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Variation in carbon, nitrogen and phosphorus partitioning between above- and belowground biomass along a precipitation gradient at Tibetan Plateau

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Abstract: Precipitation is a potential factor that significantly affects plant nutrient pools by influencing biomass sizes and nutrient concentrations. However, few studies have explicitly dissected carbon (C), nitrogen (N) and phosphorus (P) pools between above- and belowground biomass at the community level along a precipitation gradient. We conducted a transect (approx. 1300 km long) study of *Stipa purpurea* community in alpine steppe on the Tibet Plateau of China to test the variation of N pool of aboveground biomass/N pool of belowground biomass (AB/BB N) and P pool of aboveground biomass/P pool of belowground biomass (AB/BB P) along a precipitation gradient. The proportion of aboveground biomass decreased significantly from mesic to drier sites. Along the belt transect, the plant N concentration was relatively stable; thus, AB/BB N increased with moisture due to the major influences by above- and belowground biomass allocation. However, P concentration of aboveground biomass decreased significantly with increasing precipitation and AB/BB P did not vary with aridity because of the offset effect of the P concentration and biomass allocation. Precipitation gradients do decouple the N and P pool of a *S. purpurea* community along a precipitation gradient in alpine steppe. The decreasing of N:P in aboveground biomass in drier regions may indicate much stronger N limitation in more arid area.

Keywords: Biomass allocation; Nutrient concentration; Qinghai-Tibetan Plateau; Alpine steppe; *Stipa purpurea*

Abbreviations:

GSP = growing season precipitation;
TB = Total biomass;
AB = Aboveground biomass;
BB = Belowground biomass;
STP = soil total phosphorus concentration;
AB/BB = Aboveground/belowground biomass;
AB/BB N = N pool of aboveground biomass/N pool of belowground biomass;
AB/BB P = P pool of aboveground biomass/P pool of belowground biomass;
AB/BB C = C pool of aboveground biomass/C pool of belowground biomass

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Introduction

Plant biomass and nutrient allocation definitely link the evolution and adaptive strategies of organisms to the exchange of materials and energies in ecosystems (Kerkhoff et al. 2006). The allocation pattern of carbon (C), nitrogen (N) and phosphorus (P) is of central interest because these three elements play a pivotal role in the soil-plant system and because N and P availability frequently limits plant growth (Sterner and Elser 2002). Knowledge of the distribution pattern of the plant nutrient pool is fundamental to improving our understanding of many ecological processes, such as litter decomposition (Brandt et al. 2007; Posada and Schuur 2011), plant-herbivore correlations (Garibaldi et al. 2010; Marczak et al. 2013) and biogeochemical cycles (Sardans et al. 2012).

Plants have the ability to re-allocate their material between organs in the face of environmental pressure. From a whole plant perspective, when water is the typically scarcest resource, which limits plant growth, a plant would allocate more resources to the root to promote the water absorption capacity. Therefore, from mesic to drier sites, a rising proportion of belowground biomass as well-documented in many studies (Orians and Solbrig 1977; Mooney et al. 1978; Hui and Jackson 2006; Mokany et al. 2006; Fan et al. 2009). Generally, changes in external environmental factors and an organism's stoichiometric homeostasis are coupled factors that determine the variability of plant nutrient concentrations in terrestrial ecosystems (Sterner and Elser 2002; Güsewell et al. 2003; Castle and Neff 2009). Compared with N, plant P is more variable to environmental factors (i.e. temperature and precipitation) (Yu et al. 2010). Generally, with increasing precipitation, leaf P concentrations display a decreasing trend due to the larger amount of soil P leaching in wetter sites (Santiago et al. 2005; Ordoñez et al. 2009; Han et al. 2011). For leaf N, the results differed in study areas and scales. For example, Ordoñez et al. (2009) found that moisture had no effect on leaf N concentration at a global scale, whereas Han et al. (2011) observed a negative correlation between leaf N concentration and precipitation across China. Previous studies have shown that N:P ratio in plant tissues was an indicator of nutrient limitation in a given community (Koerselman and Meuleman 1996; Güsewell 2004). A leaf N:P ratio >16 generally showed P limitation, while the ratio <14 indicated N limitation (Koerselman and Meuleman1996). Notably, all studies mentioned were conducted on a species organ level (leaf, root, stem and reproduction tissue), whereas relatively little work was performed on the community level along a precipitation gradient at large scales.

