

RESEARCH ARTICLE

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Key Points:

- Warming-induced soil moisture limitation increased ecosystem water-use efficiency
- Water-use efficiency responded differently to warming at canopy and ecosystem levels
- Plant transpiration dominated the responses of canopy and ecosystem water-use efficiency to warming

Supporting Information:

- Data Set S1
- Supporting Information S1

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Transpiration Dominates Ecosystem Water-Use Efficiency in Response to Warming in an Alpine Meadow

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Abstract As a key linkage of C and water cycles, water-use efficiency (WUE) quantifies how much water an ecosystem uses for carbon gain. Although ecosystem C and water fluxes have been intensively studied, yet it remains unclear how ecosystem WUE responds to climate warming and which processes dominate the response of WUE. To answer these questions, we examined canopy WUE (WUE_c), ecosystem WUE (WUE_e) and their components including gross ecosystem productivity, ecosystem evapotranspiration (ET), soil evaporation (E), and plant canopy transpiration (T), in response to warming in an alpine meadow by using a manipulative warming experiment in 2015 and 2016. As expected, low- and high-level warming treatments increased soil temperature (T_{soil}) at 10 cm on average by 1.65 and 2.77°C, but decreased soil moisture (M_{soil}) by 2.52 and 7.6 vol %, respectively, across the two years. Low- and high-level warming increased WUE_e by 7.7 and 9.3% over the two years, but rarely changed WUE_c in either year. T/ET ratio determined the differential responses of WUE_c and WUE_e. Larger T/ET led to less difference between WUE_c and WUE_e. By partitioning WUE_c and WUE_e into different carbon and water fluxes, we found that T rather than gross ecosystem productivity or E dominated the responses of WUE_c and WUE_e to warming. This study provides empirical insights into how ecosystem WUE responds to warming and illustrates the importance of plant transpiration in regulating ecosystem WUE under future climate change.

1. Introduction

Global surface temperature has experienced rapid warming in recent decades and is predicted to rise by another 1.5°C at least by the end of this century (Intergovernmental Panel on Climate Change, 2013). The rapid warming has profound impacts on the terrestrial ecosystem, especially the carbon (C) and water cycles (Jung et al., 2010; Luo et al., 2001; Sistla et al., 2013). As a key link of the two cycles, water-use efficiency (WUE) weighs C gain against water loss and reflects the key characteristic of ecosystem function (Campos et al., 2013; Keenan et al., 2013; Niu et al., 2011; Yu et al., 2008). Although the response of leaf-level WUE to temperature rising has been investigated much (Kaminski et al., 2014; Keenan et al., 2013; Muthuri et al., 2009; Niu et al., 2011), we know little about how ecosystem-level WUE changes under climate warming, partly due to the limited understanding on the different sensitivities of ecosystem C and water fluxes to warming.

WUE reflects the coupling of C and water fluxes. Therefore, the relative responses of C and water processes will determine warming effects on WUE. Conceptually, the controlling factors of the C assimilation process are quite different from the water loss process (evapotranspiration, ET). Ecosystem C assimilation is an energy-consuming process that is mainly controlled by plant physiological activity associated with carboxylation and photosynthesis. Previous studies showed that warming would increase plant C uptake by providing optimal temperature (Niu et al., 2008; Sage & Kubien, 2007), more available nutrient (Rustad et al., 2001), or nitrogen use efficiency (Niu et al., 2010). However, warming would also have negative or neutral effects due to warming-induced water stress (Niu et al., 2008) and photosynthetic acclimation (Niu et al., 2012; Zhou et al., 2007). One of ecosystem water loss process, soil evaporation (E), is a physical process, which is usually affected by wind speed, temperature, soil moisture, and air humidity (Gong et al., 2006; Huntington, 2006; Jung et al., 2010; Mu et al., 2011; Sulman et al., 2016; Wilson et al., 2000). However, the other water loss process, plant transpiration (T), is not only influenced by these physical factors but also regulated by plant stomatal conductance and community structure (Rigden & Salvucci, 2016; Schlesinger & Jasechko, 2014; Waggoner et al., 1964; Zelitch & Waggoner, 1962). Thus, water loss from T and E are expected to have

different sensitivities to warming. Studying the relative sensitivity of ecosystem C and water fluxes to warming will provide fundamental process understanding for the responses of WUE under climate warming. However, the contribution of each C or water process in determining WUE and its response to warming has not been well quantified yet.

