LETTER

Shifting biomass allocation determines community water use efficiency under climate warming

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Abstract

Understanding how net primary production (NPP) and its allocation respond to climate warming is of fundamental importance in predicting ecosystem carbon (C) cycle and C-climate feedback. Especially, the optimal partitioning theory suggests that plants preferentially allocate photosynthates toward the above- or below-ground parts to acquire the limiting resources to maximize their growth rate and optimize resource use under environmental change. However, it remains elusive on how NPP allocation changes and regulates community water-use efficiency (WUEc) under climate warming. In this study, we conducted a manipulative warming experiment with three levels of warming treatments (control, +1.5 °C and +2.5 °C) to explore the response of NPP allocation and its regulation on WUEc in an alpine meadow. Results showed that above-ground NPP (ANPP) and below-ground NPP (BNPP) responded differently to warming. On average, W1.5 (+1.5 °C) and W2.5 (+2.5 °C) treatments increased BNPP by 28.98% and 33.28% and increased NPP by 20.05% and 38.70%, respectively, across 4 years. Whereas no consistent warming effect on ANPP was observed across years. The fraction of BNPP to total NPP (fBNPP) responded positively to warming under low ambient temperature and community biomass while it responded negatively under high ambient temperature and community biomass. Notably warming-induced changes in fBNPP negatively correlated with warming-induced changes in WUEc. These results suggested that warming effect on NPP allocation was largely contextually dependent and implied important biological regulation on WUEc. The emerging trade-offs between NPP allocation and WUEc reflect adaptation strategy of plant community under climate change.

1. Introduction

Net primary production (NPP) has long been recognized to be the key process and the driving force of global carbon (C) cycle (Norby et al 2002, Ni 2004, Fan et al 2008, Xu et al 2012). Investigating how NPP responds to climate warming is a key for critical understanding of ecosystem functions (Wu et al 2011, Xu et al 2015b) and C-climate feedbacks. However, previous studies have shown various warming impacts on NPP, including positive (Wan et al 2011), negative (Klein et al 2007) or neutral (Xu et al 2013). The uncertain response of NPP results from not only the variability in the response of above-ground NPP (ANPP) but also the limited understanding of below-ground NPP (BNPP). Despite the great efforts that have been made to explore the response of ANPP to warming, no consensus has been achieved, since results suggest that warming can either increase or decrease ANPP, depending on background temperature (Penuelas et al 2007, Arnone et al 2011, Guo et al 2017), precipitation
(Moran et al 2014, Ganjurjav et al 2016) or nutrient availability (Hutchison and Henry 2010, Natali et al 2012). In comparison with well-studied ANPP, the response of BNPP to climate warming remains largely unknown (Hui and Jackson 2006, Xu et al 2013), primarily due to the methodological difficulties in observing or measuring below-ground processes (Milchunas and Lauenroth 2001, Mokany et al 2006, Xu et al 2012). Nevertheless, BNPP usually accounts for more than half of total NPP (Hui and Jackson 2006, Luo et al 2009, Zhou et al 2012) and represents a large ecosystem C stock. It is estimated that global root C stock is around 241 Pg C and makes a great contribution to soil C input (Mokany et al 2006). Therefore, it is essential to study both ANPP and BNPP simultaneously, in order to fully understand the response of total NPP to warming and, further, gain confidence in predicting ecosystem C cycle and its feedback to climate warming.

The allocation of NPP is expressed by \( f_\text{BNPP} \), which is the fraction of BNPP to total NPP. In the majority of global terrestrial ecosystem C models, \( f_\text{BNPP} \) is a critical parameter, and its value is usually held constant due to the lack of reliable \( f_\text{BNPP} \) estimates (Wullschleger et al 2001, Agren and Franklin 2003). This will lead to a large uncertainty in C cycle, since both theoretical and empirical evidences suggested that the allocation of NPP would alter in response to environmental change (Hui and Jackson 2006, Xu et al 2012, Freschet et al 2015). Changes in \( f_\text{BNPP} \) would greatly affect ecosystem C sequestration. Plenty of empirical evidences demonstrated that the decomposition rate of root is slower than that of leaf litter (Thormann et al 2001). This is due to that (1) both roots and their decomposers are buried in the soil with relative anoxic condition, which is buffering from extreme environmental changes (Silver and Miya 2001, Mclaren and Turkington 2010, Makiranta et al 2018), and (2) roots may contain higher bound and lignin phenols and condensed tannins, which are difficult to decompose (Wang et al 2015, Xia et al 2015, Ma et al 2016). Thus, more NPP allocation to BNPP would increase the inputs of root material, thereby increasing long-term ecosystem C storage (Fan et al 2008, Shi et al 2015, Wang et al 2016).

