Interactive and individual effects of multi-factor controls on water use efficiency in Central Asian ecosystems

Shihua Zhu, Chi Zhang, Xia Fang and Liangzhong Cao

1 Shandong Provincial Key Laboratory of Water and Soil Conservation and Environmental Protection, College of Resources and Environment, Linyi University, Linyi 276000 People’s Republic of China
2 International Institute for Earth System Science, Nanjing University, Nanjing 210093 People’s Republic of China
3 Jiangsu Center for Collaborative Innovation in Geographical Information Resource Development and Application, Nanjing, People’s Republic of China
4 State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, People’s Republic of China
5 Xinjiang Institute of Engineering, Urumqi, Xinjiang 830091 People’s Republic of China
6 Research Center for Ecology and Environment of Central Asia, Chinese Academy of Sciences, Urumqi 830011, People’s Republic of China

E-mail: zc@ms.xjb.ac.cn

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Abstract

Water use efficiency (WUE) characterizes the relationship between water dissipation and carbon sequestration. Knowledge of WUE dynamics and its responses to complex climate controls are prerequisites for addressing the challenges of future climate change and human disturbance of wild lands. Owing to a lack of experimental observations and the complexity of quantifying the individual and interactive effects of different environmental factors, the mechanism of WUE dynamics and the spatiotemporal characteristics of WUE in Central Asian ecosystems remain unclear. Here, a specific Arid Ecosystem Model was used to assess WUE dynamics under environmental stresses, specifically isolating and identifying proprietary features from complex coupling effects, across different ecosystems in Central Asia from 1980 to 2014. WUE declined in southern Xinjiang but exhibited an upward trend in the Tianshan Mountains and northern Kazakhstan. Precipitation and CO₂ controlled WUE of 39% and 54% of Central Asia, respectively. The factor analysis showed that the negative effects of climate change were largely compensated by the CO₂ fertilization effect, and their interaction produced negative feedback to WUE. This resulted in inhibition of the CO₂ fertilization effect during long droughts. The negative effects of warming included increased water stress and enhanced evapotranspiration from vegetation. Based on variations in precipitation and net primary production, we determined that southern Xinjiang and the Turgay Plateau were environmentally vulnerable areas. Our study provides guidance regarding how ecologically fragile regions in Central Asia might cope with environmental pressures under extreme climate change in the future.

1. Introduction

Climate change exerts an important effect on structure and function in arid/semiarid ecosystems, especially the tightly related components of the carbon–water cycle (Liu et al. 2015, Huang et al. 2017). On a global scale, arid/semiarid ecosystems dominate the interannual variability of terrestrial net primary production (NPP) and strongly influence not only oscillation in evapotranspiration (ET) but also the regional climate system (Biederman et al. 2017, Zhang and Ren 2017). Compared with other terrestrial ecosystems, desert plants face more serious threats from complex climate and CO₂ changes (Seddon et al. 2016, Han et al. 2018a), especially water scarcity, one of the main constraints for the fragile structure and function of arid/semiarid ecosystems (Zhu et al. 2019, Fang et al. 2019a). As a key indicator that characterizes the coupling relationship between ecosystem biological and physical processes, water use efficiency (WUE) is defined here as the ratio of carbon assimilation to water loss, measuring the
trade-off between photosynthetic carbon uptakes and water that transpires from arid/semiarid ecosystems (Baldocchi 1994, Malone et al 2016). It is essential to explore the spatiotemporal features and controlling factors of WUE within the context of climate and CO$_2$ change. In particular, isolating and quantifying the individual and interactive effects of multi-factor controls on carbon–water dynamics are fundamental and critical for assessing an ecosystem’s vulnerability to environmental stresses over large areas (Zhou et al 2019).

Numerous studies have investigated climate–biosphere feedback based on the complex coupling effects of multiple environmental elements at the ecosystem level (Eamus 1991, Cramer et al 2001, Zhou et al 2016, Fang et al 2019b). However, the individual and interactive effects of multi-factor controls on WUE are still unclear, as is the relative relationship among these factors, especially in cold northern areas. For example, WUE in temperate and boreal forests in the northern hemisphere tends to respond consistently to positive CO$_2$ fertilization (Keenan et al 2013), while this positive feedback to desert plants in response to CO$_2$ enrichment is greatly suppressed under extreme drought conditions (Naumburg et al 2003). Previous investigations also indicated that forests in high latitude cold regions are sensitive to the long-term drought, and the impacts of drought depends on the type of vegetation, soil water content, duration and time of drought, etc (Krishnan et al 2006). But other studies indicated that temperate forests appeared overwhelmingly temperature restricted (Vicente-Serrano et al 2013). Contradictory results might indicate that WUE in temperate arid/semiarid ecosystems is co-affected by multiple climatic factors (temperature, precipitation, and CO$_2$), with different plants being sensitive to different factors and having inherent physiological variations. The different areas were dominated by different climate factors. In addition, some studies concluded that the interactive effects of different environmental factors on carbon–water dynamics tended to be additive rather than synergistic or antagonistic (Crain et al 2008, Zhou et al 2019). However, typical arid/semiarid ecosystems simulation results showed that elevated CO$_2$ due to climate change resulted in synergistic carbon sequestration (Li et al 2013) or even a negatively interactive effect on NPP (Zhang and Ren 2017). Therefore, considering the complexity and importance of arid/semiarid ecosystems in a regional climate system, it is critical to identify the underlying mechanism of WUE dynamics in Central Asia.