Plant nutrient pools could be dissected into biomass sizes and nutrient concentrations. Interestingly, aridity may create decreasing biomass and an increasing P concentration in aboveground tissue (Ye et al. 2015). Due to these two opposite effects, AB/BB P most likely exhibits a different tendency from AB/BB along the precipitation gradient. Furthermore, AB/BB P would remain relatively constant on the condition that the two opposite effects are equal (Ordoñez et al. 2009; Ye et al. 2015). If N concentrations of aboveground remain relatively stable with moisture, then AB/BB N would be primarily determined by AB/BB; thus, AB/BB N may show a consistent correlation with AB/BB along the precipitation gradient. The potential decoupling of nutrient pools that shift between above- and belowground could suggest implications for biogeochemical functions, particularly in the processes of plant-herbivore correlations and in the coupling correlation between plants and soil nutrients (Ye et al. 2015). The Tibet Plateau is considered the highest plateau on the earth, with a vast area of alpine steppe that is undisturbed by human activities, which provides an ideal place for exploring plant biomass and nutrient allocation in response to precipitation variability (Luo et al. 2002). Although some previous studies documented that the biomass of alpine grass was significantly influenced by environmental factors, such as soil fertility and precipitation, (Yang et al. 2009a; Yang et al. 2009b; Sun et al. 2013), few attempt has been made to estimate nutrient pools in different components of plants at the community level on the Tibet Plateau. Therefore, the paucity of data limits the accurate assessment of the amount of plant nutrients that is interchanged in biogeochemical cycling in alpine tundra.

We conducted a systematic survey of biomass and nutrient allocation in a *Stipa purpurea* community in 32 sites along a precipitation gradient on the northern Tibetan Plateau of China. Our objectives were (1) to quantify the correlation between nutrient concentrations (C, N and P) and the mean growing season precipitation (GSP) at the community level; (2) to clarify the allocation pattern of C, N and P pools in above- and belowground biomass along a precipitation gradient; and (3) to test whether AB/BB N and AB/BB P show a similar correlation with the GSP. Furthermore, we proposed that biomass sizes and nutrient concentrations would offset each other on the condition that their effect sizes are equal, which would result in a constant AB/BB P with aridity. On the contrary, a larger proportion of biomass and N pool belowground in arid region were speculated.

1 Methods

1.1 Study sites and climate

The study area was located on the northern Tibet Plateau. Most sites were above 4500 m, with annual mean temperature below 0°C and annual mean precipitation below 300 mm. Gale-force winds (wind speed > 17.2 m s^{-1}) occurred on more than 100 days per year in this area (Bai et al. 2005). In this region, *S. purpurea* and *Carex moorcroftii* are the dominant species, and the soils were belonging to alpine steppe soil (Tibet Land Administrative Bureau 1994).

This study was conducted in alpine steppe along a precipitation gradient (approx. 1300 km long) in the Tibet Autonomous Region of China (Figures 1, 2). In total, 32 natural arid and semiarid ecosystem sites were selected, which run from 31.23° - 32.31°N latitude and 80.12° - 91.35°E longitude. The growing season precipitation (GSP) (May - August) ranged from 111 to 272 mm and the mean growing season temperature (GST) (May - August) ranged from 1.23°C to 6.42°C (Appendix 1). Each two adjacent sites were at intervals of approx. 30 km. A Global Positioning System (GPS) recorded the latitude, longitude and altitude of each site. In our study, the data of precipitation was selected because it was a intuitive indicator for reflecting moisture in a certain area, and it was common used in analyses of variation of plant biomass and nutrient pools with climate conditions (Meier and Leuschner 2010; Ye et al. 2015). The

