Soil nitrogen and carbon determine the trade-off of the above- and below-ground biomass across alpine grasslands, Tibetan Plateau

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1. Introduction

Both aboveground biomass (AGB) and belowground biomass (BGB) act as primary input sources to the soil carbon pool (Sun et al., 2013b), and the allocation of AGB and BGB is widely studied because the ratio of root to shoot (R/S) is an important parameter in the carbon cycle model, such as the GRASS model and BIOME model (Enquist and Niklas, 2002; Wu et al., 2013). Moreover, the biomass allocation pattern is a key component of the plant life history and life span (Roa-Fuentes et al., 2012). Therefore, many studies have explored the mechanisms of AGB, BGB or R/S responses to such environmental changes with precipitation gradients (Edwards et al., 1992; Perkins and Owens, 2003; Roa-Fuentes et al., 2012; Zhou et al., 2009, 2012), warming (Lin et al., 2010; Wang et al., 2012; Zhou et al., 2012), elevated CO₂ or O₃ concentrations (Bernacchi et al., 2000; Eamus, 1996; Grukle and Balduman, 1999; Hattenschwiler and Korner, 1998; Laitat et al., 1999; Liu et al., 2002; Olszyk et al., 2003; Penuelas et al., 1995; Poorter and Nagel, 2000; Reich et al., 2004; Schortemeyer et al., 1999; White et al., 2012) and other environmental factors (Mao et al., 2012; Phongodume et al., 2012; Schall et al., 2012; Slot et al., 2012; Xie et al., 2012; Xue et al., 2012). In addition, there has been much debate over two important hypotheses, optimal partitioning and isometric allocation. For the former, the slope, for which biomass allocation can be quantified as the slope of log-transformed AGB versus log-transformed BGB, did not show any change due to environmental stress. For the latter, the functional equilibrium hypothesis (optimal partitioning) regards plant biomass allocation as size-independent (McConnaughay and Coleman, 1999), which suggests that plants will develop larger root systems if soil resources are limiting and will proportionally allocate more resources to stems and leaves if an aboveground resource, such as light, is limiting (Coleman and McConnaughay, 1995; Shipley and Meziane, 2002; Yang et al., 2010).

Alpine grassland is a dominant ecosystem of the Tibetan Plateau. The natural environment of the region is extremely harsh and is characterized by poor soil nutrients, aridity, and low temperatures (Sun et al., 2013a). Studies showed that the ratio of R/S increases with decreasing temperature and soil water/nutrient availability (Li et al., 2008; Liu et al., 2014a,b) in grassland ecosystems, particularly in alpine grassland where soil water/nutrient availability is limited (Sun et al., 2013b). The root–shoot interaction is species-specific in the alpine grassland, and plants may trade off morphological...
shifts within the roots and shoots to adapt to stressful environments (Song et al., 2006). The reason for these shifts is that plants allocate more photosynthates to roots in low-temperature environments, which may increase water/nutrient absorption for survival in a harsh environment due to the “root size – ability symmetric effect”, in which the soil water/nutrient uptake ability of a plant is proportional to the size of its root system (Li et al., 2011). Previous studies showed that the ratio of biomass is not fixed and may vary over time and across environments (Liu et al., 2014a; Sun et al., 2013b; Wu et al., 2013). A quantitative understanding of such patterns is of fundamental importance for modeling terrestrial carbon storage and ecological processes (Poorter et al., 2012). In this study, we developed a method to quantify the relative benefits of AGB and BGB, particularly in terms of trade-off, for which biomass allocation is shaped by environmental conditions (Walther et al., 2002).

Bradford and D’Amato (2012) established a computational formula for trade-off among individual benefits, providing a powerful tool with which to quantify the trade-off relationships of multi-objects. Therefore, the effects of environmental factors, such as the mean annual precipitation (MAP), mean annual temperature (MAT), index of aridity ($l_{dam}$), soil nitrogen content (nitrogen), soil carbon density [30 cm (SOC1), 50 cm (SOC2) and 100 cm depths (SOC3)], clay and silt, on the trade-off of biomass allocation above- and belowground across alpine grasslands, including the alpine steppe and alpine meadow, are examined. Specifically, the objectives of this study are as follows: (1) to analyze the difference in biomass allocation in alpine steppes and meadows; (2) to explore the main environmental factors associated with trade-offs between AGB and BGB across alpine grasslands; and (3) to identify the threshold and inflection point of trade-off responses to major environmental factors.