The five landlocked countries (Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan) and the Xinjiang region of China together constitute the Central Asian Geographical Entity, characterized by an arid to semi-arid climate (Huang et al 2014, Hu et al 2014). The terrestrial carbon–water cycle is uniquely affected by the Central Asian temperate desert ecosystem due to this landscape’s significant geographical heterogeneity, complex meteorological systems, and typically fragile environment (Lioubimtseva and Henebry 2009, Chen et al 2012, Li et al 2015). In recent decades, striking changes in climate have swept across Central Asia (Han et al 2018b). The winter warming trend in Central Asia has reversed, and the annual average temperature is 30% higher than the adjacent area (Hu et al 2014, Zhu et al 2017). Precipitation in this region showed strong spatial heterogeneity and significant interannual fluctuations (Gessner et al 2013, Chen et al 2014). Climate variability and intensive human disturbance have seriously affected the stability and security of Central Asian ecology and socioeconomics (Li et al 2013). Understanding the interactive effect and feedback mechanism between environment factors and desert plants, and developing strategies to adapt to future climate change, are grand challenges.

Here, a specific Arid Ecosystem Model (AEM), which was developed and optimized for typical temperate desert plants (Zhang et al 2013), was used to identify dominant climate factors and assess the relative contributions of different environmental constraints to WUE dynamics. A large number of site experiments and data from the literature were applied to the parameterization and verification of typical plant functional types (PFTs) in the AEM (Zhang et al 2013, Li et al 2013, 2018), but the AEM was not evaluated for its ability to predict ecosystems’ responses to climatic changes against field climate/CO$_2$ control experiments. In the present study, AEM was originally verified by selecting compiled data from 28 climate/CO$_2$ field control experiments. Then we performed scenario experiments in order to: (1) quantify spatiotemporal patterns of WUE in Central Asia; (2) assess the relative contribution of different environmental factors on WUE dynamics and the interactive effect between climate and CO$_2$; and (3) identify the hotspots of WUE change and the PFTs that are vulnerable to environmental stresses.

2. Data and methods

2.1. Study region

Central Asia (34.3°–55.4°N, 46.5°–96.4°E) is generally considered to be located north of the Pamir–Qinghai–Tibet Plateau, south of the Ural and Altai Mountains, and adjacent to the Caspian Sea in the west. Located in the hinterland of Eurasian continent, and own 80%–90% of the world’s cold/temperate (Li et al 2015), it is the widest temperate arid zone in the northern hemisphere (Hu et al 2014). The vegetation has its own zonal physiological and ecological characteristics under the unique mountain–oasis–desert landform profile and regional climate system (Chen et al 2013). Because the study area is located deep
inside the Eurasian continent and because the plains in the area are in the rain shadows of high mountains, the vast plains are occupied by desert shrubs or dry grasslands. The mountain areas, esp. their western slopes, have higher precipitation because of the topographic effects, whereby high mountain ranges intercept the moisture from the westerly Atlantic air masses. As the results, these mountain areas are covered by forests, alpine meadows before rising into glaciers at higher elevations. To analyze the WUE pattern of typical arid/semiarid ecosystems under the control of different environmental factors, six PFTs (Needleleaf forest, Broadleaf forest, Grassland, Non-phreatophyte shrub, Phreatophyte shrub, Cropland) were described and parameterized in AEM to represent the main characteristics of Central Asia vegetation (figure 1).

2.2. Model description

The AEM was originally designed for typical temperate ecosystems. It is a highly integrated model that couples biogeochemical processes and biophysical processes (Zhang et al 2013). AEM has an advantage over other models in describing sparse arid/semiarid vegetation due to its improvements on the vertical root distribution submodel, plant form submodel, and root–water uptake submodel. A detailed description of AEM is provided in supplementary material.

In the AEM, the water cycle is driven by absorbed solar radiation (SRAD) and photosynthesis is driven by canopy-absorbed photosynthetic active radiation (PAR) (appendix figure S1 available online at stacks.iop.org/ERL/15/084025/mmedia). The canopy is divided into sunlit and shaded fractions, in which photosynthesis and evapotranspiration (ET) were estimated independently. A fraction of SRAD is intercepted by canopy, the rest SRAD energy is absorbed by the soil surface. Likewise, a fraction of daily precipitation is intercepted by the canopy. Throughfall and irrigated water enter the soil and move downward. During this process, driven by the solar radiation absorbed by the canopy and soil surface, water leaves the ecosystem through a series of energy exchange processes: snow sublimation, evaporation, and transpiration. The energy exchanges and potential evapotranspiration rate are estimated using the Penman–Monteith approach (Wigmosta et al 1994). The actual transpiration rate is determined by two factors: the water demanded by the plants to support potential transpiration and the maximum water uptake capacity of the root system under the current soil moisture condition. Water movement through the groundwater–soil–root–canopy–atmosphere continuum is driven by the gradient of water potential between the different water compartments. Finally, a portion of the
input water will leave the ecosystem as either surface runoff or drainage flow. The evapotranspiration and photosynthesis of the sunlit and shaded canopies in an ecosystem (or forest stand) are added to derive the ecosystem/stand-level primary productivity and canopy evapotranspiration. Then the canopy evapotranspiration and the soil evaporation are added to derive the ecosystem/stand-level evapotranspiration. If a unit study area, i.e. a grid pixel, is composed by multiple ecosystem type, then the ecosystem productivity and evapotranspiration of each ecosystem are integrated by area-weighted linear combination to derive the ecosystem productivity and evapotranspiration of the unit study area. Because the processes of photosynthesis and evapotranspiration are modelled at leaf to canopy levels and then scaled up to ecosystem and regional levels, the nonlinear responses of leaf photosynthesis and stomatal conductance to climate changes from various PFTs could be conserved and integrated by our simulation.