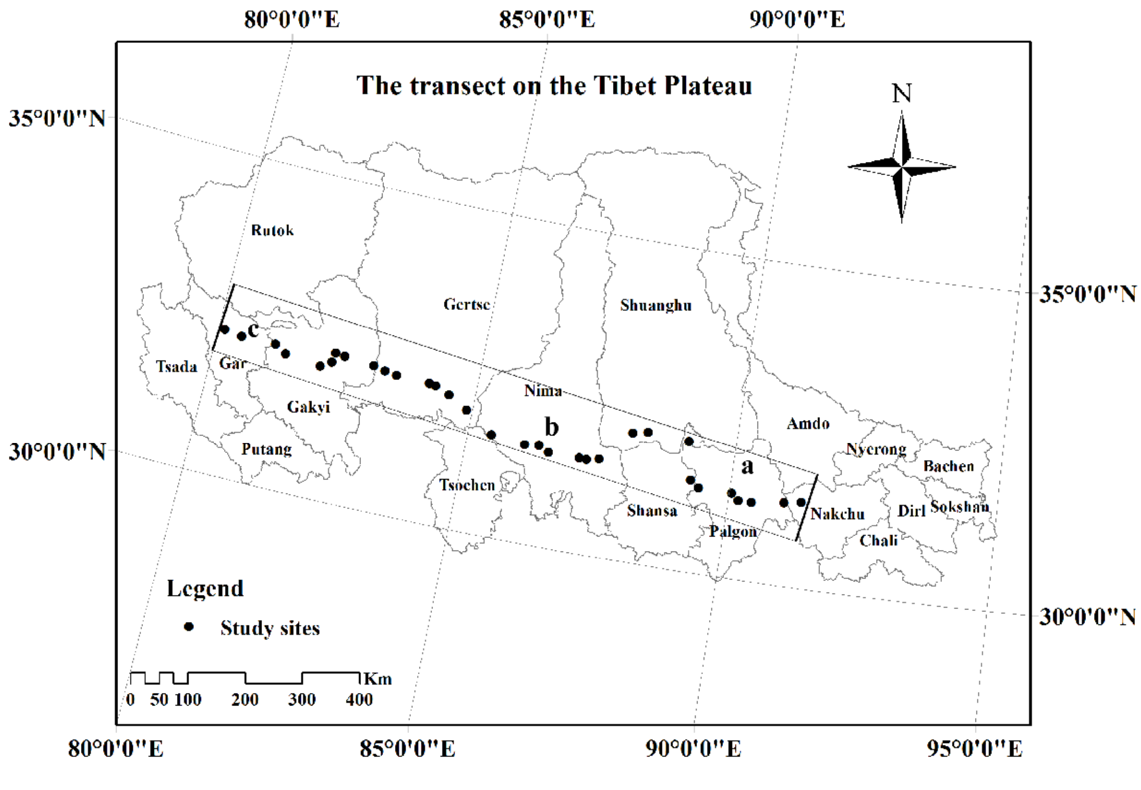

Figure 1 The geographical location of the sample sites along the precipitation gradient.

climate data for the sampling sites were extracted from the World Climate web site (www.worldclimate.com). In all sampling sites, *S. purpurea* was the dominant species, with the largest biomass in the community (Appendix 1). The sampling site was selected on flat terrain far from settlements to minimise the influence of microtopography and livestock.

1.2 Field sampling and chemical analyses

Samples along the precipitation gradient were collected in August 2012, when each site had the peak biomass for the year. Three 0.5 m × 0.5 m quadrats were randomly measured in each site. No woody species was contained in each quadrats. The living aboveground biomass was harvested by scissors. We collected belowground biomass at the depth of 0 - 15 cm, where most of belowground biomass was located (Yan et al. 2005; Li et al. 2011). Live roots were distinguished by their consistency and colour (Vogt and Persson 1991). Then, all the aboveground and belowground samples were carefully cleaned and put into separate envelopes. After being sun-dried in paper envelopes, all the plant samples were brought to the laboratory and oven-dried at 65°C for 72 h to a constant mass to determine the biomass. Then, all the plant samples were ground into fine powder with a plant-sample grinder (TAISITE, High-speed Universal Disintegrator FW80, Tian Jin, China) for chemical analyses. Three soil samples (0-15 cm depth) were collected, thoroughly mixed and air-dried from each site.

We calculated the plant C, N and P concentration of total aboveground and belowground biomass at each quadrat, respectively. The plant samples were digested in $K_2Cr_2O_7$–H_2SO_4 solution using the oil-bath heating and the C concentration was determined by titration (Institute of Soil Academia Sinica 1978). Plant N concentration was determined using the micro-Kjeldahl method (Coombs et al. 1985), and the plant P concentration was analysed using ammonium molybdate method after persulfate oxidation (Kuo 1996), standardized against known reference materials (Yu et al. 2010). Soil total phosphorus concentrations were determined by the sodium bicarbonate alkali digestion method and by

Figure 2 The landscape of the sample sites in (a) Plagon, (b) Nima and c) Gar.

molybdenum antimony colorimetry (Institute of Soil Academia Sinica 1978). We used the mean value of three samples from the same site as the plant biomass and nutrient concentrations and soil total phosphorus concentrations of each site. C, N and P data were expressed on a mass (mg g^{-1}) and N:P (quotient of [N] and [P]) ratio was also expressed on mass basis. C, N and P pools in

Table 1 Correlation coefficients between growing season precipitation (GSP) and each plant trait of the *S. purpurea* community in the transect

