



RESEARCH ARTICLE

The forb, *Ajania tenuifolia*, uses soil nitrogen efficiently, allowing it to be dominant over sedges and Graminae in extremely degraded grasslands: Implications for grassland restoration and development on the Tibetan Plateau

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Abstract

Plant growth is mainly N-limited in the alpine grasslands because of slow mineralization of soil organic matter due to low air temperature. Different plant species dominate in soils of different N concentrations. For example, more forbs occur in severely degraded alpine meadows than do sedges and Gramineae. We hypothesized that a more efficient uptake of low soil N by forbs than by sedges and Gramineae was the mechanism that allowed forbs to dominate. The amount and rate of soil N uptake and N allocation were determined in seven dominant alpine plant species using ¹⁵N isotope tracer. The plants, which included one forb, *Ajania tenuifolia*, three sedges, *Kobresia humilis*, *Carex scabrirostris*, and *Carex enervis*, and three Gramineae, *Elymus nutans*, *Festuca sinensis*, and *Stipa purpurea*, were maintained in pots with four different N concentrations (0, 50, 100, and 150 kg ha⁻¹). The forb had the highest efficiency of N utilization (N uptake rate, 60.4%) in low N soil concentration, the Gramineae had intermediate efficiencies (27.9–47.9%), and the sedges had the lowest efficiencies (5.2–34.9%), and, consequently, our hypothesis was supported. N utilization of the seven species decreased with an increase in soil N concentration, from 32.1% at N50 to 18.0% at N150, which indicated that soil N uptake by plants was affected by soil N concentration. The mechanism used by forbs to be the dominant species in severely degraded alpine meadows was a more efficient utilization of soil N than Gramineae and sedges in conditions of low soil N. We concluded that plant species have different efficiencies in soil N uptake and utilization, which allow them to adapt and survive in habitats of different soil nutrition levels. These results implied that forbs should be reduced, and that Gramineae and sedges should be planted and N be added during the restoration and development of severely degraded grasslands on the Tibetan plateau when the soil N content is low.

KEYWORDS

¹⁵N labeling, alpine meadow plants, nitrogen utilization, soil retention, Tibetan Plateau

1 | INTRODUCTION

The Qinghai-Tibetan Plateau is the largest geomorphological unit on the Eurasian continent and the largest body of low latitude frozen soil in the world (Wang, Wang, & Lu, 2009). The alpine grasslands on the plateau account for one third of the total grasslands in China (Wiener et al., 2006) and have the capacity to store large amounts of soil carbon (C) and nitrogen (N) and to provide important ecosystem functions, such as livestock production, soil and water conservation, and biodiversity (Shang et al., 2016; Yang et al., 2008). However, large areas of the alpine grasslands on the Tibetan Plateau have been severely degraded (Harris, 2009) due to anthropogenic activities such as overgrazing and natural factors such as climate change (Jing et al., 2018; Li, Dong, Wen, Wang, & Wu, 2014). The degraded grasslands are bare throughout the year and are dominated by ruderal plants, which are inedible by livestock (Dong et al., 2012; Shang, Tang, & Long, 2010). This unique feature of the degraded grasslands implies that ruderal plants may have a more efficient utilization of soil N than sedges Cyperaceae and Gramineae.

Nitrogen (N), an important nutrient in plant metabolic processes, is the primary nutrient that limits plant growth and development in many terrestrial ecosystems (Aerts & Chapin, 1999; Anbessa & Juskiw, 2012; Zhang, Cai, & Müller, 2018). Grassland degradation has resulted in a high loss of N by erosion, soil organic matter mineralization, and leaching (He & Richards, 2015; Liu, Schleuss, & Kuzyakov, 2017), and the reduced N input into the soil ultimately affects soil N cycling (Zhang et al., 2017). Low soil N concentration is widespread in alpine grasslands (Vitousek & Howarth, 1991) because of slow mineralization of soil organic matter due to low air temperature (Gao, Mo, Xu, Zhang, & Yu, 2014; Yin et al., 2019; Zhang et al., 2017).

It has been reported that plant species differ in N acquisition strategies in alpine meadows (Xu et al., 2011), which suggests that N input may have the potential to affect species composition and abundance in alpine meadows (Xu et al., 2014). Plant species composition has altered substantially in recent decades due to the intensive degradation of alpine grasslands and differences among species in the efficiency of N uptake in N-limited ecosystems (Schleuss et al., 2015). There is evidence that plants of different ecosystems are able to absorb simple soluble organic N directly (Gao et al., 2014; Liu et al., 2017; Zhang et al., 2017; Zhou et al., 2017), and it has been reported that alpine meadow plant species have adapted to low soil nitrogen concentration by absorbing different forms of nitrogen. However, little is known about N uptake and N allocation in alpine meadow plants under different levels of soil N, although this information is indispensable in assessing N utilization in the alpine meadow ecosystem.

The efficiency of nutrient utilization is one of the essential factors influencing the competitive capability of plant species (Wang et al., 2018). Differences in N uptake among plant species (Wang et al., 2012) are one of the mechanisms that could explain the dominance of certain plant species under different conditions (Jiang et al., 2018). For example, Arctic tundra vegetation became graminoid-dominated because N uptake strategies of graminoids and shrubs differed (Wang et al., 2018). Furthermore, grasses dominated when high levels of soil

N were available (Xu et al., 2014), forb species dominated in severely degraded grasslands characterized by nutrient-poor soil in alpine grasslands, and sedges dominated in nondegraded natural alpine grasslands (Zhang et al., 2014). We hypothesized that a more efficient utilization of soil N by forbs than by sedges and Gramineae was the mechanism that allowed forbs to dominate. To test our hypothesis, we determined N uptake and allocation of seven dominant alpine plant species on the Qinghai-Tibetan Plateau using ^{15}N isotope tracer in a pot experiment. Results from this study should demonstrate whether the efficiency of N utilization in plants is a mechanism of adaptation to low levels of soil N. This study should provide information: (a) on the efficiency of N utilization by plants in degraded grasslands; (b) on the mechanisms used by plants that allow them to be the dominant species in the process of grassland degradation; and (3) implications for the management and restoration of degraded grasslands on the Qinghai-Tibetan Plateau by taking into account the plant species composition and the ability and adaptation of plants to use N.

2 | MATERIALS AND METHODS

2.1 | Plant species and ^{15}N stable isotope tracer

To eliminate the effects of soil heterogeneity, interspecific competition and plant age on N uptake, the study was done with strict control of nitrogen levels in a controlled pot experiment in a greenhouse using the ^{15}N tracer method. Seven dominant alpine meadow plants, which included one forb, *Ajania tenuifolia*, three sedges, *Kobresia humilis*, *Carex scabriorostris*, and *Carex enervis*, and three Gramineae, *Elymus nutans*, *Festuca sinensis*, and *Stipa purpurea*, were examined. The sedges are the main plant species in natural alpine meadow, the Gramineae are the main plant species in artificial grasslands, and the forb is the main plant in the degraded grasslands on the Tibetan plateau (Dong et al., 2012; Zhang et al., 2019). *A. tenuifolia* is a common forb and most dominant species in degraded grasslands on the Tibetan plateau (Shi et al., 2011) and, therefore, was selected to represent forbs in this study. Seeds of the seven plants were collected from Maqu county (100°45'–102°29'E, 33°06'–34°30'N), Gannan Tibetan autonomous prefecture, in eastern Tibetan Plateau, China, in September 2012. $^{15}\text{N-KNO}_3$ was selected as the ^{15}N stable isotope tracer ($^{15}\text{N-KNO}_3$ with 10.28% ^{15}N abundance provided by the Shanghai Research Institute of Chemical Industry), as vascular plants prefer to absorb NO_3^- for development of their root systems and vascular tissue (Wang et al., 2014; Xing et al., 2015).

2.2 | Pot experiment

The study was carried out from May to September 2013, in a greenhouse at Yuzhong Experimental Station (35°57'N, 104°9'E; 1,620 m a. s.l.), Lanzhou University. Substrate soil from a cropland that had not been cultivated for several years was collected at a depth of 0–20 cm,

was mixed thoroughly, and homogenized before potting. The soil had a silt loam texture, a pH of 8.38 (water: soil ratio = 2.5:1), soil bulk density of 1.41 g·cm⁻³, total soil organic carbon of 7.43 g·kg⁻¹, total N of 0.64 g·kg⁻¹, and total P of 0.70 g·kg⁻¹. The soil was sterilized before the study at 150°C for 24 hr. The greenhouse had conditions that simulated the habitats of the plants: air temperature was 25°C from 7:00 to 21:00 and 19°C from 21:00 to 7:00, relative humidity was 65%, and light intensity was 800 μmol·m⁻²·s⁻¹ (Ma et al., 2015) over a normal growing season (from May to September) of about 100 days.

