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Original Research

Resilience of Energy and CO_2 Exchange to a Summer Heatwave in an Alpine Humid Grassland on the Qinghai-Tibetan Plateau

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Abstract

Summer heatwaves are expected to be much more frequent and severe with negative effects on terrestrial ecosystem water and carbon budgets, while the impacts on alpine grasslands remain poorly understood. Here we analyzed eddy flux and meteorological dataset of a seven-day (July 26 to August 1) summer heatwave in an alpine humid grassland in northeastern Qinghai-Tibetan Plateau in 2015. Compared with pre-heatwave, only diurnal ecosystem respiration (RES) increased by 30.7%, evidently ($P < 0.001$) during the heatwave. Diurnal sensible heat fluxes (H) and latent heat fluxes (LET) increased by 18.1% ($P = 0.08$) and 27.5% ($P = 0.02$) from 9:00 to 16:00. The heatwave did not lead to substantial increments of daily H and daily LET, while daily Bowen ratio (H/LET) decreased a little ($P = 0.07$). Daily net ecosystem CO_2 exchange increased by 76.7% ($P = 0.03$), mainly resulting from remarkable growth in daily RES ($P<0.001$) and undetectable fluctuation in daily gross primary production (GPP) ($P = 0.13$). Daily ecosystem water use efficiency (GPP/evapotranspiration) decreased by 20.8%. The little difference of energy and CO_2 fluxes between pre-heatwave and post-heatwave indicated strong resilience to the summer heatwave in the alpine humid grassland. Our results revealed that the present-day summer heatwave exerted a limited influence on energy exchange and vegetation photosynthetic activity but did stimulate ecosystem respiration, which would provide a positive feedback to climate warming with more carbon efflux from alpine grassland.

Keywords: climate change, vegetation photosynthesis, ecosystem respiration, evapotranspiration, boosted regression trees

Introduction

Summer heatwaves, induced mainly by global climate change, have become frequent and severe by model projections and *in situ* observations [1-3]. Because of greater response strengths and shorter response durations, terrestrial ecosystems are thought to be more sensitive to summer heatwaves than to gradual climate warming [4-6]. The physiological heat stress, high-light stress, and – more important – drought stress [7-8] generated by summer heatwaves have direct and concurrent effects on

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ecological processes such as transpiration, photosynthesis, respiration, and production at the leaf, ecosystem, and regional scales [8-10]. However, accurately assessing ecological response to summer heatwaves remains a key challenge because of the unpredictability and rarity of naturally occurring extreme events [11-12].

With an aggressive water-spending strategy of most herbaceous plants [13], grassland ecosystems, which are exposed to summer heatwaves during peak productivity season, evapotranspiration (hereafter ET) initially was enhanced. Along with soil water depletion and drought stress [14], ET and carbon sequestration capacity was reduced [10], even though the plant community shifted [11, 15] and thus potentially exacerbated the heating regional climate system and positively fed back to climate warming [5]. The grassland ecosystem gross primary production (GPP) dropped a little more than ecosystem respiration (RES) [7, 10] or unsubstantially affected [14] or even enhanced [16]. Specifically, heatwaves in July and not August could reduce aboveground net primary production in Konza Prairie [8]. However, a number of recent studies, both observational and experimental, have revealed that the immediate ecological response to such climatic extremity can be highly variable because of species- and/or system-specific attributes [11-12, 17]. Therefore, it is still uncertain how alpine grassland ecosystem H_2O and CO_2 exchange quantitatively responded to summer heatwaves, particularly that such an ecosystem is generally referred to as the "water towers of China" and "sensitive ecotone" over the Qinghai-Tibetan Plateau [18-19].

The alpine ecosystem is believed to be most susceptable to climate warming [15, 20], and recent research has shown that such a temperature-limited alpine grassland could provide negative feedback in climate change due to enhanced vegetation growth and prolonged growing season length and alleviated nutrient limitations [21-22]. But the impacts of summer heatwaves are thought to be more important than gradual warming [4, 9], and even to a much greater extent than experimental nutrient inputs [15]. Heat stress in summer heatwave and consequently limited soil water availability may strongly change or even reverse the function of carbon fixation and water resources of alpine grassland [9, 11, 14]. But there is little direct evidence and the response of the alpine grassland needs to be quantified [5, 7] for understanding how alpine grassland responds to a summer heatwave. We specifically addressed the question of whether or not the predominant environmental factor of ecosystem CO_2 and H_2O fluxes change during a summer heatwave.

Materials and Methods

Study Area

The study site is located near Haibei National Field Research Station of Alpine Grassland Ecosystem (hereafter Habei station, 37°37′N, 101°19′E, 3200 m a.s.l), which is situated northeast of the Qinghai-Tibetan Plateau (Fig. 1). The climate is of plateau continental type. The average annual air temperature (T_a) is -1.7ºC (monthly maxima and minima of 10.1ºC in July and -15.0ºC in January, respectively). The annual amount of precipitation is 570 mm, of which about 80% is concentrated in the plant growing season from May to September. No period is absolutely frost-free, and about a 20-day relatively frost-free period is common. Annual sunshine is 2,467 h, and annual pan evaporation is 1,238 mm [22]. The soil, which is approximately 60 cm deep, is classified as Mat Cry-gelic Cambisol, featuring high soil organic matters (0-10 cm SOM is 106.2±4.5‰) and low available nitrogen content (0-10 cm content is 21.9 ±4.9‰).

