

# Effects of soil fertility on the N:P stoichiometry of herbaceous plants on a nutrient-limited alpine steppe on the northern Tibetan Plateau

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## Abstract

**Background and aims** Plant nutrient concentrations and their correlations with soil nutrient conditions are regarded as effective tools for exploring plant adaptation and resource utilisation strategies in a severe environment. However, few comparative studies have addressed the nutrient traits of different organs along natural fertility gradients.

**Methods** We quantified the nitrogen (N) and phosphorus (P) concentrations and N:P ratios in roots and leaves of 139 plant samples from 14 species on a nutrient-limited alpine steppe on the Tibetan Plateau. Next, we explored the correlation between root and leaf nutrient

traits of different plant functional groups as well as soil fertility.

**Results** Soil P had a significant impact on plant N:P stoichiometry, whereas soil N had little effect on plant nutrient traits. Leaf P and the N:P ratio of legumes exhibited more sensitive responses to soil P than roots. Among non-legume species, however, root N and P concentrations of *Stipa purpurea* and *Orinus thoroldii* (grasses) were more sensitive than N and P concentrations of leaves to variations in soil P availability. In contrast, leaf P and the N:P ratio of *Leontopodium nanum*, *Potentilla bifurca* and ect. (forbs) exhibited more sensitive responses to soil P than roots. Both root and leaf nutrient traits of *Carex moorcroftii* (sedges) were uncorrelated with soil fertility. The N:P stoichiometry of different functional groups showed disparate responses to soil P, and even the roots and leaves of the same functional group exhibited inconsistent correlations with soil nutrients.

**Conclusions** The distinct response patterns to soil nutrient conditions across functional groups helped elucidate the diversification of alpine plant adaptations to nutrient-poor environments and offered insights into quantifying the trade-off of different organs in co-existing species between resource use/conservation “strategies” and soil fertility.

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## Introduction

Plant nutrient concentrations and their correlation with soil nutrient conditions are regarded as useful tools for exploring plant adaptation and resource utilisation strategies in a severe environment (Ordoñez et al. 2009; He et al. 2010; Geng et al. 2011). Acquisitive species tend to have high resource acquisition, high tissue nutrient concentrations, specific leaf area, net photosynthetic rate and specific root length, whereas conservative species have high resource conservation, low tissue nutrient concentrations, high nutrient resorption efficiency and high stress tolerance (Grime 1974; Díaz et al. 2004; Sterck et al. 2006, 2011). Ordoñez et al. (2009) found that soil P had a great influence on leaf nitrogen and phosphorus concentrations, while soil N was only positively correlated with leaf nitrogen concentrations from a global dataset. However, no significant relationship was observed between soil nitrogen and leaf nitrogen concentrations across Chinese grassland (He et al. 2010). Although correlations between plant functional traits and soil nutrients have been studied extensively (Chapin III 1980; Aerts and Chapin 1999; Ordoñez et al. 2009; Geng et al. 2011), studies in cold and arid areas are lacking.

Recent studies have assumed that dominant and wide-ranging species always have a stronger homeostasis or weak relationship in nutrient concentrations than non-dominant and narrow-ranging species in response to environmental factors (e.g., soil fertility) (Yu et al. 2010; Geng et al. 2011). However, these field studies have primarily focused on leaf nutrient traits. Until recently, relatively little effort has been dedicated to detecting root nutrient concentrations along natural fertility gradients on a large scale. Moreover, few attempts have been made to examine whether nutrients in different organs of the same plant would show a consistent response to soil fertility in a nutrient-limited environment.

The Tibetan Plateau is considered the “third pole” of the world, which is characterised by low temperature, low precipitation, strong solar radiation, large amount of gale-force winds and extensive permafrost (Fig. 1). Plants on the Tibetan Plateau grow in an extreme environment in nutrient-deficient conditions and are expected to be sensitive to climate change, including global

warming and changes in precipitation and N deposition (He et al. 2006; Jiang et al. 2012). Quantifying nutrient utilisation strategies of different species in this area is important for understanding plant adaptation to a harsh environment and future climate changes. Because of the cold and harsh conditions, the species diversity is very low in this alpine steppe. We conducted a systematic survey of the plant N:P stoichiometry of 139 plant samples from 14 species and seven families that covered the common species in the nutrient-limited alpine steppe of the northern Tibetan Plateau of China. We divided the 14 species into two functional groups, which included legumes and non-legumes (three sub-classes groups: grasses, sedges and forbs) (Mamolos et al. 2005; Song et al. 2012) (Table 1). Our objectives were (1) to quantify the root and leaf N and P concentrations and N:P ratios between legumes and non-legumes in the same community and (2) to clarify the correlation between the root and leaf N:P stoichiometry of the different functional groups (sub-classes groups) and soil total nitrogen (STN), soil available nitrogen (SAN), soil total phosphorus (STP) and soil available phosphorus (SAP) in the alpine tundra.

