeneity of C-flux sensitivities thus should be considered in future
studies on the ecosystem-level responses to climate change and extreme climatic events.

4.3 Modelling uncertainties and future research needs

Our model showed its ability to describe the dynamics of soil temperature, moisture content and C
effluxes measured for the studied semiarid ecosystem. The uncertainties in the modelling, however,
may exist in several aspects. Firstly, the representative land unit (RLU) was a statistical simplification
to the target ecosystem at footprint scale (Gong et al., 2016), and may not fully capture the spatially
explicitly of soil environment and biogeochemistry at ecosystem scale. For example, the model
assumed Poisson probability of mutual shading (Bégué et al., 1994), and the probability of shading
increased continuously with solar zenith (Gong et al., 2016). However, for explicit space-time,
shading is binary. This possibly explains the biases in the estimated net radiation (Gong et al., 2016)
and collar temperature around midday, which sequentially affected the simulated $F_S$ (see Fig. 3b).
Moreover, field observations showed considerable spatial variations of soil temperature, water content
and biogeochemistry (e.g. pH, litter quality and root biomass) within a distance of 3-5 meters. Such
variations could well exceed a magnitude of 10 %, and even over 100 % (e.g. Zhang et al., 2008; Feng
et al., 2013; Wang et al., 2015). Therefore, the variation of $F_S$ driven by the spatiality of soil factors
could be greater than the responses to ±2 °C in soil temperature or ±10 % in soil water content.
Therefore, future modelling may need to consider spatially explicit settings, in order to further
minimize the gaps between model settings and the reality.

Secondly, the high sensitivity of simulated $F_S$ to soil pH indicated that the uncertainties in inorganic
C processes could strongly affect the accuracy of modelling. Our modelling of CO$_2$ transport was
based on gaseous and liquid phases, whereas the solid phase was not involved, despite the high lime
content (2300–5400 kg ha$^{-1}$) in the soil (Feng et al., 2013; Wang et al., 2015). Based on soil samples
of similar lime content (2700 kg ha$^{-1}$), Buysee et al. (2013) showed that neglecting the inorganic C
exchanges by solids may underestimate $F_S$ during the heating phase of a day, but overestimate $F_S$
during the cooling phase. This is very similar to the diurnal pattern of biases in our modelling (Fig.
3d). Therefore, further improvement on the modelling may need to consider the solid phase as well.

Thirdly, the current model still lacked mechanistic descriptions on growths of plant and soil
microbes. Comparing to many other ecosystems, drylands often feature high root-shoot ratio (Jackson
et al., 1996) but low SOC storages. Changes in plant physiology and growth can readily influence root
metabolisms and labile SOC pools, hence modify F\textsubscript{S} dynamics (Wang et al., 2015). On the other hand, large fluctuation of diurnal and seasonal temperature may drive the microbial communities to shift between warm-adapted to cold-adapted (Van Gestel et al., 2013), which could largely change soil respiration and its sensitivity to freeze-thaw cycles (Van Gestel et al., 2013; Liu et al., 2016). Both the biotic controls are mixed with the legacy effects of climatic variability over annual and inter-annual courses (Sala et al., 2012; Jia et al., 2016; Shen et al., 2016), and could affect the C-water simulations cumulatively through the feedbacks between biomass accumulation and soil biogeochemistry (Bradford et al., 2016). This may explain the decreasing trend of model validity from year 2013 to 2014 (Fig. 3, Fig. 4). Therefore, the dynamics of plants and microbial communities are required in future modelling, in order to improve the F\textsubscript{S} simulations regarding inter-annual and long-term periods.

In addition, proper field data are still needed to support the future modelling work. The dataset used in our model validation mainly separated the influences of biocrusts from subsoil respirations. However, some processes like photodegradation and lateral CO\textsubscript{2} transport by root or water flows still require more support from observation. Also, respiration data from shrub-covered soil remains unavailable, as the settlement of soil collars and respiration chambers under canopy could easily interrupt the biophysiology of shrubs. The C functioning of crust organisms is especially sensitive to water content (Table 4). However, track the water content in the very thin layer of topcrust can be very challenging using hour-based meteorological data. Nocturnal water inputs (e.g. dewfalls) are important to the metabolisms of crust organisms (e.g. Liu et al., 2006), but they are hard to be quantified precisely by EC measurement, or models derived from EC data. Moreover, we presumed structural homogeneity for the crust layer and employed constant regime for crust processes. In reality, there may not be clear boundaries between topcrust and subcrust, and even topcrust itself may contain significant variations in microstructure and communities even within one centimetre (Williams et al., 2012; Raanan et al., 2016). The C sequestration of biocrust can be strongly modified by microbial communities directly (Belnap, 2003; Pointing and Belnap, 2012; Feng et al., 2014; Maestre et al., 2015) and through other factors e.g. surface albedo (Chamizo et al., 2012), dew falls (Liu et al., 2006), soil pore forming (Williams et al., 2012; Felde et al., 2014). So far, many questions remain unanswered about the mechanisms that control the colonization, adaption and succession of microbial communities and the structure-function of biocrust (Pointing and Belnap, 2012). Further knowledge on these mechanisms will be helpful to improve the modelling of crust C functioning in response to climate change and extreme climatic events.