2. Materials and methods

2.1. Data collection

Data were obtained from previous studies (Yang et al., 2007, 2009) in which samples were collected from 110 sites (74 in the alpine steppe and 36 in the alpine meadow; each site area is 10 m × 10 m) in July and August of 2005; the study sites are displayed in Fig. 1. The data package used in this study included meteorological factors, such as the mean annual temperature (MAT), mean annual precipitation (MAP), and aridity index ($l_{dam}$); soil properties, such as soil moisture, nitrogen, silt, clay, and organic carbon density at depths of 30, 50, and 100 cm, respectively; and two target variables of aboveground biomass (AGB) and belowground biomass (BGB). To represent a realistic alpine grassland ecosystem, our analyses included sites covering a wide range of alpine grassland habitats, such as alpine steppes and alpine meadows.

2.2. Calculation of trade-off

The trade-offs between AGB and BGB were calculated as described below.

Benefit for a single object (AGB or BGB) is defined as the relative deviation from the mean for a given observation. Given observations of an individual object A, the magnitude of benefit for object A ($B_A$, AGB/BGB) is calculated as (Bradford and D’Amato, 2012):

$$B_A = \frac{A_{OBS} - A_{Min}}{A_{Max} - A_{Min}}$$

where $A_{OBS}$ is the observed value of AGB/BGB and $A_{Max}$ (Maximum) and $A_{Min}$ (Minimum) are calculated from the entire population of AGB/BGB. The trade-off ranges from 0 to 1 and can be conceptualized as the proportion of possible benefit in object A (AGB/BGB). In cases in which certain objects are considered to be more valuable or important than others, individual objects (AGB/BGB) can be weighted to incorporate these differences into calculations of overall benefit and trade-off.

One simple means of quantifying the magnitude of the trade-off between AGB and BGB involves calculating the root mean square error (RMSE) of the individual benefits, AGB or BGB. The RMSE approximates the average deviation from the mean benefit and, in two dimensions, is the distance from the “1:1 line” of the zero trade-off (Bradford and D’Amato, 2012) (Fig. 2). This method represents an effective strategy for quantifying the relationships of AGB and BGB.

Fig. 1. Locations of the 110 sample sites included in this study. Black solid circles and triangles represent samples in the alpine meadow and steppe, respectively.
ecologically more plausible estimation of responses to a given variable (Ruppert et al., 2012). Therefore, the 99th percentile was used to evaluate the response of trade-off to soil properties, including soil nitrogen, SOC1, SOC2 and SOC3, as the potential constraint. In addition, we calculated the change trends of the median for the overall analysis. The segment function is as follows:

\[
t_1 = \min(t)
\]

\[
t_3 = \max(t)
\]

\[
f_1(t) = \frac{y_1 \times (T_1 - t) + y_2 \times (t - t_1)}{T_1 - t_1}
\]

\[
f_2(t) = \frac{y_2 \times (T_2 - t) + y_3 \times (t - T_1)}{T_2 - T_1}
\]

\[
f_3(t) = \frac{y_3 \times (T_3 - t) + y_4 \times (T_2 - t)}{T_3 - T_2}
\]

\[
f = \text{if}(t \leq T_1, f_1(t), \text{if}(t \leq T_2, f_2(t), \text{region } f(t)))
\]

LPQRs were computed using the quantreg package in the statistical software R (R Core Development Team, R Foundation for Statistical Computing, Vienna, Austria).

