Soil gravels and plant species configuration control vegetation restoration in Qinghai-Tibet Plateau

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Abstract

Soil gravel content strongly affects ecological restoration; however, the response and mechanism of plant traits to soil gravel content under the sensitive and fragile natural environment of Qinghai-Tibet Plateau remains unclear. Herein, soils with three gravel content (10%, 30%, 50%) in the southeastern Tibetan Plateau were selected, and three plant species (one indigenous specie of *Elymus dahuricus (Ed)*, and two introduced ones of *Festuca elata* (*Fe*) and *Medicago sativa* (*Ms*)) were used in seven planting patterns with different proportions (*Fe*, *Ed*, *Ms*, *Fe* + *Ed* (1:1), *Fe*+ *Ms* (2:1), *Ed* + *Ms* (2:1), *Fe*+ *Ed*+ *Ms* (2:2:1)). Plant traits, phytochemical properties and soil stoichiometric characteristics were measured to explore the interactive effects of soil gravels and plant species on vegetation restoration. Average plant height, coverage, shoot biomass and total biomass were most affected by plant species (F=277˜611, p<0.01), followed by gravel content (F=90˜195, p<0.01) and their interaction (F=5˜51, p<0.05); root biomass was most affected by gravel content (F=130, p<0.01). Among plant species, shoot and root biomass, total biomass overall decreased in the order of *Fe+Ed+Ms¿Fe¿Fe+Ms¿Fe+Ed¿Ms¿Ms+Ed¿Ed*. Plant total biomass, shoot biomass, root biomass and shoot/root ratio among different soils overall decreased in the order of low¿ high¿ medium gravel contents. All plant species were restricted by soil nitrogen except for *Ed* and *Ed*+ *Ms* (N:P>14). In addition, average plant height, coverage, shoot biomass and total biomass were separately negatively and positively correlated with bulk density and total porosity (r=-0.88˜-0.96 and 0.78˜0.91, p<0.05), so did for total nitrogen, total phosphorus, organic carbon, C:N and N:P of shoot fraction and rhizosphere soils (|r|=0.69˜0.97, p<0.05), indicating that gravel content affects plant growth through bulk density and nutrients. Therefore, optimizing the configuration of soil properties (mainly nitrogen and compactness) and plant species (isecologic niche plants) is an effective strategy for ecological restoration in the Qinghai-Tibet Plateau.

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Abstract: Soil gravel content strongly affects ecological restoration; however, the response and mechanism of plant traits to soil gravel content under the sensitive and fragile natural environment of Qinghai-Tibet Plateau remains unclear. Herein, soils with three gravel content (10%, 30%, 50%) in the southeastern Tibetan Plateau were selected, and three plant species (one indigenous specie of *Elymus dahuricus (Ed)* , and two introduced ones of *Festuca elata* (*Fe*) and *Medicago sativa* (*Ms*)) were used in seven planting patterns with different proportions (*Fe* , *Ed* , *Ms* , *Fe* +*Ed*(1:1), *Fe* +*Ms* (2:1), *Ed* +*Ms* (2:1),*Fe* +*Ed* +*Ms* (2:2:1)). Plant traits, phytochemical properties and soil stoichiometric characteristics were measured to explore the interactive effects of soil gravels and plant species on vegetation restoration. Average plant height, coverage, shoot biomass and total biomass were most affected by plant species (F=277˜611, p<0.01), followed by gravel content (F=90˜195, p<0.01) and their interaction (F=5˜51, p<0.05); root biomass was most affected by gravel content (F=130, p<0.01). Among plant species, shoot and root biomass, total biomass overall decreased in the order of *Fe+Ed+Ms¿Fe¿Fe+Ms¿Fe+Ed¿Ms¿Ms+Ed¿Ed* . Plant total biomass, shoot biomass, root biomass and shoot/root ratio among different soils overall decreased in the order of low¿ high¿ medium gravel contents. All plant species were restricted by soil nitrogen except for *Ed* and *Ed* +*Ms* (N:P>14). In addition, average plant height, coverage, shoot biomass and total biomass were separately negatively and positively correlated with bulk density and total porosity (r=-0.88˜-0.96 and 0.78˜0.91, p<0.05), so did for total nitrogen, total phosphorus, organic carbon, C:N and N:P of shoot fraction and rhizosphere soils (|r|=0.69˜0.97, p<0.05), indicating that gravel content affects plant growth through bulk density and nutrients. Therefore, optimizing the configuration of soil properties (mainly nitrogen and compactness) and plant species (isecologic niche plants) is an effective strategy for ecological restoration in the Qinghai-Tibet Plateau.

Keywords: Ecological restoration, Soil gravel, Plant species, Plant biomass, Tibetan Plateau.