5. Conclusions

This work represents a first attempt to integrate the CO\textsubscript{2} production, transport and surface exchanges (e.g. biocrust photosynthesis, respiration and photodegradation) in F\textsubscript{S} modelling for
dryland ecosystems with high plant-interspace heterogeneities. Our model simulated reasonably well the \( F_s \) dynamics measured from non-crusted and lichen-crusted soil collars during year 2013-2014, although introducing the gas exchanges of lichen crust decreased the model performance at the hourly scale. However, further model development may still be required on several aspects, e.g. by including: i) the spatial-explicit schemes for surface conditions and soil biogeochemistry; ii) influences of lime and solids on CO\(_2\) transport; iii) growth dynamics of plants; iv) high-resolution dynamics of surface water-thermal conditions and v) the dynamics of microstructure and microbial communities of biocrusts.

Our model simulations highlighted that, the transport processes of inorganic C and the metabolisms of biocrusts could strongly modify the CO\(_2\) efflux, and these influences are closely linked to soil hydrology. Soil rewetting could enhance CO\(_2\) dissolution and delay the emission of CO\(_2\) produced from root-zone. In addition, an ineligible fraction of respired CO\(_2\) could be removed via lateral flows and root uptake, and become “missing” from volumes under respiration chambers. The lichen-crusted soil could temporally shift from net CO\(_2\) source to sink during rewetting, as driven by the photosynthesis of lichens and the restrained CO\(_2\) emissions from subsoil. Whereas after rain events, the CO\(_2\) exchanges of lichens could be easily masked by background emissions from subsoil. Based on our modelling, the annual NPP was 9.3 gC m\(^{-2}\) by topcrust at interspace. However, the net C sequestration by topcrust could be marginal, if the photodegradation is accounted. Our modelling further showed different componental C fluxes and sensitivities between plant-covered soil and interspace. The presence of plant cover tended to decrease the root-zone CO\(_2\) production and biocrust C sequestration, but increase the temperature sensitivities of these fluxes. On the other hand, the sensitivities of root-zone emissions to water content was decreased by canopy. This may be due to the advection water flows from the interspace. To conclude, the complexity and plant-interspace heterogeneities of soil C processes should be carefully considered to extrapolate findings from chamber to ecosystem scales, and to predict the ecosystem responses to climate change and extreme climatic events. Our model can serve as a useful tool to simulate the soil CO\(_2\) efflux dynamics in dryland ecosystems.

Acknowledgement

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### Tables

**Table 1. Configuration of soil collars used in this study**

<table>
<thead>
<tr>
<th>Collars</th>
<th>C1</th>
<th>C2</th>
<th>C3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface type</td>
<td>Non-crusted</td>
<td>Lichen-crusted</td>
<td>Lichen-crusted</td>
</tr>
<tr>
<td>Chamber type</td>
<td>Opaque</td>
<td>Opaque</td>
<td>Transparent</td>
</tr>
<tr>
<td>Root biomass (g m$^{-3}$)</td>
<td>420</td>
<td>106</td>
<td>92</td>
</tr>
<tr>
<td>Gap of data (%)</td>
<td>12.9</td>
<td>10.5</td>
<td>9.85</td>
</tr>
<tr>
<td>Annual C efflux (gC m$^{-2}$) $^a$</td>
<td>259</td>
<td>194</td>
<td>192</td>
</tr>
</tbody>
</table>

$^a$ The values were calculated from the measured hourly FS data excluding data gaps.

**Table 2. Parameters for soil water retention and C turnover**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Equation</th>
<th>Unit</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a_h$</td>
<td>$^a$</td>
<td></td>
<td>0.0355$^b$</td>
</tr>
<tr>
<td>$n$</td>
<td>$^a$</td>
<td></td>
<td>1.5215$^b$</td>
</tr>
<tr>
<td>$k_1$</td>
<td>(11)</td>
<td>g g$^{-1}$ day$^{-1}$</td>
<td>0.01$^c$</td>
</tr>
<tr>
<td>$k_2$</td>
<td>(11)</td>
<td>g g$^{-1}$ day$^{-1}$</td>
<td>0.08$^d$</td>
</tr>
<tr>
<td>$k_3$</td>
<td>(11)</td>
<td>g g$^{-1}$ day$^{-1}$</td>
<td>0.001$^d$</td>
</tr>
<tr>
<td>$k_4$</td>
<td>(15)</td>
<td>g g$^{-1}$</td>
<td>0.15$^e$</td>
</tr>
<tr>
<td>$k_r$</td>
<td>(19)</td>
<td>g g$^{-1}$ s$^{-1}$</td>
<td>0.0014$^f$</td>
</tr>
</tbody>
</table>
Table 3. Simulated component CO$_2$ fluxes (gC m$^{-2}$ year$^{-1}$) for areas with plant cover and without (interspace).