Fig. 3. Comparison of the alpine steppe with the alpine meadow, and the relationships of trade-offs (AGB and BGB) with environmental factors in these grassland ecosystems. In graph A, the trade-off relationships are the distance between the dots and the 1:1 line. AS and AM represent the alpine steppe and alpine meadow, respectively. Graph B shows a comparison of the aboveground biomass and belowground biomass in AS with AM; the lower case "a" and "b" represent a significant difference at the 0.01 level. Graphs C and D represent the relationships of trade-off with environmental factors in the alpine steppe and alpine meadow, respectively. The colored solid circles represent the significant correlation (P < 0.05). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)
2.3.1. Calculation of aridity index

The index of aridity ($I_{\text{dam}}$) was calculated using the MAT and MAP data with the following formula (Sun et al., 2013b):

$$I_{\text{dam}} = \frac{P}{(T + 10)}$$

where $P$ is the average precipitation (mm) and $T$ is the average temperature (${^\circ}\text{C}$).

2.3.2. Other methods of analysis

Correlation analysis and ANOVA were performed with the SPSS 19.0 package (IBM Company Inc., Armonk, NY, USA).

3. Results

3.1. The trade-off between above- and below-ground biomass in the alpine steppe and alpine meadow

The trade-off of AGB and BGB (Fig. 3A) in the alpine steppe (0.609) was greater than in the alpine meadow (0.062). The relative frequency distribution (Fig. 4A) showed that less than 0.1 accounted for 80% of all trade-offs in the alpine steppe, with the trade-off value varying from 0 to 0.385, with a mean value of $0.058 \pm 0.069$. In the alpine meadow, the trade-off value ranged from 0.0019 to 0.740, and the mean value was $0.188 \pm 0.179$ (Fig. 4B).

AGB and BGB were significantly higher in the alpine meadow than the alpine steppe ($P<0.01$, Fig. 3B). AGB and BGB exhibited large variations between the alpine steppe and alpine meadow, ranging from 9.8 to 347.5 g/m² for AGB and 44.60 to 2784.80 g/m² for BGB in the alpine steppe (Fig. 5A and C). AGB varied from 31.80 to 255.90 g/m² and BGB varied from 82.90 to 2127.20 g/m² in the alpine meadow (Fig. 5B and D). The mean values of AGB for the alpine steppe and alpine meadow were 60.07 g/m² and 111.81 g/m², respectively. The mean values of BGB for the alpine steppe and alpine meadow were 333.83 g/m² and 725.88 g/m², respectively.

3.2. The relationships between trade-off and environmental factors in the alpine steppe and alpine meadow

Pearson's correlation (Fig. 3C and D) indicated that the trade-off between AGB and BGB was not significantly correlated with all of
3.3. The relationships between trade-off and soil properties across alpine grasslands

The response threshold and processes of trade-off were explored across the alpine grassland. We used high percentiles (99th) and the median (50th percentiles) to examine the soil properties that act as constraints on trade-off (Fig. 7).

The 99th percentile of trade-offs showed different changes for all of the soil properties, and the trade-off increased with increasing soil nitrogen content (Fig. 7A), and initially increased slightly and then increased with increasing SOC1 (Fig. 7B). However, the trade-off response to SOC2 and SOC3 showed the same trend, with a gentle increasing process (Fig. 7C and D).

Due to limitations in LPQR methodology, significance of 99th percentile could not be tested (Ruppert et al., 2012). However, regressions along the 50th percentile were calculated for illustrative purposes. All of the trends of the trade-off (50th percentile) were increased slightly and then rapidly increased with the soil nitrogen, SOC1, SOC2 and SOC3 gradients. The inflection points were 5.8 g/m² (Fig. 7A), 8.85 g/m² (Fig. 7B), 15.82 g/m² (Fig. 7C), and 23.63 g/m² (Fig. 7D), respectively.

Linear regression was used to model the relationships between trade-off and soil nitrogen ($R^2 = 0.260, P < 0.0001$), SOC1 ($R^2 = 0.273, P < 0.0001$), SOC2 ($R^2 = 0.283, P < 0.0001$) and SOC3 ($R^2 = 0.280, P < 0.0001$).