2.3. Input data for the AEM

Model-driven data can be divided into two categories: climate reanalysis data and ancillary geographical data. We downloaded the gridded climate data based on Climate Forecast System Reanalysis (CFSR) from the National Centers for Environmental Prediction (http://rda.ucar.edu/pub/cfsr.html), which performed well in characterizing arid/semiarid meteorological condition (Hu et al 2014). Climate variables provided by CFSR include precipitation, temperature, relative humidity, and shortwave radiation. The CFSR data had a spatial resolution of $0.313^\circ \times 0.313^\circ$, which roughly equaled to a spatial resolution of 35 km to 40 km in the study area. Therefore, the climate data were interpolated to 40 km $\times$ 40 km in the present study. Geographical base data included topographic maps (latitude and longitude, elevation, slope, and aspects), PFT maps, soil maps (bulk density, volumetric content of sand and clay, and pH), and the groundwater table. The PFT distribution map was derived from multiple sources (figure 1).

Firstly, we used the GlobCover 2009 land cover map (http://due.esrin.esa.int/page_globeCover.php; last visited in April 17, 2020) developed by the European Space Agency to determine the distribution of forests, shrubland, grassland, cropland, and non-vegetated areas (mobile sandy deserts, water bodies, and glaciers). Then, we used the 25-km resolution vegetation map of the five central Asian states of the former Soviet Union (Rachkovskaya 1995) and the 10-km resolution vegetation map of China (Zhang et al 2007) to identify the potential distribution of the needleleaf forest and broadleaf forest. Because majority of the croplands in Central Asia located in plains, which generally had an arid/semiarid climate background, we assumed the croplands in our study area were irrigated. This assumption, however, may lead to overestimated NPP and underestimated drought effects on those rainfed crops in the study area. Atmospheric CO$_2$ data was retrieved from the Mauna Loa Observatory (http://co2now.org). Like most similar studies, it was assumed that tropospheric CO$_2$ was well-mixed and had no significant spatial variation at regional scale (Li et al 2015, Zhang and Ren 2017, Fang et al 2019b). All model-driven data were bilinearly resampled to a unified resolution (40 km $\times$ 40 km) to match the coarse resolution of the CFSR climate data. As shown in figure 1, each grid in the study area was shared by several PFTs. The NPP or ET value of a single grid was calculated by area weighting of all vegetation types presented within that grid. WUE was calculated using this formula: $WUE = \frac{NPP}{ET}$. Each grid point runs independently and the points do not interfere with each other.

2.4. Methods

In order to isolate the individual and interactive effects of changes in environmental factors on WUE dynamics, we designed five numerical scenarios to calculate the relative contributions of different factors (table 1). The OVERALL scenario calculated the concurrent effect of the historically changed climate and CO$_2$ data. The CLIM scenario isolated the effect of climate change, in which only climate factors changed and CO$_2$ remained unchanged. The CO$_2$fert scenario was designed to simulate the effect of CO$_2$ change (i.e. CO$_2$ fertilization effect), but excluding the pairwise interactive effect between CO$_2$ and temperature or precipitation. In this experiment, AEM was driven by temporal variations in CO$_2$ and equilibrium over the

| Experiments | CO$_2$ concentration | Precipitation | Temperature$^a$ | Description |
|-------------|----------------------|---------------|----------------|-------------|
| OVERALL    | Transient            | Transient$^b$ | Transient       | Combined effect |
| CLIM       | 1980                 | Transient     | Transient       | Climate effect |
| CO$_2$fert | Transient            | Equilibrium$^c$ | Equilibrium     | Individual effect (CO$_2$) |
| PREC       | 1980                 | Transient     | Equilibrium     | Individual effect (Precipitation) |
| TEMP       | 1980                 | Equilibrium   | Transient       | Individual effect (Temperature) |

$^a$ Temperature represents the maximum, minimum, and average temperature.

$^b$ Transient indicates that AEM is driven by transient data during 1980 to 2014.

$^c$ Equilibrium is produced by the average climate state from 1980 to 1989.
course of a year, generated using the average climate data from 1980 to 1989 (Zhang et al. 2013, Fang et al. 2017). The PREC (and TEMP) scenarios isolated the effects of change in precipitation (and temperature) while holding other climate factors and CO₂ constant (equilibrium climate). The dynamic changes in NPP, ET, and WUE from 1980 to 2014 were calculated by comparing the mean values from 1997 to 2014 and from 1980 to 1997. Based on these data, we carried out factor analyses to explore the individual effects of environmental elements and their dynamic interaction on NPP, ET, and WUE as follows:

\[
\text{OVERALL}_{\text{effect}} = \text{VAR}_{1997-2014} - \text{VAR}_{1980-1997}
\]

\[
\text{TEMP}_{\text{effect}} = \text{VAR}_{1997-2014} - \text{VAR}_{1980-1997}
\]

\[
\text{PREC}_{\text{effect}} = \text{VAR}_{1997-2014} - \text{VAR}_{1980-1997}
\]

\[
\text{CO₂}_{\text{effert}_{\text{effect}}} = \text{VAR}_{1997-2014} - \text{VAR}_{1980-1997}
\]

\[
\text{CLIM}_{\text{effect}} = \text{VAR}_{1997-2014} - \text{VAR}_{1980-1997}
\]

\[
\text{CO₂} \leftrightarrow \text{CLIM} = \text{OVERALL}_{\text{effect}} - \text{CLIM}_{\text{effect}} - \text{CO₂}_{\text{effert}_{\text{effect}}}
\]

where VAR refers to NPP, ET, and WUE; and CO₂ ↔ CLIM indicates the dynamic interaction between climate and CO₂ change. The front part of the suffix of VAR indicates the period of time (e.g. 1980–1997), and the latter part denotes the specific experimental scenario (table 1).