<table>
<thead>
<tr>
<th>Surface type</th>
<th>$F_S$</th>
<th>$F_T$</th>
<th>$Rs+Ra^a$</th>
<th>$Ra$</th>
<th>$P_{C_t}$</th>
<th>$F_{C_t}$</th>
<th>$F_P$</th>
<th>$F_{C_t} - F_P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Interspace</td>
<td>244</td>
<td>249</td>
<td>295</td>
<td>113</td>
<td>54.6</td>
<td>31.1</td>
<td>26.1</td>
<td>5.0</td>
</tr>
<tr>
<td>Plant covered</td>
<td>214</td>
<td>218</td>
<td>263</td>
<td>108</td>
<td>36.3</td>
<td>18.2</td>
<td>14.6</td>
<td>3.6</td>
</tr>
</tbody>
</table>

$a$ Rs+Ra represents the total CO$_2$ production from soil respirations. $Ra$ is the total autotrophic respiration ($Ra = \sum Ra_s$, see Eq. (10)) and $Rs$ is the total heterotrophic respiration ($Rs = \sum Rs_s$, see Eq. (12)); $b$ $F_{C_t} - F_P$ represents the net CO$_2$ exchanges of topcrust, see Eq. (17) and Eq. (24) for correspondent algorithms of the variables. For definitions of other fluxes, see Eq. (1) for $F_S$, Eq. (3) for $F_T$, Eq. (17) for $F_{C_t}$, Eq. (18) for $P_{C_t}$ and Eq. (24) for $F_P$.

Table 4. Sensitivity of simulated $F_S$ and its componental fluxes to manipulations of parameter values.

<table>
<thead>
<tr>
<th>Change of parameter</th>
<th>$F_S^a$</th>
<th>$F_T$</th>
<th>$Ra+Rs^a$</th>
<th>$Ra$</th>
<th>$P_{C_t}$</th>
<th>$F_{C_t}$</th>
<th>$F_P$</th>
<th>$F_{C_t} - F_P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$n_R +20%$</td>
<td>+3.3 $^b$</td>
<td>+3.2</td>
<td>+2.7</td>
<td>+7.9</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
</tr>
<tr>
<td>$n_R -20%$</td>
<td>-2.9</td>
<td>-2.8</td>
<td>-3.4</td>
<td>-8.8</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
</tr>
<tr>
<td>$n_P +20%$</td>
<td>+1.6</td>
<td>+1.6</td>
<td>+1.0</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
</tr>
<tr>
<td>$n_P -20%$</td>
<td>/</td>
<td>/</td>
<td>-1.4</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
</tr>
<tr>
<td>$f_{aw} +20%$</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>+2.9</td>
<td>+3.8</td>
<td>+3.4</td>
<td>+6.0</td>
<td></td>
</tr>
<tr>
<td>$f_{aw} -20%$</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>+1.2</td>
<td>/</td>
<td>-5.7</td>
<td>+30</td>
<td></td>
</tr>
<tr>
<td>$Ts +2\ ^\circ C$</td>
<td>+9.5</td>
<td>+9.6</td>
<td>+7.1</td>
<td>+11</td>
<td>+4.9</td>
<td>+3.9</td>
<td>+1.5</td>
<td>+16</td>
</tr>
</tbody>
</table>

$^a$ See Eq. (26) in Gong et al. (2016). Sources of parameter values: $^b$ This study, see section 2.3.2; $^c$ Lai et al. (2016); $^d$ Gong et al. (2014); $^e$ Chen et al. (1999); $^f$ This study, see section 2.4.4 and Fig. 3; $^g$ Wang et al., 2014a.
Definitions of fluxes see Table 3 and Section 2.5.3; Value represents the percentage (%) of change ($dF$) in correspondent C flux with manipulated parameter value, as compared to the no-change condition. A positive value represents the percentage of increase in the simulated flux whereas a negative value represents the percentage of decrease; the change in simulated C flux was smaller than 1 %.

Table 5. Plant-interspace differences in the sensitivities of C fluxes to changes in soil temperature ($Ts$), water content ($\theta$) and root biomass ($M^b$).