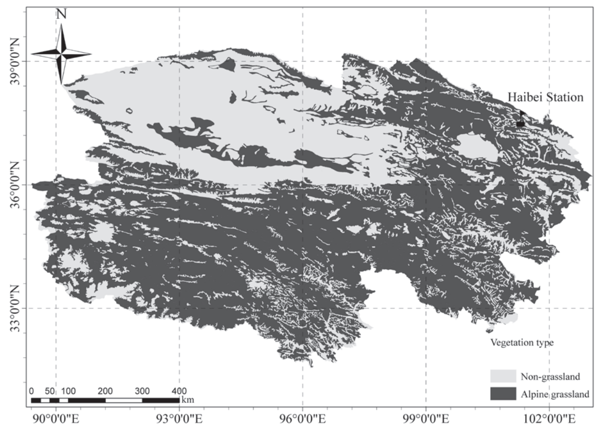

Fig. 1. Simple geographic map of the study site.

The vegetation in the area has accounted for most of the winter forage intake by livestock from a single household since the late 1970s. *Kobresia humilis* is the dominant species, followed by *Elymus nutans*, *Stipa aliena*, *Taraxacum dissectum*, *Anaphalis lacteal*, and *Potentilla anserina*, which together comprise nearly 70% of all basal study area [23]. The average canopy height and 80% of root concentrated depth is about 40 cm and 20 cm, respectively. Maximum amounts of leaf area index reach value of 4.0 $m^2 \cdot m^{-2}$ at the end of July. Tibetan sheep and yak graze lightly (3.75 sheep unit·ha^{-1}) in this area from October to the following May [24].

Measurements

Since May 2014, an open-path EC system was installed in the center of a flat (aspect < 5º), open (5 km minimum distance from mountain base), and homogenous area (average canopy coverage is above 98% in July and August) with sufficient terrain of about 12 km^2 for flux measurement. The EC system consisted of a three-dimensional ultrasonic anemometer (CSAT3, Campbell, USA) and an open-path infrared CO_2/H_2O gas analyzer (LI-7500A, LI-Cor, USA), both fixed at a height of 2.2 m above the ground. The raw data (wind speed, sonic virtual temperature, and CO_2 and H_2O concentrations) was sampled at 10 Hz. The 30-minute fluxes were calculated and logged with a SMARTFLUX system (7550-200, Campbell, USA). The CO_2/H_2O gas analyzer was calibrated during the end of each April. Zero points, CO_2 span, and water span were established using dry N_2 gas (99.999%, National Institute of Metrology, China), standard CO_2 gas (450 mg/kg, National Institute of Metrology, China), and a dew-point generator (LI-610, LI-Cor, USA), respectively.

The routine meteorological factors were measured synchronously. T_a and relative humidity (RH) was monitored by a temperature and humidity probe (HMP45C, Vaisala, Finland) at both 1.5 m and 2.5 m high, and was used to estimate vapor pressure deficit (VPD). Canopy temperature (T_c) was measured via two infrared thermocouple sensors (SI-111, Apogee, USA) at 1.5 m high. Net radiation (Rn, including inwards/outwards long-wave radiation, inwards/outwards short-wave radiation) and photosynthetic photon flux density (PPFD) were monitored with four radiometers (CM11, Kipp & Zonen, Netherlands) and a quantum sensor (LI-190SB, LI-Cor, USA), respectively, at 1.5 m high. Precipitation was collected with a rain gauge (52203, RM Young, USA) positioned 0.5 m aboveground. Soil temperature and volumetric soil water content was integratedly (Hydra probe II, Stevens, USA) measured at 5, 10, 15, 20, and 40 cm below ground. The soil heat flux (G) was measured with heat plates (HFT-3, Campbell, USA) buried at three different points at 2 cm below soil surface. The 30-minute average of meteorological data was recorded with a data logger (9210 XLITE, Sutron, USA). The system energy closure ratio (defined as the ratio between the sum of H and LE against the subtract G from Rn) was above 78.0% ($r^2 = 0.89$, $p<0.001$), which indicated that the flux measurements were reasonable [25].

Aerodynamic conductance (G_a) and canopy conductance (G_c) were estimated by the following equations:

$$\frac{1}{G_a}=\frac{W_s}{u_*^2}+6.2u_*^{-0.67};\quad \frac{1}{G_c}=\frac{\rho C_p VPD}{\gamma LET}+\frac{\beta\Delta-\gamma}{\gamma G_a}$$

…where W_s is wind speed (m·s^{-1}), u_* is friction velocity (m·s^{-1}), ρ is mean air density, C_p is specific heat of air, VPD is vapor pressure deficit (kPa), γ is the psychrometric constant (kPa·°C^{-1}), LET is the latent heat flux (W·m^{-2}, L is the latent heat of vaporization), β is the Bowen ratio (H/LET), and Δ is slope of the saturation vapor-pressure curve (kPa·°C^{-1}).

