

General comment

“Modelling the diurnal and seasonal dynamics of soil CO₂ exchange in a semiarid ecosystem with high plant-interspace heterogeneity” Gong et al. present a model development and model validation study focused on simulating soil CO₂ efflux in semiarid soils. They have improved on previous models used for these ecosystems by incorporating abiotic processes related to lateral and vertical transport of CO₂ in heterogeneous canopies as well as biotic processes related to biocrust CO₂ production and photodegradation. They evaluate their new model against two years of site-based data from semiarid shrubland ecosystem in Yanchi, northwestern China. This is an interesting and relatively new contribution to the modelling literature on this topic. The introduction is well laid out and clearly explains the context behind the work and the importance of including processes related to plant heterogeneity and biocrust dynamics in the model. From both the introduction and discussion it is clear the authors know the literature well and have a good handle on the gaps in understanding that need to be addressed.

This is a comprehensive study with a number of interesting results. Given this however, I would like to see some of the objectives framed as questions in the introduction, which would then be answered directly in the results/discussion. This would help to highlight the key points in the results section, link the results back to the context and would make the text less focused on a model description, parameterization and sensitivity study, although these aspects are important and described well in this paper. Such changes would serve to improve the structure, readability and scientific value of the paper. The authors could frame the work around questions such as: (a) What is the difference in diurnal to seasonal variability in CO₂ flux between soils with and without a biocrust? (b) Are there significant differences between the CO₂ flux from plant covered and interspace soils? (c) What are the relative contributions of different processes to total soil CO₂ efflux? Are the process of CO₂ production and emission tightly coupled during wetting and drying cycles? The paper would also benefit from a more thorough discussion of the importance of including processes related to biocrusts in regional to global scale biogeochemical models. Does the inclusion of biocrust-related processes improve the fit to the measured soil CO₂ flux at C3 compared to a model that does not include these processes (e.g. if you repeated the simulation without the inclusion of the new processes related to biocrust)? Does this represent a significant flux in semiarid ecosystem C balance at regional to global scales? Finally, please see my comment below on the aim of the sensitivity study, other than to see how robust the model is to changes in parameters. However, in a more general context, I think it would be beneficial for the study if you put the sensitivity analyses in the context of climate and anthropogenic change? What are the likely changes in temperature and moisture for this region? And what is the implication for the carbon balance and viability of the vegetation of this ecosystem in the future?”

Response to general comment:

We are very grateful for the efforts of reviewer on improving this work. We have re-organized the objectives and contents, emphasizing on the following two questions: i) the roles of componential C processes in regulating soil CO₂ effluxes, and ii) the plant-interspace differences in the C fluxes (see Lines 111-120). Sections and paragraphs in results and discussion has been re-arranged accordingly, and additional analysis (e.g. Table 5) has been added to aid the second question. We also performed a test as suggested, to see if exclusion of biocrust-related processes reduced the fitness to measured soil CO₂ flux at C3 (Line 678-683). We hope these revisions could improve the manuscript. Please find the red marks in revised manuscript for the changes.

We understand the hope of reviewer to upscale and extrapolate the current results, for large scale, long term and general implications. Extrapolating the modelling for large scale and long term applications, and

scenarios analysis for climate change and sustainable management are our future targets as well. At the moment, this could not be done by current model. Because, as described in section 4.3, the growth dynamics of shrub vegetation is not included in modelling yet. Therefore, the changes in leaf area, shading and energy partitioning, evapotranspiration and root biomass are not available for longer term iterations, considering climate change scenarios or vegetation management. Our future work addresses this issue and will aim to provide a full picture of C-N cycle in such ecosystems.

MAIN SUGGESTIONS Materials and methods Figure 1: could you incorporate a small map showing the study region? I am sure readers would find that useful. Figure 1 also is not very clear unless zoom in, therefore I think the size/resolution needs to be improved for reading on paper.

Response: We appreciate the comment and have separated Figure 1 into two different figures (Fig. 1 and 2). Into Fig. 1, we added a map showing the study region (Fig. 1a), changed the site picture (Fig. 1b) for better quality, and added photos showing the soil collars (Fig. 1c - 1e). Model framework has been moved to Fig. 2.

Line 127: You say 40% here but the value is 90% in the Gong et al. (2016) paper. Which one is correct?

Response: Both values are correct. This study was based on a different location from that in Gong et al. (2006). The two locations are about 1km apart.

Line 160: Please define PATCIS. Is it a model name, an acronym?

Response: It is the name of model.

Section 2.2.3: for the sake of clarity/completeness, it would be good to have an extra equation here showing how all the flux components sum to provide the total net biocrust flux (FB) in equation (1).

Response: We have revised all the symbols and names to keep them consistent. F_B in this question was replaced by F_{Ct} , see Line 162.

I would have Section 2.3.1 as a separate Section (e.g. just 2.3) entitled "data" or "measurements". It may not be immediately obvious that you would find a description of the data here in this section on model parameterization if you were just scanning through section headings.

Response: We have separated that paragraph to section 2.3 named "Micrometeorological and soil CO₂ efflux measurement". (Line 299-324)

Lines 308 to 309: it would be great to have pictures of these three sites to show readers new to the topic of biocrusts what they look like.

Response: The crust pictures have added to Fig. 1 (c - e).

Section 2.3.3 (and throughout Section 2.3): For many parameters, there is a clear and adequate description for the functions used to derive them, but not all – some detail appears to be missing for some. For example,

for lines 345-347: please could you give a little more detail on how the horizontal and vertical root biomass profiles were parameterized? For example, did the root biomass decrease linearly with distance from the center of the shrub crown? Another example for lines 351-352: how was the photodegradation coefficient calculated from the mass-loss rate. I am also a bit confused as to why only certain parameters are included in Table 2 and not all (e.g. why is the photodegradation coefficient not included for example)?

Response: That section (numbered as 2.4.2 in revised paper) has been checked and more information has been added. Photodegradation coefficient k_p has been added to Table 2.

Lines 377 and 379: I think the 2nd $Q_{10}()$ in equation 28 should be $Q_{10}(\theta)$ and the same in equation 30? How did you come to define equation 31 in this way? Based on the aforementioned studies? Which method did you use to perform the fits shown in Figure 2 and equations 32 and 33?

Response: The 2nd Q_{10} in equation 28 has been revised to $Q_{10}(\theta)$. For equation 31, there are not available numerical descriptions on such an rain effect so far; therefore we decided to add one to the algorithm. This equation has been tested in sensitivity analysis (see test for parameter n_p), which shows this equation may not be an important source of uncertainty. Future modelling may also consider to simplify this algorithm (Line 615). Fittings in figure 2 (Fig. 3 in revised manuscript) were performed by Matlab curve-fitting toolbox. The information has been added to Line 416 and 423.

Section 2.4.1 title should mention the meteorological forcing data. A shorter title could be “model set-up”. Do you have a reference for the PECE method?

Response: The title has been changed as suggested (Line 324). Like forward/backward Euler, PECE method can be found in many textbooks related to ordinary differential equations, e.g. Butcher, John C. (2003), Numerical Methods for Ordinary Differential Equations, New York: John Wiley & Sons, ISBN 978-0-471-96758-3. The reference has been added to the manuscript (Line 482).

Lines 502-504: How/why did you choose which parameters to include in your sensitivity analysis?

Response: The reason to choose the tested parameters has been better discussed in section 2.5.3.

Section 2.4.3: to avoid some confusion in the results later, I might have the parameter sensitivity as a separate test from the comparison between plant covered and interspace soil CO₂ flux (so add a test 5). I think this would help to emphasize the importance of the impact of plant heterogeneity in the text, given its importance in the paper title. It might be useful for the reader to have a small table summarizing all the tests, which processes they include, which site they correspond to, what the observations are measuring etc.

Response: This suggestion was taken with gratitude. We separated the contents as suggested, and organized the tests to two part: i) to demonstrate the roles of componential C fluxes in regulating surface efflux; and ii) to find out the differences between plant cover and interspace in terms of C flux rates and sensitivities. see Section 2.5.3-2.5.4.

Results What is shown on the bottom of Fig4a? Is that precipitation? It might be worth smoothing your hourly curves with a moving average window so we can see the variability better I would put precipitation on the hourly time series plots in Figure 5 as well.

Response: The figures 4 and 5 have been revised following the suggestions. 3-day moving average trends were used to show the temporal dynamics better.

Lines 540-541: It would be good to give the RMSE of C1 above as well for a comparison.