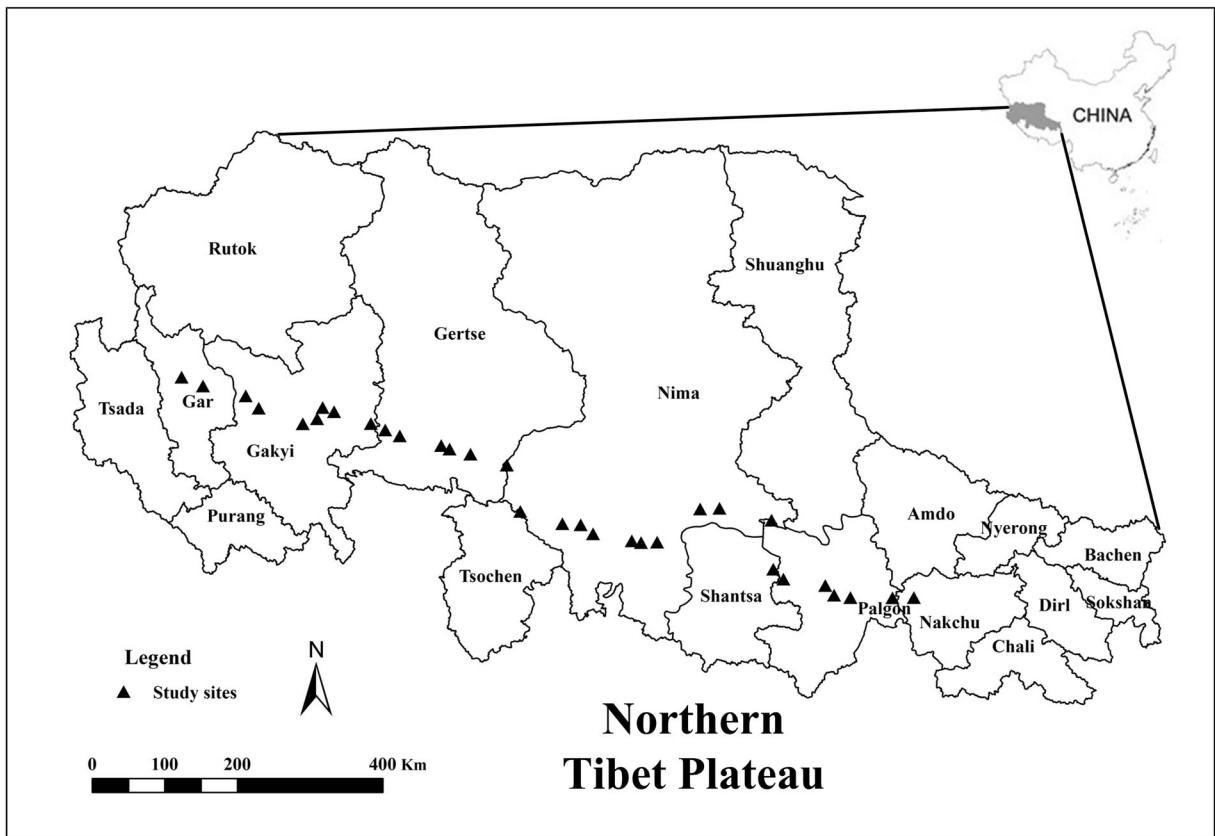
## Materials and methods

### Site descriptions

The study area was in a nutrient-limited alpine steppe, where *Stipa purpurea* and *Carex moorcroftii* were the most dominant and widely distributed species. Thirty-two sites were selected, extending from longitude 80.12 to 91.35 °E (approx. 1300 km long from east to west of the Tibetan Plateau) and latitude 31.23 to 32.31 °N, along with altitudes ranging from 4398 to 5561 m (Fig. 1). The mean annual temperature (MAT) and mean annual precipitation (MAP) ranged from −5.93 to 0.29 °C and 181 to 359 mm, respectively (data obtained from the World Climate web site, [www.worldclimate.com](http://www.worldclimate.com)).

### Plant and soil sampling

Field measurements were conducted in August 2012. To



**Fig. 1** Location of the study area and sampling sites on the northern Tibetan Plateau of China

minimise the influences of microtopography and grazing disturbances, all samples were selected on flat terrain and far from human habitats. The dominant species were selected and sampled at each of the 32 sites. However, in some species-poor sites, fewer species (as few as one) were collected (Appendix Table 2). In each site, a 10 \* 10 m quadrat was set. The soil core (15 cm in length, 15 cm in width, and 30 cm in depth), which contained a dominant species, was gathered by a spade in the quadrat. To maintain the integrity of the plant, we only collected a dominant individual plant from one soil core. Ten to twenty individuals of each species in each quadrat were collected. Then, the root and leaf samples from the same species were carefully cleaned and sundried in a paper envelope. In all, we investigated 139 plant samples for 14 species over a total of 32 sites (Table 1; Appendix Table 2).

Three soil samples (0–15 cm in depth) were collected from each site. Each sample was thoroughly mixed and air-dried. Roots in the soil were removed by hand and sieved through a 100-mesh sieve. Then, the soil was divided into four subsamples for analysing STN, SAN, STP and SAP.

#### Sample analysis

All plant samples were divided into roots and leaves (139 \* root and 139 \* leaf samples), oven-dried at 60 °C to a constant mass and ground into a fine powder in the laboratory. Soil and plant total N concentrations were analysed using the micro-Kjeldahl digestion method (Coombs et al. 1985). Plant P concentrations were analysed using the ammonium molybdate method (Institute of Soil

**Table 1** N and P concentrations and N:P ratios in the roots and leaves of 14 species on the alpine steppe of the Tibetan Plateau

F G	Species	n	Root			Leaf			
			N (mg g <sup>-1</sup> )	P (mg g <sup>-1</sup> )	N:P	N(mg g <sup>-1</sup> )	P (mg g <sup>-1</sup> )	N:P	
Legumes	<i>Oxytropis glacialis</i>	16	20.16(0.79)	0.70(0.05)	31.24(2.31)	34.40(1.57)	1.74(0.11)	20.54(1.16)	
	<i>Oxytropis microphylla</i>	13	20.00(0.81)	0.66(0.03)	30.80(1.25)	32.70(0.99)	1.77(0.16)	20.01(1.63)	
	<i>Oxytropis serioopetala</i>	6	19.42(0.74)	0.78(0.13)	27.70(3.41)	32.84(0.95)	1.88(0.22)	18.74(2.38)	
Non- Legumes	Grasses	<i>Stipa purpurea</i>	32	10.92(0.44)	0.43(0.02)	26.55(1.22)	19.26(0.53)	1.07(0.06)	19.38(0.96)
		<i>Orinus thoroldii</i>	4	11.00(1.48)	0.57(0.08)	20.31(3.11)	19.40(3.03)	1.27(0.18)	15.45(1.42)
	Sedges	<i>Carex moorcroftii</i>	16	8.09(0.44)	0.57(0.05)	16.06(0.89)	18.51(0.84)	0.90(0.04)	21.16(1.25)
	Forbs	<i>Leontopodium nanum</i>	15	11.13(0.37)	0.47(0.02)	24.64(1.39)	17.78(1.00)	1.26(0.10)	14.68(0.80)
		<i>Potentilla bifurca</i>	17	11.44(0.39)	0.71(0.05)	17.46(1.19)	21.70(0.65)	1.62(0.11)	14.28(0.91)
		<i>Youngia simulatrix</i>	3	10.80(1.34)	0.71(0.05)	15.19(0.92)	18.83(0.91)	1.13(0.03)	16.77(1.28)
		<i>Incarvillea compacta</i>	4	10.98(0.32)	0.97(0.07)	11.54(0.90)	20.10(1.54)	1.35(0.10)	15.25(1.96)
		<i>Lagotis brachystachya</i>	3	11.93(0.56)	0.71(0.10)	17.34(2.47)	21.73(1.82)	1.57(0.14)	13.94(1.01)
		<i>Artemisia wellbyi</i>	5	12.07(0.33)	0.88(0.10)	14.68(2.11)	24.47(2.43)	1.78(0.22)	14.52(2.07)
		<i>Artemisia younghusbandii</i>	1	11.06(–)	0.52(–)	21.36(–)	15.06(–)	1.41(–)	10.66(–)
		<i>Saussurea stoliczkae</i>	4	11.87(0.78)	0.53(0.07)	23.36(2.59)	21.94(0.29)	1.39(0.06)	15.87(0.86)

Values between brackets are the standard error of the mean

FG Functional groups

Academia Sinica 1978). Soil total P concentrations were determined using the sodium bicarbonate alkali digestion method and molybdenum antimony colorimetry (Kuo 1996). The soil available N concentration was analysed using the alkaline hydrolysis diffusion method (Institute of Soil Academia Sinica 1978). The available soil P concentration was extracted by sodium bicarbonate and determined using the molybdenum blue method (Institute of Soil Academia Sinica 1978). The nutrient concentrations in plant and soil samples were expressed on a mass basis. We used the mean value of three samples from the same site for the STN, SAN, STP and SAP concentrations of each site.