Data Quality Control and Gap Filling

All fluxes data and quality flags were re-calculated by Eddypro 6.0 (LI-COR inc, USA) with WPL (Webb-Pearman-Leuning) density correction, double rotation tilt correction, and time-lag compensation. After the steady state test and the developed turbulent conditions test, we discarded the flux results with a quality flag of 2, which are the worst retrieval data and widely removed in subsequent analysis [26]. Then the standard methodologies on flux data recommended by ChinaFLUX were applied [27]. The 30-minute flux data were removed when precipitation emerged or when the absolute value was above 1.0 mg CO_2·m^{-2}·s^{-1}. Nighttime (PPFD < 10 μmol·m^{-2}·s^{-1}) CO_2 flux data under low atmospheric turbulence conditions were screened using thresholds of u_*, and CO_2 flux data were removed when $u_* < 0.15$ m·s^{-1}. The missing flux data were filled by non-linear functions between environmental variables and valid flux data. In this study, the nighttime flux ($R_{eco,n}$) gaps were filled by the Van't Hoff equation, which included 5 cm soil temperature (T_s). Daytime flux (net ecosystem exchange, NEE) gaps were filled by a rectangular hyperbolic light-response function [27].

$$R_{eco,n}=R_{eco,ref}e^{\ln(Q_{10})(T_s-10)/10};$$

$$NEE=R_{eco,d}-\frac{a\times P_{max}\times PPFD}{P_{max}+a\times PPFD}$$

…where $R_{eco,ref}$ is reference ecosystem respiration rate when T_s was 10ºC and Q_{10} are the relative increase of the ecosystem respiration with the temperature increase of 10ºC, $R_{eco,d}$ is ecosystem dark respiration rate, and a and P_{max} are apparent quantum yield and saturated photosynthesis rate. $R_{eco,ref}$, Q_{10} and $R_{eco,d}$, a, and P_{max} were fitted to parameters using valid flux data with a five-day moving window in Matlab R2007a (Mathworks Inc., USA). The daytime and nighttime available flux data ratio was approximately 84.0% and 44.2% during study periods, respectively. The gaps in meteorological data, H and LET were filled using linear temporal interpolation [24].

GPP was generally derived by partitioning NEE data (GPP = NEE – ($R_{eco,d}$ + $R_{eco,n}$)) with the assumption that $R_{eco,d}$ could be estimated and extrapolated by the Van't Hoff equation based on the diurnal data of T_s. Negative and positive NEE represented the CO_2 absorbed and released by the ecosystem, respectively. By convention, GPP was shown the negative value [27].

Summer Heatwave Definition

Summer heatwave is defined as a spell of consecutive days with maximum air temperatures (T_{max}) exceeding the local 90th percentile of the 30-year period [2, 9]. Based on meteorological data from 1981 to 2011 at Haibei station, we found the seven-day-period from July 26 to August 1 in 2015 could be classified as a summer heatwave, with T_{max} ranging from 23.1°C in August 1 to 25.6ºC on July 30, which exceeded corresponding temperatures. Therefore, the period from July 1 to August 31 was studied and classified as pre-heatwave (July 1 to July 25), heatwave (July 26 to August 1), and post-heatwave (August 2 to August 31). Meanwhile, we chose the period from July 1 to August 31 in 2014 as a reference and it was somewhat arbitrary. Fortunately, T_a and rain of 2014 from July to August was 10.3±0.30°C and 160.4±2.0 mm, which was close to the corresponding T_a (10.8±0.27 ºC) and rain (150.6±13.9 mm) from 2006 to 2013, and could serve as a proxy for normal climatic conditions. It also suggested that we could distinguish the net effect of heatwave on interesting variables in 2015 from the plant phenological seasonal dynamics through simply subtracting corresponding value in reference 2014.

Statistical Analysis

The Kolmogorov-Smirnov test was first conducted and the results showed that the focused variables were normally distributed ($0.20 < P < 0.97$) without transformation. One-way ANOVA (analysis of variance) and LSD (least significant difference) tests were performed for multiple comparisons of the environmental factors and flux data among pre-heatwave, heatwave, and post-heatwave.

Because of collinearities and nonlinearities among ecological variables, we adopted the boosted regression trees (BRT), which could identify relatively important environmental variables without transformations no matter how variables distribute and whether observations are independent [28]. Therefore, BRT was performed for recognizing the relevant controlling factors (T_a, VPD, T_c, W_s, G_a, G_c, PPFD, Rn-G (AE: available energy), SWC (5 cm SWC), T_s) on variations of daytime H, LET, and RES and GPP data without gap-filling. The difference in coefficient of covariance estimate of predictive deviance between BRT and simplified BRT is less than 1.5, then we demonstrated all variables' contributions on dependent factors of BRT results. All statistical analyses were performed in R 3.03 [29].