Another knowledge gap is the unclear impact of vegetation regulations on the response of ecosystem WUE to climate warming. T/ET ratio indicates the allocation of ecosystem water flux between physical and biological processes, which reflects vegetation regulation (Hu et al., 2008; Wang et al., 2014). Thus, exploring T/ET ratio will provide an important insight into how ecosystem biological feedback regulates warming effect on ecosystem-level WUE (Wang et al., 2013). Nevertheless, currently, our empirical knowledge of T/ET responses to climate warming is very limited, consisting of only two experiments conducted in grasslands (Niu et al., 2011; Wang et al., 2013). According to the definition, ecosystem WUE is usually expressed at canopy and ecosystem levels. Canopy WUE (WUE_c) is expressed as gross ecosystem productivity (GEP)/T, while ecosystem WUE (WUE_e) is GEP/ET, which can be decomposed as a product of GEP/T and T/ET (Hu et al., 2008). Thus, T/ET ratio should determine the difference between WUE_c and WUE_e. However, previous studies usually confound WUE_c with WUE_e by using ET as a substitute for T due to the difficulty in partitioning ET into its components especially in the field (B. Yang et al., 2010). It remains unclear whether the canopy- and ecosystem-level WUE respond to warming in the same way and how T/ET ratio regulates the discrepancy between WUE_c and WUE_e.

Considering these knowledge gaps, we investigated the effects of warming on ecosystem WUE and the related C and water fluxes using a manipulative experiment in the Qinghai-Tibetan Plateau (QTP), which is the highest and largest plateau in the world and referred to as the world's "Third Pole." The magnitude of climate warming on the QTP is considerably larger than the global average (Intergovernmental Panel on Climate Change, 2013; Y. H. Yang et al., 2008). Besides, this high-altitude area is ecologically fragile and the ecosystem structure and function are considered to be sensitive to climate change (Kang et al., 2010; Tao et al., 2015; You et al., 2008). Thus, the response of ecosystem WUE of the QTP to warming may of critical importance and differ from other ecosystems. Specifically, we addressed the following questions: (1) How ecosystem WUE responds to experimental warming? (2) How T/ET ratio regulates the response of WUE_c and WUE_e? And (3) which process, GEP, E, or T, dominates the response of ecosystem WUE to warming?

2. Materials and Methods

2.1. Study Area

The study was performed in an alpine meadow located on the eastern QTP (32°84'N, 102°58'E), which is in Hongyuan County, Sichuan, China. The altitude is about 3,500 m. Over the past 60 years, the mean annual precipitation is 753 mm, mainly distributed from May to October. The mean annual temperature is 1.1°C, with January as the coldest month (−10.3°C) and July as the hottest month (10.9°C). The soil in the study site is classified as Cryumbrept following the U.S. Soil Taxonomy (Li & Sun, 2011; Shi et al., 2015). The plant species are dominated by *Deschampsia caespitosa* (Linn.) Beauv., *Koeleria cristata* (Linn.) Pers., *Gentiana sino-ornata* Balf. f., *Potentilla anserina* L., and *Anemone rivularis* Buch.-Ham.

2.2. Experimental Design

We used block design with three warming treatments and five replications each in this study. Within each of the five blocks, three 3 × 2 m plots were randomly assigned to the three treatments of control (C, ambient temperature), low-level warming (W1), and high-level warming (W2). The warmed plots were continuously heated by infrared radiators (MSR-2420, Kalglo Electronics Inc., Bethlehem, Pennsylvania, USA) suspended 1.5 m above the ground since June 2014. The output powers were 1,000 and 2,000 W for heaters in W1 and W2, respectively. In each control plot, we suspended a dummy heater, which appearance is identical to the infrared radiator at the same height to simulate the shading effect. The adjacent plots were 3 m apart.