Four treatments were applied: (a) N0 (no N added, as control); (b) N50 (50 kg·N·ha⁻¹); (c) N100 (100 kg·N·ha⁻¹); and (d) N150 (150 kg·N·ha⁻¹; Jiang et al., 2015; Liu, Schleuss, & Kuzyakov, 2017). The amounts of ¹⁴N-KNO₃ and ¹⁵N-KNO₃ applied to each treatment are presented in Table 1. Air-dried soil was passed through a 2-mm sieve, and then 3 kg of soil was placed into each plastic pot (diameter 16 cm; height 20 cm). After watering the pots for 10 days, 20 seeds of each plant species were sown uniformly per pot. All plants had four replicated pots for each treatment, except for *A. tenuifolia*, which had three replicated pots for each treatment, for a total of 108 pots. When the height of the plants reached 6–10 cm, about 40 days after sowing, the plants were thinned evenly to five seedlings per pot, at which time, KNO₃ dissolved in 100-ml distilled water was added to each pot. If there were less than five seedlings in a pot, seedlings were transplanted from spare pots to make up for the difference. Throughout the study, soil moisture was maintained at 70% of field capacity by adding distilled water every 1–3 days according to the water loss determined by weighing. The pots were placed randomly and also moved periodically in the greenhouse.

2.3 | Sampling and analyses

Plant and soil samples were collected from all pots at the end of the growing season, September 10–20. Plant samples were washed and then divided into shoots and roots. Both shoots and roots were oven-dried at 65°C to constant mass and ground to powders. The soil was mixed thoroughly in each pot, and a 200-g sample was collected. Soil samples were air-dried at room temperature and sieved through a 0.25-mm screen (the soil sample of *C. scabrostris* was inadvertently lost). The ¹⁵N/¹⁴N ratios (atom percent ¹⁵N excess) and N content of the plant and soil samples were determined using an isotope ratio mass spectrometer (DELTA V Advantage) linked to an elemental analyzer (Flash EA1112 HT, Thermo Fisher Scientific, Inc. USA).

TABLE 1 Nitrogen treatment levels with the amount of ¹⁴N-KNO₃, ¹⁵N-KNO₃, ¹⁵N, and N per pot at different N levels

N level (kg·ha ⁻¹)	N (g·pot ⁻¹)	¹⁵ N (g·pot ⁻¹)	¹⁴ N-KNO ₃ (g·pot ⁻¹)	¹⁵ N-KNO ₃ (g·pot ⁻¹)
0	0	0	0	0
50	0.1064	0.0066	0.307	0.434
100	0.2128	0.0131	0.614	0.868
150	0.3191	0.0197	0.921	1.302

2.4 | Calculations and statistics

The at%¹⁵N/¹⁴N-¹⁵N-KNO₃ is the atom percent ¹⁵N excess derived from ¹⁵N-KNO₃ (the difference in ¹⁵N atom% between labeled and unlabeled treatments); ¹⁵N (mg)_{treatment} is the mass of ¹⁵N in samples; N utilization (N uptake rate) is the percentage of ¹⁵N mass in shoot or root of the applied ¹⁵N mass; and soil retention is the percentage of ¹⁵N mass in soil of the applied ¹⁵N mass. These parameters were calculated as (Liu, Xu, Xu, Wanek, & Yang, 2018):

$$\text{at}\%^{15}\text{N}/^{14}\text{N-}^{15}\text{N-KNO}_3 = \text{at}\%^{15}\text{N}/^{14}\text{N}_{\text{treatment}} - \text{at}\%^{15}\text{N}/^{14}\text{N}_{\text{control}}$$

$$^{15}\text{N (mg)}_{\text{treatment}} = M(\text{g}) \times \text{N content (\%)} / 14 (\text{g/mol}) \times \text{at}\%$$

$$^{15}\text{N}/^{14}\text{N-}^{15}\text{N-KNO}_3 \times 15 (\text{g/mol}) \times 1,000,$$

$$\text{N utilization (\%)} = ^{15}\text{N (mg)}_{\text{plant}} / \text{Applied } ^{15}\text{N (mg)} \times 100\%,$$

$$\text{Soil retention (\%)} = ^{15}\text{N (mg)}_{\text{soil}} / \text{Applied } ^{15}\text{N (mg)} \times 100\%,$$

where at%¹⁵N/¹⁴N_{treatment} and at%¹⁵N/¹⁴N_{control} are atom percent ¹⁵N excess of treatment in the ¹⁵N source-labeled and control (unlabeled), respectively, and M and N contents are the mass and nitrogen contents of the samples, respectively (Ouyang et al., 2016).

All data are presented as means (±standard error) of the replicates. Two-way analysis of variance was used to test the effects of plant species, N level and their interaction on biomass, N content, at %¹⁵N/¹⁴N, ¹⁵N in vegetation and soil, and N utilization followed by Duncan's post hoc tests. Differences among means were considered significant at the *p* < .05 level. All statistical analyses were done with the Software Statistical Package for the Social Sciences 17.0 (SPSS Inc. Chicago, IL, USA).

3 | RESULTS

3.1 | N utilization of alpine meadow plants

In general, shoot biomass, shoot and root N content, at%¹⁵N/¹⁴N and ¹⁵N values, and N utilization differed significantly among plant species and N levels. Soil at%¹⁵N/¹⁴N and ¹⁵N values, N retention, and N loss rate also differed significantly among plant species and N levels. Root biomass differed significantly among plant species and was affected by the interaction of plant species and N levels but was not affected by N levels alone. Root N utilization differed among plant species and N levels but was not affected by the interaction of plant species and N levels (Table S1).

Shoot N utilization of the forb, *A. tenuifolia* (48%, 47%, and 35%), was the highest, whereas that of the sedges, *K. humilis* (3.9%, 3.3%, and 1.5%) and *C. scabrostris* (3.4%, 2.1%, and 2.2%), were the lowest

among the seven species at N50, N100, and N150, respectively. Root N utilization of *E. nutans* (19%, 23%, and 15%) was the highest and of *A. tenuifolia* (13%, 11%, and 9%) the second highest among the seven species at N50, N100, and N150, respectively. Shoot and root N utilization of *C. enervis*, *E. nutans*, *F. sinensis*, and *S. purpurea* decreased with an increase in soil N, whereas, for *A. tenuifolia*, shoot N utilization decreased, but root N utilization did not (Figure 1).

3.2 | Alpine meadow plants biomass and nitrogen content

Shoot biomass of the forb, *A. tenuifolia*, was the greatest, whereas those of the sedges, *K. humilis* and *C. scabrostris*, were the lowest among the seven species (Figure 2a). In addition, shoot biomasses of *A. tenuifolia* and *E. nutans* at the N50, N100, and N150 treatments

