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Rain use efficiency across a precipitation gradient on the Tibetan Plateau

Yuanhe Yang,[1] Jingyun Fang,[1] Philip A. Fay,[2] Jesse E. Bell,[3] and Chengjun Ji[1]

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[1] Our knowledge of the relationship between vegetation rain use efficiency (RUE) and precipitation is critical for predicting potential responses of grassland ecosystems to changing precipitation regimes. However, a generalized pattern of RUE along the precipitation gradient is still unavailable. Here we examined RUE variations in both Tibetan and global grasslands across precipitation gradients, using actual measurements obtained from a regional survey and a global dataset. RUE in Tibetan grasslands exhibited a unimodal pattern across the precipitation gradient, with an increasing trend in dry alpine steppe and a decreasing trend in mesic alpine meadow. RUE in alpine steppe was lower than in alpine meadow, largely due to their differences in species richness, soil texture and soil carbon content. The RUE of Tibetan grasslands was lower than global grasslands but displayed a similar trend with precipitation, suggesting the generality of a unimodal RUE pattern across diverse grassland types across broad precipitation gradients.

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1. Introduction

[2] Precipitation regimes have been predicted to shift due to global warming, with increasing inter- and intra-annual variability [*Forster et al.*, 2007]. These alterations could have significant impacts on grassland ecosystems [*Knapp et al.*, 2002; *Weltzin et al.*, 2003; *Huxman et al.*, 2004a; *Fang et al.*, 2005; *Fay et al.*, 2008; *Knapp et al.*, 2008; *Yang et al.*, 2008a]. Rain use efficiency (RUE), commonly described as the ratio of aboveground net primary production (ANPP) to mean annual precipitation (MAP), could be a critical indicator for evaluating responses of grassland ecosystems to altered precipitation patterns [*Le Houerou et al.*, 1988; *Huxman et al.*, 2004b; *Bai et al.*, 2008]. The RUE in grassland ecosystems has been observed to exhibit an increasing [*Bai et al.*, 2008], unimodal [*Paruelo et al.*, 1999] or insignificant change [*Lauenroth et al.*, 2000] across the precipitation gradient. However, a generalized pattern of RUE along the precipitation gradient is still unavailable. Moreover, current understanding of RUE variation with MAP primarily comes from temperate grasslands in North and South America [*Bai et al.*, 2008]. Thus, to obtain a global view of RUE and its variation, it is essential to investigate the pattern of RUE across the precipitation gradient in other grasslands around the world.

[3] In this study, we investigated variation in the RUE of alpine grasslands across the precipitation gradient on the Tibetan Plateau. We also compared the RUE pattern in Tibetan alpine grasslands with that in global grasslands. More specifically, this study aims to address the following four questions: (1) How does RUE in alpine grasslands change along the precipitation gradient? (2) Is the RUE pattern occurring in Tibetan alpine grasslands similar to that in global grasslands? (3) What is the difference between RUE in alpine steppe and meadow? (4) What factors could explain such a difference?

2. Materials and Methods

2.1. Study Area

[4] The Tibetan Plateau is the highest and largest plateau on Earth, with a mean elevation of ~4000 m and an area of ~2.0×10^6 km^2 [*Li and Zhou*, 1998]. The plateau is characterized by a large southeast-northwest precipitation gradient, ranging from 100 to 700 mm in MAP. Alpine grasslands consist of alpine steppe and meadow, covering 60% of the plateau. The distribution of alpine grasslands is closely associated with the precipitation gradient across the plateau. Alpine steppe occurs in arid regions and consists of cold-xerophytic grasses such as *Stipa purpurea* and *Carex moorcroftii*, mixed with alpine forbs (e.g., *Polygonum viviparum*) [*Zhang et al.*, 1988]. By contrast, alpine meadow occurs in relatively mesic portions of the plateau and is dominated by perennial grasses such as *Kobresia pygmaea*, *K. humilis* and *K. tibetica* [*Zhang et al.*, 1988].

2.2. Data Collection

[5] We conducted four consecutive sampling campaigns during the summers (July and August) of 2001–2004 and sampled 675 biomass plots and 405 soil profiles from 135 sites across the plateau [*Yang et al.*, 2008b, 2009]. These sites were sampled along the major roads due to extreme climatic conditions, limited seasonal accessibility and sparse road networks on the plateau (Figure S1 of the auxiliary material).[4] Regardless, the field sampling covered both arid

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[1] Department of Ecology and Key Laboratory for Earth Surface Processes of the Ministry of Education, College of Urban and Environmental Sciences, Peking University, Beijing, China.