2.3. WUE Component Measurement

We measured ecosystem CO₂ and water fluxes twice per month during the growing season in both 2015 and 2016, using an infrared gas analyzer (LI-6400XT, LI-COR Environmental, Lincoln, Nebraska, USA), which was attached to a transparent canopy chamber (0.5 × 0.5 × 0.5 m, polymethyl methacrylate). In order to seal the canopy chamber to the soil surface, in each plot, we installed a 0.5 × 0.5 m square aluminum frame

into the soil at the depth of 3 cm, which provided a plane interface between them (Sharp et al., 2013; Xia et al., 2009). During measurements, two small fans were installed diagonally inside the chamber and fanned continuously to mix the atmosphere. Consecutive recordings of CO₂ and water vapor concentrations were obtained once every 10 in 80 s. Net ecosystem CO₂ exchange (NEE) and ET were calculated by the slope between recording time and concentrations. Right after the NEE measurements, the chamber was lifted up and shaken slightly to exchange with the outside air. Then we covered an opaque cloth on the chamber and repeated the measurement to obtain ecosystem respiration. GEP was calculated as the difference between NEE and ecosystem respiration.

To measure E, we permanently inserted a polyvinyl chloride collar (10.5 cm in diameter) into soil surface at the depth of 3 cm in each plot. In order to exclude transpiration from the above ground components of plants inside the collars, we regularly removed them. We measured E at the same time of measuring NEE and ET, using the LI-6400 infrared gas analyzer with attached soil CO₂ flux chamber (LI-6400-09; LI-COR Environmental, Lincoln, Nebraska, USA). The E were calculated as the same way of ET calculation. T was determined by the difference between ET and E. These methods for measuring the components of WUE mainly followed Niu et al. (2011). Besides, infrared radiator did not significantly alter the microclimate in the chambers during the measurements (Wan et al., 2002); thus, the changes in ET and T between the treatments reflect the treatment-induced changes in ecosystem. These may include the warming-induced changes in leaf area index, shifts in vegetation structure (Hu et al., 2008), and phenology (Xiao et al., 2013). We defined WUEc as GEP/T and defined WUEe as GPP/ET (Niu et al., 2011; Sun et al., 2016).

2.4. Soil Temperature and Moisture

Soil temperature (T_{soil}) was measured at a 10 cm depth using a thermocouple probe connected to Li-6400XT. A 10 cm soil water content (M_{soil} , %vol) was measured using a time domain reflectometry (TDR) equipment (TDR 100, Spectrum Technologies Inc., Chicago, USA). Both T_{soil} and M_{soil} were measured at the same time when measuring WUE components. All measurements were performed under cloud-free conditions.

2.5. Data Analysis

One-way analysis of variance was performed to test the difference of seasonal mean soil moisture, temperature, C and water fluxes, and canopy and ecosystem WUE among different warming treatments. We used regression analyses to explore relationships between canopy/ecosystem WUE and their components. Structural equation modeling (SEM) was performed to analyze the pathways that may explain the warming effect on canopy/ecosystem WUE. We used multivariate stepwise analyses to evaluate the combined influence of soil microclimate variables, ecosystem C, and water fluxes on canopy/ecosystem WUE. Considering the nonlinear relationship among variables, we used the Ln-transformed data. We calculated the effect size of warming by the response ratio (RR): $\ln RR = \ln(XT/XC)$, where XT and XC were the values of warming treatment and the control groups, respectively. Statistical analyses were conducted with SPSS 22.0 (SPSS Inc., Chicago, IL, USA), R statistical software v 3.4.1 (The R Foundation for Statistical Computing, Vienna, Austria) and AMOS 21.0 (Amos Development Corporation, Chicago, IL, USA).

3. Results

3.1. Warming Effects on Soil Microclimate

Warming significantly increased T_{soil} and reduced M_{soil} at a 10 cm depth (Figure 1). On average, W1 and W2 increased seasonal mean T_{soil} at 10 cm by 1.54 and 2.62°C, respectively, in 2015, and by 1.77 and 2.91°C, respectively, in 2016. Seasonal mean M_{soil} declined by 1.34 and 7.3 vol % in W1 and W2, respectively, in 2015, and by 3.7 and 7.9 vol %, respectively, in 2016.

3.2. Canopy and Ecosystem WUE in Response to Warming

Warming effects on WUEc varied with treatments and years (Figure 2). W1 significantly reduced WUEc by 6.4%, while W2 significantly increased it by 9.9% in 2015. Neither W1 nor W2 had significant influence on WUEc in 2016. However, both warming treatments had significantly positive effect on WUEe and T/ET in the two years. Warming significantly increased WUEe by 2.6 and 12.7% in W1 and W2, respectively, in 2015, and by 12.7 and 5.9%, respectively, in 2016 (Figure 2). Warming also significantly increased T/ET by 7.3 and 1.6% in W1 and W2, respectively, in 2015, and by 2.6 and 4.1%, respectively, in 2016.