<table>
<thead>
<tr>
<th>Change of parameter</th>
<th>$F_s$</th>
<th>$F_T$</th>
<th>$Ra + R_S$</th>
<th>$Ra$</th>
<th>$P_O$</th>
<th>$F_O$</th>
<th>$F_p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Ts + 2 ^{\circ}C$</td>
<td>+0.38</td>
<td>+0.45</td>
<td>+0.87</td>
<td>+0.49</td>
<td>+1.7</td>
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<td>+1.2</td>
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<td>(+4.0)</td>
<td>(+4.7)</td>
<td>(+12)</td>
<td>(+12)</td>
<td>(+34)</td>
<td>(+70)</td>
<td>(+78)</td>
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<tr>
<td>$Ts - 2 ^{\circ}C$</td>
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<td></td>
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<td>(+14)</td>
<td>(+27)</td>
<td>/</td>
<td>(+222)</td>
<td>(+14)</td>
<td>(+615)</td>
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<tr>
<td>$\theta + 10 %$</td>
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<td>-1.5</td>
<td>-0.61</td>
<td>/</td>
<td>-0.27</td>
<td>+8.7</td>
<td>+13</td>
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<tr>
<td></td>
<td>(-49)</td>
<td>(-27)</td>
<td>/</td>
<td>(-1.9)</td>
<td>(+21)</td>
<td>(+46)</td>
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<tr>
<td>$\theta - 10 %$</td>
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<td>+0.58</td>
<td>+0.36</td>
<td>+1.5</td>
<td>-3.5</td>
<td>-4.5</td>
<td>+0.9</td>
</tr>
<tr>
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<td>(-17)</td>
<td>(-17)</td>
<td>/</td>
<td>(+10)</td>
<td>(+10)</td>
<td>(+22)</td>
<td>(+36)</td>
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<tr>
<td>$M^b + 10 %$</td>
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<td>(-4.7)</td>
<td>(-5.8)</td>
<td>/</td>
<td>/</td>
<td>/</td>
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<tr>
<td>$M^b - 10 %$</td>
<td>+0.44</td>
<td>+0.41</td>
<td>+0.65</td>
<td>+5.2</td>
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$^a$ Definitions of fluxes see Table 3 and Section 2.5.3; $^b$ Values shows the plant-interspace difference in parameter sensitivities by value (outside bracket, $dF_p - dF_T$) and by percentage (inside bracket, $100 \times (|dF_p| - |dF_T|) / |dF_T|$, where $dF_p$ and $dF_T$ are parameter sensitivities ($dF$, definitions see Table 4 and Section 2.5.3) for
plant-covered and interspace areas, respectively. A positive percentage (inside bracket) indicates a greater sensitivity \(|dF|\) of the flux at plant cover than interspace, whereas a negative value indicates a lower sensitivity. Definitions of fluxes and sensitivities see Table 3 and Section 2.5.3. The difference in sensitivity are smaller than 0.1% by value.

Figures

Figure 1. Site position (a), overlook of measured ecosystem (b), appearance of soil surface at collar C1 (c), C2 (d) and C3 (e), and layout of representative land unit (RLU, adopted from Gong et al., 2016)
Figure 2. Conceptual framework of process-based modelling. Solid arrows represent flows of masses and dash arrows represent flows of information.

Figure 3. Measured and fitted bulk respiration (a) and photosynthesis (b) of the lichen topcrust as functions of temperature and water content.
Figure 4. Measured and modelled soil temperature (a) and soil moisture content (b) at 10 cm depth for FS site, and as compared to the EC site in year 2013 by Gong et al. (2016).

Figure 5. Measured and modelled hourly F_S for non-crusted soil (a), the temporal pattern of the bias of simulated hourly F_S (b) and the comparison of measured and modelled daily F_S (c) during 2013-2014.
Figure 6. Measured and modelled $F_S$ of lichen-crusted soils for opaque (a, c) and transparent chambers (b, d) at hourly (a, b) and daily (c, d) scales during 2013-2014.

Figure 7. Diurnal patterns of biases ($\zeta$) in the simulated hourly $F_S$ for lichen-crusted soils using opaque (a) and transparent chambers (b), and the cumulative probability of the biases during wetting and drying periods (c) during 2013-2014. The wetting period included the raining days and a 1-day period after each rainfall. The drying period included the rest time of the years other than the wetting period.
Figure 8. Simulated component CO₂ exchanges by biocrust and root-zone soil (a), the simulated CO₂ fluxes before and after example rain events of 2.3 mm (b), 7.6 mm (c) and 12.8 mm (d) sizes, and the comparison of $F_T$ and $R_R$ during wetting and drying periods during 2013-2014. The wetting period included the raining days and a 1-day period after each rainfall. The drying period included the rest time of the years other than the wetting period.
Figure 9. Comparison of the measured $F_s$ from lichen-crusted surfaces using opaque and transparent chambers during a dry period (day 83-103) in spring 2013.