Introduction

As the key component of soil texture, the content and distribution of gravel particles affect soil physical structure and hydrological processes such as soil water storage, runoff, water infiltration, solute transport and water flow (Smets et al.,2011; Qiu et al.,2015; Zhang et al.,2016;Wang et al.,2019; Mahinroosta et al., 2021); they also could reduce the mechanical resistance to root extension (Alameda et al.,2012), and may cause root aggregation and growth (Clark et al.,2003). But the impact and the underlying mechanism of soil gravels are relatively complex (Han et al.,2021; Li et al.,2020). In order to better comprehensively unravel the effect of soil on plant growth, the importance of gravel cannot be ignored (Du et al.,2022).

At present, a large number of studies have shown that gravels could promote cation exchange, and store water to facilitate plant growth (Certini et al.,2004). For instance, in the foothills of the Himalayas mountains, high gravel content of up to 40% can preserve rainwater and promote better economic benefits for leguminous plants or relatively drought-tolerant crops with vigorous rootstock systems (Grewal et al.,1984). Hubbert et al. (2001) reported that in stony soil, gravel in the soil can provide 70% water for plant growth. Other studies have found that the addition of a certain amount of waste gravel can improve soil physical properties, and is conducive to the improvement of soil quality and crop yield (Ye et al.,2021; Jin et al.,2022). In the arid area of northwest China, the addition and mulching of appropriate topsoil gravel can increase the retention of soil moisture (Qiu et al.,2021) and increase the yield of *Malus pumila* , *Zea mays*and other crops (Suo et al.,2019). For the pot culture of flue-cured tobacco, adding 10%-30% volcanic ash gravel significantly promoted the plant height and maximum leaf area of the overground part of the initial flue-cured tobacco, but the influence of volcanic ash gravel on the growth of tobacco plants became weaker with the extension of planting time (Shen et al.,2012). Less gravel inhibits the development of tobacco plants, but is beneficial to the accumulation of dry matter in the later period, while the opposite is true when gravel content is too high (Luo et al.,2014).

In general, soil gravel has different effects on plant growth at different growth stages. The content of gravel in the soil also leads to a decrease in soil water retention and the lack of root-soil contact area, and the lack of resources will restrict the growth of plants (Rytter et al., 2012; Ceacero et al., 2020). Studies on the Loess Plateau have found that high gravel content (50%) restricts plant growth and dry matter accumulation (Mi et al., 2016). For grassland in the Qinghai-Tibet Plateau, gravel content was found to negatively correlate with above-ground biomass and vegetation coverage (Yu et al., 2015), and soil organic carbon and total nitrogen reserves were the highest when gravel was covered by 40-50% (Wang et al., 2011). Additonally, soil gravel could reduce plant nitrogen and phosphorus contents, and inhibit plant growth and development (Masoni et al., 2008). A potted pot study on the adaptation of legume Sandalwood to soil gravels found that with the increase of gravel content, the root/shoot ratio of seedlings showed an increasing trend, and the biomass of stems transferred to roots and leaves, especially to low-grade roots (Liu et al., 2016). Therefore, the influence of gravel content on plant traits is species-specific, and the difference response of vegetation to soil gravels varys in different ecosystems.

Large-scale projects have disturbed soil surface texture and damaged native vegetation, and if timely ecological restoration is not carried out, it may cause serious ecological consequences such as land degradation and water and soil loss (Zhang et al.,2015; Si et al.,2020; Chen et al.,2020). After the ecological environment is disturbed by engineering, scientific and effective vegetation restoration is needed to ensure ecological security (Xie et al.,2021). However, the complex geological background and unique, sensitive and fragile natural environment of the Qinghai-Tibet Plateau make ecological restoration techniques scarce (Zhang et al.,2016b; Xu et al.,2022; Li et al.,2022). Gravel soils are widely distributed in the Tibetan Plateau (Pan et al.,2017). Therefore, it is urgent to understand the mechanism of soil gravel on plant traits to carry out the effective ecological restoration. The objectives of this study were to: (i) evaluate the effects of gravel content and plant species on plant growth; (ii) explore the mechanism of action of gravel content and plant species on plant growth based on stoichiometry.

2. Material and methods

Studied site

The studied site is located in Nyingchi City, Tibet Autonomous Region, China (E94°45'25", N29°58'10"), which has a warm and semi-humid plateau climate with annual precipitation and temperature of 650 mm and 8.7, respectively. This region belongs to the upper reaches of the Yarlung Zangbo River high mountain gorge area, and the average elevation is 2940 m. The typical soil types are mountain brown soil, -yellow-brown soil and sandy loam deposited in river flats, which are generally in coarse textures and possess various gravel contents (Gao et al.,2021). The main native herbage plants include *Kobresia myosuroides* , *Stipa capillata* , *Carex hirta, Potentilla chinensis, Elymus dahuricus* .