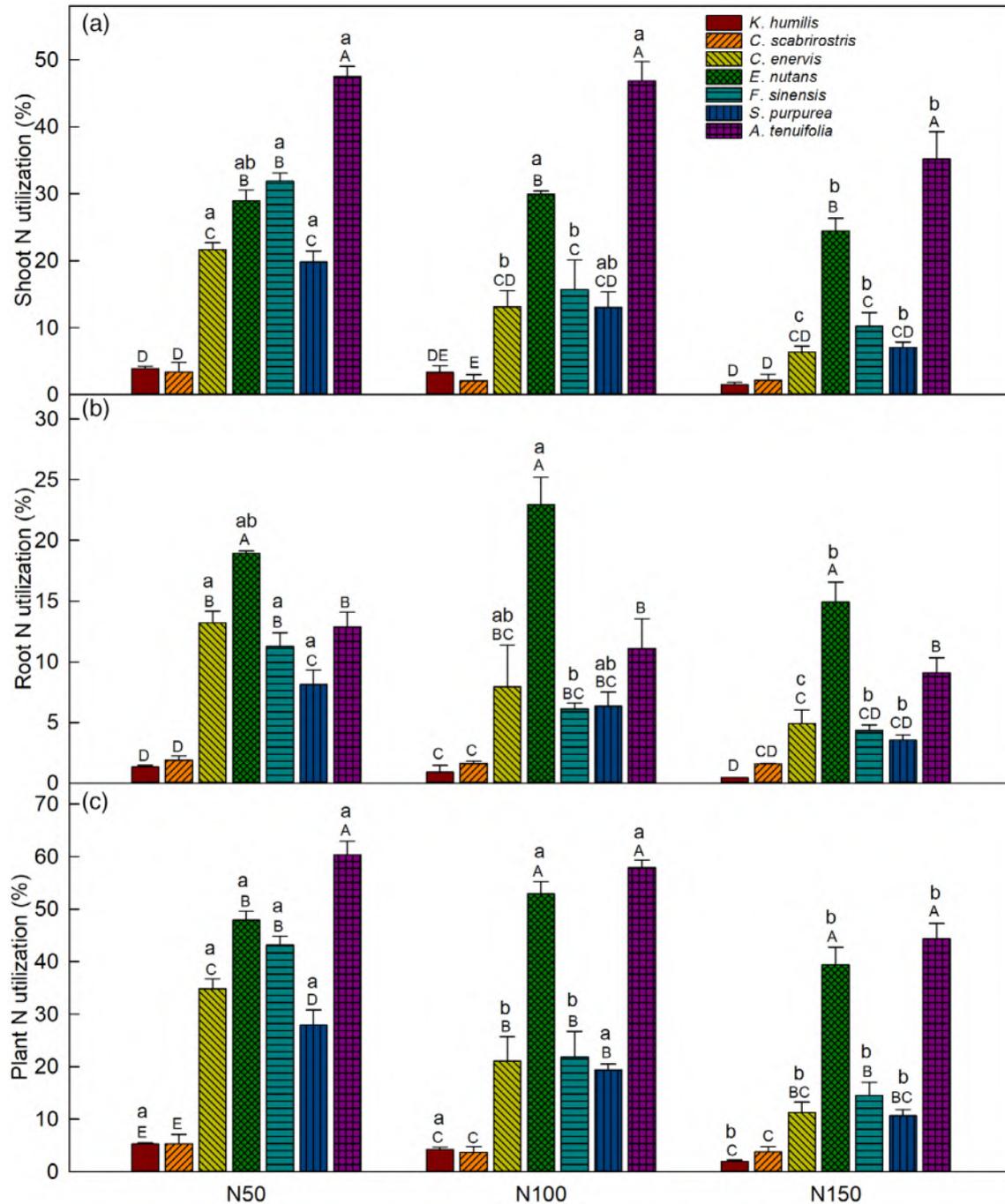


FIGURE 1 N utilization of shoot (a), root (b) and plant (shoot plus root, c) in seven plant species. N50, N100, and N150 denote the different N levels (50, 100, and 150 kg·hm⁻²). *K. humilis*, *C. scabrostris*, *C. enervis*, *E. nutans*, *F. sinensis*, *S. purpurea*, and *A. tenuifolia* represent *Kobresia humilis*, *Carex scabrostris*, *Carex enervis*, *Elymus nutans*, *Festuca sinensis*, *Stipa purpurea*, and *Ajania tenuifolia*, respectively. Different lowercase letters denote differences within a plant species at different N levels ($p < .05$); and different capital letters denote differences among the seven species at the same N level ($p < .05$). Vertical bars represent standard error of the mean, $n = 4$

were significantly greater than their N0 treatments (Figure 2a). Root biomass of *C. enervis* was the greatest among the seven species at N0 treatment, but that of *E. nutans* was the greatest, and *A. tenuifolia* was the second greatest at the N50, N100, and N150 treatments. Root biomasses of *E. nutans* at the N50, N100, and N150 treatments were significantly greater than that at the N0 treatment (Figure 2b).

The shoot, root, and soil N contents differed significantly at the different N levels and among plant species (Table S1). At the N0 treatment, shoot N content of *C. enervis* was the highest among the seven species and more than two times that of *A. tenuifolia*. Shoot N contents of *C. enervis*, *F. sinensis*, and *S. purpurea* were the highest among the seven species at the N50 treatment. Shoot N contents of *F. sinensis* at the N50, N100, and N150 treatments were higher than at the N0 treatment, and shoot N contents of *A. tenuifolia* at the N100 and N150 treatments were higher than at the N0 and N50 treatments. The contribution of soil N level to shoot N content of

C. scabrostris and *E. nutans* was as follows: $N0 < N50 < N100 < N150$ (Figure 3a). Root N content of *S. purpurea* was the highest among the seven species at N0; however, root N contents of *S. purpurea* and *A. tenuifolia* were the highest at N50, N100, and N150. Root N contents of *C. scabrostris*, *C. enervis*, *F. sinensis*, and *S. purpurea* were significantly higher at N50, N100, and N150 than at N0s (Figure 3b). This indicated that the composition of the biomass, both above- and below-ground, changed with additional soil N availability, and that a higher proportion of N content was incorporated in the plants with increased soil N.

Soil N content of *A. tenuifolia* was the highest among the seven species at N0; however, of *K. humilis* was the highest at N50, N100, and N150. Soil N contents of *K. humilis* and *C. enervis* were significantly higher at N100 and N150 than their respective N0s; however, *E. nutans*, *F. sinensis*, and *S. purpurea* were higher only at N150 than their respective N0s (Figure 3c).

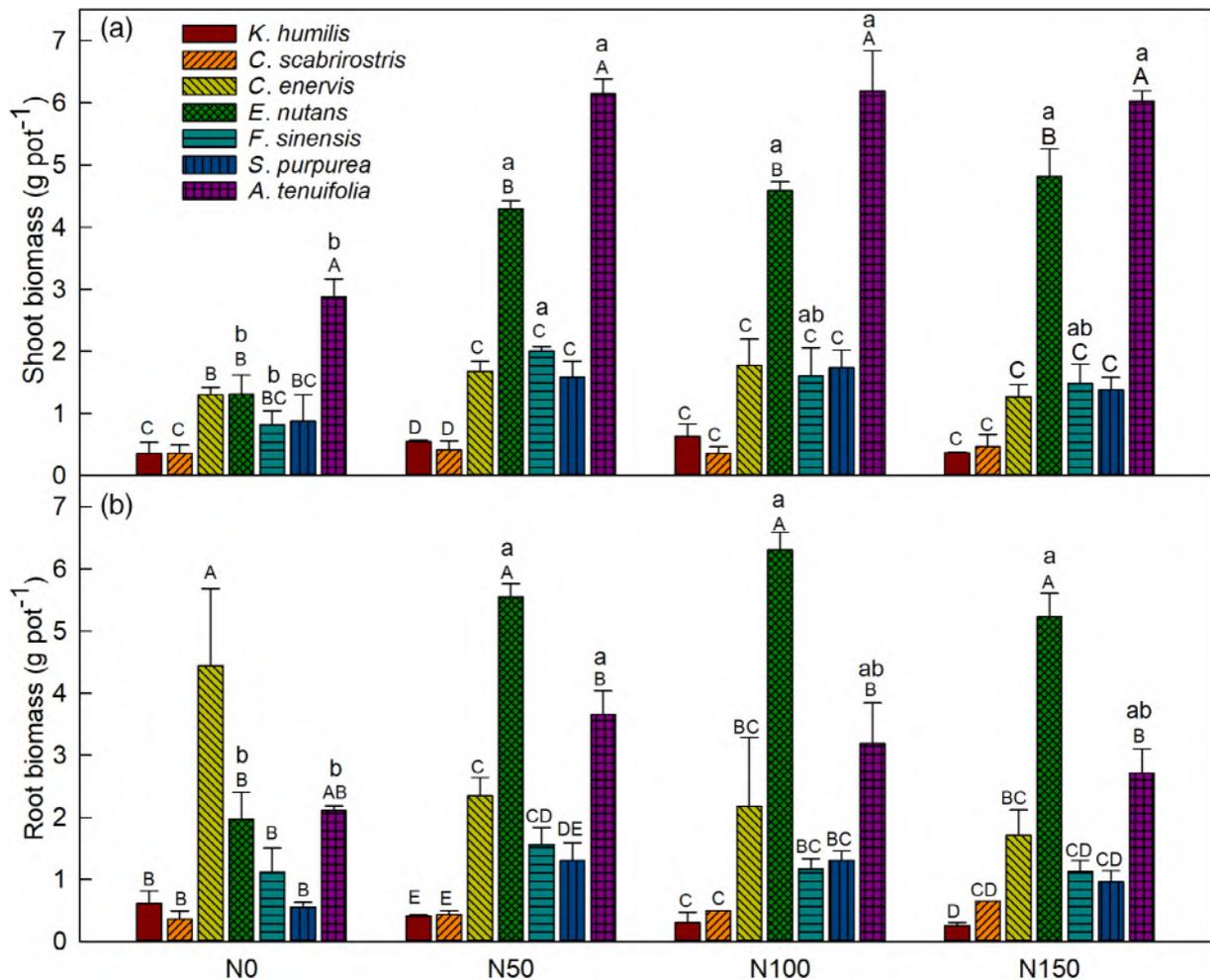


FIGURE 2 Shoot (a) and root (b) biomass of seven alpine meadow species. N0, N50, N100, and N150 denote different N levels (0, 50, 100, and 150 kg·hm⁻²). *K. humilis*, *C. scabrostris*, *C. enervis*, *E. nutans*, *F. sinensis*, *S. purpurea*, and *A. tenuifolia* represent *Kobresia humilis*, *Carex scabrostris*, *Carex enervis*, *Elymus nutans*, *Festuca sinensis*, *Stipa purpurea*, and *Ajania tenuifolia*, respectively. Different lowercase letters denote differences within a species at different N levels ($p < .05$); and different capital letters denote differences among species at the same N level ($p < .05$). Vertical bars represent standard error of the mean, $n = 4$