[2] ARS Grassland, Soil and Water Research Laboratory, USDA, Temple, Texas, USA.

[3] Department of Botany and Microbiology, University of Oklahoma, Norman, Oklahoma, USA.

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[4] Auxiliary materials are available in the HTML. doi:10.1029/2010GL043920.

and wet ends of the precipitation gradient across the plateau. The sampling was conducted at the wet end of the precipitation gradient during 2001–2003 and at the dry end in 2004. Given Tibetan Plateau did not experience large fluctuations in precipitation during the study period, the RUE pattern observed in this study should not be greatly shaped by the temporal variability in precipitation.

[6] At each site (10×10 m^2), we listed all vascular plant species in five plots (1×1 m^2) and then harvested all aboveground biomass to ground level, as a surrogate of ANPP in alpine grasslands [*Jobbágy and Sala*, 2000; *Ma et al.*, 2010a, 2010b]. Harvests took place at the growing season maximum. Biomass samples were oven-dried at 65°C to constant mass, and weighed to the nearest 0.1 g. Also, three pits were excavated to the depth of 1 meter to collect soil samples. For each profile, soil samples were taken at depths of 0–10, 10–20, 20–30, 30–50, 50–70, and 70–100 cm [*Yang et al.*, 2008b]. Soil samples were collected using a standard container (100 cm^3 in volume) for determining bulk density. Soil samples for carbon analysis were sieved through a 2-mm mesh, handpicked to remove plant detritus, and then ground in a ball mill. The volume of rock fraction >2 mm was determined using the release water method, and the volume percentage was then calculated as the ratio of the volume of the fraction >2 mm to the volume of the standard container. Soil organic carbon concentration was analyzed using the Walkley-Black method [*Nelson and Sommers*, 1982]. Soil texture was determined using a particle size analyzer (Malvern Masterizer 2000, England) after removal of organic matter and calcium carbonate. In addition, MAP for each sampling site during 2001–2004 was spatially interpolated from the records of 43 climatic stations located above an elevation of 3000 meter across the plateau [*Yang et al.*, 2008b].

2.3. Data Analysis

[7] We calculated RUE for each sampling site using equation (1). We then examined patterns of RUE in both Tibetan and global grasslands along precipitation gradients. The dataset of ANPP and MAP in global grasslands was obtained from *Yang et al.* [2008a]. We then further compared the differences of RUE in alpine steppe and meadow and in Tibetan and global grasslands through ANOVA analysis. Finally, we conducted regression analyses to investigate the relationships of RUE with species richness, silt content and soil carbon content (amount per area, kg C m^{-2}). Soil carbon content was calculated for each soil profile using equation (2) [*Yang et al.*, 2008b]. All statistical analyses were performed using the software package R [*R Development Core Team*, 2007].

$$RUE = ANPP / MAP \tag{1}$$

$$SOCC = \sum_{i=1}^{n} T_i \times BD_i \times SOC_i \times (1 - C_i / 100) / 100 \tag{2}$$

where RUE is rain use efficiency (g m^{-2} mm^{-1}), ANPP is aboveground net primary production (g m^{-2}), and MAP is mean annual precipitation (mm) [*Le Houerou et al.*, 1988; *Bai et al.*, 2008]. $SOCC$, T_i, BD_i, SOC_i, and C_i are soil organic carbon content (kg C m^{-2}), soil thickness (cm), bulk density (g cm^{-3}), soil organic carbon concentration (g kg^{-1}), and the percentage of rock fragment >2 mm, respectively.