2.2 Experimental design

The ecological restoration experiment was conducted from July to November 2020. According to the previous field survey data of highway, railway and other construction areas in Nyingchi(Soil gravel content between 10%˜50%), three classes of soils with gravel contents (>2 mm) of 10% (low), 30% (medium) and 50% (high) were selected as ecological restoration test materials. Their physical and chemical properties are summarized in Table 1. In general, as gravel content increased, the contents of sand, silt, clay, total porosity, total nitrogen and phosphorus, and organic carbon decreased. Soil with medium gravel content had the largest bulk density. These studied soils were neutral with a pH of 6.87˜6.98. These soils were packed into 1 mx 3 m test plots with a thickness of 60 cm according to native soil compactness.

Table 1 Physical and chemical properties of studied soils

Three plant species of *Festuca elata* (*Fe,*indigenous specie), *Medicago sativa* (*Ms,* introduced specie) and *Elymus dahuricus*(*Ed,* introduced specie) were selected as experimental plant materials according to the commonly used plants in ecological restoration projects and the natural vegetation of Qinghai-Tibet Plateau, Among them, *Festuca elata* and *Medicago sativa* are ecological restoration plants introduced in Qinghai Province, and*Elymus dahuricus* is a native plant in Tibet. Considering the ecological restoration effect of plants and the more obvious competition effect between plants (same or different species), the method of close planting is adopted(Huang et al., 2021; Leinauer et al., 2021), seven typical and widely used plant species communities were set on studied soils, that is, *Festuca elata* (seeding rate of 200 kg hm^{-2})), *Elymus dahuricus* (seeding rate of 200 kg hm^{-2}), *Medicago sativa* seed (seeding rate of 100 kg hm^{-2}), *Festuca elata* (seeding rate of 200 kg hm^{-2}) plus *Elymus dahuricus* (seeding rate of 200 kg hm^{-2}), *Festuca elata* (seeding rate of 200 kg hm^{-2}) plus *Medicago sativa*(seeding rate of 100 kg hm^{-2}), *Elymus dahuricus*(seeding rate of 200 kg hm^{-2}) plus *Medicago sativa* (seeding rate of 100 kg hm^{-2}), and*Festuca elata* (seeding rate of 200 kg hm^{-2}) plus *Elymus dahuricus* (seeding rate of 200 kg hm^{-2}) plus *Medicago sativa* (seeding rate of 200 kg hm^{-2}). These plant species treatments are separately denoted as *Fe* , *Ed* , *Ms* ,*Fe* +*Ed* (1:1), *Fe* +*Ms* (2:1), *Ed*+*Ms* (2:1), and *Fe* +*Ed* +*Ms* (2:2:1). Three replicates were set for each treatment, and the same planting method of evenly spreading and covering 0.2-0.5cm soil was adopted. After sowing, no additional field management (such as fertilization and watering) were conducted during the growth periods (94 days), and the experiments ended in November 2020.

2.3. Sample collection and measurement

Before the ecological restoration experiments, composited and undisturbed soil samples were taken from 0-10 cm and 10-20 cm soil layers, and then brought back to the laboratory for soil physical and chemical analysis. At the end of plant growth, plant traits including coverage, natural height, above-ground biomass and root biomass were measured. Rhizosphere soils (about 3 mm soil fractions around the roots) were collected.

Soil particle size composition was determined by the sieving-pipette method after ultrasonic dispersion; field water content by weight method after oven-dried; bulk density and total porosity by weight method on undisturbed soil cores (100 cm^3); organic carbon of soils and plant samples by potassium dichromate oxidation and titration with ferrous sulfate; total nitrogen and phosphorus contents of plant and soil samples by Smartchem200 automatic discontinuous chemical analyzer after acid digestion (Tang et al.,2022; Institute of Soil Science.,1978).

2.4. Statistical analysis

Significant differences among treatments were analyzed by the two-factor variance of analysis (ANOVA) with Duncan test ($p<0.05$) to evaluate the effect of soil gravel content, plant species and their interaction on plant traits during vegetation restoration. Pearson's correlation analysis was used to examine the relationships between plant traits and soil properties. Redundancy analysis (RDA) was conducted to analyze the relationships between plant trait indices, the content of C, N, and P and their stoichiometric characteristics and soil properties under different plant species treatments. All data analyses were performed using SPSS 20.0 and Canoco 4.5.