Results

Changes in Environmental Factors during Heatwave

The summer heatwave was caused by an eastern extension of Middle Eastern high pressure and sparked by about 10-days of less precipitation and concomitant dry soil conditions in July 2015. Compared with the environmental factors in pre-heatwave, daily T_a, T_{max}, T_c, T_s, and VPD were significantly ($P < 0.001$) increased by 56.6%, 51.5%, 56.8%, 16.9%, and 62.0%, respectively (Table 1). A notable finding was that daily T_{min} increased undetectably ($P = 0.21$) and the magnitude was only approximately one-forth that of daily T_{max} (2.3ºC compared with 8.2ºC). Daily SWC obviously declined by 31.2% ($P<0.001$). Daily PPFD increased little ($P = 0.18$), whic might be ascribed to the non-significant change in daily rain ($P = 0.88$), which generally suggested similar cloudy days. Thus, this summer heatwave was not accompanied by a rainfall deficit unexpectedly. The net effect of the heatwave through subtracting corresponding daily variations on environmental factors in reference to 2014 was above 57.0% on T_a and T_c, 31.0% on T_{max} and VPD, and below 15.0% on T_s and SWC. It was worth noting that the net effect of the heatwave declined linearly on SWC ($R^2 = 0.67$, $P = 0.06$) and T_s ($R^2 = 0.96$, $P<0.01$), and could reach a 40 cm soil layer with less than 1.3% on 40 cm SWC ($P<0.001$) and 3.2% on 40 cm T_s ($P<0.001$). Except for significant differences in SWC ($P = 0.001$) between pre-heatwave and post-heatwave, the other environmental factors recovered rapidly ($0.17<P<0.83$). Therefore, daily environmental factors excluding PPFD and rain were not resistant, while most of them omitting daily SWC were resilient to the summer heatwave in the alpine grassland (Table 1).

Table 1. Comparison of daily air temperature (T_a, ºC), maximum air temperature (T_{max}, ºC), minimum air temperature (T_{min}, ºC), daily photosynthetic photon flux density (PPFD, $\mu mol \cdot m^{2} \cdot s^{-1}$), daily vapor pressure deficit (VPD, Pa), daily precipitation (rain, mm), daily canopy temperature (T_c, ºC), daily 5 cm soil temperature (T_s, ºC), and 5 cm volumetric soil water content (SWC, $cm^3 \cdot cm^{-3}$) in reference 2014 year and heatwave 2015 year.

	2014			2015		
	Pre-heatwave (N = 25)	Heatwave (N = 7)	Post-heatwave (N = 30)	Pre-heatwave (N = 25)	Heatwave (N = 7)	Post-heatwave (N = 30)
T_a	10.3±1.7a	11.2±1.0a	8.5±2.3a	8.6±1.6B	13.4±1.0A	8.3±1.7B
T_{max}	18.1±2.9a	21.6±0.8a	16.1±2.7a	16.0±3.5B	24.2±0.8A	16.5±2.4B
T_{min}	3.6±3.5a	1.8±1.0a	2.1±3.9a	1.6±3.2A	3.9±2.2A	1.4±3.7A
PPFD	504.6±180.5a	583.6±62.9a	413.5±164.1a	485.7±158.1A	529.2±82.8A	431.2±141.2A
VPD	443.7±171.1a	534.8±75.1a	353.0±145.1a	441.1±194.6B	714.8±121.2A	412.6±152.0B
Rain	98.6±6.9a	0.2±0.1b	105.4±5.9a	36.4±2.8AB	13.3±3.2B	46.8±3.6A
T_c	11.2±1.8a	12.3±1.2a	9.2±2.4a	9.3±1.9B	14.6±1.2A	9.0±1.8B
T_s	14.0±1.1a	15.1±0.5a	13.0±1.3a	11.6±0.8B	13.6±0.7A	11.8±1.3B
SWC	0.31±0.03a	0.25±0.03a	0.29±0.04a	0.28±0.05A	0.19±0.06C	0.23±0.05B

Note: Different lowercase letters (for 2014) and uppercase letters (for 2015) mean significant differences ($P < 0.05$) among the pre-heatwave, heatwave, and post-heatwave. The values were represented by mean values ±1 standard error.

Response of Diurnal Energy and CO_2 Fluxes

One-way ANOVA showed that only diurnal RES responded significantly to the heatwave and increased by 30.7% (P<0.001), with by 36.0% (1.67 μmol·m^{-2}·s^{-1}) in daytime (P<0.001) and by 24.3% (2.28 μmol·m^{-2}·s^{-1}) in nighttime (P<0.001). Diurnal GPP decreased a little (P = 0.27), while declining significantly (P = 0.004) by -2.48 μmol·m^{-2}·s^{-1} from 9:00 to 16:00 (Fig. 2d). Consequently, diurnal NEE increased undetectably (P = 0.41). Average diurnal H (P = 0.99) and LET (P = 0.51) were unchanged. However, H and LET increased by 18.1% (P = 0.08) and by 27.5% (P = 0.02), from 9:00 to 16:00, compared with corresponding pre-heatwave daytime. G_a varied little (P = 0.58) while G_c declined significantly (P < 0.003) by about 50% during the heatwave. Such variations in diurnal G_c could be ascribed to the great increase in daytime VPD (71.0%) and little change in LET (16.4%) and Bowen ratio (-13.5%). Meanwhile, there were non-significant differences (0.30<P<0.99) of diurnal H, LET, RES, GPP, Ga, and Gc between pre-heatwave and post-heatwave, which suggested that the legacy effects derived from the summer heatwave was little on diurnal energy and CO_2 fluxes in the alpine grassland (Fig. 2).