Response: The RMSE value was added to C1 in Line 551.

Figure 6: I like the addition of the diurnal bias plots - they are very informative. I would put the same scale for all C1, C2 and C3 plots to enable an easier comparison between the tests.

Response: The scales has been set to same in Fig. 5 and Fig.7.

Lines 542-544: Looking at Figure 6b it seems to me that the pattern of diurnal biases has changed for C3 compared to C2 and C1? There is now a positive bias around noon and a negative bias in the mid-morning and afternoon? Why do you think this is?

Response: Indeed, the pattern became different in C3 compared to C2 and C1. It is probably caused by biases from photosynthesis & photodegradation, which were introduced into system in Test 3. We have revised the description in the manuscript (Line 565-568).

Table 3 caption: component fluxes. It would also be better to say “for areas with plant cover and without (interspace)”

Response: Table 3 caption has been revised as suggested.

Figure 7: You mention FS in the caption but FT in the text and figure legends. Also, you refer to net CO2 sequestration by the biocrust in the legend – isn’t this FB (or FCt), of have I misunderstood? It would be helpful to the reader to make sure all the abbreviations you use for the fluxes are uniformly used across the text and figures. In fact, I would suggest adding an extra table with all the component flux abbreviations and their long name/description, given that there are many. This may help the reader cross-reference between the figures, tables and text.

Response: We agree there have been several place with unnecessary naming. We have revised all the symbols and names to keep them consistent. Please see in the revised figure (Fig. 8).

Table 4: are all the values listed the % change in C flux after manipulation compared to the base flux, or are some of the +/- values a change in the absolute C flux magnitude? Please detail this in the table caption.

Response: Yes, all values listed in Table 4 are % changes. This point has been clarified in figure footnote.

Lines 578-583: I am a bit lost as to main message of the second part of the sensitivity analysis. What does the sensitivity analysis suggest about how important the parameters are? If changing the parameter values does not result in that much change to the fluxes, does that mean that parameter or even that process is not actually important for modelling the flux? How have you decided how much to change the parameter

values? Perhaps it would be good to explore their full range (between their upper and lower bounds) in a proper sensitivity analysis (e.g. using the Morris method) in order to determine the full impact of the parameter values.

Response: Yes, parameter sensitivity was studied to understand which parameter is more important and more likely to be the main source of uncertainty, as we have many site-specific parameters. Those parameter have high sensitivity then need to be used with extra caution, when applying the system to another space-time. For site-specific parameters like T_s , θ , M_{tot} etc., we modified the values by the same degree ($\pm 10\%$), so that their effects on C fluxes are easy to compare. Moreover, if the changes in simulated C fluxes are much smaller than the changes in certain parameter, we consider the simulated C fluxes could be insensitive to that specific parameter. Therefore, this kind of tests is a bit different from the Morris method. On the other hand, "full" impact is difficult to define. Some parameters, e.g. root biomass, may vary by several folds from one collar to another (see Wang et al., 2015, Biogeosciences). Also an artificial parameter setting (e.g. assuming extreme values for many parameters) may be unrealistic in many cases (e.g. a combination of very low moisture content and very high root biomass). Therefore, performing an Morris analysis like suggested could be difficult, while the upper/lower bounds of parameters are unclear in a combination.

Some of the results are repeated in the discussion. Given that the results section is very short, it might be better to merge the results and at least some of the discussion that is very pertinent to each particular result for each separate sub-section (e.g. validity of the results, ...) and separate out each with a sub-heading. That way the reader is not switching between different aspects of the modeling in the results before having to come back to consider the implications of these results in the discussion. It is encouraging that the authors are aware and detail all the caveats of their work; however, the manuscript might benefit from a shorter, more concise discussion, particularly given the methods section is also (necessarily) long. A brief summary of the missing features of the model such as is given in the conclusions may be enough with a few extra sentences and references. Be sure not to repeat sections of the introduction or results in the discussion, e.g. lines 726-744 is largely a repetition of context and results. I appreciate it is hard to keep the results and discussion separate, which is why I have suggested combining at least some parts of the discussion with the results in a "results and discussion" section. This would also help to reduce the length of the manuscript. Other more general parts of the discussion could be put in a final "Conclusions and future perspectives" section.

Response: We greatly appreciate these advices. In order to better structure this part, we moved a part of the discussion on model validity into result section 3.1. Now discussion (i.e. section 4.1 and 4.2) has focused on answering the two questions we proposed. The model uncertainties and further needs of research are discussed in the final section 4.3. We think this information would be helpful for future studies on experiments and modeling.

MINOR COMMENTS In general: CO₂ production, not productions. Both some missing and unnecessary "the" in places (e.g. line 95, no 'The' is needed, and occasionally the plural of a word is used where it should not be (e.g. CO₂ productions). Check the text carefully. Please could you explain this sentence more: "In dryland soils, the interactions between CO₂ transport and water cycle could also be intensive, due to the commonly high salinity/alkalinity of soils."? What do you mean by intensive?

Response: Appreciated. We revised the text as suggested, see Line 60-62.

Line 104: "However, both models focus on the patterns at the regional-scale with very simplified ecosystem processes and neglect stand-scale heterogeneities of water energy budget, and have not yet been validated by field measurements." I would turn this sentence into a positive one to highlight what you will do to add to the field and incorporate that into your following paragraph. Something like switching this sentence to read "we will build on this work by including complex processes related to... . Furthermore, we have validated our new model with extensive field measurements..."

Response: we have revised the text, see Line 107-120.

Line 384: Sponseller, 2007 and Cable et al. references missing

Response: Citation to Sponseller has been added. Cable et al. 2013 was removed.

Lines 409-411: Do you mean NPP and not NP?

Response: Yes, it should be NPP here (Line 420-422). Corrected.

Line 429: litterfall Line 456: probability, not probably?

Response: Corrected as suggested (Line 439 and 466).

Line 464: "The model simulation employed half-hourly meteorological factors" "the model was run with half-hourly meteorological variables"

Response: Corrected as suggested (Line 474).

Line 496: "contributed to the soil CO2..."?

Response: Corrected (Line 505).

Line 506: "It was also studied" "Furthermore, we studied" Line 507: "regarding the" "due to"

Response: This paragraph has been revised (section 2.5.3).

Line 521: pronounced

Response: Revised as suggested (Line 542).

Line 703: "should" instead of "shall"

Response: This paragraph has been revised.

Lines 705-709 reads more like "Conclusions"

Response: This paragraph has been re-organized.

Final Response to reviewer #2

General comment:

This study concerns the development and application of a highly detailed physically based patch-scale land-atmosphere energy, water and carbon balance model for a semiarid ecosystem with high plant-interspace heterogeneity. The model represents an expansion of the model developed by Gong et al. (2016. Ag. Forest Met) that compared patch scale water and energy exchange into soil-plant C exchanges. The model represents most of the C stocks and fluxes that you expect to be relevant for dryland ecosystems, but which are not normally represented in ecosystem C models like photodegradation, biocrust photosynthesis and respiration, gas and liquid phase CO₂ transport, etc. The model is used to simulate bare and plant shaded surfaces as well as biocrust covered surfaces and compared to measurements. The model was shown to be very capable of accurately simulating measured soil temperatures, soil moisture and soil respiration(Rs). The main findings were that total CO₂ production in the soil and Rs could deviate substantially from one another due to root uptake, crust respiration and photosynthesis, and variations in CO₂ dissolution, emphasizing the processes beyond heterotrophic and autotrophic respiration and highly heterogeneous nature of CO₂ cycling in patchy ecosystems. These results shed some light on the importance of these other processes that are not commonly represented in ecosystem models as well as our ability to represent them in ecosystem models. The paper is well written. The authors do a great job in discussing the background literature in the Introduction as well as tying their findings to previous studies in the discussion. The paper is very long, but this should probably be expected given the highly detailed modeling work that is being presented. Overall, there is nothing fundamentally flawed with the paper and I expect that this work will be of interest to ecosystem modelers, particularly those interested in dryland ecosystems.

My main complaint about the paper involves equifinality of the model results and the lack of data to be able to validate their findings on the relative roles of the different component fluxes. A model with far fewer parameters and processes is likely to be equally as capable of simulating soil moisture, temperature, and Rs for these cases or tests so how can one have much confidence that extra capabilities of the model (to represent the individual fluxes and transports like photorespiration, crust photosynthesis/respiration, CO₂ uptake by roots) are valid? Table 3 is great, but it could be entirely fictitious. While I'm excited to see models being built with these processes considered, I wonder how we can build confidence that they are any better than simple, more empirical models already out there.