#### Statistical analyses

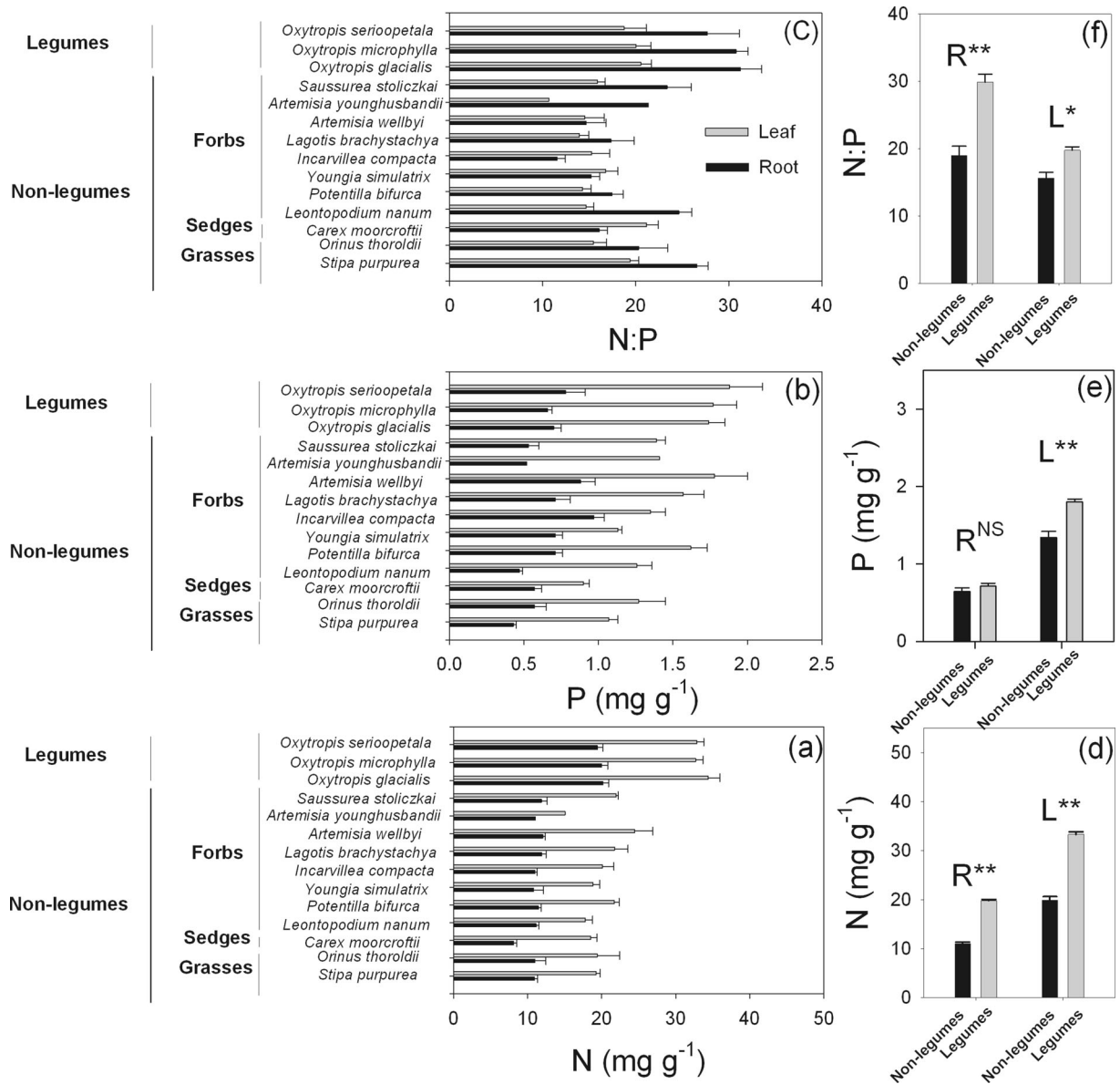
Differences in the root and leaf N and P concentrations and N:P ratios between legumes and non-legumes species was processed using Mann–Whitney U-test. The correlation between plant nutrient traits (N and P concentrations and N:P ratios) and soil fertility (STN, SAN, STP and SAP) was analysed using simple regression

analyses. Plant nutrient traits (N, P and N:P ratios) and soil fertility (STN, SAN, STP and SAP) were log-transformed to normalise the statistical distribution where necessary. All statistical analyses were performed using the SPSS version 16.0 software (SPSS Inc., Chicago, IL, USA), and cartograms were plotted using the SigmaPlot 11.0 software (Systat Software, Inc., Richmond, USA).

#### Results

Patterns of the N and P concentrations and N:P ratios in root and leaf between different plant functional groups

Leaf nitrogen and phosphorus concentrations were nearly double that of root both in legumes and non-legume species (Fig. 2). Mean value of root N and P concentrations of legumes were 19.86 mg g<sup>-1</sup> and 0.71 mg g<sup>-1</sup>. Non-legumes had lower root N concentrations than legumes (mean value for root N: 11.03 mg g<sup>-1</sup>) ( $P < 0.05$ ) (Fig. 2). Root N:P of legumes was higher than non-legumes ( $P < 0.05$ ). The mean value were



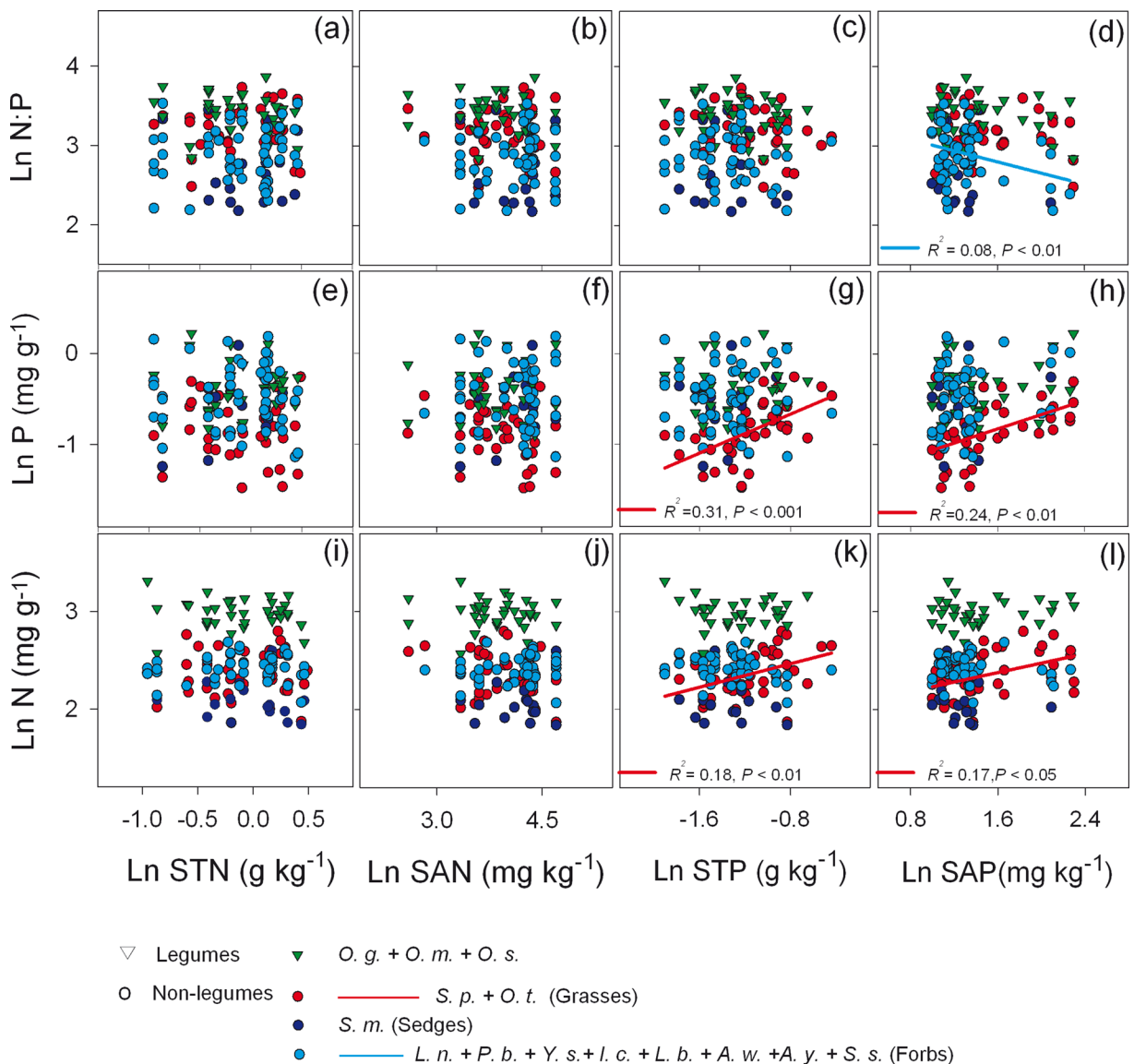
**Fig. 2** N and P concentrations and N:P ratios in the roots and leaves of 14 species and different functional groups on the alpine steppe of the Tibetan Plateau. Legumes included *Oxytropis glacialis*, *Oxytropis microphylla* and *Oxytropis serioopetala*. Non-legumes species included *Stipa purpurea*, *Orinus thoroldii*, *Carex moorcroftii*, *Leontopodium nanum*, *Potentilla bifurca*,