Generally, plants preferentially invest photosynthates to the organ that acquires the limiting resources to maximize their growth rate and optimize resource use (Agren and Franklin 2003, Luo et al 2012). However, it remains unknown how changes in NPP allocation alter community resource use efficiency, especially, the community water-use efficiency (WUEc), which is the tradeoff between C gain and water loss and represents the coupling of ecosystem C and water cycle. Given that previous studies have suggested plants tend to shift allocations of carbohydrates toward aboveground part to provide C assimilation and toward belowground part for root development to increase water uptake (Joslin et al 2000, Hui and Jackson 2006, Zong et al 2018), we expected that changes in NPP allocation in response to climate warming would result in changes in WUEc. However, no study so far has explored the regulation of NPP allocation on WUEc.

To fill these knowledge gaps, we conducted a field warming experiment with three treatments (control, + 1.5 °C, + 2.5 °C) on the Qinghai-Tibet Plateau (QTP). As the world’s tallest and largest plateau with a mean elevation of 4000 m above sea level, the QTP is experiencing more rapid climate warming than the global average (Chen et al 2013, IPCC 2013, Shen et al 2015). Specifically, we aimed to address the following questions: (1) how ecosystem NPP and its allocation respond to warming? (2) how changes in NPP allocation regulate the response of WUEc to warming?

### 2. Materials and methods

#### 2.1. Study area

The study was conducted in an alpine meadow located on the eastern Qinghai-Tibetan Plateau (32°48’N, 102°33’E), which is in Hongyuan County, Sichuan, China. The altitude here is about 3500 m. Long term (1961–2013) mean annual precipitation is 747 mm with approximately 80% occurring in May to September and mean annual temperature is 1.5 °C with monthly temperature ranging from −9.7 °C in January to 11.1 °C in July. The soil in the study site is classified as Mat Cry-gelic Cambisol according to Chinese classification (Li and Sun 2011). The plant species in this alpine meadow are dominated by Deschampsia caespitosa (Linn.) Beauv., Koeleria cristata (Linn.) Pers., Gentiana sino-ornata Balf. f., Potentilla anserina L. and Anemone rivularis Buch.-Ham (Quan et al 2018).

#### 2.2. Experimental design

A complete random block design with three warming treatments and five replications was used in this study. Three \( 3 \times 2 \) m plots laid out in each of five blocks were randomly assigned to the three treatments of control, low-level warming (W1.5, + 1.5 °C) and high-level warming (W2.5, + 2.5 °C). The warming plots were heated continuously since June 2014 by 165 \( \times 15 \) cm Infrared radiators (MSR-2420, Kalglo Electronics Inc. Bethlehem, Pennsylvania, USA) suspended in the center, 1.5 m above the ground. The heaters for the low level warming treatments were set at a radiation output of approximately 1000 W, while the heaters for the high level warming treatments were set at a radiation output of approximately 2000 W. In each control plot, a dummy heater with the same size and shape as the infrared radiator was suspend at the same height to simulate the shading effect. The adjacent two plots were 3 m apart.
2.3. ANPP and BNPP measurements and f_{BNPP} estimation