Plant traits		N	Spearman's Correlation	Sig.(2-tailed)
Biomass	AB	32	0.773	**0.000**
	BB	32	0.777	**0.000**
	TB	32	0.785	**0.000**
	AB/BB	32	0.418	**0.017**
Carbon	C concentration of aboveground biomass	32	-0.425	**0.015**
	C concentration of belowground biomass	32	0.159	0.386
	C pool of aboveground biomass	32	0.739	**0.000**
	C pool of belowground biomass	32	0.681	**0.000**
	AB/BB C	32	0.278	0.123
Nitrogen	N concentration of aboveground biomass	32	-0.100	0.586
	N concentration of belowground biomass	32	0.048	0.794
	N pool of aboveground biomass	32	0.748	**0.000**
	N pool of belowground biomass	32	0.712	**0.000**
	AB/BB N	32	0.461	**0.008**
Phosphorus	P concentration of aboveground biomass	32	-0.568	**0.001**
	P concentration of belowground biomass	32	-0.331	0.064
	P pool of aboveground biomass	32	0.677	**0.000**
	P pool of belowground biomass	32	0.571	**0.001**
	AB/BB P	32	0.135	0.463
Nutrient ratios	N:P of aboveground biomass	32	0.545	**0.001**
	N:P of belowground biomass	32	0.268	0.138

Note: Bold values indicate $P < 0.05$. AB = aboveground biomass; BB = belowground biomass.

different components were calculated by multiplying the nutrient concentrations and biomass.

1.3 Statistical analyses

Plant C, N and P concentrations and pools were log-transformed to normalise the statistical distribution. The correlation between each plant trait and the GSP was analysed using Spearman's correlation analysis. The correlation between biomass and nutrient was processed by linear regression. Differences of above- and belowground plant traits were processed by independent samples *t*-test. The relationship between AB/BB C, AB/BB N and AB/BB P were processed by linear regression. All statistical analyses were performed using the software SPSS version 16.0 (SPSS Inc., Chicago, IL, USA), and cartograms were plotted using the software SigmaPlot 11.0 (Systat Software, Inc., Richmond, USA).

2 Results

2.1 Plant biomass and its allocation

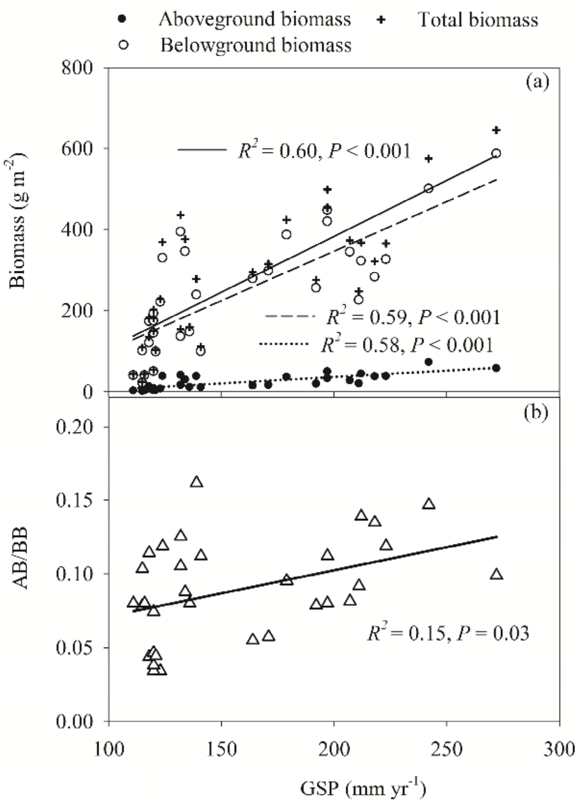

Figure 3 Correlations between GSP, biomass, and AB/BB along a precipitation gradient on the northern Tibetan Plateau. AB = aboveground biomass; BB = belowground biomass.

Aboveground, belowground and total vegetation biomass were positively correlated to the GSP (Table 1, Figure 3 a, P < 0.001). AB/BB (varying from 0.03 to 0.16) was positively associated with the GSP (Table 1, Figure 3b, P < 0.05).

2.2 Plant C, N and P concentrations and N:P ratio

The C concentration of above- and belowground biomass ranged from 281.46 mg g^{-1} to 556.09 mg g^{-1} and 340.50 mg g^{-1} to 512.67 mg g^{-1}, respectively (Table 2). The C concentration of aboveground biomass had a significant positive correlation with the GSP (Table 1, Figure 4a, P < 0.05), whereas the C concentration of belowground biomass was uncorrelated with the GSP (Table 1, Figure 4a, P > 0.05).