2D Graph 1

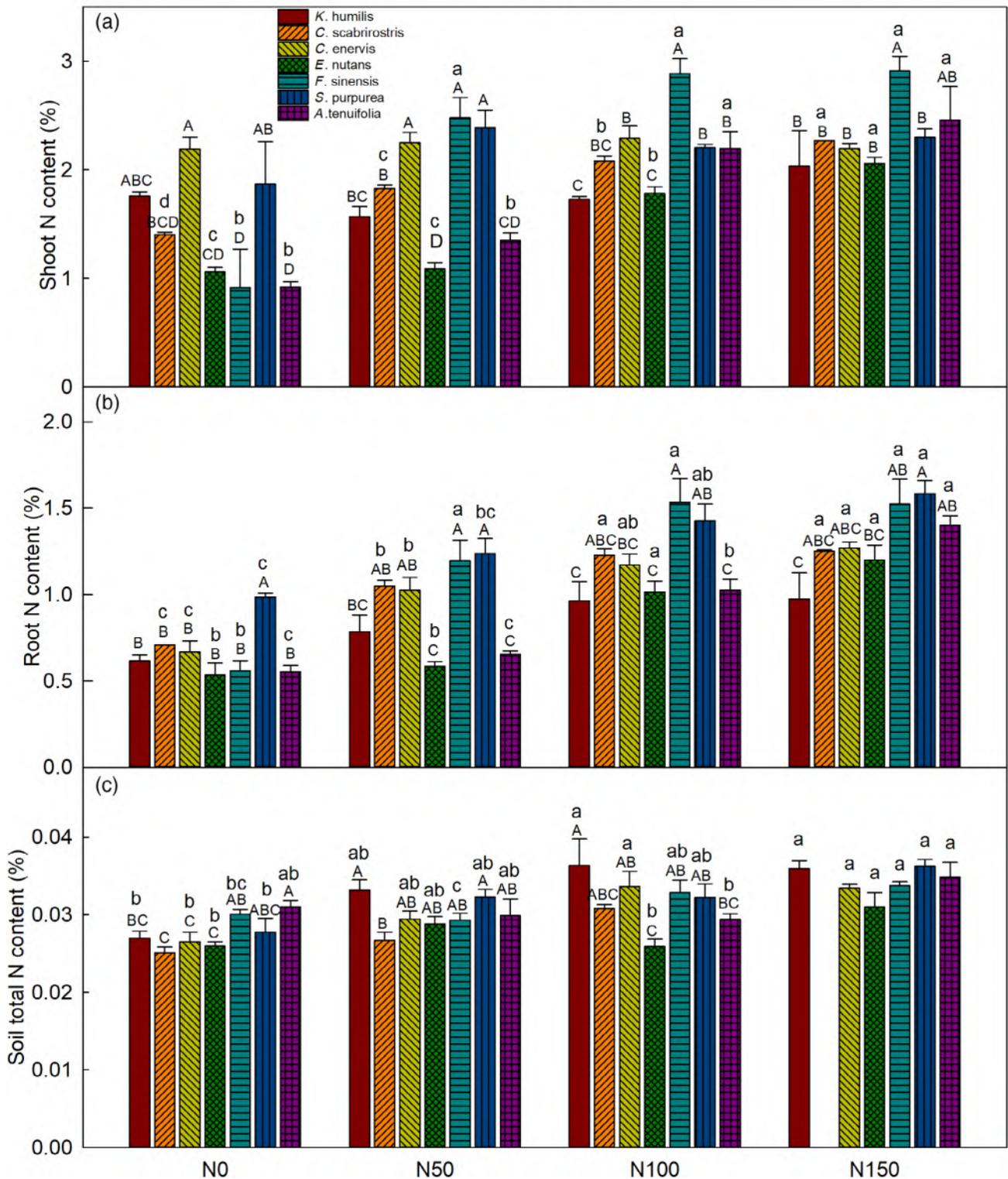


FIGURE 3 N content in shoot (a), root (b), and soil (c) of seven alpine meadow species. N0, N50, N100, and N150 denote the different N levels (0, 50, 100, and 150 kg·hm⁻²). *K. humilis*, *C. scabrirostris*, *C. enervis*, *E. nutans*, *F. sinensis*, *S. purpurea*, and *A. tenuifolia* represent *Kobresia humilis*, *Carex scabrirostris*, *Carex enervis*, *Elymus nutans*, *Festuca sinensis*, *Stipa purpurea*, and *Ajania tenuifolia*, respectively. Different lowercase letters denote differences within a plant species at different N levels ($p < .05$); and different capital letters denote differences among plant species at the same N level ($p < .05$). Vertical bars represent standard error of the mean, $n = 4$

3.3 | ^{15}N uptake by plants and retention in soil

The ^{15}N uptake by shoots of *A. tenuifolia* was the highest and by *E. nutans* the second highest; whereas, that of *K. humilis* and *C. scabrostris* were the lowest among the seven species at N50, N100, and N150. In addition, ^{15}N uptake by shoots of *A. tenuifolia* and *E. nutans* increased significantly with an increase in soil N. The

^{15}N uptake by roots of *E. nutans* was the highest and of *A. tenuifolia* the second highest among the seven species at N50, N100, and N150. Furthermore, ^{15}N uptake in roots of *A. tenuifolia*, *E. nutans*, and *C. scabrostris* increased significantly with an increase in soil N concentration. However, ^{15}N retentions in the soil of *K. humilis* and *C. scabrostris* were the highest at N50 and N100 and of *A. tenuifolia* and *E. nutans* were the lowest at N50, N100, and N150 among the