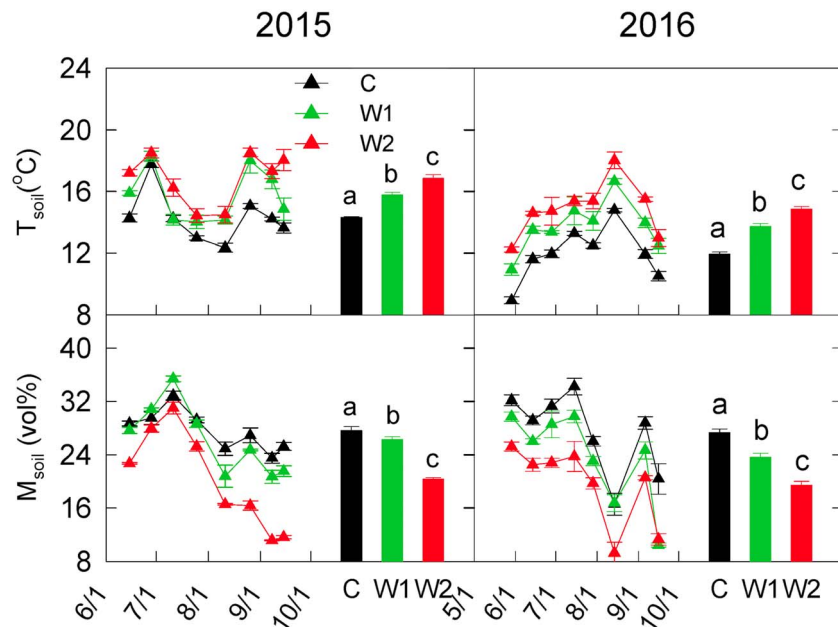


Figure 1. Seasonal dynamics and means of soil temperature (T_{soil}) and soil moisture (M_{soil}) at the depth of 10 cm under three warming treatments in 2015 and 2016. C: control; W1: low-level warming; W2: high-level warming. Different letters close to the bars indicate significant differences between treatments.

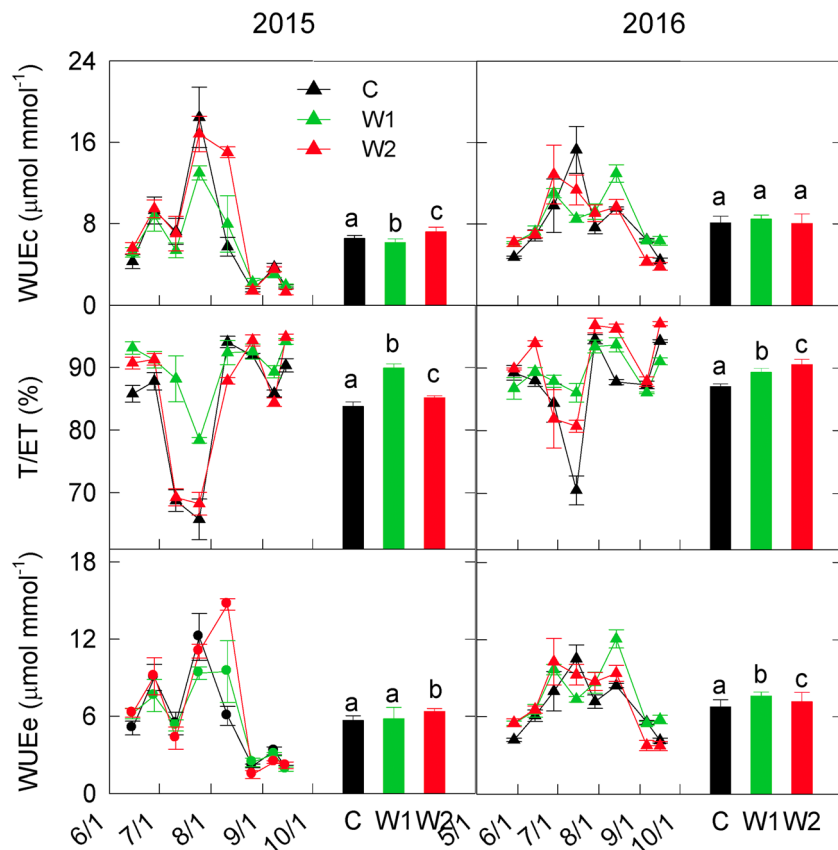


Figure 2. Seasonal dynamics and means of canopy water-use efficiency (WUEc), ecosystem water-use efficiency (WUEe), and the ratio of T/ET under three warming treatments in 2015 and 2016. C: control; W1: low-level warming; W2: high-level warming. Different letters close to the bars indicate significant differences between treatments.