The N concentration of aboveground biomass was greater than that in belowground biomass (P < 0.05) (Table 2). The GSP had no significant influence on the N concentration of either aboveground or belowground biomass (Table 1, Figure 4b, P > 0.05).

Aboveground biomass had a higher P concentration than that for belowground biomass (P < 0.05) (Table 2). With increasing GSP, the P concentration appeared to decrease significantly in aboveground biomass (Table 1, Figure 4c, P = 0.001), whereas the P concentration of belowground biomass was uncorrelated with the GSP (Table 1, Figure 4c, P > 0.05).

The N:P ratio of aboveground biomass had a significant positive correlation with the GSP , while the N:P ratio of belowground biomass was uncorrelated with the GSP (Table 1, P < 0.05).

The aboveground biomass was negatively correlated to the C and P concentrations (Figure 5a,

Table 2 Descriptive statistics of plant biomass (g m^{-2}), C concentration(mg g^{-1}), N concentration (mg g^{-1}), P concentration (mg g^{-1}), N:P, C pool (g m^{-2}), N pool (g m^{-2}) and P pool (g m^{-2}) of 32 sample sites

Plant traits		Mean	Range	CV
Biomass	AB	23.16	2.32-73.60	0.80
	BB	242.64	22.40-587.32	0.59
	TB	265.80	24.72-645.44	0.60
	AB/BB	0.09	0.03-0.16	0.38
C concentration	AB	421.84 ^{a}	281.46-556.09	0.13
	BB	433.77 ^{a}	340.50-512.67	0.07
N concentration	AB	18.35 ^{b}	12.29-28.94	0.20
	BB	12.18 ^{a}	8.17-20.73	0.24
P concentration	AB	1.30 ^{b}	0.69-3.09	0.41
	BB	0.52 ^{a}	0.24-0.91	0.27
N:P ratios	AB	15.72 ^{a}	5.60-27.41	0.32
	BB	25.51 ^{b}	10.97-45.13	0.34
C pool	AB	9.30 ^{a}	1.02-31.99	0.80
	BB	106.04 ^{b}	10.12-258.06	0.61
N pool	AB	0.40 ^{a}	0.03-1.19	0.76
	BB	2.81 ^{b}	0.27-5.93	0.57
P pool	AB	0.024 ^{a}	0.004-0.076	0.67
	BB	0.125 ^{b}	0.011-0.385	0.69

Notes: Different superscript letters (a, b) indicate significant differences (adjusted P < 0.05) in plant traits between above- and belowground biomass. AB = aboveground biomass; BB = belowground biomass.

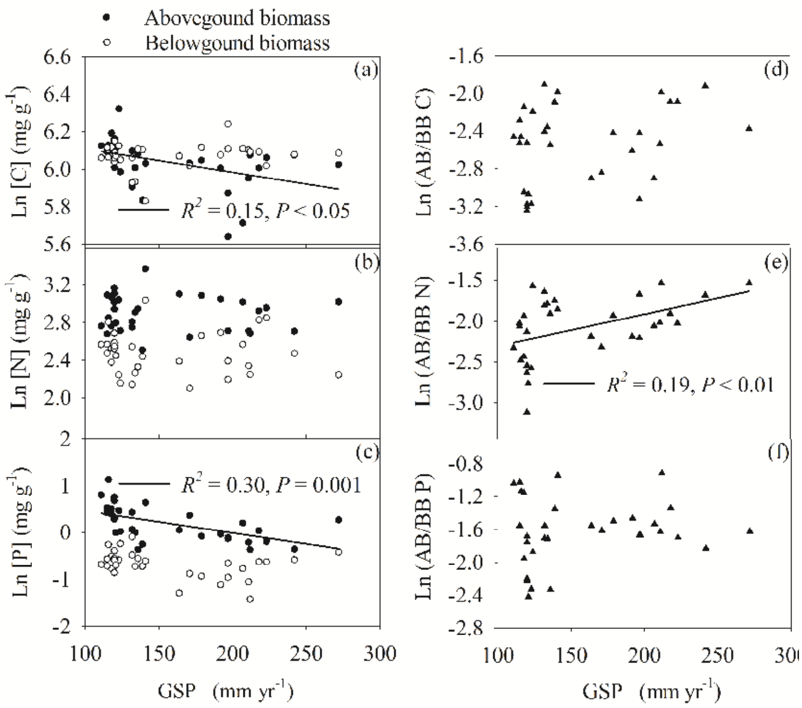

Figure 4 Correlations between growing season precipitation (GSP), C, N and P concentrations and AB/BB C, AB/BB N and AB/BB P along a precipitation gradient on the northern Tibetan Plateau. AB = aboveground biomass; BB = belowground biomass.