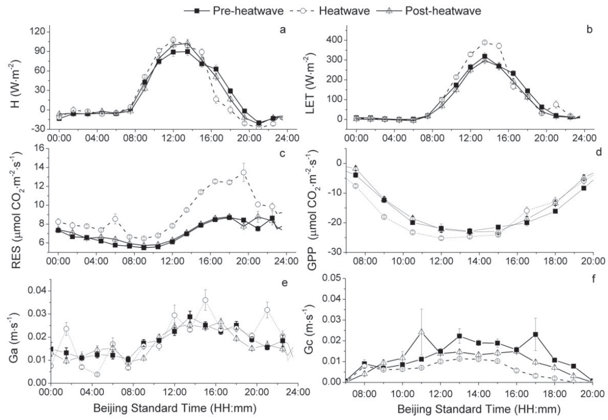

Fig. 2. Variations of average diurnal energy and CO_2 fluxes (sensible heat fluxes (H, a), latent heat fluxes (LET, b), ecosystem respiration (RES, c), and gross primary production (GPP, d), aerodynamic conductance (G_a, e) and canopy conductance (G_c, f) during the heatwave.

Response of Daily Energy Exchange

Shortwave radiation did not increase significantly (P>0.24, Table 2). As a direct heating effect of the heatwave, daily longwave radiation was promoted with inward radiation by 7.8% (31.8 W·m^{-2}, P<0.001) and outward radiation by 7.6% (41.7 W·m^{-2}, P<0.001). Therefore, there was little difference in daily R_n (P = 0.12) between pre-heatwave and heatwave. Daily G increased evidently by 74.6% (3.2 W·m^{-2}, P<0.001). Daily AE accordingly increased little (P = 0.29). Daily H fluctuated undetectably among pre-heatwave, heatwave, and post-heatwave in 2015 (P = 0.96) and in corresponding reference 2014 (P = 0.55). Daily LET declined significantly by 24.2% (28.0 W·m^{-2}, P = 0.014) only from heatwave to post-heatwave in 2015. However, such a decrease could be ascribed to normal seasonal dynamics rather than the summer heatwave, because daily LET also dropped by 28.1% (31.9 W·m^{-2}, P = 0.008) in reference to 2014. Daily LET seemed to consume little more AE during the heatwave, with the ratio of LET to AE increasing to 0.72 (P = 0.34), and those of H declined to 0.14 (P = 0.43) with

Table 2. The comparison of daily shortwave radiation inward (Rs in, W·m^{-2}), daily shortwave radiation outward (Rs out, W·m^{-2}), daily longwave radiation inward (Rl in, W·m^{-2}), daily longwave radiation outward (Rl out, W·m^{-2}), daily net radiation (Rn, W·m^{-2}), daily soil heat flux (G, W·m^{-2}), daily sensible heat flux (H, W·m^{-2}), daily latent heat flux (LE, W·m^{-2}) and daily Bowen ratio (H/LE) in reference 2014 year and heatwave 2015 year.

	2014			2015		
	Pre-heatwave (N = 25)	Heatwave (N = 7)	Post-heatwave (N = 30)	Pre-heatwave (N = 25)	Heatwave (N = 7)	Post-heatwave (N = 30)
Rs in	256.3±91.1a	298.1±31.4a	215.0±84.2a	268.6±85.1A	286.1±43.9A	240±77.9A
Rs out	52.1±17.6a	62.7±6.3a	45.3±16.8a	49.3±15.3A	50.9±8.2A	44.3±13.8A
Rl in	467.3±28.5a	465.0±8.3a	459.1±29.5a	449.6±23.9B	484.9±13.1A	453.1±19.1B
Rl out	526.7±12.6a	532.9±8.8a	510.4±17.7a	512.1±13.7B	551.1±10.4A	509.4±13.9B
Rn	144.8±47.7a	167.4±17.3a	118.5±47.9a	156.8±46.8A	169.0±25.9A	139.4±48.6A
G	5.7±4.0a	5.3±1.8a	1.8±3.6b	4.3±2.9B	7.6±1.6A	2.1±2.6A
H	15.8±7.3a	19.3±3.3a	17.3±8.8a	23.4±9.8A	22.4±6.7A	23.5±9.7A
LE	95.8±31.2a	113.6±11.8a	81.7±27.2a	99.8±27.2AB	115.8±13.2A	87.9±27.7B
Bowen	0.16±0.06a	0.17±0.03a	0.19±0.09a	0.23±0.07A	0.19±0.04A	0.26±0.08A

Note: Different lowercase letters (for 2014) and uppercase letters (for 2015) mean significant differences (P<0.05) among the pre-heatwave, heatwave, and post-heatwave. The values were represented by mean values ±1 standard error.

comparison to the pre-heatwave (LET: 0.66, H: 0.21) and the post-heatwave (LET: 0.64, H: 0.22). Thus, the Bowen ratio decreased marginally significantly ($P = 0.07$). Overall, this summer heatwave just led to available energy partitioned a little more into LET without magnitude fluctuations of total heat exchange.

Response of Daily CO_2 Fluxes

Daily NEE increased by 76.7% ($P = 0.03$) from -2.15±0.31 g C·m^{-2}·d^{-1} during pre-heatwave to -0.50±0.63 g C·m^{-2}·d^{-1} during the heatwave (Fig. 3). This resulted from daily RES increasing clearly by 30.7% ($P<0.001$) and daily GPP decreasing little by 6.1% ($P = 0.13$). The net effect of the heatwave on daily GPP, daily RES, and daily NEE was -10.7%, 23.7%, and -125.7%, respectively. Daily GPP, RES, and NEE of the corresponding period of heatwave and post-heatwave changed significantly ($P<0.02$) in reference 2014. However, such clear declines in daily GPP ($P = 0.08$) and daily NEE ($P = 0.22$) were weakened, and increases in daily RES ($P<0.001$) were enhanced by the heatwave in 2015. These results suggest that daily GPP was resistant while daily RES exhibited good acclimation to the summer heatwave (Fig. 3).