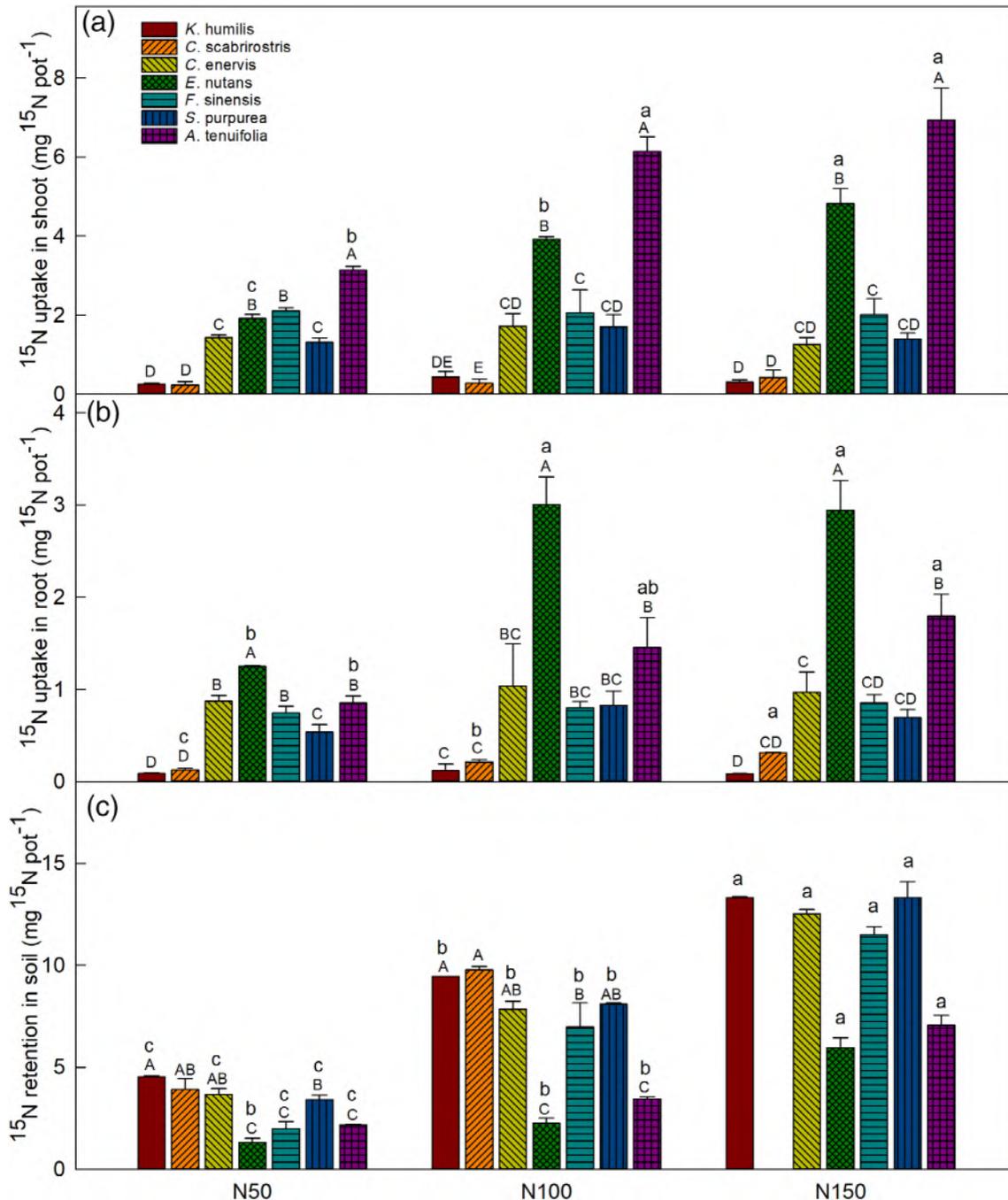


FIGURE 4 The ^{15}N uptake of shoot and root of seven plant species, and ^{15}N retention in soil ($\text{mg } ^{15}\text{N} \cdot \text{pot}^{-1}$) at three levels of soil N. N50, N100, and N150 denote the different N levels (50, 100, and 150 $\text{kg} \cdot \text{hm}^{-2}$). *K. humilis*, *C. scabrostris*, *C. enervis*, *E. nutans*, *F. sinensis*, *S. purpurea*, and *A. tenuifolia* represent *Kobresia humilis*, *Carex scabrostris*, *Carex enervis*, *Elymus nutans*, *Festuca sinensis*, *Stipa purpurea*, and *Ajania tenuifolia*, respectively. Different lowercase letters denote differences within a plant species at different N levels ($p < .05$); and different capital letters denote differences among the seven species at the same N level ($p < .05$). Vertical bars represent standard error of the mean, $n = 4$

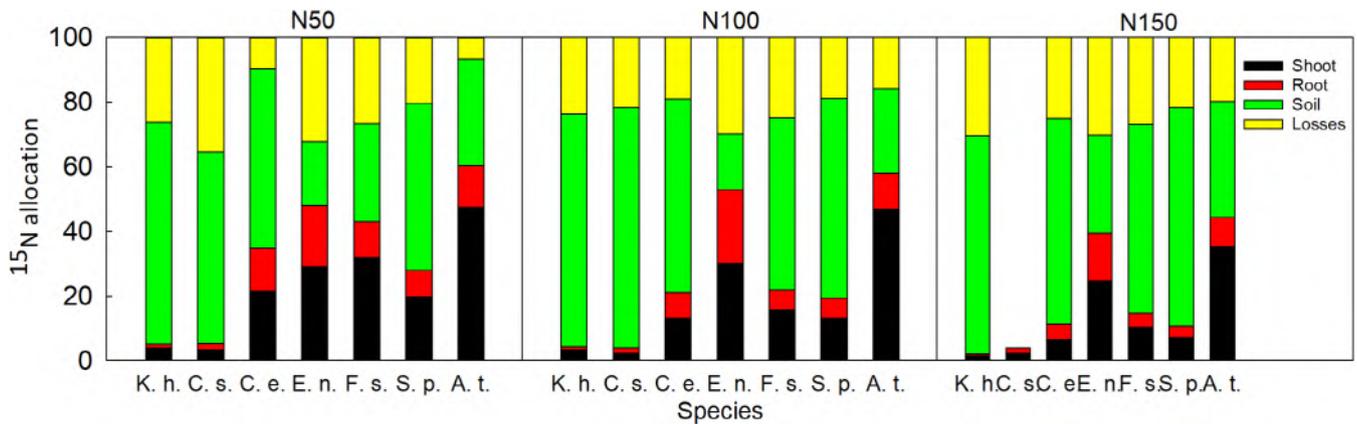


FIGURE 5 ^{15}N allocation of seven alpine meadow plants at N50, N100, and N150. Shoot, root, soil, and losses represent shoot uptake, root uptake, soil retention, and loss rate, respectively. K. h., C. s., C. e., E. n., F. s., S. p., and A. t. denote *Kobresia humilis*, *Carex scabrostris*, *Carex enervis*, *Elymus nutans*, *Festuca sinensis*, *Stipa purpurea*, and *Ajanía tenuifolia*, respectively

seven species. The ^{15}N retention in soil of *K. humilis*, *C. enervis*, *E. nutans*, *F. sinensis*, *S. purpurea*, and *A. tenuifolia* increased significantly with an increase in soil N (Figure 4).

3.4 | ^{15}N allocation in plants and soil

The percentage of ^{15}N in plants and soil of the seven species exhibited a similar pattern at N50, N100, and N150. Much of the ^{15}N remained in the soil, and some was lost, in particular in the sedges and Gramineae. The percent of ^{15}N in *K. humilis* and *C. scabrostris* was less than 6% at N50, N100, and N150, whereas in *C. enervis*, *E. nutans*, and *F. sinensis*, it ranged from 28% to 48%, 19% to 53%, and 11% to 39% at N50, N100, and N150, respectively, and in *A. tenuifolia*, it was the highest with 60%, 58%, and 44% at N50, N100, and N150, respectively (Figure 5).

More N was utilized by the forb, and, consequently, less N was left in the soil, whereas more N was lost by the sedges and Gramineae. The percent of ^{15}N in the soil of the sedges was 60% to 67%, of the Gramineae was 30% to 49%, and of the forb was 26 to 36%. The N loss for sedges was 20%, 21%, and 27%, for Gramineae was 28%, 26%, and 27%, and for the forb was 7%, 16%, and 20% at N50, N100, and N150, respectively (Figure 6), that is, the soil N loss for forbs was less than that of sedges and Gramineae.

4 | DISCUSSION

4.1 | Effect of N addition on plant biomass and N content

In a meta-analysis using 89 studies and 67 sites from peer-reviewed journals, You et al. (2017) reported that the addition of N to natural grasslands increased the above-ground biomass of all plants by 31% and of grasses by 79%, but forbs showed little response and may have

actually decreased by 6%. In addition, it emerged that above-ground biomass increased with each additional increase in N, as was found for the plant species in the present study. High N uptake is an important mechanism in sustaining high rates of primary production (Iversen, Bridgman, & Kellogg, 2010; Lü, Feike, Kong, Wang, & Han, 2014), which would explain the higher biomass of *A. tenuifolia* and *E. nutans* than the other plant species. Alpine grassland ecosystems have stabilized primary production as a result of shifting plant species composition in response to climate change. For example, warming and drought had no effect on total net primary production, but grass abundance increased at the expense of sedges and forbs (Liu et al., 2018). Nitrogen addition also had no effect on total above-ground biomass; however, grasses biomass increased, but legumes decreased, whereas forbs showed little response and quickly switched from being N deficient to N excess (Xu et al., 2014). In addition, Li, Yang, Liu, and Shao (2018) reported that the addition of N and water increased the total above-ground productivity and biomass of grasses but decreased the biomass of forbs. Under natural conditions, forbs are out-competed by grasses (You et al., 2017), which are then able to show the greatest response of all plant types to N application. N requirements for forbs are relatively low, and, in the present study, forbs were able to use the N efficiently for above-ground growth. Consequently, the difference in response of the forbs between the present study and previous studies could have been due to lack of interspecific competition for the forbs in the current study. The N content of the seven alpine meadow plant species increased with an increase in N level, which agreed with the report that increased N availability leads to an increase in plant N content (Xia & Wan, 2008).