Response to general comment:

We sincerely appreciate the comments of reviewer. The manuscript has been revised in light of the comments, with several main changes in the structure, figures and tables. All the revised texts have been marked in red color.

For the complaint on equalfinality, we fully are aware that over-complexity and over-parameterization could be important sources of uncertainties for process-based models; and that also, a well-trained empirical model with less parameters may still yield good fitting, for environmental conditions assumed not to change. In this work, we have aimed to understand the role of componential fluxes under varying environmental conditions.

For the complaint on lack of data support, we are aware that only one chamber for each step may not be enough, and fluxes like photorespiration and CO₂ removed by root or lateral flows are still lack of support

from field data. These uncertainties, along with several other possible aspects, have been discussed in revised section 4.3.

“A couple of relatively minor issues: 1. There could be better setup in the introduction. What are the objectives and rationale of this study? Major questions or hypotheses? ”

Response to minor issue 1:

This issue is pointed out by both reviewers and we have re-organized the manuscript to answer two specific objectives: i) to investigate the roles of componential C processes in regulating soil CO₂ effluxes in the studied ecosystem, and ii) to analyze the plant-interspace differences in the componential C processes. These issues has been discussed in introduction (Line 111-120). The results (section 3.2, 3.3) and discussion (section 4.1 and 4.2) have been re-organized accordingly.

“2. Figure 8 used as an estimate of photorespiration. How do you separate the effects of greenhouse effect under the clear chamber versus the shade effect of the opaque one? In other words, the opaque chamber shields the surface and reduces the heating when the chamber is closed. The clear chamber, by allowing solar radiation in and blocking thermal radiation out, is going to be heated much more potentially during the measurement cycle, potentially increasing heterotrophic respiration. Is Rs higher because of higher temps or because of photorespiration? ”

Response to minor issue 2:

The C fluxes are measured by automatic chambers, which only seals the collar during measurement (2.5 minutes), then move away from the collar. Therefore, the collar was not blocked by chamber in most of time, and the temperature disturbance by measurement are marginal. As suggested by Figure 8, flux signals during the daytime nearly doubled during those periods; it is difficult to be explained as heating effect, as even 2 degree heating lead to < 10% changes in efflux (Table 4, sensitivity analysis). Also, the period was dry and with almost no rain event (see Fig. 6 in revised manuscript). Therefore, photorespiration by crust organisms is also unlikely.

“Text specific comments: L13. This sentence is an unusual way to open up an Abstract. I am wondering if it could be replaced with a sentence that provides context and rationale for the study ”

Response: The abstract opening has been revised (Line 13-17), based on the revised objectives and contents.

L54. cannot

Response: Revised to “may not” (Line 57).

L55. periods

Response: Revised to “periods” (Line 58) as suggested.

L58 intensive? Also, why would water and CO₂ transport be more intensive in the drylands?

Response: We agree that this sentence is unclear. It has been revised to “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” (Line 60).

L62. Here’s another paper with the relevance of abiotic C with fluxes on the diurnal time scale. Hamerlynck, Erik P., et al. "Nocturnal soil CO₂ uptake and its relationship to subsurface soil and ecosystem carbon fluxes in a Chihuahuan Desert shrubland." *Journal of Geophysical Research: Biogeosciences* 118.4 (2013): 1593-1603.. There are several papers out that seem to show that inorganic C uptake is unlikely to be a very significant flux...see e.g. review in Schlesinger, William H. "An evaluation of abiotic carbon sinks in deserts." *Global change biology* 23.1 (2017): 25-27.

Response: It is true that inorganic C uptake may not be very significant flux in many cases. Our simulation also showed that such a flux was only about 15% of total emission from collar, and those C may still emit somewhere during the transport and have even less impact at ecosystem level. The main idea to include the transport processes are to better explain the variations of point-scale efflux, which may not necessarily link to changes in total soil C pool, but are just noises caused by transportation processes.

L69. matter

Response: Revised as suggested (Line 71).

L70. “could maintain inactive”?

Response: Revised to “could be inactive” (Line 72).

L77. Might consider H. Throop’s work here, e.g., Throop, Heather L., and Steven R. Archer. "Resolving the dryland decomposition conundrum: some new perspectives on potential drivers." *Progress in botany*. Springer Berlin Heidelberg, 2009. 171-194. If you can’t find this chapter, she has several articles about photodegradation.

Response: Good suggestion. Citation of Throop et al. 2009 has been added (Line 80).

L79. periods

Response: Revised as suggested (Line 81)

L95 Define “global change”

Response: Revised to “global climate change” (Line 97)

L104. “works”

Response: Revised as suggested (Line 106)

L114-115. This sentence seems out of place. If this represents an advance of Gong et al. you should cover what this model development is.

Response: This paragraph has been revised to better state the aims and objectives of this study and the advance of this modeling (Line 111-120).

L118. How about "Model Overview"

Response: Revised as suggested (Line 124).

L119. modeling work was based on measurements?

Response: Reworded as "... model was build based on ..." (Line 125)

L128. Don't understand this sentence

Response: The sentence has been reworded (Line 134).

L456 "probably"?

Response: Revised as suggested (Line 466).

L491. Later on, Test 4 is mentioned, but it should probably be included in this paragraph

Response: Test 1-3 are for model validation, Test 4-5 are for sensitivity analysis, so we consider that it would be better to separate them into different sections.

L503. component

Response: This paragraph has been revised (section 2.5.3).

L521. "was more pronounced"

Response: Revised as suggested (Line 542).

L523-525. I don't know of many soil C3 water probes that are good at measuring frozen water content. Are you sure the measurements are valid during these times?

Response: It is true that water content measurement during freezing period may not be reliable. We have changed the statement here (Line 543-544).

L534 4b?

Response: revised to 5b (Line 554).

L554. All the variables need to be clearly redefined in the Table caption so that this paragraph is much easier to understand.

Response: Table 3 has been revised and the definition of variables has been added to footnote

L565. Compared to

Response: The paragraph has been revised (Line 587).

L566 ,irrespective of the size...

Response: Revised as suggested (Line 588).

L573. "compared"

Response: Revised as suggested (Line 604).

L598. "our model capably reproduced the time series for the water and energy fluxes at ..."

Response: Revised as suggested (Line 547).

L605 Suggest using another heading before this paragraph, something like "modeling uncertainties"

Response: This has been suggested by both reviewer and we have reorganized this part to section 4.3

L705. provides L708 caution L709 Our simulations showed that a

Response: The result section has been reorganized. Those sentences has been rewritten or removed.

L773. uptake

Response: revised as suggested (Line 792).

L785 Are the model and data available for others to use ?

Response: So far, it is distributed among several collaborators but yes. We are still trying to include the aboveground vegetation before wider distribution.

Table 3. All terms need to be defined in this table caption including Fs, Fft PCT

Response: Revised. Definitions have been added to table footnote.

Figure. 1. The photo is really too small to see much of anything. Suggest deleting this so there is more space for the conceptual figure

Response: Revised. The conceptual framework has been displayed separately as Fig. 2.

Fig. 4. Ppt is not labeled or given a scale

Response: Revised (see Fig. 5).

Fig. 6. Greek letter is not defined in the caption.

Response: Revised (see Fig. 7).

Fig. 7. This figure is very hard to see. Could you use more colors for the different symbols so that it is easier to see?

Response: We revised the figure by differentiating the coloring (Figure 8). The resolution of initial figure was also limited by the file-size restrictions of discussion paper. We will upload bigger images with better qualities in the final submission.