3.Results

3.1 Plant traits

ANOVA results (Table 2) showed that average plant height, cover, shoot biomass and total biomass were most affected by plant species (F=277˜611, $p<0.01$), followed by gravel content (F=90˜195, $p<0.01$) and their interaction (F=5˜51, $p<0.05$); root biomass was most affected by gravel content (F=130, $p<0.01$). Plant total biomass, shoot biomass, root biomass and their biomass ratio(shoot/root) among different soils overall decreased in the order of low¿high¿medium gravel content(Fig 1). In addition, different types of plants shoot biomass, root biomass and total biomass overall decreased in the order of*Fe+Ed+Ms* ¿*Fe* ¿*Fe+Ms* ¿*Fe+Ed* ¿*Ms* ¿*Ms+Ed* ¿*Ed* . Among them, *Ms* (2.15kg m^{-2}) and*Fe+Ed+Ms* (2.08kg m^{-2}) on low gravel content soil had the highest total biomass, while *Ed*(l0.69˜0.74kgm^{-2}) had the lowest total biomass and showed no significant difference among three gravel soils ($p>0.05$).

Table 2 ANOVA results of the effects of gravel content, plant species and their interaction on plant traits.

Fig 1 . The changes of total, shoot, root biomass and their ratio with gravel content for different plant species. Error bars refer to standard deviation. Different lowercase letters indicate significant differences among different gravel soils; different capital letters indicate significant differences among all treatments ($p<0.05$). Fe, *Festuca elata* ; Ed,*Elymus dahuricus* ; Ms, *Medicago sativa* ; Fe+Ed,*Festuca elata plus Elymus dahuricus* ; Fe+Ms, *Festuca elata plus Medicago sativa* ; Ms+Ed, *Medicago sativa plus Elymus dahuricus* ;Fe+Ms+Ed, *Festuca elata plus Medicago sativa plus Elymus dahuricus* .

Fig. 2 The changes of plant height and coverage with gravel content for different plant species. (a), Total coverage; (b), Plant height; (c), Coverage of different plant species; (d), Height of different plant species. Error bars refer to standard deviation. Different lowercase letters indicate significant differences among different gravel soils ($p<0.05$). Fe, *Festuca elata* ; Ed,*Elymus dahuricus* ; Ms, *Medicago sativa* ; Fe+Ed,*Festuca elata plus Elymus dahuricus* ; Fe+Ms, *Festuca elata plus Medicago sativa* ; Ms+Ed, *Medicago sativa plus Elymus dahuricus* ;Fe+Ms+Ed, *Festuca elata plus Medicago sativa plus Elymus dahuricus* .

Fig. 2 shows that plant average height, and coverage among different gravel contents overall decreased in the order of low¿ high¿ medium gravel content. Among different soils, the average height of *Ms*and *Fe+Ed+Ms* decreased in the order of low¿medium¿high; the average coverage of *Ed* decrease in the order of low¿medium¿high, while that of *Fe+Ed* , *Fe+Ed+Ms* followed an opposite trend.

3.2 Carbon, nitrogen, phosphorus content and stoichiometry of plant and soil

Fig. 3 Content and stoichiometric characteristics of organic carbon, total nitrogen, and total phosphorus in plant root and shoot fractions and rhizosphere soils with different gravel contents. Error bars refer to standard deviation Different lowercase letters indicate significant differences among different gravel soils ($p<0.05$).

As shown in Fig. 3, OC, TN, TP, C: N, C:P, and N:P of different soils have significant differences($p<0.05$). TP of shoot, root and rhizosphere decreased in the order of low¿medium¿high gravel content; TN was larger for low than for medium and high gravel contents; organic carbon content showed no significant difference among different gravel soils (p¿0.05). C:N of rhizosphere soil was larger for high than for medium and low gravel contents; TP of shoot and root fractions decreased in the order of high¿medium¿low gravel content; N:P of shoot and root fractions was larger for high than for medium and low gravel contents.

Fig. 4. Content and stoichiometric characteristics of organic carbon, total nitrogen, and total phosphorus in plant root and aboveground fractions and rhizosphere soils for different plant species. Error bars refer to standard deviation; respectively. Different lowercase letters indicate significant differences among different plant species ($p<0.05$). Fe, *Festuca elata* ; Ed, *Elymus dahuricus* ; Ms, *Medicago sativa* ; Fe+Ed, *Festuca elata plus Elymus dahuricus* ; Fe+Ms, *Festuca elata plus Medicago sativa* ; Ms+Ed, *Medicago sativa plus Elymus dahuricus* ;Fe+Ms+Ed,*Festuca elata plus Medicago sativa plus Elymus dahuricus* .