ANPP was measured by clipping all living plants at the ground level in a 0.1 × 1 m quadrat in each plot, in the middle of August every year from 2015 to 2018 when biomass peaked. All plants were oven-dried at 65 °C for 48 h and weighed. The root ingrowth-core method was used to measure BNPP (Zhou et al., 2012, Wilcox et al., 2015). Previous studies at this site showed that more than 90% of the plant roots were distributed within the top 20 cm of the soil, whereas nearly 100% was distributed within the top 40 cm, thus, root sampling at 40 cm depth could well represent root biomass (Song et al., 2017, Zhang et al., 2017a). Soil cores (9.0 cm in diameter, 40 cm in depth) were taken from permanent position in each plot in 2014 at peak biomass. Then, these cores were immediately filled with sieved root-free soil from the shallow (0–20 cm) and deep (20–40 cm) soil layers outside of the plots related to the same layers in the cores and then packed to a density approximate of natural conditions. From 2015, soil cores (40 cm in depth) from the same hole in each plot were taken once a year using the same method by a soil auger (7.5 cm in diameter). Then, these holes were filled again with sieved root-free soil, which is obtained from the same soil layer outside the plots, for next year’s measurement. These soil cores were washed by wet sieving (0.25 mm) under gently flowing water to remove attached soil and obtain root samples. All living roots were dried at 65 °C for 48 h and weighted. Measured ANPP and BNPP for each plot were added up to the total NPP. f_{BNPP} was calculated as f_{BNPP} = BNPP/(ANPP + BNPP) (Hui and Jackson, 2006, Xu et al., 2012).

2.4. Ecosystem carbon and water fluxes measurements

In order to accurately quantify the impact of biomass allocation on ecosystem C and water cycles, we measured ecosystem CO₂ and water fluxes within 1 week of ANPP and BNPP sampling in every year, under cloud-free sunny days, with a transparent canopy chamber (0.5 × 0.5 × 0.5 m, Polymethyl Methacrylate) attached to an infrared gas analyzer (LI-6400XT, LI-COR Environmental, Lincoln, Nebraska, USA). We installed a 0.5 × 0.5 m square aluminum frame into the soil in each plot to provide not only a plane base between the canopy chamber and soil surface but also a higher seal performance. Two small fans ran continuously to mix the air inside the chamber during the measurement period. CO₂ and water vapor concentrations were recorded once every 10 s in 80 s after steady-state conditions were achieved in the chamber. The time-course of the concentration of CO₂ and water vapor were used to determine the net ecosystem CO₂ exchange (NEE) and evapotranspiration (ET). After the NEE measurement, the chamber was vented and covered with an opaque cloth to measure ecosystem respiration (ER). Gross ecosystem productivity (GEP) was calculated as the difference between NEE and ER.

One PVC soil collar (10.5 cm in diameter) was permanently inserted 3 cm into the soil in the middle of each plot for the measurement of soil evaporation (E), living plants inside the collars were prohibited regularly by hand-removing to eliminate above-ground plant transpiration. E were measured at the same time as measurements of NEE and ET, using the LI-6400 infrared gas analyzer with attached soil CO₂ flux chamber (991 cm² in total volume; LI-6400-09; LI-COR Environmental, Lincoln, Nebraska, USA). The E was calculated as the same as the NEE, ER and ET calculation, using the following equation:

\[ F = \frac{10VP_0 \times 1 - W/1000}{RST_0 + 273.15} \times F_{slope} \]

Where F is the C (µmol m⁻² s⁻¹) and water fluxes (mmol m⁻² s⁻¹), V is volume of chamber (cm³), P₀ is the initial pressure in the chamber (kPa), W is the initial water vapor mole fraction (mmol mol⁻¹), R is gas constant (8.314 Pa m³ K⁻¹ mol⁻¹), S is the soil surface area (cm²), T₀ is the temperature (°C) in the chamber, and F_{slope} is the slopes of CO₂ and H₂O content over measuring time in the chamber (Niu et al., 2008).

Canopy transpiration (T) was determined by the difference between ET and E. These methods for measuring the components of WUE mainly followed Niu et al. (2011) and WUEc was defined as GEP/T (Niu et al., 2011, Sun et al., 2016).