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Modelling the diurnal and seasonal dynamics of soil CO₂ 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 CO₂ 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 CO₂ 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-crust and two lichen-crust plots during a two-year period. The model simulation showed that, soil rewetting could enhance CO₂ dissolution and delay the emission of CO₂ produced from root-zone. In addition, an ineligible fraction of respired CO₂ might be removed from soil volumes under respiration chambers by lateral water flow and root uptake. During rewetting, the lichen-crust soil could shift temporally from net CO₂ source to sink, due to the photosynthesis of lichens and restricted CO₂ emissions from subsoil. The presence of plant cover could decrease the root-zone CO₂ 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 CO₂ 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 (F_S) 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 F_S 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 F_S 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ production with the transport of gas and heat (Šimuněk 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 CO₂ components in regulating soil CO₂ effluxes in the studied ecosystem, and ii) to estimate the plant-interspace differences in the componential C processes. For these purposes, we developed a process-based model, which considered simultaneously the CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 $1.4 \times 10^5 \text{ J cm}^{-2}$ 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) CO_2 dissolution, transport and efflux; (ii) Autotrophic and heterotrophic CO_2 production in the soil profile; (iii) CO_2 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): CO_2 transport, dissolution and efflux

For soil fraction x (see Fig. 1f for RLU settings), CO_2 exchange (F_s , upward positive) was the sum of CO_2 exchange by biocrust (F_{Ct}), photodegradation (F_p) and the emission from soil under the biocrust layer (F_T):

$$F_{Sx} = F_{Ct_x} + F_{T_x} + F_{P_x} \quad (1)$$

where F_{Ct} is the net balance between biocrust photosynthesis (P_{Ct}) and respiration (R_{Ct}), and $F_{Ct} = P_{Ct} - R_{Ct}$ (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 CO_2 concentration and C flows were calculated as follows:

$$\frac{\partial C_{x,i}}{\partial t} = \frac{\partial}{\partial z} (F_{dg}^v + F_{ag}^v + F_{dw}^v + F_{aw}^v) + \frac{\partial}{\partial h} (F_{dg}^h + F_{ag}^h + F_{dw}^h + F_{aw}^h) + S_{x,i} \quad (2)$$

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:

$$F_{Tx} = F_{dg_{x,1}}^v + F_{ag_{x,1}}^v + E_{x,1}^S C_{w_{x,1}} \quad (3)$$

where $E_{x,1}^S$ is the soil evaporation at section x (see Eq. (17) in Gong et al., 2016); C_w is the equivalent CO_2 concentrations in the solution of the topmost soil. For layer (x, i) , C_w is linked to the gaseous CO_2 concentrations (C_g):

$$C_{x,i} = C_{g_{x,i}}(V_{x,i} - \theta_{x,i}) + C_{w_{x,i}}\theta_{x,i} \quad (4)$$

where V is the total porosity; and θ 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):

$$\text{CO}_2(g) + \text{H}_2\text{O}(l) \rightleftharpoons \text{H}_2\text{O}(l) + \text{CO}_2(aq) \quad K_H = P_C / \text{CO}_2^{aq} \quad (5)$$

$$\text{CO}_2(aq) + \text{H}_2\text{O}(l) \rightleftharpoons \text{H}_2\text{CO}_3 \quad K_0 = \text{CO}_2^{aq} / [\text{H}_2\text{CO}_3] \quad (6)$$

$$\text{H}_2\text{CO}_3 \rightleftharpoons [\text{H}^+] + [\text{HCO}_3^-] \quad K_1 = [\text{H}^+][\text{HCO}_3^-] / [\text{H}_2\text{CO}_3] \quad (7)$$

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

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 $[\text{H}^+]$ 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 CO_2^{aq} , H_2CO_3 , HCO_3^- and 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 uptake by roots:

$$S_{x,i} = R_{s_{x,i}} + R_{a_{x,i}} - E_{x,i} C_{w_{x,i}} \quad (9)$$

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 (R_m) and growth respiration (R_g):

$$Ra_{x,i} = Rm_{x,i} + Rg_{x,i} \quad (10)$$

To simulate Rs , 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} , 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):

$$m_{x,i}^r = M_{x,i}^r k_r f(Ts_{x,i}) f(\theta_{x,i}) f(O_{x,i}) dt \quad (11)$$

where superscript r denotes the type of SOM pool ($r=1$ for M_{deb} , $r=2$ for M_{mic} , and $r=3$ for M_{hum}); m is mineralized SOM during time step dt ; k is the decomposition constant; dt is time step; $f(Ts_{x,i})$, $f(\theta_{x,i})$ 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). $f(Ts_{x,i})$ 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):

$$Rs_{x,i} = r_E m_{x,i}^r \quad (12)$$

where r_E is the gas production rate ($r_E \in [0, 1]$), 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:

$$M_{x,i}^r = (1 - r_E) m_{x,i}^{r-1} - m_{x,i}^r + A_{x,i}^r dt \quad (13)$$

where A is the SOM input rate ($A=0$ for M_{mic} and M_{hum}); superscript $r-1$ denotes the source SOM pools.

$Rm_{x,i}$ was calculated in a similar way to $Rs_{x,i}$ (e.g. Chen et al., 1999; Fang and Moncrieff, 1999). $Rg_{x,i}$ was calculated as a fraction of photosynthetic assimilates, following Chen et al. (1999):

$$Rm_{x,i} = M_{x,i}^R k_R f(Ts_{x,i}) f(\theta_{x,i}) f(O_{x,i}) dt \quad (14)$$

$$Rg_{x,i} = k_g P_g f r_{x,i} \quad (15)$$

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_{max} , and maximum rate of electron transport, J_{max}), foliage temperature (T_c) and stomatal conductance (g_s). The values of V_{max}

and J_{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. NH_4^+ and 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_{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:

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

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

2.2.3 Submodel (iii): CO₂ 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:

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

$$R_{Ct} = M_{Ct} k_{cr} f_{RC}(T_{Ct}) f_{RC}(\theta_{Ct}) \quad (19)$$

where α_C is the apparent quantum yield, P_{Cm} is the maximal rate of photosynthesis, and was a function of the moisture content (θ_{Ct}) and temperature (T_{Ct}) in topcrust; A_{PAR} is the photosynthetically active radiation (PAR); M_{Ct} is the total C in the SOM of topcrust; k_{cr} 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 ($M'_{x,l}$) and temperature and moisture content of crust layer (i.e. $T_{s_{x,l}}$ and $\theta_{x,l}$; 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:

$$M_{Ct} = M_{CA} + M_{CH} \quad (20)$$

$$\frac{dM_{CA}}{dt} = P_{Ct} - R_{Ct} \frac{M_{CA}}{M_{Ct}} - k_m M_{CA} - k_b M_{CA} \quad (21)$$

$$\frac{dM_{CH}}{dt} = k_m M_{CA} - R_{Ct} \frac{M_{CH}}{M_{Ct}} - k_b M_{CH} - F_P \quad (22)$$

$$\frac{dM_{Cs}}{dt} = k_b M_{Ct} - R_{Cs} \quad (23)$$

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:

$$F_{Px} = M_{surf} k_p Rad_x \quad (24)$$

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 CO₂ 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-crusts 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 θ 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 5m×5m 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 F_s 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 (θ_{sat}), bulk density and residual water content (θ_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 α_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. 60cm 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 ($M^S = 0.2917 * \pi(0.5D)^2$, 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 ($M^R = 0.47M^S$, 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):

$$k_R = k_{R0}(1 + n_R L_l / L_{max}) \quad (25)$$

where k_{R0} 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_{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 CO₂ production

Based on the empirical study of Wang et al. (2014a), the steady-state sensitivity of CO₂ production to soil temperature and water content (i.e., $f(Ts)f(\theta)$, Eq. (11)) can be described as a logistic-power function:

$$f(Ts)f(\theta) = f(Ts, \theta) = \{1 + \exp[a(b - Ts)]\}^{-1}(\theta/\theta_{sat})^c \quad (26)$$

where a , b and c are empirical parameters. This function represents the long-term water-thermal sensitivity of CO₂ production over the growing seasonal, yielding an apparent temperature sensitivity Q_{10} of 1.5 for the emitted CO₂ (Wang et al. 2014a). However, this could underestimate the short-term sensitivities of CO₂ 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} :

$$f(Ts)f(\theta) = f(Ts_{short}, \theta_{short}) + [f(Ts, \theta) - f(Ts_{short}, \theta_{short})]Q_{10}^{(Ts - Ts_{short})/10} \quad (27)$$

$$Q_{10} = \max [Q_{10}(Ts_{short}), Q_{10}(\theta_{short})] \quad (28)$$

$$Q_{10}(Ts_{short}) = -0.42 Ts_{short} + 12.4 \quad (29)$$

$$Q_{10}(\theta_{short}) = 18010 \theta_{short}^{3.721} + 1.604 \quad (30)$$

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

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_{pulse}):

$$f_{pulse} = \max[1, (\theta/\theta_{72h})^{n_p}] \quad (31)$$

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. θ_{72h} is the 72-hour moving average of θ . For tests on model sensitivities to different parameterization of f_{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 $\mu\text{mol C cm}^{-3}$) were collected from a 20 m \times 20 m area. The samples were wetted and incubated under controlled T_{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 exchanges 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, θ_{Ct} was measured every 20 min. For more details see Feng et al. (2014).