$P < 0.05$). However, the N concentration of aboveground biomass was uncorrelated with the aboveground biomass (Figure 5a, $P > 0.05$). The belowground biomass was negatively correlated to the N concentrations (Figure 5b, $P < 0.05$), whereas the C and P concentration of belowground biomass were uncorrelated with the belowground biomass (Figure 5b, $P > 0.05$).

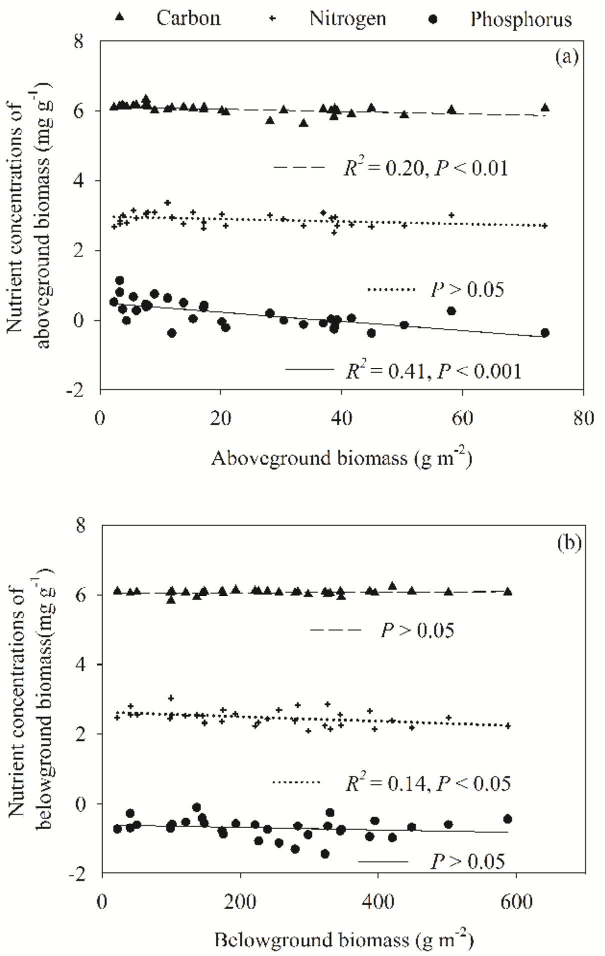

Figure 5 Correlations between plant biomass and nutrient concentrations on the northern Tibetan Plateau. The natural logarithm transformation was used to express nutrient concentrations in the figure.

2.3 C, N and P pools of above- and belowground biomass

C, N and P pools of aboveground, belowground and total vegetation biomass were positively correlated with the GSP (Table 1). The GSP had no effect on AB/BB C (Table 1, Figure 4d, $P > 0.05$). A positive correlation was detected between GSP and AB/BB N, whereas the GSP had no effect on AB/BB P (Table 1, Figure 4e, f). AB/BB C, AB/BB N and AB/BB P were positively related to each other (Figure 6, $P < 0.05$).

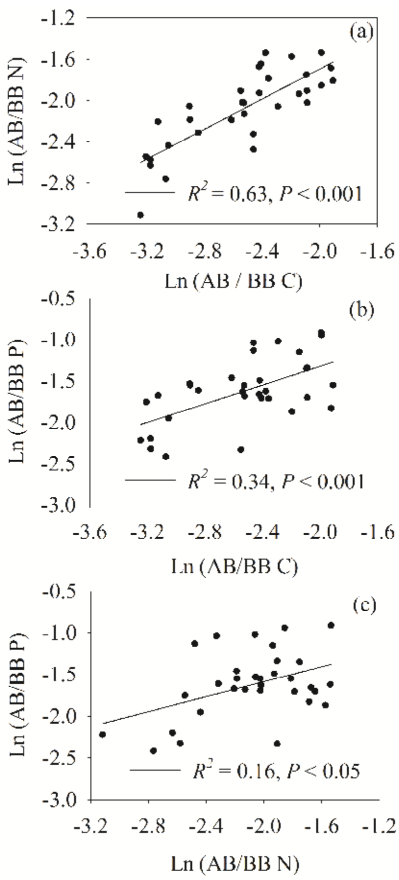

Figure 6 Correlations between the AB/BB C, AB/BB N and AB/BB P on the northern Tibetan Plateau. AB = aboveground biomass; BB = belowground biomass.