2.5. Statistical analysis

One-way ANOVA was used to test the difference of ANPP, BNPP, NPP and f_{BNPP} among different warming treatments. Repeated measures ANOVA were performed to examine the main and interactive effects of warming and year on ANPP, BNPP, NPP and f_{BNPP}. We calculated the effect size of warming by the response ratio (RR): InRR = ln (XT/XC), where XT and XC were the values of warming treatment and the control groups, respectively. We used regression analyses to explore relationships between variables. Statistical analyses were conducted with SPSS 22.0 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Warming effects on ANPP, BNPP and NPP

Warming had significant impacts on ANPP (table 1), which varied with years (table 1; figure 1). In 2015, W2.5 significantly increased ANPP by 162.86%, while in 2016 and 2017, W2.5 had no significant effects, and in 2018, W2.5 significantly decreased ANPP by 33.82% (figure 1). W1.5 had no significant impact on ANPP in any year. Warming significantly increased BNPP and NPP (table 1; figure 1). Overall, across 4 years, W1.5 and W2.5 increased BNPP by 28.98% and 33.28% and increased NPP by 20.05%
Our results indicated that warming-induced changes in fBNPP negatively correlated with warming-induced changes in WUEc (figure 5). Furthermore, the warming response ratio of fBNPP was significantly positively correlated with the response ratio of transpiration (T) rather than GEP (figure 6).

4. Discussion

4.1. Warming effects on ANPP

Our results showed various warming effects on ANPP, either positive or negative, depending on the study years and background environment. This was in line with some previous studies, which also suggested that warming effects on ANPP varied over time. Generally, warming would increase ANPP through enhancing plant photosynthesis (Liang et al. 2013), prolonging growing season length (Starr et al. 2000, Lafleur and Humphreys 2008, Natali et al. 2012) or increasing nutrient availability (Treseder et al. 2016, Xue et al. 2016, Zhang et al. 2017b). However, ANPP would also respond negatively to warming due to warming-induced drought effect in tall-grass prairie (Sherry et al. 2008) or grassland ecosystems (De Boeck et al. 2007). Moreover, Henry et al. (2015) demonstrated that the significant positive warming effect on ANPP only occurred when warming significantly advanced the beginning of growing season in early spring in temperate old field. Whether experiencing the late spring frost or not would also lead to opposite response of ecosystem to warming. For example, warming might accelerate snow melting and enhance water availability for plant growth during the early spring and hence increase ANPP, while the melting of snow cover might also lead to severe frost in late spring and thereby reducing ANPP (Henry et al. 2015). In our study, we found that the response of ANPP to warming depended on warming-induced changes in soil water content (SWC) (figure S1(in the supplementary material available at https://stacks.iop.org/ERL/15/094041/mmedia)). W1.5 did not alter ANPP across 4 years, and similarly W1.5-induced decrease in SWC did not change over time, either. However, the response of ANPP to W2.5 changed from positive to negative over time, while W2.5-induced decrease in SWC significantly changed over time (figures 1 and S2). These suggested that warming and its induced drought determine the warming response of ANPP, which is in line with our previous findings on the warming response of gross primary productivity and net ecosystem productivity (Quan et al. 2019).

In addition, previous studies showed evidences that the response of plant biomass to climate warming largely depended on the changes in plant species and functional types (Lin et al. 2010, Arnone et al. 2011, Wang et al. 2012), mainly due to their different responses to warming-induced changes in temperature, soil moisture or nitrogen availability (van Wijk et al. 2003, Wan et al. 2005, Arnone et al. 2011, Mowll et al. 2015). In our study, by classifying plants into two functional groups (grass and forb), we also found that the warming effect on ANPP negatively correlated with warming effect on grass/forb ratio in community (figure S3). It indicated that changes in plant community composition also regulate the response of ANPP to warming.

Warming had positive effect on BNPP in this study. On the one hand, the direct warming effect would promote root biomass by increasing plant photosynthesis (Danby and Hik 2007). On the other hand, the indirect warming effect of decreasing SWC would also promote root growth or allocate root biomass to deeper soil layers, to alleviate water limitation (Osonubi and Davies 1981, Joslin et al. 2000). In particular, not only changes in plant morphology,

and 38.70%, respectively. Results also showed that, overall, the warming response ratio of NPP positively correlated with the warming response ratio of BNPP, but not with that of ANPP (figure 2). This was due to that the response patterns of NPP to warming was similar to that of BNPP in each year, and BNPP also accounted for a larger proportion of NPP over the 4 years (figure 1).