Fig. 4 illustrates the contents and stoichiometric characteristics of OC, TN and TP of plant shoot, root fractions and rhizosphere soils among different plant species. For plant shoot fraction, TN content was the largest and the lowest for *Ms* (30.76 g kg^{-1}) and *Fe* (11.40 g kg^{-1}), respectively; TP content of *Ed* (2.23g kg^{-1}), *Ms* (2.13g kg^{-1}), *Fe+Ed* (2.19g kg^{-1}),*Fe+Ms* (1.81g kg^{-1}), *Ed+Ms* (1.92g kg^{-1}) were significantly larger than that of *Fe*(1.57g kg^{-1}) and *Fe+Ed+Ms* (1.55g kg^{-1}); OC content was the lowest for *Ms+Ed*(422.99 g kg^{-1}) among plant species. C:N was significantly different ($p<0.05$), while C:P was not statistically significant (p¿0.05). N:P of *Ms* (14.71g kg^{-1}) and *Ms+Ed* (14.01g kg^{-1}) was significantly higher than that of *Fe* (7.42g kg^{-1}) and *Fe+Ed* (8.21g kg^{-1}). For plant root fraction, TN, TP, C: N, C:P and N:P had significant differences($p<0.05$), among which the OC content of *Ms*(468.35 g kg^{-1}) and *Fe+Ms* (469.38g kg^{-1}) was larger than that of *Fe* (406.33g kg^{-1}) and *Fe+Ms+Ed* (408.22g kg^{-1}). The OC, TP, C:N and C:P of rhizosphere soils showed no significant differences among plant species except*Fe+Ms* .

3.3 Linkage between plant traits with rhizosphere and soil properties

Correlation analysis indicated (Table 3) that all plant traits were positively correlated with soil organic carbon (r=0.69˜0.76, $p<0.05$), and C:P (r=0.72˜0.85, $p<0.05$) and total porosity (r=0.78˜0.91, $p<0.05$); and negatively correlated with bulk density (r=-0.96˜-0.88, $p<0.01$). Among these plant traits, shoot and total biomass were positively correlated with total nitrogen (r=0.71 and 0.69, $p<0.05$). In addition, all plant traits were positively correlated with rhizosphere total nitrogen (r=0.81˜0.96, $p<0.01$), and total phosphorus (r=0.70˜0.89, $p<0.05$) and N:P (r=0.71˜0.93, $p<0.05$); and negatively correlated with C:N (r=-0.68˜-0.85, $p<0.05$). Plant height, shoot and total biomass were positively correlated with rhizosphere organic carbon (r=0.71 and 0.69, $p<0.05$).

Table3 Pearson correlation coefficients between plant growth indices with non-rhizosphere and rhizosphere soil properties (n = 9)

Root organic carbon, C:N,C:P were positively correlated with soil organic carbon, and C:N (r= 0.67˜0.78, $p<0.05$); total nitrogen (TN), and total phosphorus (TP) were positively correlated with total porosity (r=0.73 and 0.67, $p<0.05$); N:P was positively correlated with bulk density and pH (r=0.72 and 0.78, $p<0.05$). There was a significant positive correlation between C:P, bulk density, pH and soil C:N (r=0.77, 0.78, 0.72 and 0.82, $p<0.05$); TP was negatively correlated with soil C:N (r=0.80, $p<0.01$), were positively correlated with C:P,N: P (r=-0.68 and 0.68, $p<0.05$).

Root total phosphorus was positively correlated with rhizosphere total nitrogen (r=0.67, $p<0.05$); root total nitrogen and total phosphorus were positively correlated with total phosphorus (r=0.83 and 0.93, $p<0.01$); root C:P was negatively correlated with total phosphorus (r=-0.91, $p<0.01$); root total phosphorus was positively correlated with rhizosphere soil organic carbon (r=0.72, $p<0.05$), root organic carbon, C:N, C:P and N:P were negatively correlated with rhizosphere organic carbon (r=-0.92˜ -0.72, $p<0.05$); root total nitrogen and total phosphorus was positively correlated with C:N (r=0.96 and 0.83, $p<0.01$), and root C:P was negatively correlated with C:N (r=0.80, $p<0.05$); root C:P and N:P were positively correlated with C:P (r=0.74 and 0.98, $p<0.05$); N:P was positively correlated with root N:P (r=0.73, $p<0.05$).

There was a significant positive correlation between shoot total nitrogen and organic carbon and rhizosphere total nitrogen (r=0.73 and 0.82, $p<0.05$); shoot total nitrogen and total phosphorus positively correlated with (r=0.88 and 0.86, $p<0.01$), and shoot C:N,C:P was a negative correlation with total phosphorus (r=-0.93 and -0.78, $p<0.05$); shoot total phosphorus and total phosphorus was positively correlated with (r=0.68 and 0.86, $p<0.05$), and shoot C:P and N:P were negatively correlated with rhizosphere soil organic carbon (r=-0.86 and -0.75, $p<0.05$); shoot total nitrogen and phosphorus was positively correlated with C:N (r=0.82 and 0.69, $p<0.01$), and shoot C:N was negatively correlated with C:N (r=-0.96, $p<0.01$); shoot C:P and N:P was positively correlated with C:P (r=0.76 and 0.76, $p<0.05$), and shoot total phosphorus was significantly negatively correlated with (r=-0.78, $p<0.05$).