4.2 | Plant species N uptake and utilization

N availability and utilization have large impacts on plant growth in the alpine grassland ecosystem (Schleuss et al., 2015; Xu et al., 2014), where growth is limited by low air temperature, high solar radiation,

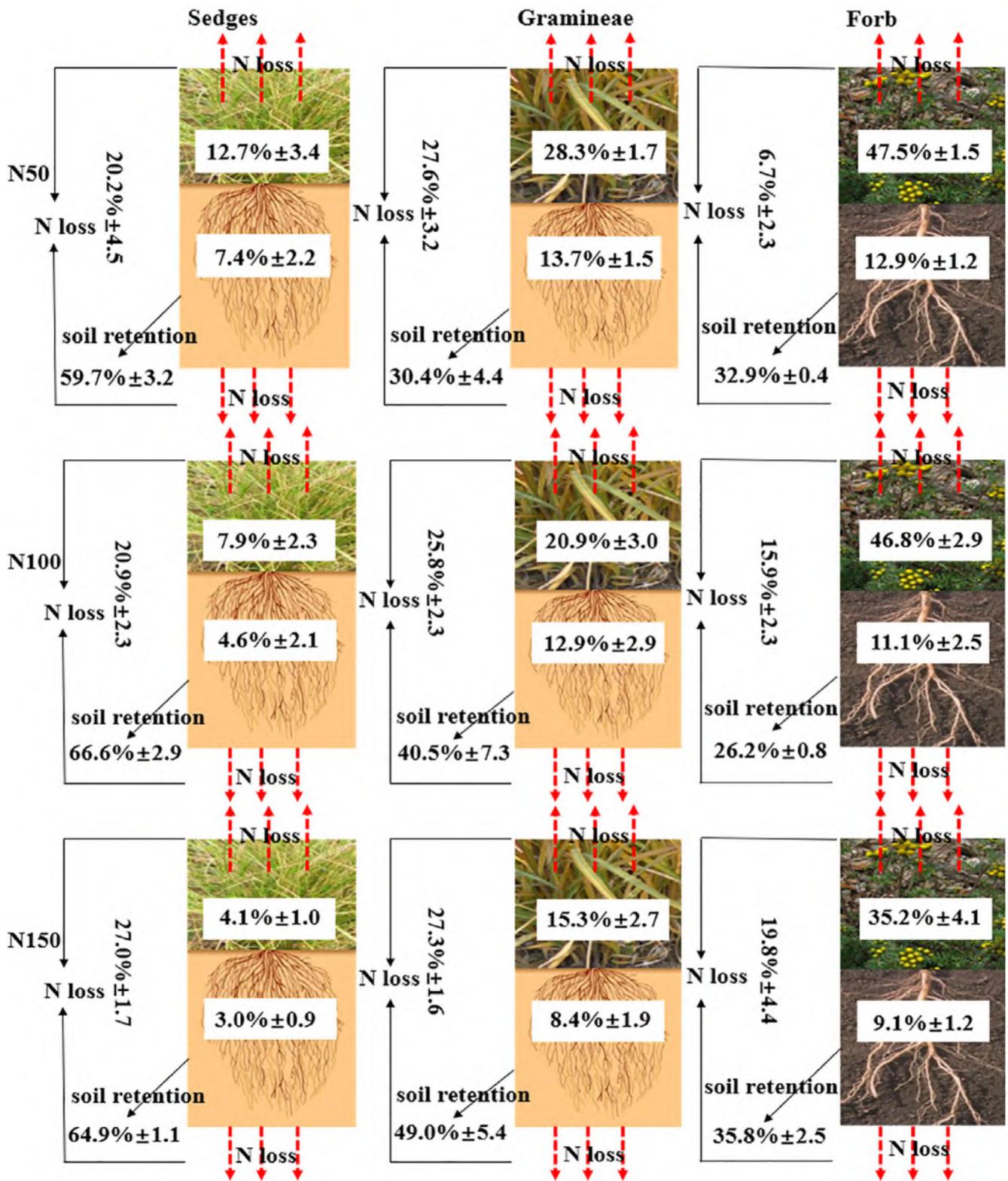


FIGURE 6 ¹⁵N allocation of different plant functional groups at N50, N100, and N150. N loss includes N_xO_y emissions and nitrate leaching

and nutrient deficiency (Callaway et al., 2002; Hermans, Hammond, White, & Verbruggen, 2006; Yin et al., 2019), especially N. Alpine plants compete under these harsh conditions by developing specific survival and reproduction strategies (Choler, 2005; Onipchenko

et al., 2009). At N50, the lowest soil N level treatment in the current study, the forb, *A. tenuifolia*, had the highest uptake rate of soil N, the Gramineae, *E. nutans*, *F. sinensis*, and *S. purpurea*, had intermediate uptake rates, whereas the sedges, *K. humilis*, *C. scabrostris*,

and *C. enervis*, had the lowest uptake rates, and, consequently, our prediction was supported. The better ability of forbs to absorb soil nitrogen was the mechanism that conferred them an advantage over Gramineae and sedges in poor soil N conditions and could explain the dominance of forbs over sedges and Gramineae at severely degraded alpine meadows (Zhang et al., 2014). The difference in ^{15}N recovery by plants may have resulted, to some extent, from the different plant functional groups that can affect mineral nitrogen content in the soil differently through rhizosphere processes.

Plant N utilization of the seven species increased with a decrease in soil N, which agrees with findings in earlier reports (Iversen et al., 2010; Liu et al., 2013; Yang et al., 2015). Most forbs are annual broad-leaf, tall weeds, and compete well for light resources (Tilman, 1987), which can increase soil N use, as N is needed for the synthesis of enzymes involved in photosynthesis (Hungate et al., 2004). This feature allows forbs to be more efficient than sedges and Gramineae in utilizing soil N. However, with the addition of N, species composition shifted to more productive grasses, whereas legumes and upright forbs decreased (Sun, Yu, Shugart, & Wang, 2016; You et al., 2017), and the soil carbon pool increased (Wang et al., 2017). N deposition enhanced the dominance of grasses over forbs in alpine meadows due to the greater ability of grasses to absorb nutrients under relatively higher N levels (Li et al., 2018). This implied that N addition should be taken into account when planting Gramineae species in the restoration and development of severely degraded grasslands on the Tibetan Plateau.

The highest ^{15}N was recovered in the shoot, which is in contrast with a previous study (Schleuss et al., 2015), where it was in the root. This may be due, at least in part, to the difference in length between the two studies. The study of Schleuss et al. (2015) lasted only 45 days, less than half the time of the present study (100 days) and, consequently, less N moved to the shoot. In the study of Schleuss et al. (2015), plant N utilization ranged between 49% and 70%, and about 18% was used in the shoot. The utilization in the current study was lower and ranged from 5% to 60%, 4% to 58%, and 2% to 44% in the N50, N100, and N150 treatments, respectively. Differences in utilization between studies may also have been a result of the difference in the lengths, and perhaps, less N was lost in the shorter study by Schleuss et al. (2015). The ^{15}N retention in the soil in the present study ranged between 26% and 67%, which is similar to the range of previous studies of 28% to 85% in the soil of grasslands (Delgado, Mosier, Valentine, Schimel, & Parton, 1996; Epstein, Burke, & Mosier, 2001). The soil N loss, which resulted mainly from nitrous oxide emission and nitrate leaching (Pervanchon et al., 2005; Zhou et al., 2013), was less for forbs than for sedges and for Gramineae. More knowledge is required on nitrogen utilization patterns in individual species with mixed plantings and interspecies competition. It is planned to fill this gap in future studies.

5 | CONCLUSIONS

Experimental evidence has demonstrated that alpine grassland plant species have different uptake rates in soil N. Our results suggested that at

the lowest soil N level treatment, the forb had the highest uptake rate of soil N (60.4%), the Gramineae had intermediate uptake rates (27.9–47.9%), and the sedges had the lowest (5.2–34.9%). Consequently, the forb (*A. tenuifolia*) was most efficient in soil N uptake at a low soil N level. We reasoned that the difference in N uptake could be the mechanism that explains the dominance of forbs at severely degraded grasslands with poor soil nutrients. This could have important implications in that it suggests that forbs should be reduced, as was practiced by Shi et al. (2011), and Gramineae and sedges should be planted and N be added for the restoration and development of severely degraded grasslands on the Tibetan plateau, when soil N content is low. Mean N utilization of the seven species decreased with an increase in soil N, from 32.1% at N50 to 18.0% at N150, which indicated that plant species N utilization was affected by the ecosystem nutrient level. Results of this study on plant N uptake and N allocation provide insights on plant adaptation to nutrient-poor soils. In addition, the findings could be used in the restoration of grasslands with N-limited soils and in the management of artificial grasslands, and the data could be a basis for future studies and model simulations of global grassland plant N utilization within the context of increased grassland degradation.