Daily RES linearly correlated with daily GPP ($RES = -0.19GPP - 5.46$, $R^1 = 0.23$, $P<0.001$) in reference to 2014, and daily RES consumed much more daily GPP ($RES = -0.31GPP - 4.55$, $R^1 = 0.16$, $P<0.001$) during the 2015 heatwave. Moreover, there was little difference in slope during the pre-heatwaves between 2014 and 2015 (Fig. 4a), which partly confirmed that much proportion of daily RES from GPP was a consequence of the heatwave. Daily NEE was less controlled by daily GPP, with R^2 of 0.51 in heatwave 2015 and 0.85 in reference 2014. WUE (GPP/ET) was 1.25 g C·mm^{-1} during pre-heatwave and increased to 1.80 g C·mm^{-1} in reference 2014, and it was 1.17 g C·mm^{-1} and also increased to 1.46 g C·mm^{-1} in heatwave 2015. Therefore, the heatwave could decrease WUE by 20.8% and weaken the coupling relationship of carbon and water, suggesting a lack of evolutionary adaption to scarce temperature rapid rising of the alpine grassland.

Environmental Controls on Daytime Energy and CO_2 Fluxes

Daytime H was linearly controlled by daytime AE ($H = 0.18AE - 0.23$, $R^1 = 0.78$, $P<0.001$) in the pre-heatwave, while the effect of AE was weakened by 29.5% during the heatwave and recovered to 90.6% during the post-heatwave, which suggested that the response of daytime H was sensitive and lagged little (Fig. 5a). Interestingly, daytime PPFD rather than daytime AE regulated daytime LET ($LET = 0.22AE - 29.0$, $R^1 = 0.86$, $P<0.001$) and its effect seemed to be a little stronger by 12.7% with comparison to the pre-heatwave (Fig. 5b), which might reflect that ET was greatly regulated by plant transpiration activity. As an extrapolation of nocturnal RES, daytime RES was primarily determined by daytime

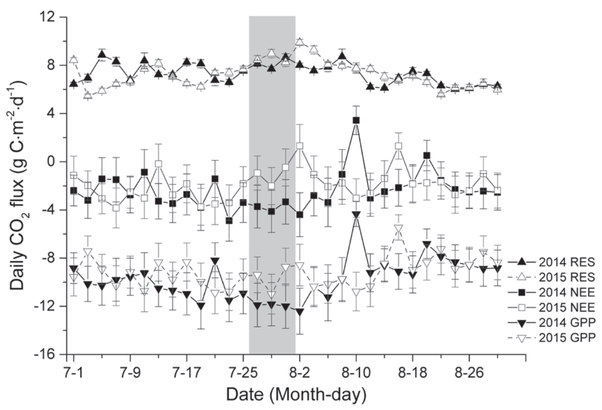

Fig. 3. Variations of daily CO_2 fluxes during reference 2014 and heatwave 2015.

T_s, and the effect of daytime SWC was demonstrated only during the heatwave (Fig. 5c). Surprisingly, daytime GPP was also controlled by daytime AE with a similar rectangular hyperbolic light-response function $\left(GPP = -5.88 - \frac{0.086AE28.2}{0.086AE + 28.2},\ R^2 = 0.58,\ P < 0.001\right)$ during pre-heatwave and post-heatwave, while daytime G_c asymptotically regulated daytime GPP ($GPP = -773 - 13.6 \ln(Gc + 0.0087)$, $R^1 = 0.28$, $P<0.001$) during the heatwave. Overall, the predominant environmental controls of daytime H, LET, and RES stayed steady while that of GPP changed.

Discussion

Heat Fluxes Responded to Summer Heatwave

Compared with the pre-heatwave, LET from 9:00 to 16:00 increased significantly while H changed undetectably, which was consistent with the findings that the heating effect of a summer heatwave is suppressed by increasing ET with evaporative cooling around the grassland [1, 5, 17]. However, the response of daily LET and H was undetectable, which might be ascribed to little variations of AE induced by unchanged daily R_n. Moreover, the increased and decreased proportion of LET and H against AE, together with a lower Bowen ratio (Table 2), seemed to confirm that the behavior of LET consuming much more AE would facilitate mitigating the negative effect of a short-term temperature increase, especially over a humid grassland ecosystem [14]. Meanwhile, such short-term increasing variations of LET should be caused by plant transpiration more than by soil evaporation because of higher vegetation coverage of more than 95% [30], fast shallow soil moisture depletion (Table 1), and aggressive water use strategy [5, 13]. Furthermore, the minimal SWC was 0.15 cm^3·cm^{-3} during the heatwave, which was much above the wilting point (0.09 cm^3·cm^{-3}), and also did not