To establish a baseline for all scenario experiments, two uniform steps were used to initialize carbon–water pools in the AEM. First, we used CO₂ data from the initial year (1980) and equilibrium climate to run the AEM for 3000 years, to ensure that ecosystem carbon and water pools reach a system equilibrium under specific climate and PFTs. Secondly, a 1000-year (100 spins × 10 years) spin-up run was designed for AEM to wipe out possible deflection of the conversion from the equilibration state to the transient state. The driven data for this phase are the detrended climate data produced based on the CFSR from 1980 to 1989 and CO₂ in 1980 (Fang et al. 2017, Zhu et al. 2019). Finally, AEM performs transient simulations based on different experimental designs (table 1).

2.5. Model validation

In previous studies, we used a large amount of measured data, including ET, NPP, vegetation, and soil carbon density at fixed experimental stations and over 350 field plots in Central Asia, to evaluate and verify the accuracy and consistency of the AEM (Li et al. 2015, Zhang and Ren 2017, Zhu et al. 2019). The site experiments confirmed that the AEM performed satisfactorily in the carbon–water cycle simulation in Central Asia. The present study further validated the simulation accuracy of AEM for ET estimation by using the newly acquired site data from Fukang desert station (44.29°N, 87.93°E). Furthermore, we selected surveys from 28 experimental sites to assess the AEM’s performance in predicting the responses of typical temperate PFTs to variations in precipitation, temperature, and CO₂ (table S1 in supporting information). The AEM-captured and replicated site-scale response results are prerequisites for large-scale numerical simulation prediction. In the present study, we compared the Change/Ambient (C/A) ratios of AEM-simulated responses of different PFTs with data from observations (figure 2).

3. Results and analysis

3.1. Evaluating the performance of AEM in simulating NPP and ET

We selected 28 sites with different PFTs to evaluate the NPP responsiveness simulated by the AEM to changes in precipitation, temperature, and CO₂ concentration (figures 2(a)–(c), and table S1). The validation results indicated that the AEM is able to accurately capture observed climate/CO₂ fertilization effects in different typical PFTs in Central Asia. We found higher R² and lower RMSE (R² > 0.86, RMSE < 0.07) values for the simulated NPP for CO₂ and precipitation than for temperature at the experimental site (R² = 0.52, RMSE = 0.19). The response of arid/semiarid ecosystems to temperature change is more complicated, especially among shrubs, which exhibit great unpredictability (figure 2(b)). The reason may be that the temperature not only directly affects the photosynthetic process of desert vegetation, but also indirectly aggravates evaportranspiration. Stressed by both temperature (cold in winter and heat stress in summer) and water deficit, desert vegetation shows great variability in response to temperature. As shown in figure 2(d) (ET fluxes for the T. ramosissima measured by a flux tower at the Fukang Station of Desert Ecology, 44.29°N, 87.93°E), the simulated daily ET is highly consistent with the observed ET (ET_observed = 0.8° ET_simulated + 0.05; R² = 0.82, p < 0.01). Any discrepancy between simulated ET and observations is likely to result from observation error caused by instrument damage (DOY60-90) or insufficient data used to parameterize the model.
3.2. Changes in NPP, ET, and WUE from 1980 to 2014

As shown in figure 3, Central Asia experienced severe climate variability from 1980 to 2014. Precipitation decreased significantly by 4.67 mm yr\(^{-1}\) (p-value < 0.05), while the temperature increased significantly by about 0.2 °C/10 years (p-value < 0.05). Although there was a consistent warming trend throughout the region, precipitation changes showed significant spatial heterogeneity (figure 4(d)). The precipitation decrease mainly occurred in northern Kazakhstan and southern Xinjiang, while the northern slope of Tianshan Mountain showed a slightly increasing trend, with a unique switch from ‘warm dry’ to ‘warm and wet’. Precipitation in Central Asia was correlated negatively (p < 0.05) with temperature, especially during the global La Niña phenomenon (but no significant correlation during the El Niño periods was found) from 1998 to 2008; precipitation during this time only accounted for 80% of the climatological normal (according to http://ggweather.com/enso/oni.htm, last visited in Jan 24, 2020). Excluding this anomalous period (1998–2008), the changes in temperature would be insignificant.

In response to the coupling effect of multiple environmental factors (precipitation, temperature and CO\(_2\) change) over the past 35 years, the NPP and ET in Central Asia showed significant interannual fluctuations (figure 3), with a significant declining trends of 0.82 g C m\(^{-2}\) yr\(^{-1}\) (p < 0.05) and 1.41 mm yr\(^{-1}\) (p < 0.05), respectively (OVERALL scenario). Although linear regression showed an increasing trend (0.001 g C kg\(^{-1}\) H\(_2\)O yr\(^{-1}\)) in WUE, but the trend was not significant during the study period. This indicated that the ET reduction (−1.41 mm yr\(^{-1}\)) caused by climate change was almost balanced by the NPP changes (−0.82 g C m\(^{-2}\)). NPP and ET showed similar patterns in variation, which were significantly affected by precipitation. For example, before the mid-1990s, the interannual variation in precipitation was small, and NPP and ET remained relatively stable. The long-term drought (as the precipitation decreasing by 20%, temperature increasing by 0.6 °C) from 1998 to 2008 led to a significant decrease in NPP and ET, with the lowest values appearing in 2001 and 2008. Previous studies indicated the severe drought in Central Asia might be related to the protracted La Niña episodes during 1998–2008 (Barlow et al 2002, Syed...
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Figure 3. Interannual variations in Precipitation, NPP, ET, and WUE. Precipitation and temperature data were from Climate Forecast System Reanalysis (CFSR), ET, NPP, and WUE were simulated by AEM model. La Niña records were obtained from http://ggweather.com/enso/oni.htm.