*Youngia simulatrix*, *Incarvillea compacta*, *Lagotis brachystachya*, *Artemisia wellbyi*, *Artemisia younghusbandii* and *Saussurea stoliczkai*. \*, \*\* indicated significant differences in root (R) and leaf (L) between legumes and non-legumes species at 0.1 and 0.05. NS indicated no significant differences between legumes and non-legumes species

33.31 mg g<sup>-1</sup>, 1.80 mg g<sup>-1</sup> and 19.76 for leaf N and P concentrations and N:P ratios of legumes, respectively (Table 1). Legumes had higher leaf N and P concentrations than non-legumes ( $P < 0.05$ ) (Fig. 2).

The correlations between the N and P concentrations of different plant functional groups and soil fertility

For legumes and non-legumes species, both root and leaf N and P concentrations, as well as the

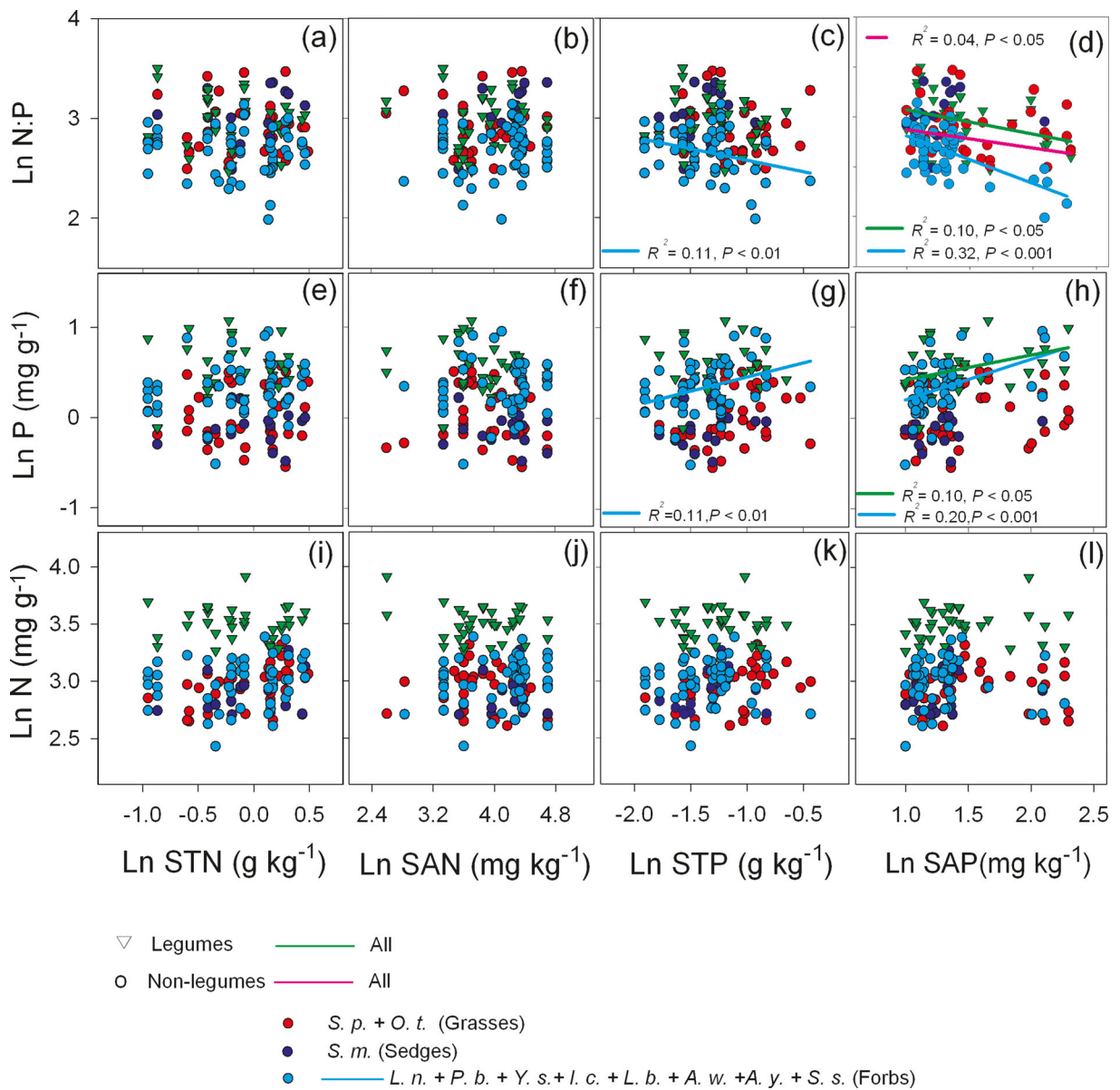


**Fig. 3** Correlations between nutrient traits (N, P and N:P ratios) of the root and soil nutrients (STN, SAN, STP and SAP) across the different functional groups. Legumes included *Oxytropis glacialis* (*O.g.*), *Oxytropis microphylla* (*O.m.*) and *Oxytropis serioopetala* (*O.s.*). Non-legumes species included three sub-classes groups. *Stipa purpurea* (*S.p.*) and *Orinus thoroldii* (*O.t.*) belonged to

grasses; *Carex moorcroftii* (*C.m.*) belonged to sedges; *Leontopodium nanum* (*L.n.*), *Potentilla bifurca* (*P.b.*), *Youngia simulatrix* (*Y.s.*), *Incarvillea compacta* (*I.c.*), *Lagotis brachystachya* (*L. b.*), *Artemisia wellbyi* (*A.w.*), *Artemisia younghusbandii* (*A. y.*) and *Saussurea stoliczkaei* (*S.s.*) belonged to forbs

N:P ratios, were uncorrelated with STN and SAN (Figs. 3 and 4,  $P > 0.05$ ). Positive linear correlations were detected between the leaf P concentrations of legumes and SAP (Fig. 4h,  $P < 0.05$ ), whereas the N:P ratios were negatively associated

with SAP (Fig. 4d,  $P < 0.05$ ). Weakly positive correlation was detected between the leaf N:P concentrations of non-legumes and SAP (Fig. 4d,  $P < 0.05$ ). Among non-legume species, however, the root N and P concentrations of *Stipa purpurea*