3.2. Warming effects on fBNPP

The main and interactive effects of warming and year were significant on fBNPP (table 1; figure 1). W2.5 significantly decreased fBNPP from 0.65 ± 0.03 to 0.44 ± 0.10 in 2015, but increased it from 0.77 ± 0.11 to 0.88 ± 0.05 in 2018 (figure 1). Warming-induced changes in fBNPP were due to the warming-induced changes in both ANPP and BNPP. The response ratio of fBNPP negatively correlated with the response ratio of ANPP and positively correlated with that of BNPP (figure 2).

The regression analyses also showed various warming effects on fBNPP. There was a quadratic relationship between soil temperature and fBNPP (figure 3). Moreover, warming effects on fBNPP depended not only on the background soil temperature but also on the background NPP of community. Warming effects on fBNPP changed from positive to negative when background soil temperature and community biomass changed from low to high (figure 4).

3.3. Regulation of NPP partition on WUEc

Table 1. Repeated measure ANOVA results (F values) on the effects of warming, year and their interactions on above-ground net primary production (ANPP), below-ground net primary production (BNPP), total net primary production (NPP) and the fraction of BNPP to NPP (fBNPP). Level of significance: \( *P < 0.01; \quad **P < 0.001; \quad ***P < 0.0001 \); \( P \leq 0.05 \) in 2018 (figure 1).

|                | ANPP  | BNPP  | NPP   | fBNPP |
|----------------|-------|-------|-------|-------|
| Warming        | 9.46* | 3.91* | 6.36* | 4.69* |
| Year           | 26.74*** | 7.79*** | 7.60*** | 24.97*** |
| Warming × Year | 7.83*** | 1.04* | 2.03* | 3.32* |

In addition, previous studies showed evidences that the response of plant biomass to climate warming largely depended on the changes in plant species and functional types (Lin et al. 2010, Arnone et al. 2011, Wang et al. 2012), mainly due to their different responses to warming-induced changes in temperature, soil moisture or nitrogen availability (van Wijk et al. 2003, Wan et al. 2005, Arnone et al. 2011, Mowll et al. 2015). In our study, by classifying plants into two functional groups (grass and forb), we also found that the warming effect on ANPP negatively correlated with warming effect on grass/forb ratio in community (figure S3). It indicated that changes in plant community composition also regulate the response of ANPP to warming.
but also altered community structure in response to warming would lead to increase in BNPP. Combining a 4-year manipulative experiment with a meta-analysis across alpine meadow ecosystem on the Tibetan Plateau, Liu et al (2018) found that warming would increase the abundance of grasses but decrease the abundance of forbs, which indicated a shift community composition toward deeper-rooting species.
and consequently led to increase BNPP. Here, the positive response of BNPP to warming from our study implied a longer ecosystem C turnover time and a potential increase in ecosystem soil C storage as a consequence of the increasing soil C input from root materials in a warmer world.

4.2. The response of NPP allocation to warming

The allocation of NPP represents an adaptive strategy for plants to cope with environmental changes. We found that warming impact on $f_{\text{BNPP}}$ varied with ambient temperature and environmental conditions. The temperature-dependent production allocation was previously found in plant-level, which suggested that the fraction of root mass to total plant mass decreased with increasing temperature (Poorter et al 2012). Our results provided empirical evidence that on the community level, the warming effects on $f_{\text{BNPP}}$ were also temperature-dependent. The effects of warming on $f_{\text{BNPP}}$ changed from positive to negative as ambient temperature increased. It was mainly due to that $f_{\text{BNPP}}$ responded to temperature change in a quadratic pattern, which increased with soil temperature to a maximum value and then decreased with further increasing soil temperature (figure 3). Thus, moderate warming would increase $f_{\text{BNPP}}$ while severe warming would decrease it. Previous studies suggested that plants would invest more carbohydrates in root growth to cope with warming-induced water limitation, therefore leading to positive response of $f_{\text{BNPP}}$ to moderate warming in tall-grass prairie ecosystems (Xu et al 2012, 2013). Furthermore, altered plant community composition (Liu et al 2018) and enhanced interspecific competition for increased soil nutrient availability (van Wijk et al 2003) in response
to moderate warming would also lead to increasing $f_{\text{BNPP}}$. However, exorbitant warming would advance the growing season in spring and increase the early growth and abundance of annuals (Hoeppner and Dukes 2012), which usually invested less in root system development than perennials (Geng et al 2007), thereby leading to decreased $f_{\text{BNPP}}$. Moreover, a synthesis analysis in arctic and alpine tundra revealed that ANPP responded more positively to warming than roots, as a consequence, exorbitant warming may increase aboveground competition for light and thereby increasing allocation to ANPP (Wang et al 2016).