Figure 4. The spatial pattern of the change rate of (a) ET, (b) WUE, (c) NPP and (d) Precipitation during 1980–2014. Dotted areas indicated significant trend (p < 0.05).

et al 2006, Li et al 2015). In average, the regional NPP and ET decreased $2.87 \pm 24.48 \text{ g C m}^{-2} \text{ yr}^{-1}$ and $4.83 \pm 20.50 \text{ mm yr}^{-1}$, respectively, during the La Niña events. Excluding the anomalous period of 1998–2008, the decreasing trend of NPP ($-0.46 \text{ g C m}^{-2} \text{ yr}^{-1}$; p < 0.05) would be much gentler than the trend for the whole study period (i.e. $-0.82 \text{ g C m}^{-2} \text{ yr}^{-1}$). The WUE trend would have increased from $0.001 \text{ g C kg}^{-1} \text{ H}_2\text{O yr}^{-1}$ to $0.004 \text{ g C kg}^{-1} \text{ H}_2\text{O yr}^{-1}$ if the anomalous period of 1998–2008 were excluded, though the trends were not significant in both situations. The lowest WUE values were found in 2001 and 2008 when the protracted La Niña events caused unusual decline in
precipitation (Barlow et al. 2002, Syed et al. 2006, Li et al. 2015).

WUE showed spatial heterogeneity and complexity and exhibited a large gradient across Central Asia (figure 4). WUE increases mainly occurred in northern Kazakhstan, the Altay Mountains and Tianshan Mountains; while in hyper-arid areas with exacerbated drought like southern Xinjiang, WUE exhibited a significant decreasing trend (p < 0.05) (figures 4(b), (d). The growth in WUE in the northern Tianshan Mountains and Altay Mountains was mainly owing to the increase in NPP caused by precipitation. However, the WUE increase in the grasslands of northern Kazakhstan was mainly owing to the decrease in ET caused by long-term drought. Due to a severe drought (meteorological observations show decreases in precipitation as high as 10 mm yr$^{-1}$; nsidc.org/data/g02174; figure 4(d)), both NPP and ET declined significantly in the Turgay Plateau at the north of the Kazakhstan (figures 4(a), (c). Although the WUE in the Turgay Plateau did not change significantly, the degradation of ecosystem functions was notable in that area. Based on precipitation and NPP changes, we concluded that southern Xinjiang and the Turgay Plateau were environmentally vulnerable areas, especially in the southern Xinjiang, where a significant decrease in WUE indicated degradation (and possibly decoupling) of important ecosystem functions like NPP and ET.

3.3. Identification of dominant factors and their relative contributions

Precipitation dominated the interannual variations in NPP and ET in Central Asia ecosystems (figure 3). There were significant positive correlations between precipitation and NPP ($R^2 = 0.68$, p < 0.01), and between precipitation and ET ($R^2 = 0.67$, p < 0.01). However, no clear relationships were found between temperature and NPP ($R^2 = 0.16$), nor between temperature and ET ($R^2 = 0.11$). Figure 5 indicated the individual contributions of climate and CO$_2$ and their interactive effects on NPP, ET, and WUE dynamics in Central Asia. The multi-factor combined numerical experiment (OVERALL scenario) showed that NPP decreased by 24 g C m$^{-2}$ yr$^{-1}$ during the study period. The precipitation effect had a negative effect on NPP in Central Asia, with a reduction of 42 g C m$^{-2}$ yr$^{-1}$. Although the CO$_2$ fertilization effect and warming somewhat alleviated the negative effects caused by the decline of precipitation, the weak warming effect (+6.8 g C m$^{-2}$ yr$^{-1}$) was obviously insufficient to compensate for the NPP loss caused by long-term drought. The interactive effect between climate and CO$_2$ also led to a reduction in NPP of 5.7 g C m$^{-2}$ yr$^{-1}$. Similarly, ET decreased by 28.7 mm yr$^{-1}$ during the study period, mainly due to long-term drought. CO$_2$ enrichment had a positive effect on NPP but had little effect on ET. Therefore, the interactive effect between climate and CO$_2$ had no significant effect on ET. Also, although temperature promoted the growth of NPP and ET in Central Asia, it exerted negative feedback on WUE. The positive effect of temperature on ET was much greater than that on NPP.

Further analyses showed that different PFTs had distinct responses to environmental change, and different terrestrial ecosystems were dominated by different climatic controls. Figure 6 showed the mean changes in temperature and precipitation during the study period as well as the ecosystems’ responses for each PFT. The precipitation generally decreased in Central Asia and had stronger impacts on the ecosystems than the rising temperature. The precipitation decline was most prominent in the ENF and crop-lands (i.e. CRP). Such precipitation change generally had negative effects on NPP and ET of various PFTs. PFTs were sensitive to precipitation in the following
order: forests > shrubs > grass > cropland. This was because the magnitude of precipitation decline in the forest areas was the highest in the study area, while the managed crops received sufficient water and fertilizer and were not limited by natural resource constraints. Among the forest types, ENF generally distributed in the upper-mountain-forest areas where the background precipitation was high and temperature was low when compared with that of the BDF that mainly distributed in the valleys (Chen and Luo 2013). Therefore, BDF was more sensitive to drought than the ENF, though the ENF experienced more severe precipitation decrease than the BDF. Temperature had no significant effect on forest, shrub, and grassland NPP, but it increased their ET, which led to negative feedback of WUE on temperature rise. In comparison, the NPP of the irrigated cropland was less sensitive to water limitation but benefitted greatly from the rising temperature (0.2 °C decade−1) in this temperate region (regional mean temperature = 7°C) (figure 6(a)). Therefore, the enhanced NPP offset the enhanced ET in cropland, making cropland’s WUE insensitive to temperature change (figure 6(c)). The different NPP and WUE responses between the irrigated croplands and the non-irrigated natural ecosystems (i.e. forests, shrubs, and grasslands) indicated the possibility of using irrigation as a climate modulation tool in drought-stressed areas like Central Asia. The interactive effect negatively affected NPP, but the effect on ET was not obvious, so the interactive effect on the WUE of different PFT was negative.