Fitting measured Rd to T_{Ct} and θ_{Ct} (see Fig. 3a) using Matlab[®] (2012a) curve-fitting tool. The obtained multipliers in Eq. (19) are as following:

$$f_{RC}(T_{Ct})f_{RC}(\theta_{Ct}) = Q_{Ct}^{\frac{(T_{Ct}-20)}{10}}(a_{RC} + b_{RC}\theta_{Ct} + c_{RC}\theta_{Ct}^2) \quad (32)$$

where Q_{Ct} , a_{RC} , b_{RC} , c_{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_{Ct} and θ_{Ct} of each measurement. P_{Cm} was determined by subtracting the simulated respiration rate from the NPP measured under light-saturated conditions. Then P_{Cm} was fitted to T_{Ct} and θ_{Ct} in Matlab[®] (2012a) curve-fitting tool using following equation (Fig. 3b):

$$P_{Cm} = f_{Pt}(T_{Ct}) f_{Pw}(\theta_{Ct}) \\ = (a_{Pt} + b_{Pt}T_{Ct} + c_{Pt}T_{Ct}^2 + d_{Pt}T_{Ct}^3)(-a_{Pw} + b_{Pw}\theta_{Ct} - c_{Pw}\theta_{Ct}^2 + d_{Pw}T_{Ct}^3) \quad (33)$$

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

It should be addressed that T_{Ct} and θ_{Ct} could change more rapidly than the mean conditions of the crust (i.e. $T_{s,I}$ and $\theta_{s,I}$). In this work, T_{Ct} was calculated from the surface temperature (T_s , see Eq. (13) in Gong et al., 2016) and $T_{s,I}$ by linear interpolation. The calculation of θ_{Ct} , on the other hand, depended on the drying-rewetting cycle. During drying phases, θ_{Ct} was interpolated linearly from $\theta_{s,I}$

and surface moisture content (θ_x); whereas during wetting phases, the mass balance of water input P and evaporation loss ($E_{x,1}^s$, see Eq. (17) in Gong et al., 2016) was considered:

$$T_{Ct} = \frac{T_x Z_{Ct} + T_{s_{x,1}} Z_{s_{x,1}}}{Z_{Ct} + Z_{s_{x,1}}} \quad (34)$$

$$\theta_{Ct} = \max \left[\frac{\theta_x Z_{Ct} + \theta_{x,1} Z_{s_{x,1}}}{Z_{Ct} + Z_{s_{x,1}}}, \theta_{Ct} + \frac{P - E_{x,1}^s}{Z_{Ct}} \right] \quad (35)$$

where $Z_{s_{x,1}}$ is the thickness of the biocrust; and Z_{Ct} is the thickness of the topcrust. θ_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 ($A_{x,i}^1$, Eq. (13)) were linked to the mortality of roots, which was calculated following Asaeda and Karunaratne (2000).

$$A_{x,i}^1 = k_{mo} Q_{mo}^{T_{s_{x,i}} - 20} M_{x,i}^R \quad (36)$$

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, $f_m(\theta_{Ct})$, to describe the impact of abrupt θ_{Ct} changes on k_m :

$$A_{Cm} = k_{mc} Q_{mo}^{T_{Ct} - 20} f_m(\theta_{Ct}) M_{CA} \quad (37)$$

$$f_m(\theta_{Ct}) = \max[0.01, 1 - \min(\theta_{Ct}, \theta_{Ct7}) / \max(\theta_{Ct}, \theta_{Ct7})] \quad (38)$$

where k_{mc} is the optimal mortality rate at 20°C; Q_{mo} is the temperature sensitivity parameter (Asaeda and Karunaratne, 2000); θ_{Ct7} is the forward 7-day moving average of θ_{Ct} .

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:

$$k_b = \frac{k_{sand}}{\rho_{bulk}} \frac{1}{Z_{Ct}} \quad (39)$$

where ρ_{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_{Cs}) 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, T_a , 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-crust soils. In this case, F_T in Eq. (1) was the only term affecting F_S ($F_B=0$ and $F_P = 0$), 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 (R_{Cr}), and set $F_B = R_{Cr}$ and $F_P = 0$. Test 3 considered all the flux components (F_T , F_P and F_B). 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 the those measured from the collar C1 – C3, respectively. Linear regressions were used to compare the modelled and measured values. The biases (ζ) 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 componential CO₂ fluxes and their parameter sensitivities

Using the validated model, we simulated the temporal trends of C flux components (i.e. P_{Cr} , R_{Cr} , 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 componential 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_m), to understand their effects on model uncertainties. F_S and componential 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 (dF) 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 CO₂ efflux, Test 5 simulated annual F_S and componential 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 (650 gC m⁻²) and root biomass (200 g m⁻²) 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 (T_s), water content (θ) 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 θ 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 T_s and θ 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 T_s . 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 $0.43 \text{ umol m}^{-2} \text{ s}^{-1}$ and $0.29 \text{ umol m}^{-2} \text{ s}^{-1}$ 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 $0.25 \text{ umol m}^{-2} \text{ s}^{-1}$ and $0.35 \text{ umol m}^{-2} \text{ s}^{-1}$ 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 componential C processes and their parameter sensitivities.

3.2 Modelled C flux components of F_S

Test 4 showed that, R_s 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 ($R_s + R_a$) 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 (R_s+R_a) 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. $36 \text{ gC m}^{-2} \text{ year}^{-1}$), whereas the loss of dissolved CO_2 via seepages or pore-mediated horizontal flows were limited (i.e. $7.4 \text{ gC m}^{-2} \text{ year}^{-1}$). The photosynthesis rate of topcrust was $31.1 \text{ gC m}^{-2} \text{ year}^{-1}$ 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. $< 5 \text{ gC m}^{-2} \text{ year}^{-1}$).

Analysis of parameter sensitivity showed that, the modelled F_S and the component fluxes were more sensitive to $\pm 2 \text{ }^\circ\text{C}$ in T_s or $\pm 10 \text{ } \%$ in θ , **compared** to the effects of $\pm 10 \text{ } \%$ or $\pm 20 \text{ } \%$ in the other parameters (Table 4). Varying θ by $10 \text{ } \%$ produced greater impacts on the simulated R_P and crust-related fluxes (i.e. P_{Ct} , R_{Ct} and F_P), as compared to changing T_s by $\pm 2 \text{ }^\circ\text{C}$. Increasing θ by $10 \text{ } \%$ enhanced the simulated P_{Ct} and F_{Ct} by $41 \text{ } \%$ and $28 \text{ } \%$, and doubled the net C sequestration ($F_{Ct} - F_P$) 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 θ , the simulated efflux was also sensitive to changes in root biomass (M^R). Manipulating root biomass by $\pm 10 \text{ } \%$ changed the annual F_T and F_S by about 7%, and such effects were 100% greater than $\pm 10 \text{ } \%$ 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_{mc} , M_{Ct} and M_{CA} : M_{CH} . 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 produced 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 ($R_s + R_a$) 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_{Ct}) was 34% lower under canopy. This reduced the under-canopy F_{Ct} 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 $1.4 \text{ gC m}^{-2} \text{ year}^{-1}$).

We further compared the flux sensitivities at plant cover and interspace to the changes in three most effective parameters (i.e. T_s , θ and M^R , see Table 5). For subsoil-mediated fluxes (i.e. F_S , F_T , R_a , R_s), 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_{Ct} , F_{Ct} , 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 θ . On the other hand, the plant cover reduced the sensitivity of CO_2 effluxes to changes in root biomass. P_{Ct} , F_{Ct} and F_P were generally more sensitive to warming and θ manipulations at plant cover than interspace, except that plant cover decreased the

sensitivity of F_p to -10 % changes in θ . 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 CO₂ 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 CO₂. 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 CO₂ production and emission during the wetting-drying cycle, as regulated by the CO₂ transport in soil profile. The simulated CO₂ 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 CO₂ dissolution, instead of the reduced respiration rates by low O₂ 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 CO₂ could be stored temporally in soil pore-space after rainfalls. The dissolved CO₂ 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 CO₂ 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 CO₂ produced could be removed by root uptake and leave the volume measured by the respiration chamber. Bloemen et al. (2016) showed that the CO₂ 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 CO₂ 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 CO₂ 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_{Cr} 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 CO₂ 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 CO₂ efflux, removing the biocrust processes would significantly reduce the model validity. For example, the goodness of fitting (i.e. R²) in Test 3 dropped from 0.65 to 0.45 for the two-year period, if F_{Ct} 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 semiarid 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 $\pm 10\%$ 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_{Ct} 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_{Cl}) 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 CO₂ 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_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_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 CO₂ 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 CO₂ production, transport and surface exchanges (e.g. biocrust photosynthesis, respiration and photodegradation) in F_s modelling for

dryland ecosystems **with** high plant-interspace heterogeneities. Our model simulated reasonably well the F_s dynamics measured from non-crust and lichen-crust 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-crust 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 **componential 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.**