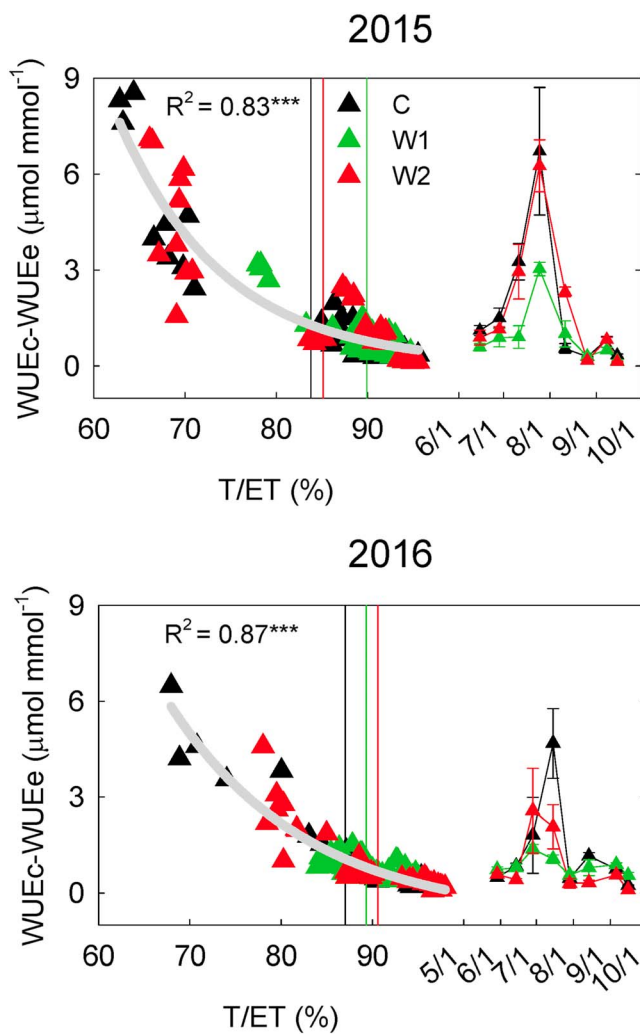


Figure 3. Relationships of T/ET ratio and the difference between canopy- and ecosystem-level water-use efficiency (left, the vertical black, green, and red line represent the means of T/ET under the control, W1, and W2 treatments, respectively) and the seasonal dynamics of the differences between canopy- and ecosystem-level water-use efficiency (right) in 2015 and 2016.

The differences between WUEc and WUEe exponentially decreased with the increase of T/ET ratio (Figure 3). The differential warming impacts on WUEc and WUEe were also closely related to T/ET ratio (Figure 3).

3.3. Transpiration Dominates Water-Use Efficiency in Response to Warming

The RRs of WUEe and WUEc to warming were dominated by the warming-induced changes in T. The RR of WUEe and WUEc were significantly correlated with the RR of T across treatments in both 2015 and 2016 ($p < 0.05$), but not with GPP, or E in either year (Figure 4). The SEM indicated that T was the main pathway that determined the response of WUE to warming, which was reflected by the high standardized path coefficient (Figure 5). The standardized total effects derived from the SEM also showed that the total effects of T and GEP were -0.92 and 0.22 for WUEc and the total effects of T, GEP, and E for WUEe were -0.84 , 0.32 , and -0.26 , respectively (Figure 6). Besides, the correlations showed that T explained most of the variation of WUEc and WUEe, while GEP and E explained much less (Figure S1). Multivariate analysis also showed that for WUEc, the proportions of variance explained by GEP and T were 8.57 and 47.37%, respectively, and for WUEe, GEP, E, and T explained 13.67, 19.82, and 58.97% of the variance, respectively (Table S1 and Figure S2).