3. Results and Discussion

3.1. RUE Varies Across the Precipitation Gradient

[8] RUE in alpine grasslands exhibited an initial increase and a subsequent decrease along the precipitation gradient ($r^2 = 0.14$, $P < 0.05$) (Figure 1a). Moreover, the relationship of RUE with MAP differed between alpine steppe and meadow. RUE increased with MAP in alpine steppe, which occupies the drier parts of the precipitation gradient ($r^2 = 0.08$, $P < 0.05$). In contrast, RUE decreased with MAP in alpine meadow, which occupies the wetter portions of the precipitation gradient ($r^2 = 0.17$, $P < 0.05$). Thus, RUE for the two alpine grasslands combined peaked at 400 mm of MAP (Figure 1a). The opposing relationships of RUE with precipitation observed in alpine steppe and meadow may be due to contrasting limitations on vegetation growth in these two grassland types. ANPP in alpine steppe was positively correlated with MAP ($r^2 = 0.43$, $P < 0.05$), while ANPP in alpine meadow was not correlated with MAP ($P > 0.05$) (Figure 1b), suggesting that vegetation growth is limited by precipitation in alpine steppe, but not in alpine meadow [*Li and Zhou*, 1998]. Other factors, such as nitrogen availability [*Paruelo et al.*, 1999; *Yang et al.*, 2009], may have constrained the responses of plant production to increased MAP in alpine meadow, resulting in lower RUE under humid environments.

[9] The pattern of RUE variation with MAP in alpine grasslands was different from that observed in China's temperate grasslands by *Bai et al.* [2008], who found that RUE increased across the precipitation gradient in Inner Mongolia (100–600 mm). Our results also differed from those of *Lauenroth et al.* [2000], who observed no significant change in RUE across the precipitation gradient in the central Great Plains of the United States (300–900 mm). However, our results concurred with *Paruelo et al.* [1999], who reported a unimodal pattern across various grassland types along a broad precipitation gradient (200–1200 mm). Moreover, the pattern of RUE variation with MAP occurring in Tibetan alpine grasslands was similar to but located below that in global grasslands (Figures 1c and 1d). These results highlight the generality of a unimodal pattern of RUE across diverse grassland types across broad precipitation gradients. These results also suggest that RUE in Tibetan alpine grasslands is lower than the global level, possibly due to the limitation of low temperature on plant growth in high-altitude regions [*Yang et al.*, 2009]. In addition, these results imply that RUE in Tibetan alpine grasslands may potentially increase under future global warming scenarios. However, warming-induced drought may weaken its positive effects on RUE of alpine grasslands.

3.2. Effects of Environmental Factors on RUE

[10] RUE in alpine meadow was significantly higher than in alpine steppe ($P < 0.05$) (Figure 2), possibly due to differences in vegetation composition, soil texture or soil carbon content (Figure 3). RUE in alpine grasslands was positively related to species richness ($r^2 = 0.31$, $P < 0.05$) (Figure 3a). Also, RUE in both alpine steppe and meadow increased with species richness, respectively ($P < 0.05$)

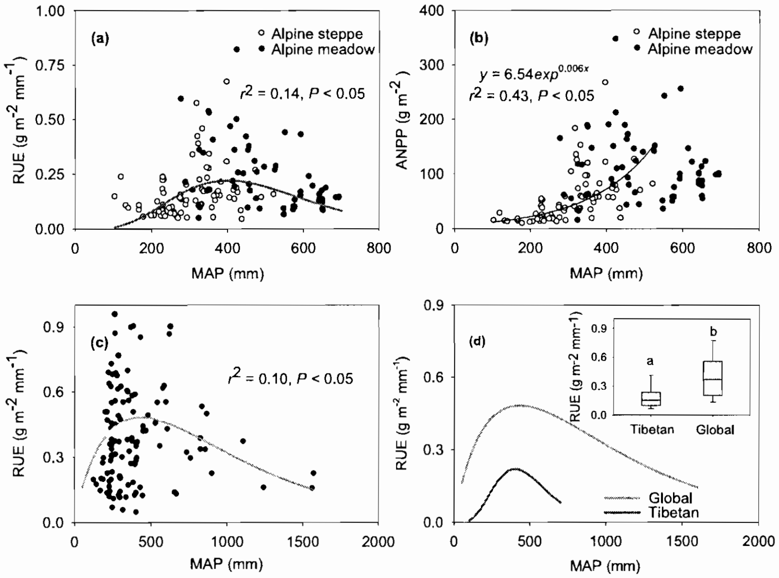

Figure 1. Patterns of (a) RUE and (b) ANPP in Tibetan alpine grasslands, (c) changes in RUE across global grasslands along the precipitation gradient, and (d) the comparison of RUE pattern between Tibetan and global grasslands. An empirical function is used to characterize the relationship between RUE and precipitation in Tibetan grasslands ($RUE = \frac{0.001MAP^{5.213}}{\exp^{(0.013MAP)}}$, $r^2 = 0.14$, $P < 0.05$). The pattern of RUE in global grasslands can also be quantified using the similar function ($RUE = \frac{0.006MAP^{0.865}}{\exp^{(0.002MAP)}}$, $r^2 = 0.10$, $P < 0.05$). The inset shows the differences between RUE in Tibetan and global grasslands. Different letters denote significant differences between them (Tukey test, $P < 0.05$).