Fig. 5 RDA of the relationships among plant traits, soil properties, and their stoichiometric characteristics for different plant species. TN, soil total nitrogen; TP, soil total phosphorus; SOC, soil organic carbon;S-C/N, soil C/N ratio; S-C/P, soil C/P ratio; S-N/P, soil N/P ratio; PH, soil pH; BD, bulk density; *e* , total porosity; PTN, plant total nitrogen; PTP, plant total phosphorus; POC, plant organic carbon; P-C/N, plant C/N ratio; P-C/P, plant C/P ratio; P-N/P, plant N/P ratio; RTN, root total nitrogen; RTP, root total phosphorus; ROC, root organic carbon; R-C/N, root C/N ratio; R-C/P, root C/P ratio; R-N/P, root N/P ratio; H, Plant height; Tc, total coverage; Ab, aboveground biomass; Rb, root biomass; B, total biomass.

RDA shows that the accumulation of the first two axes in different plant growth indexes (>93%) (Fig. 5). The changes of plant trait properties (*Ms* , *Ed+Ms* , *Fe+Ed+Ms*) were mainly explained by the first axis, and those of other plants were mainly determined by the second axis. Bulk density is negatively correlated with *Fe* , *Fe+Ed* , *Ed* , *Fe+ Ms* , *Fe+Ed+Ms*(r=-0.99˜0.69, $p<0.05$), and positively correlated with *Ms* ,*Ed+Ms* (r=0.89 and 0.96, $p<0.01$); total porosity was positively correlated with*Fe* , *Ed* , *Fe+Ed* , *Fe+ Ms* , *Fe+Ed+Ms*(r=0.91,0.79,0.95,0.93 and 0.73, $p<0.05$); TN and SOC were positively correlated with *Fe* , *Fe+Ed* , *Fe+Ms*(r=0.74,0.92,0.76; r=0.75,0.80,0.79, $p<0.05$); TP and N:P were positively correlated with *Fe+Ed* (r=0.77 and 0.80, $p<0.05$). Bulk density is positively correlated with*Fe+Ed* (r=0.71, $p<0.05$), total porosity was significantly negatively correlated with *Ms* and *Ed+Ms*(r=-0.91 and -0.81 $p<0.05$); *Ms* was positively correlated with TN (r=0.97, p<0.05)and negatively with TN, TP, SOC and N:P (r=-0.92~0.74, , p<0.05);*Ed+Ms* had negative correlations with TN, TP, SOC, and N:P (r=-0.91~-0.70, p<0.05); *Fe+Ed+Ms* was negatively correlated with TN and N:P (r=-0.84,-0.83, p<0.05), and positively correlated with C:N (r=0.70, p<0.05)

Discussion

4.1 Effects of gravel content on vegetation restoration

The differences in soil physical structure and nutrients with different gravel contents directly affect the development of vegetation communities (Bhattacharya., 2021; Briat et al., 2020). The results of our study in the southeast Tibetan cold wet regions are different from that in other alpine arid areas in Tibet (Wang et al., 2011).The physical and chemical properties of soil with low gravel content are better than medium and high gravel content (Table 1). An increase in soil gravel content does not necessarily promote soil total porosity and plant biomass, indicating that the interaction between gravel and fine soil changed the soil skeleton structure, so that soil with high gravel content had more large voids than soil with medium gravel content, which reduced root mechanical resistance. Increased soil water content in the soil available space promoted the development of plant traits (Table.1, 2, Fig. 1) (Clark et al., 2003; Shi et al.,2012; Zhang et al.,2016). Appropriate gravel content would maintain low bulk density and high porosity (Gargiulo et al., 2016), which is conducive to water infiltration and solute migration (Zhou et al., 2009), and further to the absorption and utilization of nutrients by plants. This lays a foundation for the vigorous metabolism of plants and adequate formation of photosynthates (Ye et al., 2021). However, excellent water infiltration and solute migration in soil with 50% gravel content will inevitably lead to poor soil water retention and nutrient loss, resulting in water and nutrient stress on plants (Wang et al., 2011; Ceacero et al., 2020). In our study, there was a significant positive correlation between plant traits and total porosity (p<0.01), continuous rainfall during the growing season alleviated soil water stress and provided abundant water resources and concentrated transport capacity of soil nutrients for plants in the eastern Tibetan Plateau (Table 3 and 4).