In addition, we found that the effect of warming on $f_{\text{BNPP}}$ depended on community biomass. Poorter et al (2012) found that at plant-level, the allocation of biomass was size-dependent and varied among functional groups. However, it remains unknown whether the biomass allocation was also size-dependent at community-level in response to climate change. Our results showed that warming tended to promote the allocation toward BNPP at low community biomass while tended to promote the allocation toward ANPP at high community biomass. It might be due to that under low community biomass, plant growth may be more limited by water or nutrient rather than light, thereby warming would promote the allocation to belowground for root development. However, under high community biomass, species would compete for light, thus warming may promote the allocation to ANPP.

Our results suggested that warming effects on $f_{\text{BNPP}}$ was contextually dependent and would change over time. Thus, instead of a constant $f_{\text{BNPP}}$, our results imply that the possible temporally varied $f_{\text{BNPP}}$ should be taken into account in terrestrial models, to
improve the projection of ecosystem C sequestration and the climate warming-C cycling feedback. However, more studies are still needed to reveal the mechanisms that govern the response of f_{BNPP} to climate change.

4.3. The regulation of NPP allocation on WUEc
Plenty of empirical and model evidences suggest that the allocation of NPP reflects plant adaptation to environmental changes in order to optimize resource use and maximize the growth (Bloom et al 1985, Chapin et al 1987, Agren and Franklin 2003). However, it remains unknown how changes in NPP allocation influence community resource use efficiency under climate warming, especially for WUEc, which links ecosystem C and water cycles. The paucity of this knowledge is largely due to the fact that few studies have monitored ecosystem C and water processes simultaneously. In our study, we linked ecosystem C cycle process including ANPP, BNPP and GEP to ecosystem water flux T, to explore how the allocation of NPP regulated WUEc under climate warming. Results showed that WUEc decreased with increasing f_{BNPP}. The warming response of f_{BNPP} was negatively correlated with the warming response of WUEc, which was due to the negative relationship between the warming response of f_{BNPP} and the warming response of T, rather than GEP. Increased biomass allocation to root system might enable plant communities to acquire more water, therefore increasing water loss from T (Zhou et al 2012, Xu et al 2015a), and resulting in the reduction of WUEc. This was consistent with our previous study in this alpine meadow, which suggested that T was the main process that dominated changes in WUEc (Quan et al 2018). In addition, Hu et al (2008) found that climate-warming-induced changes in leaf area index can largely control the variations in WUE and emphasized the critical role of biological regulation on ecosystem C and water cycles. Moreover, our results implied that NPP allocation would also be a new key mechanism underlying WUEc changes, and provide new insights into the coupled ecosystem C and water cycles in response to warming.

5. Conclusions
In summary, our results from the 4-year warming experiment in the alpine meadow suggested that ANPP and BNPP responded differently to climate warming. Warming had various impacts on ANPP but significantly increased BNPP and NPP across the 4 years. In addition, f_{BNPP} responded positively to warming under low temperature and community size while responded negatively under high temperature and community size, which suggested that the warming response of NPP allocation was largely contextually dependent. This further implies that models should use dynamic f_{BNPP} to more accurately predict ecosystem C cycle. Moreover, by partitioning ecosystem C and water fluxes into different components, this study provides an unique field evidence that changes in NPP allocation would regulate WUEc, and gives new insights into the biological regulation on community resource use efficiency. In all, this study will help us to better understand and predict ecosystem functions under climate warming.

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Conflict of interest
The authors declare no competing financial interests.

Data availability statements
All data that support the findings of this study are included within the article and supplementary information files.

Author contributions
SN and QQ conceived the ideas and designed the study; QQ, FZ, CM and QZ collected the data; QQ and SN analyzed data and led the writing of the manuscript draft. All authors contributed to the drafts and gave final approval for publication.

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