(Figures 3b and 3c). Thus, the higher species richness in alpine meadow than in alpine steppe (22 *vs.* 11 (Figure S2a)) could contribute to the larger RUE in alpine meadow than in alpine steppe. Higher species richness could lead to larger RUE in the following two ways. First, more species may mean more complete use of the available water because of niche complementarity. For instance, *Bai et al.* [2004] observed that compensatory effects among various individual species or functional groups led to a decrease of temporal variation in aboveground biomass from species to plant functional groups to community level in Inner Mongolian temperate grasslands. Second, high species richness may also mean that ecosystems are more likely to contain functional groups that can respond to higher precipitation. For example, ecosystems dominated by mesophytic grasses responded more strongly to changes in precipitation than systems dominated by xerophytic grasses [*Paruelo et al.*, 1999].

[11] RUE in alpine grasslands was positively correlated with silt content ($r^2 = 0.15$, $P < 0.05$) (Figure 3d). Moreover, RUE in both alpine steppe and meadow exhibited positive associations with silt content, respectively ($P < 0.05$) (Figures 3e and 3f). Thus, the higher silt content in alpine meadow than in alpine steppe (30% *vs.* 18% (Figure S2b)) could also result in the larger RUE in alpine meadow than in alpine steppe. Soil texture may alter vegetation growth and RUE in alpine grasslands through their effects on soil water availability [*Noy-Meir*, 1973; *Bai et al.*, 2008]. The loamy soils usually have high water-holding capacity and thus could be favorable for higher RUE in alpine meadow [*Sala et al.*, 1988; *Epstein et al.*, 1997]. In contrast, the sandy soils hold less water than loamy soils and may lose more water by drainage or evaporation, resulting in lower RUE in alpine steppe [*Sala et al.*, 1988; *Epstein et al.*, 1997]. In Tibetan alpine grasslands, soil moisture in the top 10 cm was positively correlated with silt content ($r^2 = 0.45$, $P < 0.05$) (Figure S3). Thus, the positive effects of silt content on RUE in alpine grasslands may be largely driven by its indirect effects on water availability for plant growth.

[12] RUE in alpine grasslands increased with soil carbon content ($r^2 = 0.18$, $P < 0.05$) (Figure 3g). Moreover, RUE in both alpine steppe and meadow was positively correlated with soil carbon content, respectively ($P < 0.05$) (Figures 3h and 3i). Thus, the higher soil carbon content in alpine meadow

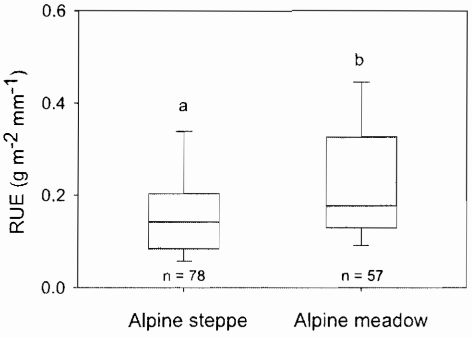

Figure 2. Box and Whisker plots showing the differences between RUE in alpine steppe and alpine meadow on the Tibetan Plateau. Different letters denote significant differences between them (Tukey test, $P < 0.05$). The number is the sample size for alpine steppe and meadow, respectively.