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Tables

Table 1. Configuration of soil collars used in this study

Collars	C1	C2	C3
Surface type	Non-cruled	Lichen-cruled	Lichen-cruled
Chamber type	Opaque	Opaque	Transparent
Root biomass (g m ⁻³)	420	106	92
Gap of data (%)	12.9	10.5	9.85
Annual C efflux (gC m ⁻²) ^a	259	194	192

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

Table 2. Parameters for soil water retention and C turnover

Parameter	Equation	Unit	Value
α_h	- ^a	-	0.0355 ^b
n	- ^a	-	1.5215 ^b
k_1	(11)	g g ⁻¹ day ⁻¹	0.01 ^c
k_2	(11)	g g ⁻¹ day ⁻¹	0.08 ^d
k_3	(11)	g g ⁻¹ day ⁻¹	0.001 ^d
k_g	(15)	g g ⁻¹	0.15 ^e
k_{cr}	(19)	g g ⁻¹ s ⁻¹	0.0014 ^f

k_p	(24)	$\text{g g}^{-1} \text{ year}^{-1}$	0.23 ^g
k_{R0}	(25)	$\text{g g}^{-1} \text{ day}^{-1}$	0.002 ^e
a	(26)	-	0.1 ^h
b	(26)	-	24 ^h
c	(26)	-	0.89 ^h
Q_{Ct}	(32)	-	1.585 ^f
a_{RC}	(32)	-	-0.0525 ^f
b_{RC}	(32)	-	2.602 ^f
c_{RC}	(32)	-	-1.653 ^f
a_{Pt}	(33)	-	0.9837 ^f
b_{Pt}	(33)	-	-0.1385 ^f
c_{Pt}	(33)	-	0.0095 ^f
d_{Pt}	(33)	-	-1.6318E-4 ^f
a_{Pw}	(33)	-	-0.3501 ^f
b_{Pw}	(33)	-	5.5884 ^f
c_{Pw}	(33)	-	-7.1783 ^f
d_{Pw}	(33)	-	2.6837 ^f

^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.

Table 3. Simulated component CO₂ fluxes ($\text{gC m}^{-2} \text{ year}^{-1}$) for areas with plant cover and without (interspace).

Surface type	F_S	F_T	$Rs+Ra^a$	Ra	P_{Ct}	F_{Ct}	F_P	$F_{Ct} - F_P^b$
Interspace	244	249	295	113	54.6	31.1	26.1	5.0
Plant covered	214	218	263	108	36.3	18.2	14.6	3.6

^a $Rs+Ra$ represents the total CO₂ production from soil respirations. Ra is the total autotrophic respiration ($Ra = \sum_i Ra_i$, see Eq. (10)) and Rs is the total heterotrophic respiration ($Rs = \sum_i Rs_i$, see Eq. (12)); ^b $F_{Ct} - F_P$ represents the net CO₂ 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_{Ct} , Eq. (18) for P_{Ct} and Eq. (24) for F_P .

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

Change of parameter	F_S^a	F_T	$Ra+Rs$	Ra	P_{Ct}	F_{Ct}	F_P	$F_{Ct} - F_P$
$n_R +20\%$	+3.3 ^b	+3.2	+2.7	+7.9	/ ^c	/	/	/
$n_R -20\%$	-2.9	-2.8	-3.4	-8.8	/	/	/	/
$n_P +20\%$	+1.6	+1.6	+1.0	/	/	/	/	/
$n_P -20\%$	/	/	-1.4	/	/	/	/	/
$f_m +20\%$	/	/	/	/	+2.9	+3.8	+3.4	+6.0
$f_m -20\%$	/	/	/	/	+1.2	/	-5.7	+30
$Ts +2\text{ }^\circ\text{C}$	+9.5	+9.6	+7.1	+11	+4.9	+3.9	+1.5	+16

T_s -2 °C	-9.0	-9.2	-8.1	-11	-1.3	-2.9	/	-20
θ +10 %	+3.6	+5.6	+7.5	+14	+41	+28	+14	+102
θ -10 %	-5.0	-5.6	-8.1	-14	-16	-13	-8.4	-34
M_{tot} +10 %	+2.9	+2.8	+2.0	/	/	/	/	/
M_{tot} -10 %	-2.5	-2.4	-3.1	/	/	/	/	/
M^R +10 %	+7.0	+6.8	+6.8	+8.8	/	/	/	/
M^R -10 %	-7.0	-6.8	-7.1	-8.9	/	/	/	/
N_{tot} +10 %	/	/	/	/	/	/	/	/
N_{tot} -10 %	/	/	/	/	/	/	/	/
k_I +10 %	+2.9	+2.8	+2.4	/	/	/	/	/
k_I -10 %	-2.5	-2.4	-3.1	/	/	/	/	/
k_{mo} +10 %	+4.1	+4.0	+3.4	/	/	/	/	/
k_{mo} -10 %	-3.3	-3.2	-3.7	/	/	/	/	/
k_{mc} +10 %	/	/	/	/	/	/	+1.5	-8.0
k_{mc} -10 %	/	/	/	/	/	/	-2.3	+8.0
M_{Ct} +10 %	/	/	/	/	/	/	/	/
M_{Ct} -10 %	/	/	/	/	/	/	/	/
$M_{CA}:M_{CH}$ +10 %	/	/	/	/	/	/	/	/
$M_{CA}:M_{CH}$ -10 %	/	/	/	/	/	/	/	/
pH +5 %	-8.6	-8.4	/	/	/	/	/	/
pH -5 %	+7.0	+6.8	/	/	/	/	/	/

^a Definitions of fluxes see Table 3 and Section 2.5.3; ^b 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; ^c 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 (T_s), water content (θ) and root biomass (M^R).

Change of parameter	F_s ^a	F_T	$Ra+R_s$	Ra	P_{Ct}	F_{Ct}	F_P
T_s +2 °C	+0.38 ^b (+4.0)	+0.45 (+4.7)	+0.87 (+12)	+0.49 (+4.6)	+1.7 (+34)	+2.7 (+70)	+1.2 (+78)
T_s -2 °C	-1.6 (+18)	-1.3 (+14)	-0.61 (+7.4)	/ ^c	-2.8 (+222)	-0.40 (+14)	-3.1 (+615)
θ +10 %	-1.8 (-49)	-1.5 (-27)	/	-0.27 (-1.9)	+8.7 (+21)	+13 (+46)	+2.9 (+20)
θ -10 %	+0.84 (-17)	+0.58 (-10)	/	+1.5 (-10)	-3.5 (+22)	-4.5 (+36)	+0.9 (-11)
M^R +10 %	-0.44 (-6.3)	-0.41 (-6.0)	-0.31 (-4.7)	-0.52 (-5.8)	/	/	/
M^R -10 %	+0.44 (-6.3)	+0.41 (-6.0)	+0.65 (-9.2)	+5.2 (-5.8)	/	/	/

^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, $dF_p - dF_i$) and by percentage (inside bracket, $100 \times (|dF_p| - |dF_i|) / |dF_i|$), where dF_p and dF_i 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. ^c the difference in sensitivity are smaller than 0.1% by value.