In the present study, the positive fertilization effects of atmospheric CO₂ enrichment on different PFTs had significant spatial heterogeneity, although tropospheric CO₂ was well-mixed and had no significant spatial variation at regional scale (Zhang and Ren 2017, Fang et al 2019b). The CO₂ fertilization effect was limited by different environment controls and regulated by different PFTs. For example, we found that the CO₂ fertilization effect was low when precipitation decreased and ET increased. The positive feedback of CO₂ was greater in moist forests than in dry grasses and shrubs.

Synthesizing the response characteristics of plants to environmental controls and factor analysis results, we identified the main factors that affected NPP, ET, and WUE in different regions of Central Asia (figures 7(a)–(c)). Precipitation was the main controlling factor for NPP in 71% of the area of Central Asia, mainly in the extremely hot and dry southern Xinjiang and Central Asia deserts. Temperature was the dominant effect for 10% of the area of Central Asia, mainly in the high-latitude meadows of Kazakhstan and the alpine regions of the Tianshan Mountains. CO₂ fertilization effect dominated 17% of the region, mainly in areas with good water and temperature conditions, such as the northern windward
slope of the Tianshan Mountains. Increased CO₂ concentration promoted vegetation productivity, but slightly affected ET (figures 6, 7(b)). Temperature and precipitation dominated the ET of 15% and 84% of the entire area, respectively. Figure 7(c) indicates the dominant climate controls on WUE dynamics of Central Asia. Precipitation and CO₂ fertilization effects controlled WUE of 39% and 54% of Central Asia, respectively. CO₂ fertilization effect promoted photosynthesis and reduced stomatal conductance and the vegetation transpiration rate, thus increasing vegetation WUE (Xu et al 2013). However, vegetation’s responses to CO₂ fertilization effect could be complicated by the interactive effects between CO₂ and climate change (i.e. CO₂ ↔ CLIM) (Xu et al 2016). As found in the northern Kazakhstan, the benefit from CO₂ fertilization are usually more prominent in face of decreased precipitation, due to the improved WUE under higher CO₂ (Sreeharsha et al 2015), (figure 4(b)). In areas that experienced severe drought (like the Turgay Plateau in the northern Kazakhstan) or hyper-arid ecosystems that suffered exacerbated drought (like the southern Xinjiang), however, water shortage could cause ecosystem degradation (e.g. severe defoliation) and inhibit plant’s response to CO₂ fertilization, leading to negative CO₂ ↔ CLIM effect (Zhang and Ren 2017). As shown in figure 7, the dominant districts of the CO₂ ↔ CLIM effect were scattered in the southern Xinjiang and the Turgay Plateau.

4. Discussion

4.1. Comparing Central Asia WUE dynamics with previous studies

The AEM confirmed that simulations of Central Asian WUE were accurate by comparing them with previous studies that used field observations or satellite-retrieved or model-simulated WUE (table 2). For example, the annual WUE of Central Asia (0.88 g C kg⁻¹ H₂O) was slightly lower than the global mean WUE (0.92 g C kg⁻¹ H₂O) (Ito and Inatomi 2012), comparable to typical semi-arid (0.8 g C kg⁻¹ H₂O) and arid ecosystems (1.2 g C kg⁻¹ H₂O) in the world (Huang et al 2017). Studies found that the WUE of forests and irrigated cropland was highest in Central Asia. The reason may be that forests and irrigated crops had better hydrothermal conditions and higher productivity, while grasslands and shrubs with lower productivity were mostly located in arid areas with extreme water shortages and stronger ET. A similar WUE spatial pattern was also found in global scale studies (Ito and Inatomi 2012, Liu et al 2015). The present study showed that the WUE in Central Asia was mostly dominated by changes in precipitation and CO₂, and the areas affected by precipitation were mostly distributed in southern Xinjiang and the Central Asia desert, while the CO₂-dominated areas were mainly distributed in the northern Kazakhstan farmland and the low-altitude windward slope of the Tianshan Mountains. The results are consistent with previous
Table 2. Comparisons of simulated Water Use Efficiency (WUE: g C/kg H₂O) for major PFTs (Plant Functional Types) with previous reports. BDF: broadleaf forest, ENF: evergreen needleleaf forest, PS: phreatophytic shrub, NPS: non-phreatophytic shrub, GRS: grassland, and CRP: cropland.