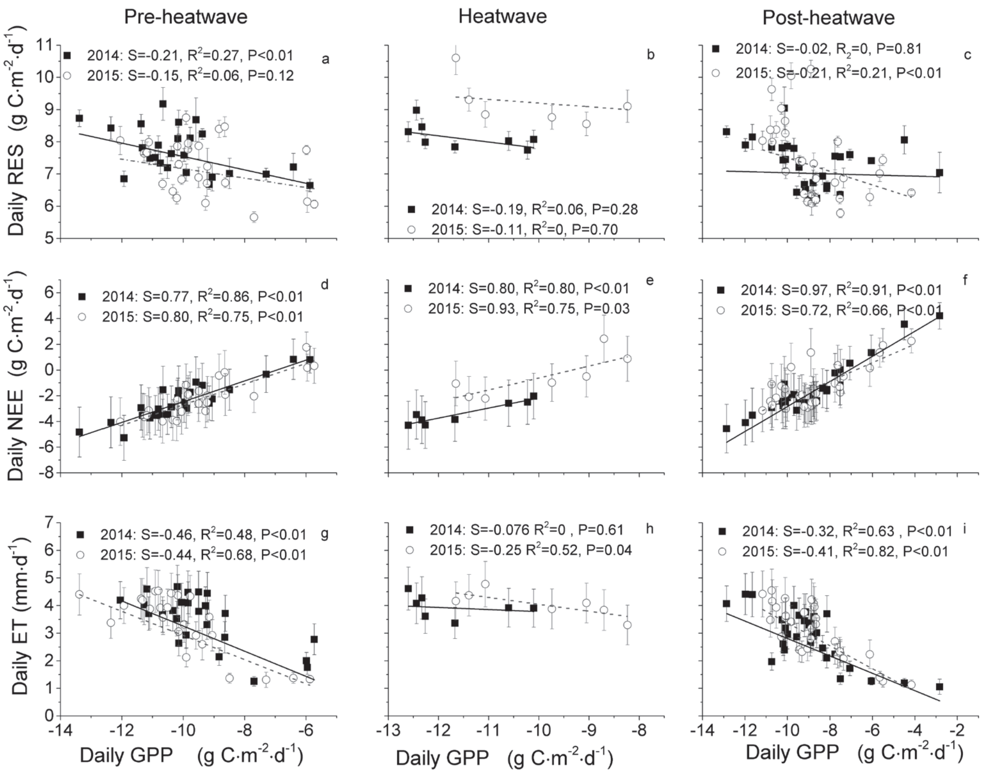

Fig. 4. Correlation of daily GPP with daily RES (a, b, c), daily NEE (d, e, f) and daily ET (g, h, i) during reference 2014 and heatwave 2015.

lead to a substantial decline of stomatal opening and ET in mountain grasslands [14].

But such an increasing response of ET would spark a substantial consequence of plant community transition [11], downstream water supply [14], and ecological health [19] of the alpine region under a much more severe summer heatwave. This consequence may be further amplified by declining growing season precipitation over alpine grasslands on the Qinghai-Tibetan Plateau [22].

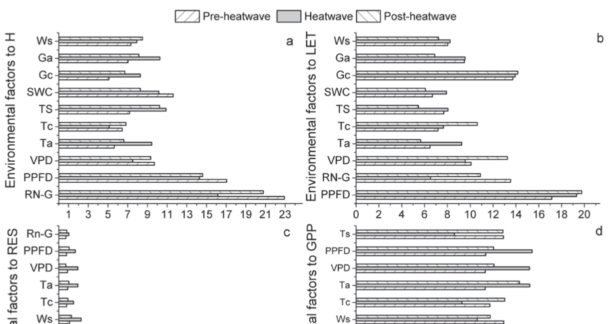

Fig. 5. Relative contribution of environmental variables on daytime sensible heat fluxes (H, a), latent heat flux (LET, b), RES (c), and GPP (d) during the heatwave.

Given that typical ET was 4.0 mm·d^{-1} and rooting depth (0-40 cm) SWC was 0.26 cm^3·cm^{-3} during July and August, it could simply be estimated that a 16-day rainless heatwave will be required before reaching soil wilting point. Thus, we reasonably speculated that soil drought stress induced by the current summer heatwave would not substantially impair ecosystem physiological activity.

CO_2 Fluxes Responded to Summer Heatwave

In contrast with the findings that a dramatic reduction of RES and GPP induced by soil drought stress rather than heat stress during Europe 2003 summer heatwave [7, 10], the summer heatwave without concurrent extreme dry soil conditions had significant positive impacts only on RES. The result was consistent with the reports that reduced CO_2 uptake during the summer heatwave mainly induced by enhancing RES [15] rather than GPP variations [14]. This partly confirmed that the effect of a summer heatwave without soil drought stress would be substantially different on alpine grassland [8-9]. But both diurnal and daily GPP showed a decreasing trend (Figs 2-3). The potential reasons for increasing tendency of ecosystem photosynthetic activity were as follows:

1. The alpine plant photosystem II has a higher tolerance for high temperatures [13] and re-adjustments of the temperature optimum of alpine plant photosynthesis to prevailing temperatures is relatively fast [20].