4. Discussion

4.1. Transpiration Dominates the Responses of WUEc and WUEe to Climate Warming

Results show that T dominated the response of WUEc and WUEe to warming in the study area. The close relationships between the RR of WUEe, WUEc, and the RR of T suggest that the response of WUEe and WUEc to warming was mainly determined by the warming-induced changes in T, rather than GEP or E (Figure 4). SEM results further confirm that T was the main pathway that determined the response of canopy and ecosystem WUE to warming (Figures 5 and 6). In addition, although the coefficients from the stepwise regression showed that WUEc and WUEe were sensitive to both GEP and T (Table S1), T explained a larger proportion of the variances of WUEc and WUEe than

GEP and E (Figures S1 and S2). All these above indicate that warming-induced changes in T dominate the response of WUEe and WUEc to climate warming.

The relative role of C gain versus water loss in causing WUE changes has not been quantitatively addressed in previous studies, although their responses to warming have been studied. For example, Allen et al. (2003) found that warming decreased WUE as it enhanced ET more than canopy GPP. Niu et al. (2011) reported that warming decreased GEP but had no significant effect on ET thus reduced WUEe. In contrast, Huang et al. (2015) and Zhang et al. (2014) proposed that warming stimulated GPP while not change ET due to stomatal regulation and consequently led to increasing WUE. Comparing with those previous studies, our study made an advance by quantifying the relative contributions of C and water processes responsible for WUE changes and illustrating their impacting pathways (Figure 5).

Previous studies reported inconsistent warming effects on ET. Warming increased ET (Allen et al., 2003; Qiao et al., 2014) through enhancing E (Xie et al., 2016) or T (Reddy et al., 1995). However, many field experiments and modeling analyses also showed that warming reduced ET. For example, Jung et al. (2010) demonstrated that global ET increased with rising temperature from 1982 to 1997, but then declined in recent years due to limited moisture supply. On the one hand, warming-induced water limitation could reduce water supply for soil evaporation and hence decrease E (Figure S3). On the other hand, stomatal closure induced by high

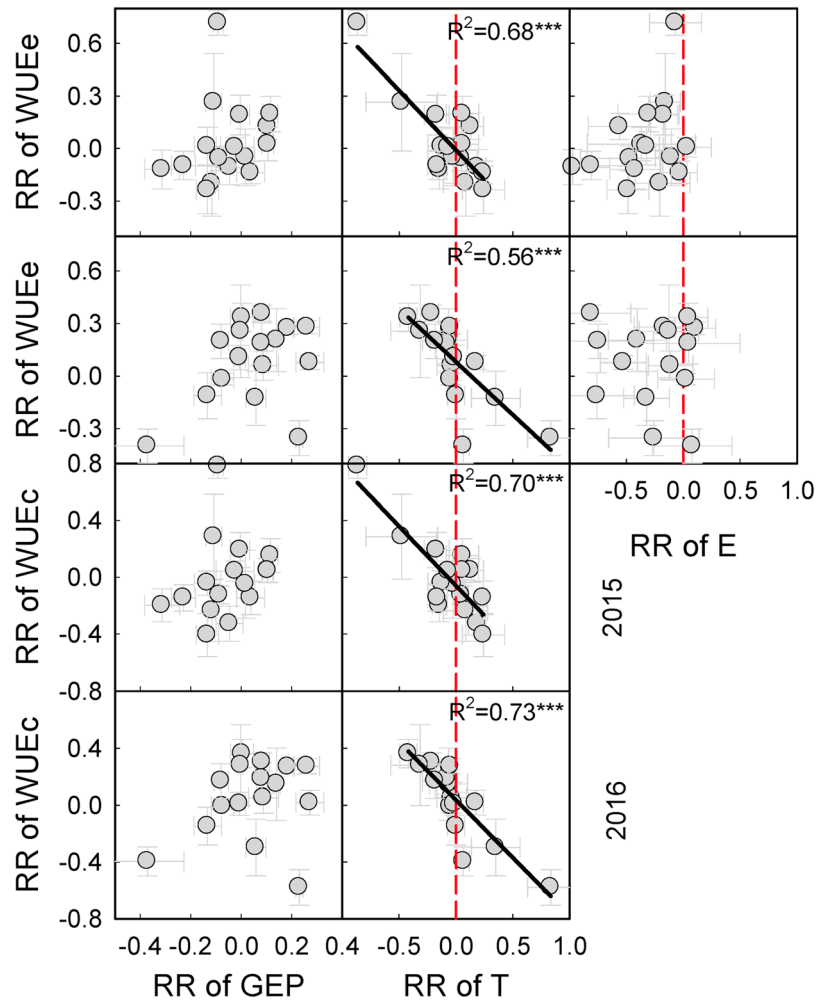


Figure 4. Relationships of the response ratio of ecosystem water-use efficiency (WUEe) and canopy water-use efficiency (WUEc) with the response ratio of gross ecosystem productivity (GEP), soil evaporation (E), or plant transpiration (T) and in 2015 and 2016.