3 Discussion

Plant biomass and its elements concentrations are important components for evaluating nutrient pool sizes of terrestrial ecosystems (i.e., carbon stocks) (Mokany et al. 2006). Changes in C:N:P stoichiometry and biomass that are associated with C, N, and P pools between roots and shoots along a precipitation gradient are likely to have great impacts on the structure and function of a terrestrial ecosystem (Jefferies and Maron 1997; Gilliam 2006; Clark and Tilman 2008).

Aboveground, belowground and total biomass increased significantly with rising moisture (Figure

3a). This trend supports the existing result that moisture availability is the important environmental factor that influences plant biomass in dry alpine steppe of the Tibet Plateau (Sun et al. 2013). More biomass was allocated belowground in alpine steppe with a decreasing moisture gradient, although this relationship had a great dispersion (Figure 3b), which is consistent with other studies that have been conducted on arid and semi-arid lands (Hui and Jackson 2006; Mokany et al. 2006; Snyman 2009). The N and P concentrations of belowground biomass were lower than that of aboveground biomass in this *S. purpurea* community (Table 2) because leaves are the most important photosynthetic organs, which require high nutrient concentrations to improve the capacity of photosynthesis (Kerkhoff et al. 2006).

Although few attempts have been made to examine the variation in plant nutrient concentrations on the community level along a precipitation gradient, we could learn from previous studies of plant leaves. The phenomenon that P concentrations in leaves were greater in dry versus wet sites was found across all plant functional types in China (Han et al. 2011), in lowland tropical forests in Central Panama (Santiago et al. 2005), and in a global meta-analysis (Ordoñez et al. 2009). However, N concentrations in leaves have a high degree of uncertainty with precipitation due to the differences in study areas and scales. For example, Han et al. (2011) found a negative correlation between leaf N and precipitation, but the correlation coefficient (r) between precipitation and leaf N (r = 0.06, P = 0.005) was much lower than leaf P (r = 0.35, P < 0.001). No significant correlation was detected between the leaf N concentration and the degree of wetness in many areas (Santiago et al. 2005; Ordoñez et al. 2009; Wu et al. 2012). We found that the P concentration of aboveground biomass decreased with increasing precipitation, whereas the N concentration was unrelated to moisture on the community level. Generally, the homeostatic regulation coefficient of P was lower than that of N (Sterner and Elser 2002); thus, P had a weaker stoichiometric homeostasis and a more variable concentration in plant tissue than N (Yu et al. 2010). Moreover, the stronger influence of precipitation on the P concentration of aboveground biomass could be explained by the notion that P cycling is vulnerable to climate variability. Climate condition had an effect on soil N by means of influencing organic matter decomposition. Unlike soil N, however, P in soil is a deuterogenic element that was derived from rock weathering and its dispersal ability in soil solution is relatively low (Lambers et al. 1998; Aerts and Chapin III 2000). Therefore, the P concentration in plant tissue was strongly affected by shifts in precipitation, which were associated with the mutability of soil P (Figure 5; Figure 7). Furthermore, with the precipitation increased, the aboveground biomass was also increased. The increased aboveground biomass may dilute the P concentration (Figure 5). To some extent, P concentrations of aboveground biomass at the community level showed a similar variation trend with other studies that were conducted at the leaf level (Ordoñez et al. 2009; Wu et al. 2012).

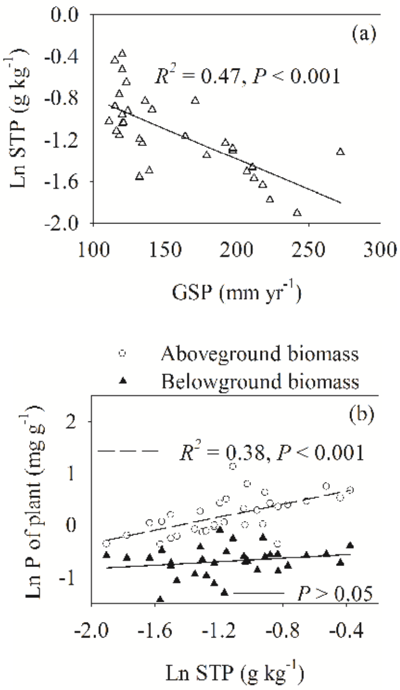

Figure 7 Correlations between soil total phosphorus concentration (STP), growing season precipitation (GSP), and plant P concentrations.