Figures

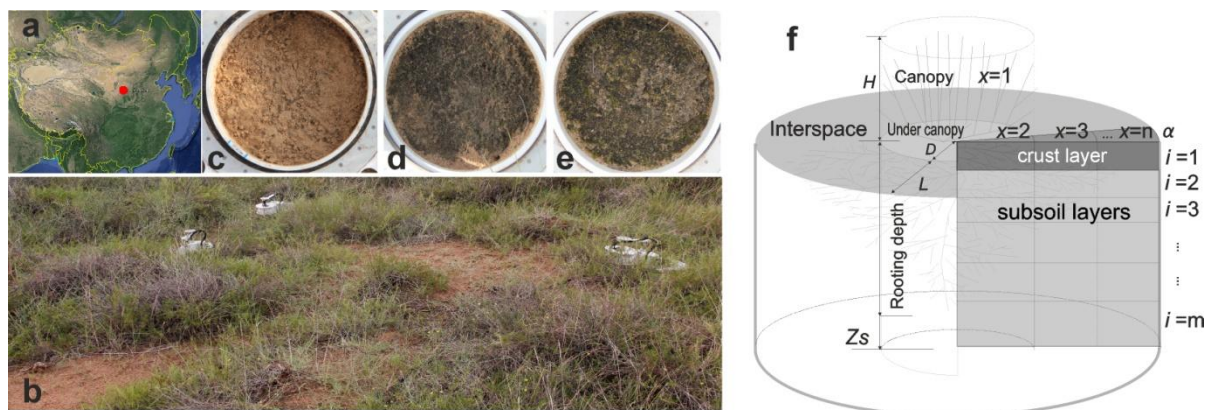


Figure 1. Site position (a), overlook of measured ecosystem (b), appearance of soil surface at collar C1 (c), C2 (d) and C3 (e), and layout of representative land unit (RLU, adopted from Gong et al., 2016)

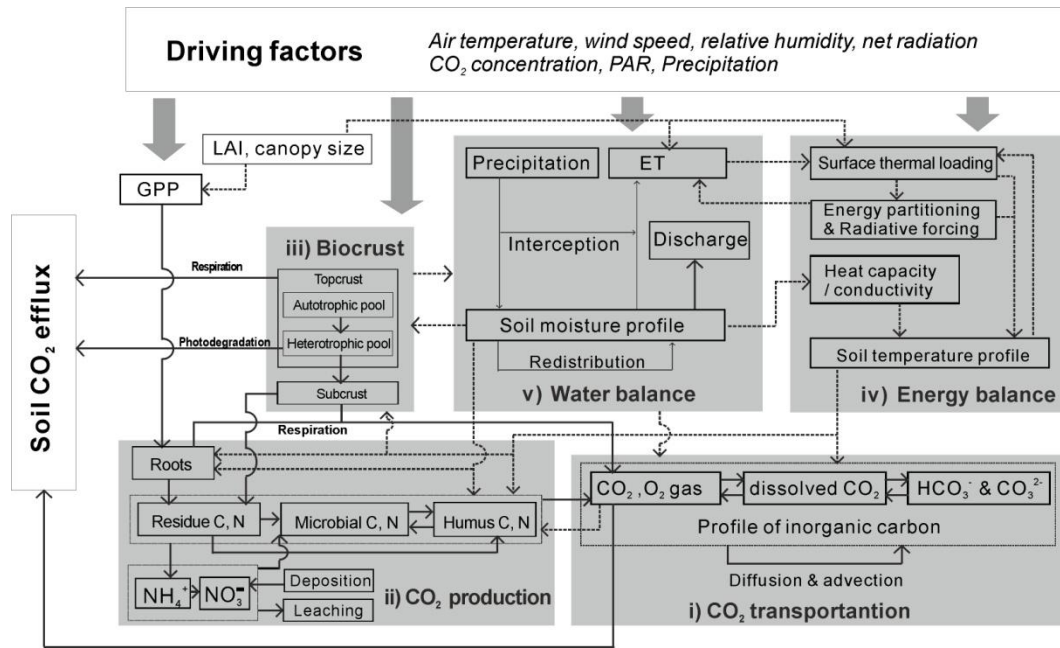


Figure 2. Conceptual framework of process-based modelling. Solid arrows represent flows of masses and dash arrows represent flows of information.

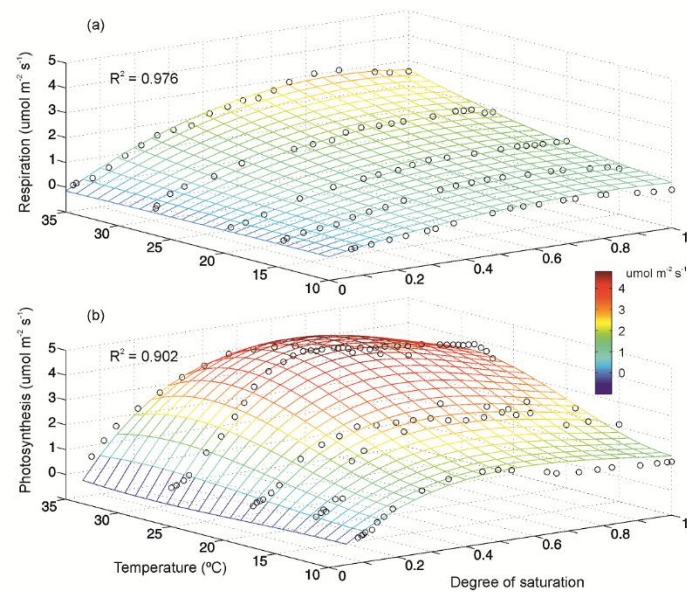


Figure 3. Measured and fitted bulk respiration (a) and photosynthesis (b) of the lichen topcrust as functions of temperature and water content.

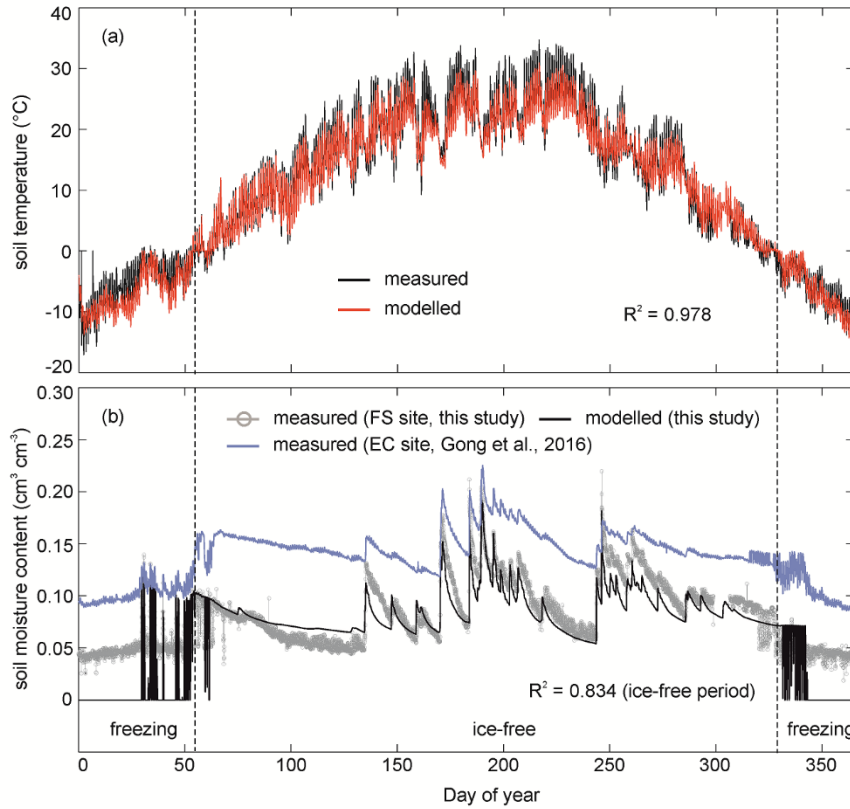


Figure 4. Measured and modelled soil temperature (a) and soil moisture content (b) at 10 cm depth for FS site, and as compared to the EC site in year 2013 by Gong et al. (2016).

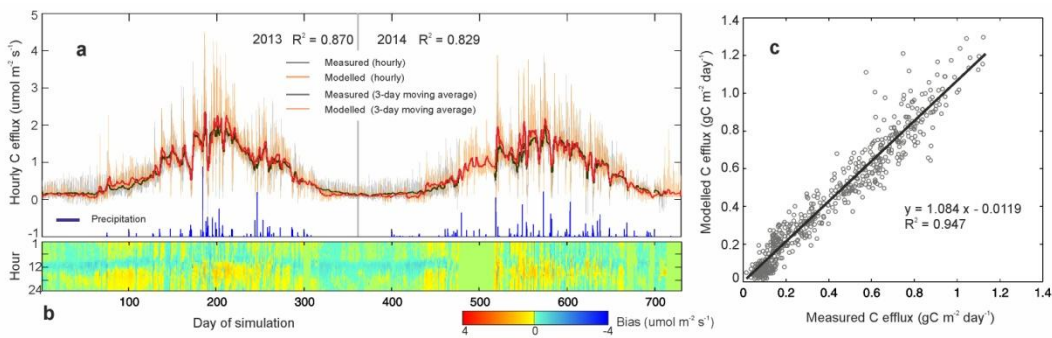


Figure 5. Measured and modelled hourly F_s for non-crustified soil (a), the temporal pattern of the bias of simulated hourly F_s (b) and the comparison of measured and modelled daily F_s (c) during 2013-2014.