4. Discussion

4.1. Comparison of the trade-off in steppes and alpine meadows

Previous studies suggested that root competition is higher at lower nutrient levels (Kiaer et al., 2013). Moreover, the grassland type was the main factor influencing soil nutrients and soil organic carbon, and the soil nitrogen and phosphorous contents were significantly higher in the alpine meadow than alpine steppe.
4.2. Effects of environmental factors on trade-off in alpine steppe and alpine meadow

Environmental factors have insignificant effects on the trade-off of AGB and BGB in the alpine steppe and meadow, respectively (Fig. 3C and D). However, soil nitrogen and organic carbon are related to the trade-off at the regional scale in both the alpine steppe and meadow (Figs. 4 and 6).

The significant difference in AGB, BGB (Fig. 3B) and soil nutrients between the alpine steppe and meadow (Cao et al., 2013) result in significant differences of trade-off between AGB and BGB. Furthermore, the relationships between trade-off and environmental factors were analyzed at different scales; therefore, there is a scale effect.

Plants may trade off as a result of competition shifts within the root and shoot to adapt to stressful environments, such as the alpine grassland (Song et al., 2006). Moreover, the overall trade-off of the root and shoot increased significantly with the nutrient level (Klaer et al., 2013). Our results also indicated that the trade-off slightly increased with increasing soil properties when the soil nitrogen, SOC1, SOC2 and SOC3 were lower than the threshold levels of 5.8 g/m², 8.85 g/m², 15.82 g/m² and 23.63 g/m², respectively (Fig. 7), but markedly increased when the soil properties were higher than this threshold level. Such a threshold for the soil nutrient limitation is a new finding, and our hope is that thresholds will become powerful tools for resolving the difficulties of vegetation restoration and grassland management on the Tibetan Plateau.

Evolution selection based on the trade-off between AGB and BGB causes plants in particular habitats to exhibit certain characteristic allocation patterns (Roa-Fuentes et al., 2012). We propose that the plant allocated more biomass belowground because of the arid and frigid environment in the long run. The precipitation and temperature therefore had insignificant effects on trade-off. Most importantly, plant tradeoffs demonstrate adaptability and a timely response to climate conditions and soil nutrition, respectively. Despite plants allocating more biomass to roots in sites with fewer soil resources (Paz, 2003), the trade-off increased with increasing soil nitrogen and organic carbon in alpine grasslands (Fig. 7).

We hypothesize that the trade-off (AGB and BGB) is dependent on soil properties. A previous study reported that low temperature resulted in restricted microbe activity, thereby reducing the microbial decomposition of soil organic matter, leading to lower soil nutrients (Sun et al., 2013b). This suggests that soil organic matter generally conserves the supply of soil nutrients and that greater soil organic carbon results in more soil nutrients. More soil nutrients result in intensified competition of AGB and BGB. The soil carbon density and soil nitrogen thus showed positive relationships with trade-off because vegetation in alpine regions always suffers from nitrogen/soil nutrient limitation (Wu et al., 2013).

5. Conclusion

In the present study, the trade-off of AGB and BGB significantly increased with increasing soil nitrogen and organic carbon across the alpine grassland. Notably, the trade-off mechanism of biomass is determined not only by environmental conditions but is also driven by plant physiology. However, the mechanism of plant self-regulation must be explored further in future studies, the quantified trade-off is an ideal interpretation for the relationship between AGB and BGB. Therefore, our results have important consequences for the use of trade-offs as an ecological indicator and tool in ecological management and decision-making.

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References


(Cao et al., 2013). Therefore, a higher trade-off was demonstrated in the alpine steppe (Fig. 4). The R/S (ratio of root to shoot) in the alpine steppe was also higher than in alpine meadows, and the variation of AGB and BGB values (Fig. 5) in the present study are consistent with other reports (Wang et al., 2010, 2014; Wu et al., 2013). According to the environmental conditions and plant physiology, the higher R/S in alpine grasslands may be ascribed to the slower root turnover (Yang et al., 2009) and low respiration rates (Wang et al., 2010) and poor soil quality.