**Fig. 4** Correlations between the nutrient traits (N, P and N:P ratios) of leaf and soil nutrients (STN, SAN, STP and SAP) across the different functional groups. Legumes included *Oxytropis glacialis* (*O.g.*), *Oxytropis microphylla* (*O.m.*) and *Oxytropis serioopetala* (*O.s.*). Non-legumes species included three subclasses groups. *Stipa purpurea* (*S.p.*) and *Orinus thoroldii* (*O.t.*)

belonged to grasses; *Carex moorcroftii* (*C.m.*) belonged to sedges; *Leontopodium nanum* (*L.n.*), *Potentilla bifurca* (*P.b.*), *Youngia simulatrix* (*Y.s.*), *Incarvillea compacta* (*I.c.*), *Lagotis brachystachya* (*L. b.*), *Artemisia wellbyi* (*A.w.*), *Artemisia younghusbandii* (*A. y.*) and *Saussurea stoliczkai* (*S.s.*) belonged to forbs

and *Orinus thoroldii* (grasses) were positively correlated with STP and SAP (Fig. 3g, h, k, l;  $P < 0.01$  for root N with STP;  $P < 0.05$  for root N with SAP;  $P < 0.001$  for root P with STP;  $P < 0.01$  for root P with SAP). The leaf P concentrations of

*Leontopodium nanum*, *Potentilla bifurca* and ect. (forbs) were positively correlated with STP and SAP (Fig. 4g, h,  $P < 0.01$  for leaf P with STP;  $P < 0.001$  for leaf P with SAP). The leaf N:P of forbs was negatively associated with STP and SAP

(Fig. 4c, d,  $P < 0.01$  for leaf N:P with STP;  $P < 0.001$  for leaf N:P with SAP). All of the nutrient traits of *Carex moorcroftii* (sedges) were uncorrelated with soil fertility ( $P > 0.05$ ) (Figs. 3 and 4).

## Discussion

Patterns of the N and P concentrations and N:P ratios in roots and leaves between different functional groups

Legumes have abundant nitrogen-fixing bacteria, which help the plant to use atmospheric- $N_2$  for growth and enable the plants to adapt to barren soil (Vitousek et al. 2002). Thus, leguminous plants always have higher N concentrations than other functional groups. In the present study, legumes also have higher leaf P concentrations; this result was inconsistent with a previous study that demonstrated that there was no significant difference in plant P concentrations between legumes and non-legumes across Chinese grasslands (He et al. 2008). This result was most likely due to the ability of leguminous species to trigger some special physiological mechanisms related to improving their absorptive capacity of P in poor quality soil on alpine steppes to prevent nutritional imbalances (Yadav and Tarafdar 2001; Houlton et al. 2008). Olde Venterink (2011) found that legumes had higher root phosphomonoesterase activity (improving absorptive capacity for P) than non-legumes. The result could help explain why the leguminosae species showed relatively high P concentrations in our study.

The root N and P concentrations were positively correlated with the leaf N and P concentrations across all species (Hong et al. 2014). The consistency of the root-leaf N and P relationship was consistent with a previous meta-analysis (Kerkhoff et al. 2006) and indicated that this general nutrient allocation rule also applies to alpine plants (Geng et al. 2014). In the present study, we took insufficient account of the root length, mycorrhizal hyphal length and root longevity, which are closely linked with the plant N:P stoichiometry (Olde Venterink and Güsewell 2010). These important

morphological and physiological ecological characteristics will be considered in our future research.

Influence of soil nutrients on the N and P concentration and N:P ratios among different functional groups

Soil N concentrations have almost no significant effects on plant nutrient traits, whereas soil P concentrations have varying degrees of impact on the plant N and P concentrations and N:P ratios across all functional groups. This stronger influence of soil P on plant nutrients was consistent with previous studies (Elser et al. 2000; Ordoñez et al. 2009; Fujita et al. 2010; Chen et al. 2011). Plants, especially legumes, not only make use of soil available N but also N in the atmosphere with the help of multiple nitrogen-fixing bacteria (Fitter et al. 1998; Aerts and Chapin 1999). In contrast, the soil P for absorbed by plants was primarily derived from rock weathering, and its diffusivity was significantly lower. Therefore, the soil available P supply was strongly influenced by climate variation, and it consequently affects plant P concentrations (Chen et al. 2011). With multiple-channels for obtaining N, plants obtain more stable N than P.

Interestingly, the N:P stoichiometry of different plant functional groups (sub-classes groups) showed disparate responses to soil P, and even organs (root and leaf) of the same functional group appeared to exhibit inconsistent correlations with soil nutrient conditions. Although the N:P stoichiometry represents part of a multivariate aspect of a phenotype that is influenced by complicated factors (biotic and abiotic factors), this difference could provide valuable means and implicit information for linking the perspective of ecology and evolution on plant organs and environmental factors (Elser et al. 2000; Kay et al. 2005). In addition, this pattern might reflect different phenological times between leaf and root growth; this pattern may also reflect a trade-off between resource allocation and investment, which is related to ecological success in a nutrient-limited steppe (Yu et al. 2011). Because roots belong to the “structural” component and leaves belong to the “metabolic” component, the nutrient concentrations of the two organs may be affected by different regulatory mechanisms. For instance, the plant size within species had a marked



impact on the nutrient concentration of roots with little or no effect observed among leaves (Kerkhoff et al. 2006).

The leaf P and N:P ratios of legumes displayed more sensitive responses to SAP. The reduced leaf phenotypic variation of legumes may be an important factor, which increases the susceptibility to external environmental variability (Walck et al. 1999; Lloyd et al. 2002). Because of the weak leaf internal self-regulation of multifactorial physiological traits of narrow-ranging, distributed and accompanying species, these plants were more sensitive to environmental variables, particularly soil fertility (Futuyma and Moreno 1988; Sultan et al. 1998; Geng et al. 2011).

Among non-legume species, the root N and P concentrations of *Stipa purpurea* and *Orinus thoroldii* (grasses) were positively correlated with soil P in the present study. The increase in the root N concentration with increasing soil P may be because an improvement in the P supply by a different pathway of N-fixation would promote plant N uptake (Ekblad and Huss-Danell 1995; Iversen et al. 2010). Under low temperatures, such as alpine or arctic ecosystems, inorganic P is always released during frozen ground thaws; however, the intensity of the freeze-thaw varies its inter-annual variability (Øien 2009). In severe and long-lasting frost years, more soil P is released and absorbed by grasses during the growing season (Richardson and Marshall 1986; Moen 1990), and then the plant allocates the extra P to roots (storage strategy) (Øien 2009). The extra nutrients that were stored in roots would reduce the dependence of grasses on soil fertility availability particularly when grasses require a sizeable demand of nutrients for growth (e.g., in early spring) (Lambers et al. 1998). *Stipa purpurea* and *Orinus thoroldii* (grasses) have adopted a storage strategy below-ground for potentially limited nutrients in infertile environments, which is consistent with other plants that dominate infertile soils (Chapin III 1980). Intense responses of sedges to soil N were observed in alpine grasslands in the Great Pyrenees and Teberda (Sebastià 2006; Onipchenko et al. 2012). However, root and leaf nutrients of *Carex*

*moorcroftii* had no relationship with soil N in our study. Compared with other study areas and plants, our study was conducted on a dry grassland, in which the roots of *Carex moorcroftii* were in the upper soil layers; therefore, extensively low surface soil moisture may constrain nitrogen uptake for the sedges. The leaf P and N:P ratios of *Leontopodium nanum*, *Potentilla bifurca* and ect. (forbs) displayed more sensitive responses to STP and SAP. The result may derive from the weak leaf internal self-regulation of multifactorial physiological traits of forbs which is the same with other narrow-ranging and accompanying species (e.g. legumes) (Futuyma and Moreno 1988; Sultan et al. 1998; Geng et al. 2011).