vapor pressure deficit under warming and water stress could reduce T (Rigden & Salvucci, 2016; Scott et al., 2004; Serrat-Capdevila et al., 2011). Thus, ET changes will depend on soil water condition. Indeed, we found that warming-induced changes in T were positively correlated with soil water content ($p < 0.05$; Figure S4). The positive warming effect on T occurred when soil water content was high (on average above 29.5%) and the negative effect occurred when soil water was low. To represent the normal weather condition and avoid rainfall pulse effect (Placella et al., 2012; Unger et al., 2010), our measurements were carried out mostly on the sunny days, which was usually a few days after rainfall and soil water content might become more likely limited. Thus, warming overall reduced water loss (Figure 4; the more negative values of RR of E and T) and increased WUEe.

4.2. WUEe and WUEc Respond Differently to Warming

This study is one of a few field manipulative experiments studying warming effects on WUE at the canopy and ecosystem levels. Although various approaches have been used to study the response of WUEe to temperature changes, such as the eddy covariance fluxes, tree-ring isotopes, or the process models (Andreu-Hayles et al., 2011; Brownlee et al., 2016; Conley et al., 2001; Gagen et al., 2011; Huang et al., 2015; Linares et al., 2009; Sun et al., 2016; B. Yang et al., 2010), most of them studied WUE response to warming by correlating WUE with temperature changes with multiple confounding factors of changing precipitation, CO₂, nutrient availability, or radiation (Brownlee et al., 2016; Campos et al., 2013; Linares et al., 2009; Tong et al., 2014;

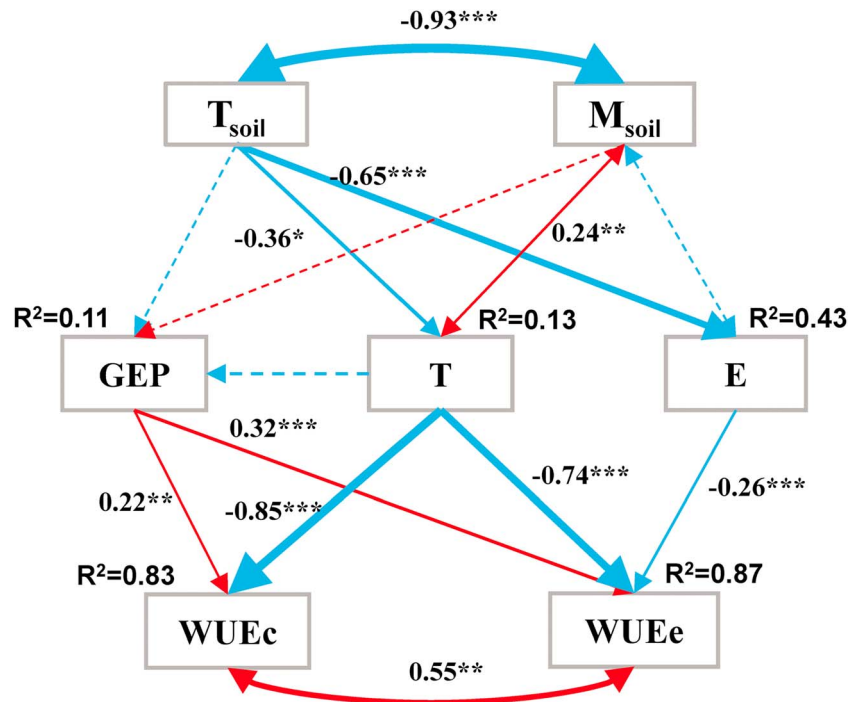


Figure 5. Results of structure equation model analysis examining the effect of warming on canopy and ecosystem water-use efficiency (WUE_c and WUE_e) via pathways of soil temperature (T_{soil}), soil moisture (M_{soil}), gross ecosystem productivity (GEP), soil evaporation (E), and plant transpiration (T). The red and blue arrows indicate positive and negative relationships, respectively. The solid and broken arrows connecting the boxes indicate significant and insignificant effects, respectively. The values adjacent to arrows are standardized path coefficients, which reflect the effect size of the relationship; significant level: ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$. R^2 values associated with variables indicate the proportion of variation explained by relationships with other variables.