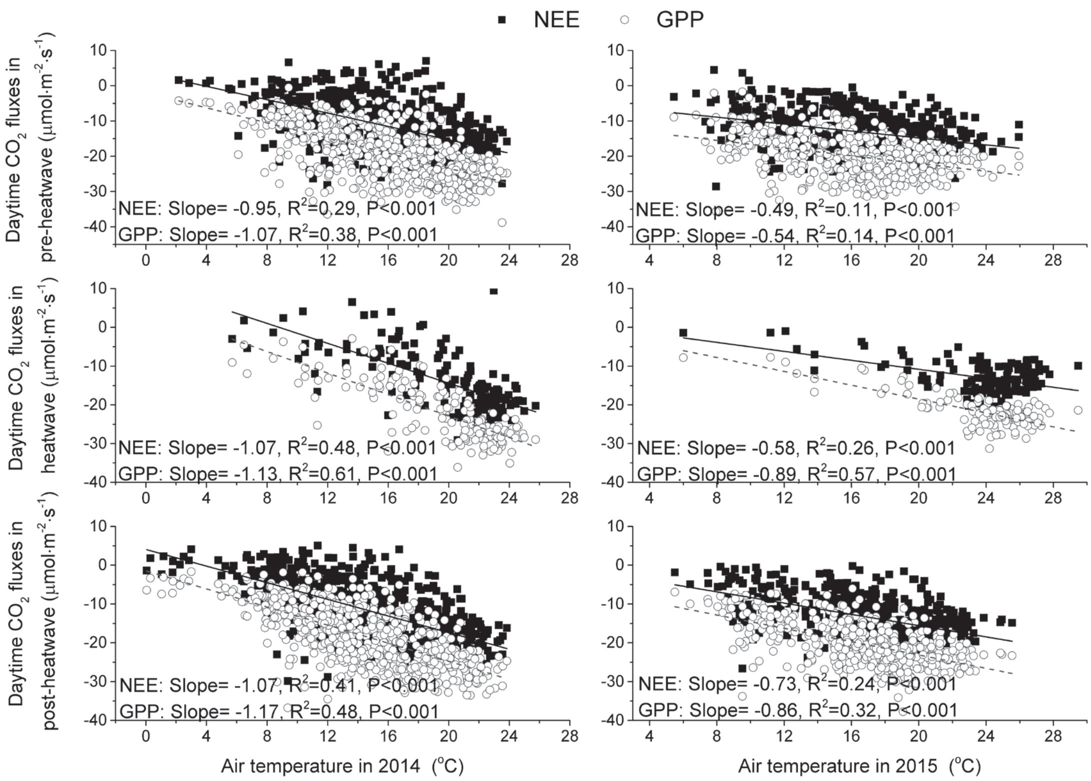

Fig. 6. Relationship between daytime CO_2 fluxes and air temperature during reference 2014 and heatwave 2015.

Moreover, the non-significant difference of GPP between pre-heatwave and post-heatwave suggested that fast recovery in GPP after raining events, which might be induced by strong resilient graminoid grasses [11], and its absolute coverage was above 65% [23]. Additionally, such a present-day heatwave would not lead to the presence of biochemical or photochemical damage in alpine plants because such impairment recovered slowly [14]. This was partly supported by the fact that the maximum T_c (27.9±0.18ºC) during the heatwave was far below the heat-tolerance threshold (above 40ºC) of alpine plants [20].

2. The alpine ecosystem was nutrient-limited, and a warming scenario could stimulate nutrient availability and light-saturated photosynthesis [24], carbon assimilation, and productivity [21-22]. This was partly approved by the relationship between diurnal GPP and diurnal T_a (Fig. 6). The slope of GPP against T_a decreased by 5.8% in reference 2014, while it decreased by 64.8% in 2015 during the heatwave in comparison with the pre-heatwave. In addition, soil drought stress induced by a present-day heatwave would not substantially decline or even promote GPP in mountain grasslands with sufficient moisture supply [14, 16].

Theoretically expected positive direct effects of increasing temperature [4, 6, 17] with normal precipitation input on respiration (Figs 2-3), especially on heterotrophic respiration, was found in an alpine region [15], which is partially confirmed by a weaker correlation between GPP and RES (Fig. 4b). The increasing RES could be explained by improved soil oxygen availability, which stimulated microbial respiration under abundant substrate supply and less drought stress [8]. Moreover, such stimulation derived from the summer heatwave was more direct and stronger in RES than in GPP (Figs 2-3). Therefore, the increase in daily NEE and daily RES (on the order of 76.7% and 30.7%, respectively), represented climate-change feedback that, when they occur over lager spatial and temporal scales, would accelerate the pace of climate warming by reducing the magnitude of alpine grassland CO_2 sinks (although plant photosynthetic production was little enhanced). This partly confirmed that the alpine grassland acted as a carbon source during the longer European 2003 heatwave [7]. Additionally, we also observed significant positive correlation between NEE and T_a above 25ºC (R^2 = 0.10, P<0.01, N = 53).

Conclusions

Our ground-based observation showed that the seven-day summer heatwave coincided only with significantly increasing temperature and did not accompany extreme dry soil conditions, which led to undetectable response of daily energy fluxes. Diurnal and daily RES, rather than those of GPP, was enhanced remarkably. Consequently, NEE was increased significantly, indicating a weakening ecosystem carbon fixation capacity. Those results suggested that such an ecological response was physiological and was relatively resilient to the current summer heatwave in the humid alpine grassland. However, LET of diurnal temperature peak (from 9:00 to 16:00) significantly increased and such cooling feedback thus suppressed H at the cost of aggressive ecosystem water spending, which indicated that the future long-term (more than 16 days) or severe intensity heatwave would substantially weaken ecosystem function of water resources and carbon sequestration capacity when soil water threshold would be crossed. A much wider coverage of alpine grassland response to heatwaves may thus become a necessity.

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