## Conclusion

The present study is a large-scale field comparative study to explicitly dissect the correlation between nutrient traits in different organs of the same plant group and soil fertility in an alpine tundra. Our results highlight that soil P has a significant impact on the plant N and P concentrations and N:P ratios, whereas soil N has relatively little effect on plant N:P stoichiometry along natural fertility gradients. The differences in the nutrient traits and their correlations with soil fertility among the different functional groups indicate that coexisting species have different nutrient use/conservation strategies in one community. Further studies will focus on combining more global data between root and leaf nutrient concentrations with soil fertility.

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## Appendix

**Table 2** Positional information, soil nutrients and plant species in 32 sample sites on the northern Tibet Plateau of China

Site 1	Species	Family	Functional group
Nakchu 31.34 °N, 91.35 °E, 4565 m MAT: -0.84 °C; MAP: 359 mm STN:0.89 g kg <sup>-1</sup> ; SAN :78.8 mg kg <sup>-1</sup> STP: 0.27 g kg <sup>-1</sup> ;SAP:3.8 mg kg <sup>-1</sup>	<i>Stipa purpurea</i>	Gramineae	Grass
	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
	<i>Leontopodium nanum</i>	Compositae	Forb
	<i>Potentilla bifurca</i>	Rosaceae	Forb
	<i>Saussurea stoliczkai</i>	Compositae	Forb
Site 2 Palgon 31.30 °N, 91.04 °E, 4929 m MAT: -2.21 °C; MAP: 320 mm STN:0.39 g kg <sup>-1</sup> ; SAN :28.1 mg kg <sup>-1</sup> STP: 0.15 g kg <sup>-1</sup> ;SAP:3.1 mg kg <sup>-1</sup>	Species	Family	Functional group
	<i>Stipa purpurea</i>	Gramineae	Grass
	<i>Leontopodium nanum</i>	Compositae	Forb
	<i>Oxytropis glacialis</i>	Leguminosae	Legume
	<i>Potentilla bifurca</i>	Rosaceae	Forb
	<i>Youngia simulatrix</i>	Compositae	Forb
Site 3 Palgon 31.23 °N, 91.43 °E, 5002 m MAT: -2.78 °C; MAP: 291 mm STN:0.82 g kg <sup>-1</sup> ; SAN :71.8 mg kg <sup>-1</sup> STP: 0.17 g kg <sup>-1</sup> ;SAP:2.9 mg kg <sup>-1</sup>	<i>Incarvillea compacta</i>	Bignoniaceae	Forb
	Species	Family	Functional group
	<i>Stipa purpurea</i>	Gramineae	Grass
	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
	<i>Leontopodium nanum</i>	Compositae	Forb
	<i>Oxytropis glacialis</i>	Leguminosae	Legume
Site 4 Palgon 31.23 °N, 90.19 °E, 5297 m MAT: -4.19 °C; MAP: 275 mm STN:1.19 g kg <sup>-1</sup> ; SAN :109.7 mg kg <sup>-1</sup> STP: 0.23 g kg <sup>-1</sup> ;SAP:3.1 mg kg <sup>-1</sup>	<i>Youngia simulatrix</i>	Compositae	Forb
	<i>Potentilla bifurca</i>	Rosaceae	Forb
	<i>Saussurea stoliczkai</i>	Compositae	Forb
	Species	Family	Functional group
	<i>Stipa purpurea</i>	Gramineae	Grass
	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
	<i>Leontopodium nanum</i>	Compositae	Forb
Site 5 Palgon 31.33 °N, 90.04 °E, 4887 m MAT: -3.10 °C; MAP: 286 mm STN:0.66 g kg <sup>-1</sup> ; SAN :52.8 mg kg <sup>-1</sup> STP: 0.19 g kg <sup>-1</sup> ;SAP:3.4 mg kg <sup>-1</sup>	<i>Oxytropis glacialis</i>	Leguminosae	Legume
	<i>Oxytropis microphylla</i>	Leguminosae	Legume
	<i>Potentilla bifurca</i>	Rosaceae	Forb
	Species	Family	Functional group
	<i>Stipa purpurea</i>	Gramineae	Grass
	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
Site 6 Palgon 31.33 °N, 89.42 °E, 5118 m MAT: -3.41 °C; MAP: 265 mm STN:1.16 g kg <sup>-1</sup> ; SAN :79.5 mg kg <sup>-1</sup> STP: 0.22 g kg <sup>-1</sup> ;SAP:3.4 mg kg <sup>-1</sup>	<i>Leontopodium nanum</i>	Compositae	Forb
	<i>Saussurea stoliczkai</i>	Compositae	Forb
	<i>Potentilla bifurca</i>	Rosaceae	Forb
	<i>Lagotis brachystachya</i>	Scrophulariaceae	Forb
	<i>Incarvillea compacta</i>	Bignoniaceae	Forb
	<i>Artemisia wellbyi</i>	Compositae	Forb