Table4 RDA sequencing of soil properties affecting plant traits.

Note: Fe, *Festuca elata* ; Ed, *Elymus dahuricus* ; Ms,*Medicago sativa* ; Fe+Ed, *Festuca elata plus Elymus dahuricus* ; Fe+Ms, *Festuca elata plus Medicago sativa* ; Ms+Ed,*Medicago sativa plus Elymus dahuricus* ;Fe+Ms+Ed, *Festuca elata plus Medicago sativa plus Elymus dahuricus* ; TN, soil total nitrogen; TP, soil total phosphorus; SOC, soil organic carbon; BD, bulk density; *e* , total porosity.

The abundance of soil nutrients will promote plant growth (Vesic et al., 2020; Wu et al., 2022). For instance, soil with 10% gravel content had richer nutrients, better water retention, and lower bulk density, resulting in significantly better plant growth than soil with 50% and 30% gravel content (Table 2 and Fig. 1) (Yang et al., 2022). Further study showed that the contents of TN, TP and SOC in rhizosphere soil, roots and plant aboveground parts of low gravel soil were significantly higher than those in soil containing 50% gravel and soil containing 30% gravel. Plant traits were closely related to the measurement characteristics of C, N and P. With the increase in growth rate, the N:P and C:P of plant organs tended to decrease. P content showed an increasing trend (Fig. 2) (Yan, 2022). At the same time, TN content in the above-ground parts of plants with 50% and 30% gravel content is lower than that in other parts of China, while TP content is higher than that in other parts of China, and there is a positive and significant correlation between TN and above-ground parts of plants, indicating that plant growth in the soil with 50% and 30% gravel content is also limited by nitrogen (Table.4) (Tang et al., 2018).

4.2 Effects of plant species on vegetation restoration

Plant functional trait expression is closely related to plant environmental adaptability and ecosystem structure and function. Due to the harsh, unique and sensitive natural environment and short growing season, the average height and total biomass of *Festuca elata* and*Medicago sativa* were significantly lower than those of Inner Mongolia and the Loess Plateau (Fang et al. 2021; Ren et al. 2022; Liu et al. 2022). At the same time, the average height, total coverage and total biomass of *Festuca elata* and *Medicago sativa* plants in our study were significantly higher than those of *Elymus dahuricus* ($p<0.05$) (Fig. 1), indicating that in the ecological restoration of the Qinghai-Tibet Plateau, Both *Festuca elata* and*Medicago sativa* can achieve good ecological restoration effect (McNickle and Brown 2014, Weidlich et al. 2018), but monotone landscape effect is easy to be formed by unicast plants. Moreover, the single life history strategy of *Festuca elata* and *Medicago sativa*unicast communities is difficult to cope with the long-term changes of soil with high gravel content and complex ecological environment in the Tibetan Plateau (Bennett et al. 2016) (Fig. 1 and 2). At the same time, it was also confirmed that the mixed planting effect of different niche plants such as *Festuca elata* and *Medicago sativa* was better than that of single planting of *Festuca elata* and*Medicago sativa* in the ecological restoration of the Tibetan Plateau, because the mixed sowing of Gramineae and legumes avoided the interspecific competition to a certain extent. The intraspecific competition was alleviated, the harmonious growth relationship was presented, and the community biomass was promoted (Sturludottir, xie et al., 2020; Diaz et al. 1998), however, *Festuca elata plusElymus dahuricus* with heterogeneous and niche plants had adverse effects on community productivity due to the same life-history strategies and similar soil resource requirements (Huangfu et al., 2021, Miao et al. 2022) .

In general, soil bulk density and total porosity were the main factors affecting plant traits in all planting patterns (Fig. 1, 2, 5). However, the responses of plant traits to soil physical structure varied greatly among different plant species and planting patterns and the community may not be affected by nutrients, For example *Medicago sativa* and*Medicago sativa* plus *Elymus dahuricus* were affected by soil compactness ($p<0.05$). Total porosity had the strongest explanatory power for shallow-rooted, fast-growing tall fescue ($p<0.01$) (Persi et al. 2022) (Fig. 1, 4, 5). *Elymus dahuricus* was less affected by nutrients in terms of nitrogen fixation of root rhizobium and higher TP content in the soil, However, soil with 30% and 50% gravel content could not provide enough nutrients for*Festuca elata* and *Festuca elata* plus *Elymus dahuricus* . Plant growth is limited by TN (Gusewell et al., 2004; Narangerel, 2022; Leinauer, 2021) (Fig. 4, 5). Most previous studies on the Qinghai-Tibet Plateau focused on the restriction of soil nitrogen and phosphorus on plant growth (Shaver et al., 1980; Hong et al., 2014). In our study, SOC all had a significant positive correlation with*Festuca elata* , *Lymus dahuricus* , *Festuca elata plus Elymus dahuricus* , and *Festuca elata plus Medicago sativa*($p<0.01$), which may be due to the low organic matter in the gravel soils, which prevented plants from absorbing water-soluble organic matter and inhibited the development of plant roots and shoot parts (Jones et al., 2012; Christ et al., 1996). The study also found that the total biomass of *Festuca elata plus Medicago sativa plus Elymus dahuricus* was significantly higher than that of other seeding modes ($P<0.05$), but did not receive nutrient restriction. This may be due to the relatively reasonable proportion of ecological factors of each component in mixed sowing, which can enhance spatial complementary, increase water and nutrient availability, reduce climate pressure or improve soil stability, and thus promote community yield in the short term (Chen et al. 2022; Huangfu et al. 2022; Craine et al. 2006) (Fig 1, 4, 5).