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REFERENCES

- Aerts, R., & Chapin, F. S. (1999). The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Advanced Ecology Research*, 30(8), 1–67. [https://doi.org/10.1016/S0065-2504\(08\)60016-1](https://doi.org/10.1016/S0065-2504(08)60016-1)
- Anbessa, Y., & Juskiw, P. (2012). Review: Strategies to increase nitrogen use efficiency of spring barley. *Canadian Journal of Plant Science*, 92, 617–625. <https://doi.org/10.4141/cjps2011-207>
- Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., ... Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417(6891), 844–848. <https://doi.org/10.1038/nature00812>
- Choler P (2005) Consistent shifts in alpine plant traits along a meso-topographical gradient. *Arctic, Antarctic, and Alpine Research* 37(4): 444–453. [http://doi.org/10.1657/1523-0430\(2005\)037\[0444:CSIAPT\]2.0.CO;2](http://doi.org/10.1657/1523-0430(2005)037[0444:CSIAPT]2.0.CO;2)
- Delgado, J. A., Mosier, A. R., Valentine, D. W., Schimel, D. S., & Parton, W. J. (1996). Long term ^{15}N studies in a catena of the

- shortgrass steppe. *Biogeochemistry*, 32(1), 41–52. <https://doi.org/10.1007/BF00001531>
- Dong, S. K., Wen, L., Li, Y. Y., Wang, X. X., Zhu, L., & Li, X. Y. (2012). Soil-quality effects of grassland degradation and restoration on the Qinghai-Tibetan Plateau. *Soil Science Society of American Journal*, 76, 2256–2264. <http://doi.org/10.2136/sssaj2012.0092>
- Epstein, H. E., Burke, I. C., & Mosier, A. R. (2001). Plant effects on nitrogen retention in shortgrass steppe 2 years after ^{15}N addition. *Oecologia*, 128(3), 422–430. <http://doi.org/10.1007/s004420100670>
- Gao, J. Q., Mo, Y., Xu, X. L., Zhang, X. W., & Yu, F. H. (2014). Spatiotemporal variations affect uptake of inorganic and organic nitrogen by dominant plant species in an alpine wetland. *Plant and Soil*, 381(1–2), 271–278. <https://doi.org/10.1007/s11104-014-2130-9>
- Harris, RB (2009). Rangeland degradation on the Qinghai-Tibetan Plateau: A review of the evidence of its magnitude and causes. *Journal of Arid Environments* 74, 1–12. <https://doi.org/10.1016/j.jaridenv.2009.06.014>
- He, S. Y., & Richards, K. (2015). Impact of meadow degradation on soil water status and pasture management—A case study in Tibet. *Land Degradation & Development*, 26, 468–479. <https://doi.org/10.1002/ldr.2358>
- Hermans, C., Hammond, J. P., White, P. J., & Verbruggen, N. (2006). How do plants respond to nutrient shortage by biomass allocation? *Trends Plant Science*, 11, 610–617. <https://doi.org/10.1016/j.tplants.2006.10.007>
- Hungate, B. A., Stiling, P. D., Dijkstra, P., Johnson, D. W., Ketterer, M. E., Hymus, G. J., ... Drake, B. G. (2004). CO_2 elicits long-term decline in nitrogen fixation. *Science*, 304(5675), 1291–1291. <https://doi.org/10.1126/science.1095549>
- Iversen, C. M., Bridgman, S. D., & Kellogg, L. E. (2010). Scaling plant nitrogen use and uptake efficiencies in response to nutrient addition in peatlands. *Ecology*, 91(3), 693–707. <https://doi.org/10.1890/09-0064.1>
- Jiang, J., Shi, P. L., Zong, N., Fu, G., Shen, Z. X., Zhang, X. Z., & Song, M. H. (2015). Climatic patterns modulate ecosystem and soil respiration responses to fertilization in an alpine meadow on the Tibetan Plateau, China. *Ecological Research*, 30, 3–13. <https://doi.org/10.1007/s11284-014-1199-1>
- Jiang, L. L., Wang, S. P., Zhe, P., Xu, X. L., Kardol, P., Li, Y. M., ... Jones, D. L. (2018). Plant organic N uptake maintains species dominance under long-term warming. *Plant and Soil*, 433, 243–255. <https://doi.org/10.1007/s11104-018-3836-x>
- Jing, X., Chen, X., Xiao, W., Lin, L., Wang, C., He, J. S., & Zhu, B. (2018). Soil enzymatic responses to multiple environmental drivers in the Tibetan grasslands: insights from two manipulative field experiments and a meta-analysis. *Pedobiologia*, 71, 50–58. <https://doi.org/10.1016/j.pedobi.2018.10.001>
- Li, J. J., Yang, C., Liu, X. L., & Shao, X. Q. (2018). Inconsistent stoichiometry response of grasses and forbs to nitrogen and water additions in an alpine meadow of the Qinghai-Tibet Plateau. *Agriculture, Ecosystems and Environment*, 279, 178–186. <https://doi.org/10.1016/j.agee.2018.12.016>
- Li, Y. Y., Dong, S. K., Wen, L., Wang, X. X., & Wu, Y. (2014). Soil carbon and nitrogen pools and their relationship to plant and soil dynamics of degraded and artificially restored grasslands of the Qinghai-Tibetan Plateau. *Geoderma*, 213, 178–184. <https://doi.org/10.1016/j.geoderma.2013.08.022>
- Liu, H., Mi, Z., Lin, L., Wang, Y., Zhang, Z., Zhang, F., ... He, J. S. (2018). Shifting plant species composition in response to climate change stabilizes grassland primary production. *Proceedings of the National Academy of Sciences*, 115(16), 4051–4056. <https://doi.org/10.1073/pnas.1700299114>
- Liu, M., Li, C., Xu, X., Wanek, W., Jiang, N., Wang, H., & Yang, X. (2017). Organic and inorganic nitrogen uptake by 21 dominant tree species in temperate and tropical forests. *Tree Physiology*, 37, 1–12. <https://doi.org/10.1093/treephys/tpx046>
- Liu, M., Xu, F., Xu, X., Wanek, W., & Yang, X. (2018). Age alters uptake pattern of organic and inorganic nitrogen by rubber trees. *Tree Physiology*, 38, 1685–1693. <https://doi.org/10.1093/treephys/tpy031>
- Liu, S., Schleuss, P. M., & Kuzyakov, Y. (2017). Responses of degraded Tibetan Kobresia pastures to N addition. *Land Degradation & Development*, 29, 303–314. <https://doi.org/10.1002/ldr.2720>
- Liu, Y., Xu, X.-R., Wei, X., Wang, D., Wang, Y., & Wang, Y. (2013). Plant and soil responses of an alpine steppe on the Tibetan Plateau to multi-level nitrogen addition. *Plant and Soil*, 373(1–2), 515–529. <https://doi.org/10.1007/s11104-013-1814-x>
- Lü, X. T., Feike, A. D., Kong, D. L., Wang, Z. W., & Han, X. G. (2014). Plant nitrogen uptake drives responses of productivity to nitrogen and water addition in a grassland. *Scientific Reports*, 4, 4817. <https://doi.org/10.1038/srep04817>
- Ma, L., X. X. R., Liu, T. J., Liu, Y. K., Yang, Y. J., & Liu, J. R. (2015). Effects of reclaimed water on soil nutrient of cool-season turfgrass in Lanzhou. *Pratacultural Science*, 32(2), 182–187. <https://doi.org/10.11829/j.issn.1001-0629.2014-0072>
- Onipchenko, V. G., Makarov, M. I., Van Logtestijn, R. S. P., Ivanov, V. B., Akhmetzhanova, A. A., & Tekeev, D. K. (2009). New nitrogen uptake strategy: Specialized snow roots. *Ecological Letters*, 12(8), 758–764. <https://doi.org/10.1111/j.1461-0248.2009.01331.x>
- Ouyang, S., Tian, Y., Liu, Q., Zhang, L., Wang, R., & Xu, X. (2016). Nitrogen competition between three dominant plant species and microbes in a temperate grassland. *Plant and Soil*, 408(1–2), 1–12. <https://doi.org/10.1007/s11104-016-2904-3>
- Pervanchon, F., Bockstaller, C., Amiaud, B., Peigné, B. P. Y., Vertès, F., Fiorelli, J.-L., & Plantureux, S. (2005). A novel indicator of environmental risks due to nitrogen management on grasslands. *Agriculture, Ecosystems and Environment*, 105(1), 1–16. <https://doi.org/10.1016/j.agee.2004.06.001>
- Schleuss, P. M., Heitkamp, F., Sun, Y., Miehe, G., Xu, X., & Kuzyakov, Y. (2015). Nitrogen uptake in an alpine Kobresia, pasture on the Tibetan Plateau: localization by ^{15}N labeling and implications for a vulnerable ecosystem. *Ecosystems*, 18(6), 946–957. <https://doi.org/10.1007/s10021-015-9874-9>
- Shang, Z., Yang, S., Wang, Y., Shi, J., Ding, L., & Long, R. (2016). Soil seed bank and its relation with above-ground vegetation along the degraded gradients of alpine meadow. *Ecological Engineering*, 90, 268–277. <https://doi.org/10.1016/j.ecoleng.2016.01.067>
- Shang, Z. H., Tang, Y., & Long, R. J. (2010). Allelopathic effect of aconitum pendulum (ranunculaceae) on seed germination and seedlings of five native grass species in the Tibetan Plateau. *Nordic Journal of Botany*, 29, 488–494.
- Shi, J. J., Hong, F. Z., Ma, Y. S., Zhang, D. G., Wang, Y. L., Yang, S. H., ... Li, S. X. (2011). Effects of fertilization and herbicide on plant community of artificial grassland in the three rivers area. *Acta Agrestia Sinica*, 19(5), 724–728.
- Sun, X., Yu, K., Shugart, H. H., & Wang, G. (2016). Species richness loss after nutrient addition as affected by N:C ratios and phytohormone GA (3) contents in an alpine meadow community. *Journal of Plant Ecology*, 9(2), 201–211. <https://doi.org/10.1093/jpe/rtv037>
- Tilman, D. (1987). Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs*, 57(3), 190–214. <https://doi.org/10.2307/2937080>
- Vitousek, P. M., & Howarth, R. W. (1991). Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry*, 13(2), 87–115. <https://doi.org/10.1007/BF00002772>
- Wang, D., He, H. L., Gao, Q., Zhao, C. Z., Zhao, W. Q., Yin, C. Y., ... Liu, Q. (2017). Effects of short-term N addition on plant biomass allocation and C and N pools of the *Sibiraea angustata* scrub ecosystem. *European Journal of Soil Science*, 68, 212–220. <https://doi.org/10.1111/ejss.12414>