| Regions or PFTs          | Reported WUE       | Methods   | Sources          | This study (Range) |
|--------------------------|---------------------|-----------|------------------|-------------------|
| Forest                   |                     |           |                  |                   |
| ENF in China             | 1.11 (0.40–2.00)    | IBIS model| Zhu et al 2011   | 0.99 (0.80–1.21)   |
| BDF in China             | 1.21 (0.41–2.01)    | IBIS model| Zhu et al 2011   | 1.51 (1.24–1.77)   |
| Global forests           | 1.1                 | VISIT model| Ito and Inatomi 2012 |                      |
| South_USA forests        | 0.93                | DLEM model| Tian et al 2010  |                   |
| China forests            | 0.84                | BEPS model| Liu et al 2015   |                   |
| GRS in China             | 0.90 (0.27–2.39)    | IBIS model| Zhu et al 2011   | 0.75 (0.61–0.89)   |
| Grass                    |                     | VISIT model| Ito and Inatomi 2012 |                   |
| Global grassland         | 0.81                |           |                  |                   |
| South_USA grassland      | 0.58                | DLEM model| Tian et al 2010  |                   |
| Xinjiang grassland       | 0.34–0.84           | Biome-BGC | Huang et al 2017 |                   |
| Shrub                    |                     | VISIT model| Ito and Inatomi 2012 | 0.82 (0.53–1.00)   |
| PS                       |                     |           |                  | 0.74 (0.47–0.97)   |
| Global dense shrubland   | 0.8                 | VISIT model| Ito and Inatomi 2012 |                   |
| China dense shrubland    | 1.05 (0.32–1.86)    | IBIS model| Zhu et al 2011   |                   |
| Global open shrubland    | 0.67                | VISIT model| Ito and Inatomi 2012 |                   |
| China open shrubland     | 0.76 (0.17–1.53)    | IBIS model| Zhu et al 2011   |                   |
| Crop                     |                     | VISIT model| Ito and Inatomi 2012 | 1.22 (1.10–1.31)   |
| Global croplands         | 0.85                |           |                  |                   |
| China croplands          | 1.17                | BEPS model| Liu et al 2015   |                   |

reports which illustrated that precipitation dominated carbon–water changes in Central Asia and that croplands were more sensitive to the CO₂ fertilization effect under drought stress (Zhang and Ren 2017).

4.2. Knowledge of individual and interactive effects from the complex combined effect

A long-term study of WUE is a necessary precondition for measuring the relative contribution of environmental elements and identifying the main controlling factors (Khalifa et al 2018). Due to the limitations in data and methods, field or satellite observations of WUE were concentrated in short-term, small-scale, and combined effect studies. It was difficult to isolate and quantify the individual or interactive effects of climate change from the local factors (e.g. land-use change, air pollution) (Malone et al 2016, Fang et al 2017). Here, several numerical experiments were conducted to calculate and separate the contribution of different environmental factors on WUE. Results indicated not only that CO₂ and precipitation were the main controlling factors driving the WUE changes in Central Asia, but that the positive effect of CO₂ fertilization on the WUE was about 1.2 times and 4.3 times that of the negative effects of precipitation and temperature change, respectively (figure 5). Furthermore, we found that the negative climate change effect could be compensated by the positive CO₂ fertilization effect (figure 5). CO₂ fertilization mainly dominated in areas with relatively abundant precipitation or river water supply. This finding was consistent with previous studies which confirmed that the increase in global terrestrial WUE mainly results from the increase in NPP caused by the precipitation promotion effect (Ito and Inatomi 2012).

With the exception of the irrigated farmland, which was not restricted by water stress, precipitation dominated WUE variation in 39% of Central Asia and had a negative effect on WUE. The negative relationship between WUE variation and a decline in precipitation was also reported by a similar drylands study in the southern United States (Tian et al 2010). Although some studies concluded that the cold regions of the northern hemisphere were temperature-controlled (or heat-limited) (Huang et al 2016, Zhang and Ren 2017), we found that WUE in Central Asia was insensitive to or even negatively correlated with temperature changes. The WUE in diverse PFTs in response to temperature changes was regulated by photosynthesis and transpiration (Zhou et al 2014). A rising temperature in Central Asia not only stimulated the activity of photosynthesis in its temperate ecosystems (Zhang and Ren 2017), but also enhanced evapotranspiration, leading to a relatively stable WUE (Du et al 2018). In addition, the temperature sensitivities and ecological adaptabilities of desert plants offset each other, allowing the plants to exhibit temperature-insensitive regional characteristics. Thus, the rapid warming of the arid region in Central Asia may not have a direct, obvious impact on ecosystem WUE. Assessments of climate effects should pay more attention to the potential evapotranspiration and water stress enhancement caused by rising temperature.

Previous studies reported that the interactive effects of multiple global climate change factors on carbon dynamics were often additive rather than synergistic or antagonistic (Zhou et al 2019). However, we found that the interactive effect between climate change and CO₂ negatively influenced NPP and ET, thus WUE (figure 5), in typical Central Asian drylands during the past 35 years. This finding was supported by several Free-Air Carbon dioxide
Enrichments that the WUE of dryland plants, mainly ephemerals and annuals, tended to be less sensitive to CO$_2$ changes under severe drought stresses (Naumburg et al 2003, Zhang and Ren 2017). In that case, droughts clearly altered desert plant phenology, allocating more photosynthates to underground roots and resulting in leaf area declination or even leaf abscission and dormancy (Zhang and Ren 2017). Climate change dominated the interactive effect, and the CO$_2$ fertilization effect was not enough to offset the negative effects caused by extreme climate changes.

4.3. Implications for ecosystem models and future experiments

WUE was heterogeneous at different spatial and temporal scales in response to complex biological and meteorological conditions (Zhu et al 2011). Even under similar climate environments, different PFTs also showed diametrically different response patterns (figures 6, 7). The main controlling factor map that we developed helps to identify ecologically vulnerable areas and climate change hotspots (figure 7), in order to rationally allocate resources to alleviate the negative effects of climate change. Although precipitation change dominated NPP and ET of the vast grassland and desert shrubland in Central Asia (figures 7(a)–(b), it usually reduced both NPP and ET, thus not strongly affected WUE in most areas. However, in hyper-arid areas that faced exacerbated drought like the southern Xinjiang, WUE declined with NPP due to degraded ecosystem functions (Li et al 2015, figures 4 and 7). Ecological protection/conservation and restoration projects, such as grazing prohibition, returning cultivated land to pastures, and ecological water conveyance, are recommendable to maintain ecological securities in these areas (Ye et al 2009, Hao and Li 2014). In contrast, the WUE increased in the Guerbantunggurt Desert of northern Xinjiang, the northern Kazakhstan grassland and the oasis in the southern Central Asia, mainly due to the CO$_2$ fertilization effect (figures 4 and 7). These areas either experienced increased precipitation (in the Guerbantunggurt Desert) or were not facing water deficit (in the northeastern Kazakhstan and oasis). Therefore, it will be possible to increase grazing intensity in the northern Xinjiang to compensate for economic loss due to grazing prohibition in the southern Xinjiang. Until recently, the NPP of the oasis could benefit greatly from CO$_2$ fertilization effect because of the abundant water supply from major rivers. However, rising temperature is threatening the glaciers and the river flow in Central Asia (Sorg et al 2012). Therefore, it is important to conserve agricultural water usage and select crops/cultivars with low water demand and high heat demand in the oasis.