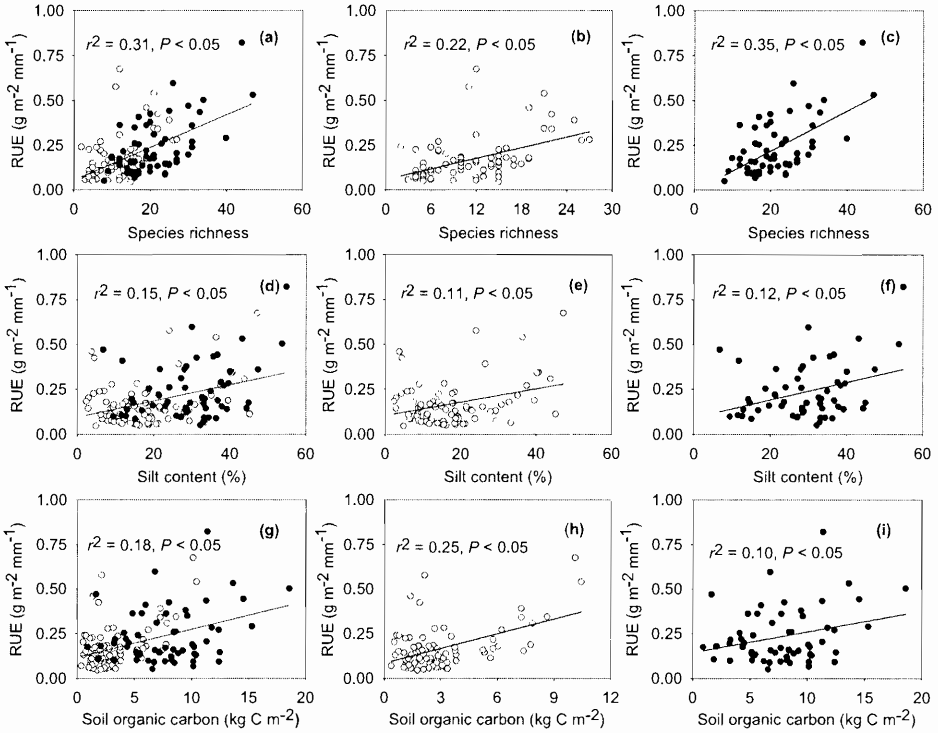

Figure 3. Relationships of RUE in alpine grasslands with (a–c) species richness, (d–f) silt content, and (g–i) soil carbon content. The open circle indicates alpine steppe, while the closed circle denotes alpine meadow.

than in alpine steppe (7.9 *vs.* 3.1 kg C m^{-2} (Figure S2c)) could potentially explain the larger RUE in alpine meadow than in alpine steppe. Considering that soil carbon content is usually related to soil nitrogen availability in grassland ecosystems [*Burke et al.*, 1997; *Bai et al.*, 2008], the positive relationship between RUE and soil carbon content may indicate nitrogen limitation on plant growth in these grasslands [*Huxman et al.*, 2004b; *Bai et al.*, 2008]. A recent analysis by *Ren et al.* [2010] demonstrated that nitrogen addition significantly stimulated plant production in an alpine grassland community on the Tibetan Plateau. In addition, higher-carbon soils also tend to be finer-textured soils, with better water holding capacity [*Brady and Weil*, 2004], and thus could be favorable for higher RUE in grassland ecosystems.

4. Concluding Remarks

[13] This study provided a comprehensive analysis of patterns of RUE in both Tibetan and global grasslands along precipitation gradients. Our results indicated that RUE in alpine grasslands varied across the precipitation gradient, with an increasing trend in dry alpine steppe and a decreasing trend in mesic alpine meadow. The different patterns of RUE variation with precipitation in these two alpine grassland types suggest that they may have differing responses to changing precipitation patterns. The higher RUE in alpine meadow than in alpine steppe could result from their differences in species richness, soil texture and soil carbon content, supporting the hypothesis that RUE in grassland ecosystems is determined by both vegetational and biogeochemical constraints [*Paruelo et al.*, 1999; *Huxman et al.*, 2004b]. The RUE of Tibetan alpine grasslands was lower than global grasslands but displayed a similar trend with precipitation, suggesting the generality of a unimodal RUE pattern across diverse grassland types across broad precipitation gradients. Patterns and controls of RUE observed in this study should be incorporated into land surface models when projecting potential responses of grassland ecosystems to changing precipitation regimes.

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J. E. Bell, Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019, USA.

J. Fang, C. Ji, and Y. Yang, Department of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China. (yhyang@water.pku.edu.cn)

P. A. Fay, ARS Grassland, Soil and Water Research Laboratory, USDA, 808 E. Blackland Rd., Temple, TX 76502, USA.