**Table 2** (continued)

Site 1	Species	Family	Functional group
Site 7	Species	Family	Functional group
Palgon	<i>Stipa purpurea</i>	Gramineae	Grass
31.43 °N, 89.25 °E, 5163 m	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
MAT: -3.74 °C; MAP: 252 mm	<i>Leontopodium nanum</i>	Compositae	Forb
STN:1.33 g kg <sup>-1</sup> ; SAN :78.8 mg kg <sup>-1</sup>	<i>Oxytropis glacialis</i>	Leguminosae	Legume
STP: 0.27 g kg <sup>-1</sup> ;SAP:3.9 mg kg <sup>-1</sup>	<i>Potentilla bifurca</i>	Rosaceae	Forb
	<i>Artemisia wellbyi</i>	Compositae	Forb
Site 8	Species	Family	Functional group
Shantsa	<i>Stipa purpurea</i>	Gramineae	Grass
32.02 °N, 89.11 °E, 4560 m	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
MAT: -0.93 °C; MAP: 274 mm	<i>Leontopodium nanum</i>	Compositae	Forb
STN:0.42 g kg <sup>-1</sup> ; SAN :28.1 mg kg <sup>-1</sup>	<i>Oxytropis glacialis</i>	Leguminosae	Legume
STP: 0.21 g kg <sup>-1</sup> ;SAP:3.0 mg kg <sup>-1</sup>	<i>Potentilla bifurca</i>	Rosaceae	Forb
	<i>Youngia simulatrix</i>	Compositae	Forb
	<i>Lagotis brachystachya</i>	Scrophulariaceae	Forb
	<i>Oxytropis microphylla</i>	Leguminosae	Legume
Site 9	Species	Family	Functional group
Nima	<i>Stipa purpurea</i>	Gramineae	Grass
32.06 °N, 88.32 °E, 4631 m	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
MAT: -1.06 °C; MAP: 252 mm	<i>Leontopodium nanum</i>	Compositae	Forb
STN:1.16 g kg <sup>-1</sup> ; SAN :81.6 mg kg <sup>-1</sup>	<i>Oxytropis glacialis</i>	Leguminosae	Legume
STP: 0.28 g kg <sup>-1</sup> ;SAP:3.7 mg kg <sup>-1</sup>	<i>Saussurea stoliczkai</i>	Compositae	Forb
	<i>Incarvillea compacta</i>	Bignoniaceae	Forb
Site 10	Species	Family	Functional group
Nima	<i>Stipa purpurea</i>	Gramineae	Grass
32.01 °N, 88.04 °E, 4609 m	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
MAT: -0.78 °C; MAP: 247 mm	<i>Leontopodium nanum</i>	Compositae	Forb
STN:0.92 g kg <sup>-1</sup> ; SAN :69.6 mg kg <sup>-1</sup>	<i>Oxytropis glacialis</i>	Leguminosae	Legume
STP: 0.29 g kg <sup>-1</sup> ;SAP:3.0 mg kg <sup>-1</sup>	<i>Potentilla bifurca</i>	Rosaceae	Forb
	<i>Oxytropis serioopetala</i>	Leguminosae	Legume
	<i>Incarvillea compacta</i>	Bignoniaceae	Forb
Site 11	Species	Family	Functional group
Nima	<i>Stipa purpurea</i>	Gramineae	Grass
31.52 °N, 87.50 °E, 4776 m	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
MAT: -0.94 °C; MAP: 231 mm	<i>Oxytropis glacialis</i>	Leguminosae	Legume
STN:0.66 g kg <sup>-1</sup> ; SAN :47.1 mg kg <sup>-1</sup>	<i>Potentilla bifurca</i>	Rosaceae	Forb
STP: 0.26 g kg <sup>-1</sup> ;SAP:4.2 mg kg <sup>-1</sup>	<i>Oxytropis serioopetala</i>	Leguminosae	Legume
	<i>Oxytropis microphylla</i>	Leguminosae	Legume
Site 12	Species	Family	Functional group
Nima	<i>Stipa purpurea</i>	Gramineae	Grass
31.48 °N, 87.27 °E, 4758 m	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
MAT: -1.03 °C; MAP: 222 mm	<i>Leontopodium nanum</i>	Compositae	Forb
STN:1.55 g kg <sup>-1</sup> ; SAN :109.7 mg kg <sup>-1</sup>	<i>Oxytropis glacialis</i>	Leguminosae	Legume
STP: 0.44 g kg <sup>-1</sup> ;SAP:3.9 mg kg <sup>-1</sup>	<i>Potentilla bifurca</i>	Rosaceae	Forb

**Table 2** (continued)

Site 1	Species	Family	Functional group
Site 13	Species	Family	Functional group
Nima	<i>Stipa purpurea</i>	Gramineae	Grass
31.48 °N, 87.13 °E, 4795 m	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
MAT: -1.29 °C; MAP: 214 mm	<i>Leontopodium nanum</i>	Compositae	Forb
STN:1.59 g kg <sup>-1</sup> ; SAN :73.2 mg kg <sup>-1</sup>	<i>Oxytropis glacialis</i>	Leguminosae	Legume
STP: 0.31 g kg <sup>-1</sup> ;SAP:3.7 mg kg <sup>-1</sup>	<i>Potentilla bifurca</i>	Rosaceae	Forb
Site 14	Species	Family	Functional group
Nima	<i>Stipa purpurea</i>	Gramineae	Grass
31.48 °N, 86.55 °E, 5561 m	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
MAT: -5.67 °C; MAP: 183 mm	<i>Leontopodium nanum</i>	Compositae	Forb
STN:1.37 g kg <sup>-1</sup> ; SAN :76.0 mg kg <sup>-1</sup>	<i>Oxytropis glacialis</i>	Leguminosae	Legume
STP: 0.29 g kg <sup>-1</sup> ;SAP:3.8 mg kg <sup>-1</sup>	<i>Potentilla bifurca</i>	Rosaceae	Forb
	<i>Lagotis brachystachya</i>	Scrophulariaceae	Forb
	<i>Oxytropis microphylla</i>	Leguminosae	Legume
Site 15	Species	Family	Functional group
Nima	<i>Stipa purpurea</i>	Gramineae	Grass
31.56 °N, 86.35 °E, 5467 m	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
MAT: -5.07 °C; MAP: 181 mm	<i>Oxytropis glacialis</i>	Leguminosae	Legume
STN:0.82 g kg <sup>-1</sup> ; SAN :34.5 mg kg <sup>-1</sup>	<i>Potentilla bifurca</i>	Rosaceae	Forb
STP: 0.21 g kg <sup>-1</sup> ;SAP:3.3 mg kg <sup>-1</sup>	<i>Oxytropis serioopetala</i>	Leguminosae	Legume
	<i>Oxytropis microphylla</i>	Leguminosae	Legume
Site 16	Species	Family	Functional group
Nima	<i>Stipa purpurea</i>	Gramineae	Grass
31.53 °N, 86.08 °E, 4851 m	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
MAT: -1.55 °C; MAP: 197 mm	<i>Oxytropis glacialis</i>	Leguminosae	Legume
STN:0.71 g kg <sup>-1</sup> ; SAN :36.6 mg kg <sup>-1</sup>	<i>Potentilla bifurca</i>	Rosaceae	Forb
STP: 0.22 g kg <sup>-1</sup> ;SAP:2.7 mg kg <sup>-1</sup>	<i>Leontopodium nanum</i>	Compositae	Forb
	<i>Oxytropis microphylla</i>	Leguminosae	Legume
Site 17	Species	Family	Functional group
Nima	<i>Stipa purpurea</i>	Gramineae	Grass
31.58 °N, 85.44 °E, 5289 m	<i>Carex moorcroftii</i>	Cyperaceae	Sedge
MAT: -5.93 °C; MAP: 187 mm	<i>Oxytropis glacialis</i>	Leguminosae	Legume
STN:1.14 g kg <sup>-1</sup> ; SAN :60.5 mg kg <sup>-1</sup>	<i>Potentilla bifurca</i>	Rosaceae	Forb
STP: 0.40 g kg <sup>-1</sup> ;SAP:8.1 mg kg <sup>-1</sup>	<i>Leontopodium nanum</i>	Compositae	Forb
Site 18	Species	Family	Functional group
Gerts	<i>Stipa purpurea</i>	Gramineae	Grass
31.88 °N, 84.89 °E, 5230 m	<i>Oxytropis microphylla</i>	Leguminosae	Legume
MAT: -3.38 °C; MAP:190 mm	<i>Artemisia wellbyi</i>	Compositae	Forb
STN:1.19 g kg <sup>-1</sup> ; SAN :64.7 mg kg <sup>-1</sup>			
STP: 0.32 g kg <sup>-1</sup> ;SAP:3.7 mg kg <sup>-1</sup>			
Site 19	Species	Family	Functional group
Gerts	<i>Stipa purpurea</i>	Gramineae	Grass
32.06 °N, 84.51 °E, 5115 m			
MAT: -3.60 °C; MAP:191 mm			