The plant tissue was complicated at the community level and with multiple organs (leaves, roots, stems and reproductive organs), which added a slightly larger degree of uncertainty to the evaluation of the effect of precipitation on the N concentration of aboveground biomass. For example, the stem is a structural organ with a low

N concentration, whereas the leaf is the photosynthetic tissue with a high N concentration (Kerkhoff et al. 2006). Therefore, our result was inconsistent with a study that was conducted on the Inner Mongolia steppe at even the micro-scale (leaf level), which found that the proportion of N pools of above- and belowground biomass remained relatively constant (Ye et al. 2015).

To explore aboveground nutrient pools/belowground nutrient pools, we integrated both biomass allocation and its nutrient concentrations. The P concentration of aboveground biomass decreased significantly with moisture, whereas the proportion of aboveground biomass increased significantly with precipitation. For the pool size of P, these two components appeared to change in opposite directions, and we expected that changes in AB/BB P might be the result of the synthetical influence of the relative effect sizes of the two aspects. If their effect sizes were equal, then the two trends would offset each other, which would result in a constant AB/BB P along an aridity gradient. Similar to our null hypothesis above, no significant correlation between AB/BB P and precipitation was observed in our study (Figure 4f). A similar correlation was also found in AB/BB C (Figure 4d). However, N concentrations above- and belowground remained stable with increasing GSP; therefore, the influence of biomass played a decisive role in controlling the variation trend of AB/BB N with GSP. N:P ratio is a useful indictor for plant nutrient limitation in most terrestrial ecosystems (Koerselman and Meuleman 1996; Güsewell 2004). In present study, the decreasing of N:P in aboveground biomass in drier regions may indicate much stronger N limitation in more arid area.

The *S. purpurea* community on the Tibetan Plateau has an exceptionally low AB/BB ratio (range of AB/BB: 0.03 - 0.16). Compared with other alpine areas, such as the Rocky Mountains at an altitude of 3000 m (range of AB/BB: 1.25 - 2.00) (Scott and Billings 1964) and Austrian Central Alps at an altitude from 2600 - 3200 m (range of AB/BB: 0.30 - 4.50) (Körner and Renhardt 1987), the relatively low value of AB/BB in our study indicated that herbaceous plants in this harsh ecological environment invested more photosynthates in the root system, possibly due to the following two reasons: firstly, the shortage in water and frequent gale-force winds (wind speed > 17.2 m s^{-1}) function together to cause extremely low soil moisture in the northern Tibetan Plateau (Bai et al. 2005). A large proportion of belowground biomass could help the plant to absorb and to store more water for prolonged water-limiting conditions. Secondly, such a pattern may be associated with the survival strategy of species under a high grazing pressure (particularly wild animals, such as *Pantholops hodgsonii*) because most dominant species (*S. purpurea* and *C. moorcroftii*) in the northern Tibetan Plateau were perennial clone plants and their roots were supposed to be the vital storage organ of carbohydrates to support plant growth and reproduction.

Based on the former research on a single plant or species, it is hard to estimate how much of the nutrient pools (leaves, roots, stems and reproductive organs) are involved in biogeochemical cycles at a larger scale (i.e., community). From mesic towards dry regions, we proposed some possible ecological effects of a larger proportion of biomass and N pool allocation belowground at the community level. For example, many shoots are eaten by herbivorous animals every year in dry sites, which reduce the amount of litter that are restituted to soil. However, an increasing proportion of belowground N pool with increasing aridity could alleviate the shortage of organic matter that is returned into soil at low precipitation regions. Moreover, root biomass could improve soil physical properties, such as aggregate and structural stability (Li et al. 1992; Ghidey and Alberts 1997). As a result, drier sites have similar soil total N concentrations with the mesic sites along the precipitation gradient in our study area (our unpublished data). A larger proportion of belowground biomass and N pool could improve the soil quality in arid sites.

4 Conclusions

Precipitation is an important factor that affects plant biomass and nutrient allocation. From mesic to drier sites, plants allocated a rising proportion of belowground biomass. N concentrations remained relatively stable with changes in water availability, whereas P concentrations of aboveground biomass exhibited a negative correlation with GSP. Thus, a shift to a greater proportion of belowground N pool size and consistent AB/BB P in more arid sites were found in our study. It appears that precipitation decouples the N and P pools of the *S. purpurea* community along the moisture gradient in alpine steppe.

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