Many studies evaluating the relative contributions of climate factors to vegetation have been conducted on individual factors, but it is difficult for single-factor experiments to represent natural conditions (Fang et al 2017). Thus, studies are shifting to focus on the interaction among multiple factors and their impact on physiological and ecological mechanisms. In the present study, the adverse effect of climate change on WUE overrode the positive CO$_2$ fertilization effect. However, the rapid warming of the arid region in Central Asia in the 21st century may not have an evident impact on the ecosystem WUE by stimulating NPP and ET. In dynamic simulations of the carbon–water cycle and the assessment of climate effects on WUE in arid/semiarid ecosystems, more attention should be paid to the water stress.

As a newly developed biogeochemical model, the AEM has great advantages in simulating the carbon–water cycle of arid ecosystems. However, there is still uncertainty around the model structure and its depiction of ecosystems. For example, although the model considers groundwater depth and the impact of anthropogenic irrigation on some farmland ecosystems, it cannot simulate changes in rivers and groundwater supply patterns due to climate change factors. In the future, when the Central Asian region has undergone extensive warming, the mountain plains are certain to be affected by melting water from the mountains. In some areas with more developed agriculture, groundwater depth and vegetation growth will change due to the heavy use of groundwater. In addition, the AEM model does not consider the impact from soil erosion, which might increase 18%-19% in the early 21st century and causing considerable loss of ecosystem services (e.g. NPP, carbon sequestration, soil water retention) in Central Asia, particularly in the vast arid/semiarid plains (Li et al 2020). Finally, AEM does not consider the competition among the vegetation in ecosystem, and thus unable to reflect the climate-change effects on vegetation dynamics and redistribution. Therefore, our study had to use a fix vegetation (PFT) map to represent the vegetation distribution during the study period. As discussed below, overlooking land-cover changes might cause our study to miss some of the non-linearity behavior in time, because different PFT types could have distinct responses to climate change (figure 6).

Although we have implemented parameterized verification of different PFTs in Central Asia in combination with measured data, the uncertainty of the input data may still lead to deviations in the simulation results. For example, our study only focuses on the climate change effect but overlooked the process of land-use/land-cover change (LULCC), which could have affected both the carbon and water processes. Previous study showed the cropland area in Central Asia decreased dramatically (as much as 22%) after the collapse of the Soviet Union, followed by a fast recovery since the mid-2000 s (Han et al 2012). Although cropland only occupied a small area in Central Asia and the net change in cropland area was even smaller, this LULCC could alter ecosystem
carbon and water dynamics (at least temporarily) in some important oasis in Central Asia. The forest areas also changed during the study time, although the net impacts on ecosystem’s functions was small according to previous studies (Chen et al 2015). Although the grassland area barely changed during the study time, the privatization of pastures seemed to have caused an unexpected NDVI increase in the northern Kazakhstan grasslands (Fan et al 2012). Analysis Model projections also indicated that climate change may trigger redistribution of dominant species like Haloxylon in Central Asia at multidecadal-centennial time scale (Li et al 2019).

In addition, due to the scarcity of climate sites in Central Asia, we used the CFSR reanalysis dataset to drive the model. This dataset performs well in Central Asia, but its precipitation data contains a certain degree of overestimation (Hu et al 2014).

Typical PFTs in Central Asia have been influenced by drought stress for a long time, which have enhanced their tolerance to drought and favored the evolution of physiological characteristics that allow them to adapt to extreme environments. For example, Haloxylon persicum (NPS) enters a summer dormancy period in August, and Tamarix elongata (PS) also shows growth stagnation in July and August. Therefore, we have refined the root water absorption characteristics of NPS and PS shrubs, as special or detailed physiological characteristics are not yet accurately described in AEM.

5. Conclusions

Accurately quantifying the sensitivity of different ecosystems to environmental factors is an essential prerequisite for addressing extreme climate change. We evaluated the response patterns of WUE to climate change and CO₂ in typical temperate forests and arid/semiarid ecosystems, including identifying proprietary features from complex coupling effects, with simulations based on the AEM. The results showed that precipitation and CO₂ controlled WUE of 39% and 54% of Central Asia, respectively. The factor analysis results indicated the negative effects of climate change were largely compensated for by the CO₂ fertilization effect. Their interactive effects exhibited a negative feedback on WUE; in other words, the CO₂ fertilization effect was inhibited during long-term droughts. The negative effects of warming were manifested by increasing water stress and enhancing vegetation evapotranspiration. Future warming may not directly reduce WUE by inhibiting NPP growth. Based on precipitation, NPP and WUE variations, we found that the Taklimakan Desert areas of southern Xinjiang and the Turgay Plateau were environmentally vulnerable areas. Therefore, in the future, more attention should be paid to the indirect effects of potential evapotranspiration and water stress enhancement caused by rising temperatures in Central Asia.

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Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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