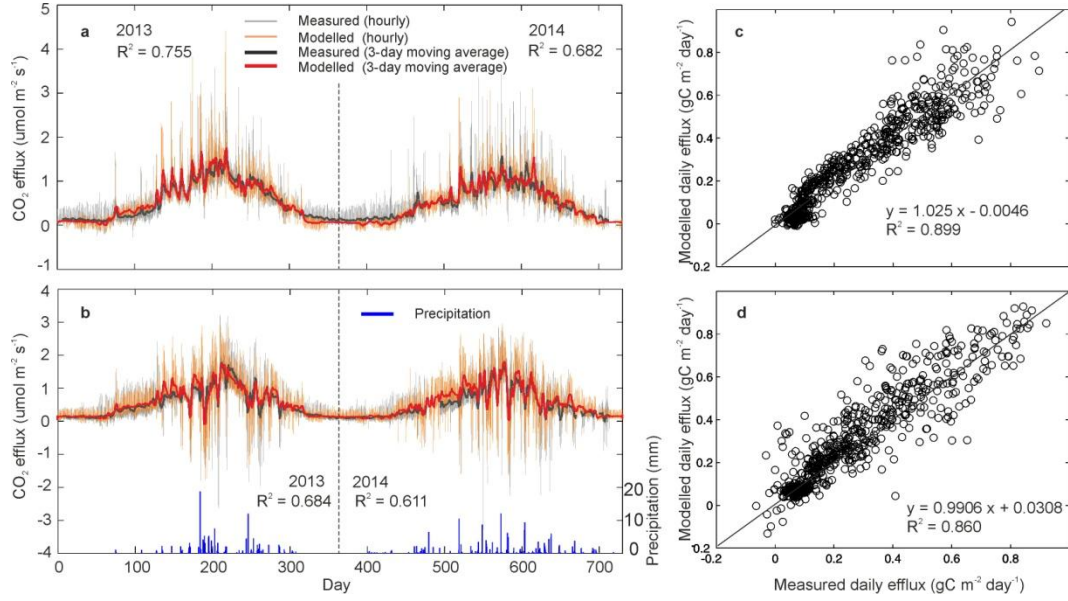


Figure 6. Measured and modelled F_s of lichen-crusted soils for opaque (a, c) and transparent chambers (b, d) at hourly (a, b) and daily (c, d) scales during 2013-2014.

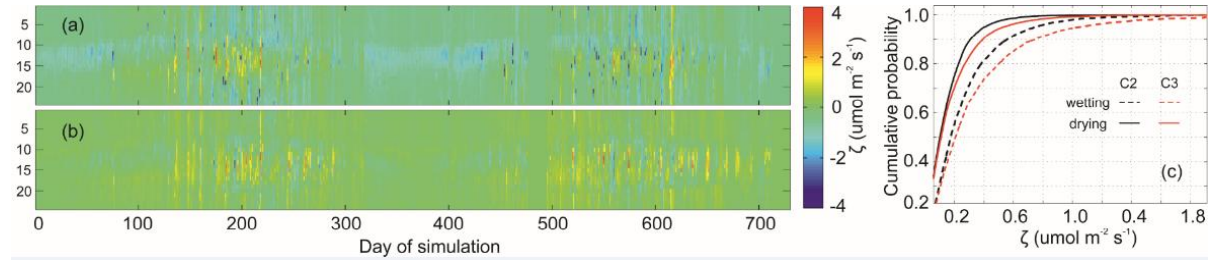


Figure 7. Diurnal patterns of biases (ζ) in the simulated hourly F_s for lichen-crusted soils using opaque (a) and transparent chambers (b), and the cumulative probability of the biases during wetting and drying periods (c) during 2013-2014. The wetting period included the raining days and a 1-day period after each rainfall. The drying period included the rest time of the years other than the wetting period.

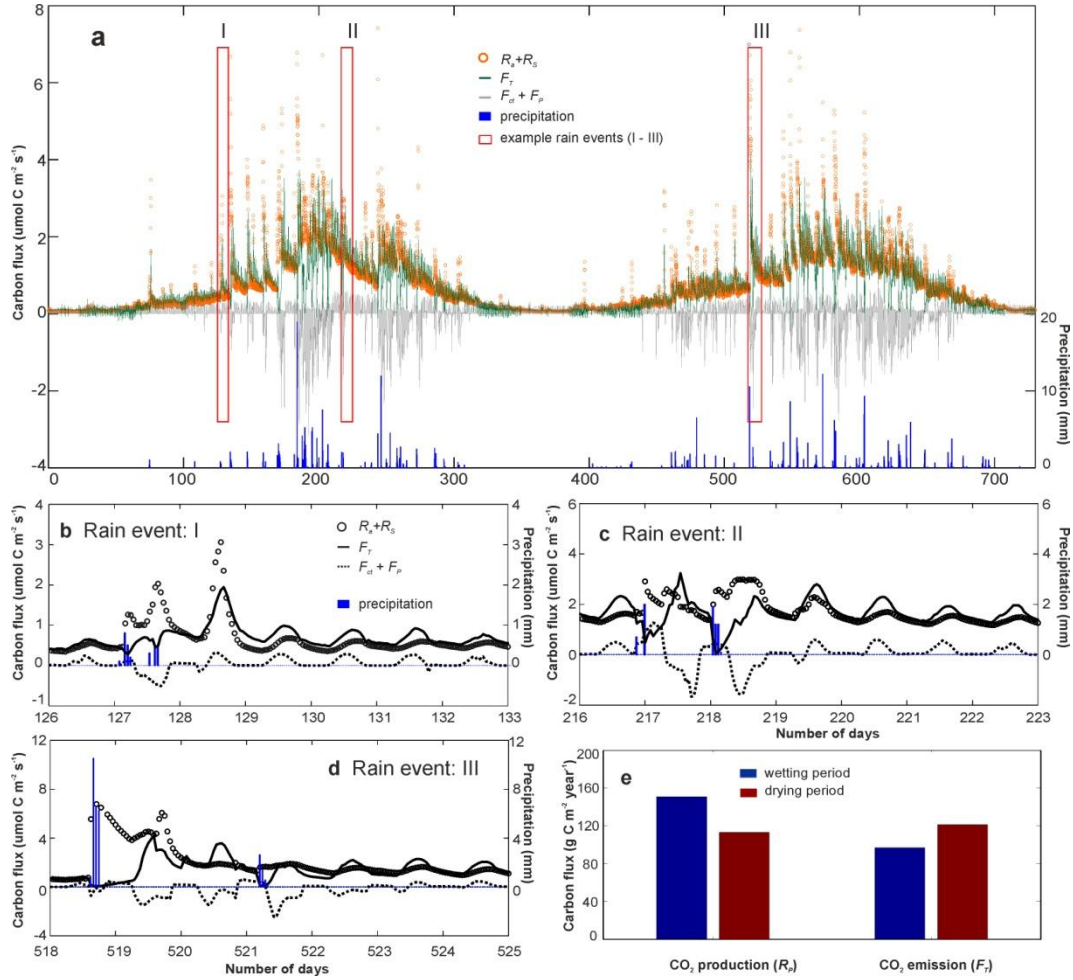
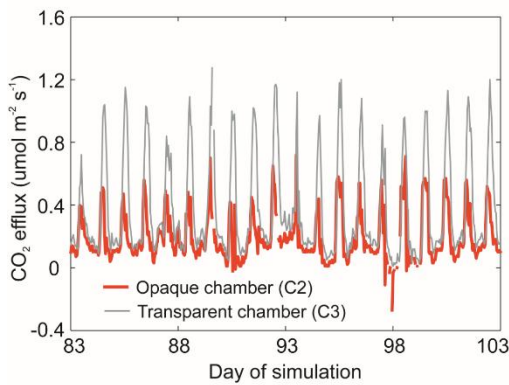


Figure 8. Simulated component CO₂ exchanges by biocrust and root-zone soil (a), the simulated CO₂ fluxes before and after example rain events of 2.3 mm (b), 7.6 mm (c) and 12.8 mm (d) sizes, and the comparison of F_T and R_R during wetting and drying periods during 2013-2014. The wetting period included 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.



1189 **Figure 9.** Comparison of the measured F_s from lichen-crusted surfaces using opaque and transparent
1190 chambers during a dry period (day 83-103) in spring 2013.