**Table 2** (continued)

Site 1	Species	Family	Functional group
STN:1.63 g kg <sup>-1</sup> ; SAN :76.0 mg kg <sup>-1</sup> STP: 0.46 g kg <sup>-1</sup> ;SAP:2.8 mg kg <sup>-1</sup>			
Site 20	Species	Family	Functional group
Gerts	<i>Stipa purpurea</i>	Gramineae	Grass
32.15 °N, 84.23 °E, 5265 m	<i>Oxytropis microphylla</i>	Leguminosae	Legume
MAT: -4.08 °C; MAP:191 mm STN:1.25 g kg <sup>-1</sup> ; SAN :52.1 mg kg <sup>-1</sup> STP: 0.41 g kg <sup>-1</sup> ;SAP:6.3 mg kg <sup>-1</sup>			
Site 21	Species	Family	Functional group
Gerts	<i>Stipa purpurea</i>	Gramineae	Grass
32.17 °N, 84.10 °E, 5022 m	<i>Artemisia wellbyi</i>	Compositae	Forb
MAT: -3.20 °C; MAP:195 mm STN:1.10 g kg <sup>-1</sup> ; SAN :41.5 mg kg <sup>-1</sup> STP: 0.33 g kg <sup>-1</sup> ;SAP:4.3 mg kg <sup>-1</sup>			
Site 22	Species	Family	Functional group
Gerts	<i>Stipa purpurea</i>	Gramineae	Grass
32.18 °N, 83.47 °E, 4398 m	<i>Oxytropis microphylla</i>	Leguminosae	Legume
MAT: 0.29 °C; MAP:222 mm STN:1.37 g kg <sup>-1</sup> ; SAN :56.3 mg kg <sup>-1</sup> STP: 0.52 g kg <sup>-1</sup> ;SAP:5.0 mg kg <sup>-1</sup>			
Site 23	Species	Family	Functional group
Gerts	<i>Stipa purpurea</i>	Gramineae	Grass
32.21 °N, 83.24 °E, 4856 m			
MAT: -2.36 °C; MAP:212 mm STN:0.61 g kg <sup>-1</sup> ; SAN :87.9 mg kg <sup>-1</sup> STP: 0.59 g kg <sup>-1</sup> ;SAP:5.1 mg kg <sup>-1</sup>			
Site 24	Species	Family	Functional group
Gerts	<i>Stipa purpurea</i>	Gramineae	Grass
32.25 °N, 83.01 °E, 4887 m	<i>Oxytropis microphylla</i>	Leguminosae	Legume
MAT: -2.76 °C; MAP:211 mm STN:1.16 g kg <sup>-1</sup> ; SAN :36.6 mg kg <sup>-1</sup> STP: 0.38 g kg <sup>-1</sup> ;SAP:9.6 mg kg <sup>-1</sup>			
Site 25	Species	Family	Functional group
Gakyi	<i>Stipa purpurea</i>	Gramineae	Grass
32.29 °N, 82.44 °E, 4808 m	<i>Artemisia wellbyi</i>	Compositae	Forb
MAT: -2.23 °C; MAP:210 mm STN:0.99 g kg <sup>-1</sup> ; SAN :43.6 mg kg <sup>-1</sup> STP: 0.69 g kg <sup>-1</sup> ;SAP:5.7 mg kg <sup>-1</sup>			
Site 26	Species	Family	Functional group
Gakyi	<i>Stipa purpurea</i>	Gramineae	Grass
32.31 °N, 82.26 °E, 4748 m			
MAT: -1.62 °C; MAP:210 mm STN:1.34 g kg <sup>-1</sup> ; SAN :32.4 mg kg <sup>-1</sup> STP: 0.35 g kg <sup>-1</sup> ;SAP:4.9 mg kg <sup>-1</sup>			

**Table 2** (continued)

Site 1	Species	Family	Functional group
Site 27	Species	Family	Functional group
Gakyi	<i>Stipa purpurea</i>	Gramineae	Grass
32.16 °N, 82.22 °E, 5389 m	<i>Potentilla bifurca</i>	Rosaceae	Forb
MAT: -5.18 °C; MAP:225 mm	<i>Orinus thoroldii</i>	Gramineae	Forb
STN:0.80 g kg <sup>-1</sup> ; SAN :40.8 mg kg <sup>-1</sup>	<i>Oxytropis microphylla</i>	Leguminosae	Legume
STP: 0.30 g kg <sup>-1</sup> ;SAP:5.3 mg kg <sup>-1</sup>			
Site 28	Species	Family	Functional group
Gakyi	<i>Stipa purpurea</i>	Gramineae	Grass
32.06 °N, 82.03 °E, 4600 m	<i>Oxytropis serioopetala</i>	Leguminosae	Legume
MAT: -0.88 °C; MAP:252 mm	<i>Orinus thoroldii</i>	Gramineae	Grass
STN:1.28 g kg <sup>-1</sup> ; SAN :39.4 mg kg <sup>-1</sup>	<i>Oxytropis microphylla</i>	Leguminosae	Legume
STP: 0.40 g kg <sup>-1</sup> ;SAP:4.4 mg kg <sup>-1</sup>			
Site 29	Species	Family	Functional group
Gakyi	<i>Stipa purpurea</i>	Gramineae	Grass
32.12 °N, 81.34 °E, 5272 m	<i>Oxytropis serioopetala</i>	Leguminosae	Legume
MAT: -4.96 °C; MAP:227 mm	<i>Orinus thoroldii</i>	Gramineae	Grass
STN:0.55 g kg <sup>-1</sup> ; SAN :54.9 mg kg <sup>-1</sup>	<i>Potentilla bifurca</i>	Rosaceae	Forb
STP: 0.43 g kg <sup>-1</sup> ;SAP:8.3 mg kg <sup>-1</sup>			
Site 30	Species	Family	Functional group
Gakyi	<i>Stipa purpurea</i>	Gramineae	Grass
32.23 °N, 81.11°E, 5039 m	<i>Oxytropis serioopetala</i>	Leguminosae	Legume
MAT: -3.75 °C; MAP: 199 mm	<i>Orinus thoroldii</i>	Gramineae	Grass
STN:0.56 g kg <sup>-1</sup> ; SAN :36.6 mg kg <sup>-1</sup>			
STP: 0.35 g kg <sup>-1</sup> ;SAP:10.0 mg kg <sup>-1</sup>			
Site 31	Species	Family	Functional group
Gar	<i>Stipa purpurea</i>	Gramineae	Grass
32.22 °N, 80.46 °E, 4887 m	<i>Oxytropis glacialis</i>	Leguminosae	Legume
MAT: -3.01 °C; MAP:181 mm	<i>Oxytropis microphylla</i>	Leguminosae	Legume
STN:0.93 g kg <sup>-1</sup> ; SAN :13.4 mg kg <sup>-1</sup>			
STP: 0.36 g kg <sup>-1</sup> ;SAP:7.3 mg kg <sup>-1</sup>			
Site 32	Species	Family	Functional group
Gar	<i>Stipa purpurea</i>	Gramineae	Grass
32.26 °N, 80.12 °E, 5084 m	<i>Artemisia younghusbandii</i>	Compositae	Forb
MAT: -4.22 °C; MAP:187 mm			
STN:0.73 g kg <sup>-1</sup> ; SAN :16.9 mg kg <sup>-1</sup>			
STP: 0.64 g kg <sup>-1</sup> ;SAP:7.4 mg kg <sup>-1</sup>			

MAT mean annual temperature; MAP mean annual precipitation; STN soil total nitrogen; SAN soil available nitrogen; STP soil total phosphorus; SAP soil available phosphorus

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