- Wang, J., Shi, F., Xu, B., Wang, Q., Wu, Y., & Wu, N. (2014). Uptake and recovery of soil nitrogen by bryophytes and vascular plants in an alpine meadow. *Journal of Mountain Science*, 11(2), 475–484. <http://ir.imde.ac.cn/handle/131551/6859>
- Wang, P., Limpens, J., Nauta, A., Huissteden, C. V., Rijssel, S. Q. V., & Mommer, L. (2018). Depth-based differentiation in nitrogen uptake between graminoids and shrubs in an arctic tundra plant community. *Journal of Vegetation Science*, 29(1), 34–41. <https://doi.org/10.1111/jvs.12593>
- Wang, W. Y., Ma, Y. G., Jin, X., Wang, H. C., Zhu, J. F., & Zhou, H. K. (2012). The uptake diversity of soil nitrogen nutrients by main plant species in *Kobresia humilis*, alpine meadow on the Qinghai-Tibet plateau. *Science China Earth Sciences*, 55(10), 1688–1695. <https://doi.org/10.1007/s11430-012-4461-9>
- Wang, W. Y., Wang, Q. J., & Lu, Z. Y. (2009). Soil organic carbon and nitrogen content of density fractions and effect of meadow degradation to soil carbon and nitrogen of fractions in alpine *Kobresia* meadow. *Science in China*, 52(5), 660–668. <https://doi.org/10.1007/s11430-009-0056-5>
- Wiener, G., Han, J., & Long, R. (Eds.). (2006). *The Yak* (second ed.). FAO: Bangkok. <http://www.fao.org/3/ad347e/ad347e00.htm>
- Xia, J. Y., & Wan, S. Q. (2008). Global response patterns of terrestrial plant species to nitrogen addition. *New Phytologist*, 179(2), 428–439. <https://doi.org/10.1111/j.1469-137.2008.02488.x>
- Xing S, Wang J, Zhou Y, Bloszies SA, Tu C, & Hu S (2015) Effects of NH₄⁺-N/NO₃⁻-N ratios on photosynthetic characteristics, dry matter yield and nitrate concentration of spinach. *Experimental Agriculture* 51 (01): 151–160. <https://doi.org/10.1017/s0014479714000192>
- Xu, X., Wanek, W., Zhou, C., Richter, A., Song, M., Cao, G., ... Kuzyakov, Y. (2014). Nutrient limitation of alpine plants: Implications from leaf N:P stoichiometry and leaf $\delta^{15}\text{N}$. *Journal of Plant Nutrition and Soil Science*, 177(3), 378–387. <https://doi.org/10.1002/jpln.201200061>
- Xu, X. L., Ouyang, H., Cao, G. M., Richter, A., Wanek, W., & Kuzyakov, Y. (2011). Dominant plant species shift their nitrogen uptake patterns in response to nutrient enrichment caused by a fungal fairy in an alpine meadow. *Plant and Soil*, 34, 495–504. <https://doi.org/10.1007/s11104-010-0662-1>
- Yang, C., Xu, S., Liu, L., Min, H., Zheng, T., Wei, S., ... Jiang, L. (2015). Nitrogen uptake and utilization by no-tillage rice under different soil moisture conditions—A model study under simulated soil conditions. *Plant Production Science*, 18(2), 118–127. <https://doi.org/10.1626/pp.s.18.118>
- Yang, Y., Fang, J., Tang, Y., Ji, C., Zheng, C., He, J., & Zhu, B. (2008). Storage, patterns and controls of soil organic carbon in the Tibetan grasslands. *Global Change Biology*, 14(7), 1592–1599. <https://doi.org/10.1111/j.1365-2486.2008.01591.x>
- Yin, Y., Wang, Y., Li, S., Liu, Y., Zhao, W., Ma, Y., & Bao, G. (2019). Soil microbial character response to plant community variation after grazing prohibition for 10 years in a Qinghai-Tibetan alpine meadow. *Plant and Soil*. <https://doi.org/10.1007/s11104-019-04044-7>
- You, C., Wu, F., Gan, Y., Yang, W., Hu, Z., Xu, Z., ... Ni, X. (2017). Grass and forbs respond differently to nitrogen addition: A meta-analysis of global grassland ecosystems. *Scientific Reports*, 7(1), 1563. <https://doi.org/10.1038/s41598-017-01728-x>
- Zhang J, Cai Z, Müller C (2018) Terrestrial N cycling associated with climate and plant-specific N preferences: A review. *European Journal of Soil Science* 69: 488–501. <https://doi.org/10.1111/ejss.12533>
- Zhang, L., Unteregelsbacher, S., Hafner, S., Xu, X., Schleuss, P. M., Miehe, G., & Kuzyakov, Y. (2017). Fate of organic and inorganic nitrogen in crusted and non-crusted *Kobresia* grasslands. *Land Degradation and Development*, 28(1), 166–174. <https://doi.org/10.1002/ldr.2582>
- Zhang, R., Bai, Y. F., Zhang, T., Henkin, Z., Degen, A. A., Jia, T. H., ... Shang, Z. (2019). Driving factors that reduce soil carbon, sugar and microbial biomass in degraded alpine grasslands. *Rangeland Ecology and Management*, 72, 396–404. <https://doi.org/10.1016/j.rama.2018.10.001>
- Zhang, R., Wang, Y., Ma, L., Sang, C., Wang, L., Guo, R., ... Shang, Z. (2014). Species diversities of plant communities of degraded artificial grassland, “heitutan” and natural grassland in the “Three-river Headwaters” region. *Acta Agrestia Sinica*, 22(6), 1171–1178. <https://doi.org/10.11733/j.issn.1007-0435.2014.06.004>
- Zhou, B., Zhang, L., Yang, W., Mao, Y., Chen, C., & Xing, S. (2017). Differential uptake of soluble organic and inorganic nitrogen by two fruit species: *Dimocarpus longan* Lour. and *Eriobotrya japonica* Lindl. *Journal of Soils and Sediments*, 17(6), 1579–1587. <https://doi.org/10.1007/s11368-016-1635-7>
- Zhou, M., Zhu, B., Butterbach-Bahl, K., Zheng, X., Wang, T., & Wang, Y. (2013). Nitrous oxide emissions and nitrate leaching from a rain-fed wheat-maize rotation in the Sichuan basin, china. *Plant and Soil*, 362 (1–2), 149–159. <https://doi.org/10.1007/s11104-012-1269-5>

SUPPORTING INFORMATION

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