Xiao et al., 2013; B. Yang et al., 2010). Manipulative experiments, which effectively control the target factor but exclude the potential impacts of confounding factors, can adequately quantify the responses of ecosystem to climate warming and partition the canopy and ecosystem WUE (Niu et al., 2011; K. Zhu et al., 2016).

The results showed that warming enhanced WUE_e in both years but rarely changed WUE_c . This difference was explained by the ratio of T/ET (Figure 3). T is a vegetation-controlled water loss process, and the changes of T/ET in response to warming provide insights into biological feedback of the ecosystem water cycle to climate warming (Hu et al., 2008; X. J. Zhu et al., 2014). T/ET ranged from 0.65 to 0.94 in this study. While previous studies suggested a wide T/ET range from 0.48 to 0.9 determining by the plant coverage, surface wetness, and soil water content (Cao et al., 2010; Gerten et al., 2005; Schlesinger & Jasechko, 2014; Wang et al., 2010). Warming increased T/ET ratio in both years, which was consistent with the result of a study in the tall-grass prairie (Wang et al., 2013). Since WUE_e can be expressed as GEP/T (WUE_c) times T/ET , the changes in WUE_e in response to warming can be attributed to changes in WUE_c and/or T/ET (Hu et al., 2008; X. J. Zhu et al., 2014). Rising air temperature could increase T/ET ratio and consequently increase WUE_e (X. J. Zhu et al., 2014).

Water loss from E is a physical and nonproductive process, while water loss from T is a physiology-based productive process, which is closely associated with ecosystem C uptake. Thus, the high ecosystem T/ET ratio under warming condition implies that ecosystem losses water more from T and is more linked to C gain, in comparison with the

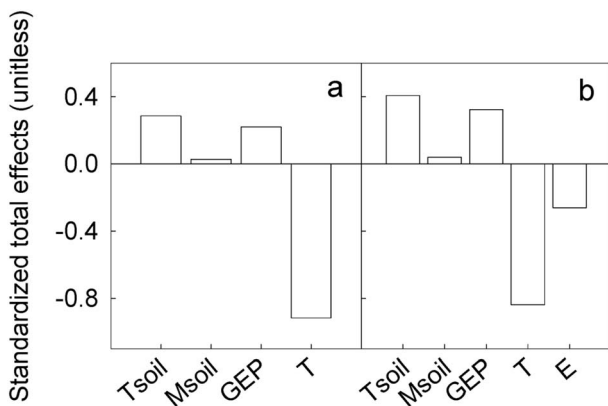


Figure 6. Standardized total effects derived from the structural equation modeling for (a) WUE_c and (b) WUE_e . The numbers adjacent to bar are the standardized coefficients in structural equation modeling.

control. This provides a mechanistic understanding for our observation that WUEc responded less strongly than WUEe to warming. For example, in 2015, although WUEc in W1 was less than control, the high T/ET ratio under W1 led to high WUEe than control. This was consistent with a model study, which showed that WUEc displays a declining trend but WUEe showed an increasing trend (Huang et al., 2015). By revealing the fundamental controlling mechanisms of WUEe response, this study showed that the discrepancy between WUEc and WUEe reduced with increasing T/ET ratio, implying the contribution of different water fluxes involved in WUEc and WUEe and the underlying uncertainty in estimating the WUEc by using ET as a substitute for T (Huang et al., 2015).

5. Conclusions

Based on a manipulative experiment, this study provides unique field evidence that warming increased ecosystem WUE at the ecosystem-level. The different responses of canopy and ecosystem-level WUE to warming indicate that caution should be taken when up scaling WUE from small to large scales. We partitioned the flux components involved in ecosystem WUE and quantified the contribution of each C and water process to the changes in WUEc and WUEe in response to warming. The results showed that T is the dominant process controlling the responses of WUE to warming. Our findings indicate that the change of plant transpiration is critical in regulating alpine meadow ecosystem WUE under future climate warming. The study will help us better understand and predict ecosystem carbon and water coupling under climate warming.

Acknowledgments

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