Conclusion

An appropriate proportion of gravels in the soil can improve the availability of soil water and promote plant growth, but the lower TN and SOC contents in soils with 30% and 50% gravel content also limit the plant growth. In addition, the introduced and domesticated plants*Festuca elata* and *Medicago sativa* had better short-term ecological restoration effects than native plants *Elymus dahuricus* . However, if *Festuca elata* plus *Elymus dahuricus* were mixed with different species and niche plants, the same life history strategy and similar soil resource requirements would enhance the competitiveness of plants for nutrients and water in gravel soils. With the participation of ecologic niche plants, the ecological factors of each component have a relatively reasonable proportion, which can make the space complimentary. Gravel soil can increase the availability of water and nutrients, and promote the community yield in the short term. Therefore, in the process of ecological restoration on the Qinghai-Tibet Plateau, TN and SOC should be added for coarse soil textures with high gravel content, and ecologic niche plants should be mixed to achieve an ideal ecological restoration effect.

CRediT authorship contribution statement

Conceptualization by: You Y, Wu X, and Zhou J. Methodology by: You Y and Wu X. Field and indoor experimental setup and analysis by: Lu,Y; Han,L. and Dong Q. Writing original draft by: You Y and Wu X. Supervision by: Rebi A, Wang L. and Zhang P. All authors read and approved the final manuscript.

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Table 1 Physical and chemical properties of studied soils

Gravel class	Particle size composition (%) Gravel	Particle size composition (%) Sand	Particle size composition (%) Silt	Particle size composition (%) Clay	BD (g cm^{-3})	*e* (%)	TN (g kg^{-1})	TP (gkg^{-1})	SOC (g kg^{-1})
Low	10.0c	62.5a	18.4a	9.1a	1.14c	55.04a	0.49a	0.45a	12.23a
Medium	30.0b	51.8b	11.9b	6.3b	1.34b	46.05b	0.37b	0.39bc	7.17bc
High	50.0a	37.5c	8.0c	4.5c	1.45a	42.66c	0.10c	0.35c	5.33bc

Note: Gravel, >2 mm; Sand, 0.05-2 mm; Silt, 0.002-0.05 mm; Clay, <0.002 mm; BD, bulk density; *e* , total porosity; TN, total nitrogen; TP, total phosphorus; SOC, soil organic carbon. The same lowercase letters after mean values indicate no significant differences at p<0.05.

Table 2 ANOVA results of the effects of gravel content, plant species and their interaction on plant traits

Variables	Gravel content *F*	Gravel content *p*	Plant species *F*	Plant species *p*	Gravel×Plant species *F*	Gravel×Plant sp *p*
Plant height	188.3	<0.01	277.3	<0.01	4.7	<0.01
Plant coverage	131.2	<0.01	304.6	<0.01	56.3	<0.01
Shoot biomass	195.2	<0.01	488.1	<0.01	26.5	<0.01
Root biomass	127.1	<0.01	33.1	<0.01	49.5	<0.01
Total biomass	118.1	<0.01	388.7	<0.01	29.4	<0.01

Table3 Pearson correlation coefficients between plant growth indices with non-rhizosphere and rhizosphere soil properties (n = 9)

		Non-rhizosphere soils TN	Non-rhizosphere soils TP	Non-rhizosphere soils SOC	Non-rhizosphere s C:N
Plant height	Plant height			0.69^{*}	
Plant coverage	Plant coverage				
Shoot biomass	Shoot biomass	0.71^{*}		0.76^{*}	
Root biomass	Root biomass			0.73^{*}	
Total biomass	Total biomass	0.69^{*}		0.76^{*}	
Root	TN				
	TP				
	OC				0.68^{*}
	C:N				0.67^{*}
	C:P				0.78^{*}
	N:P				
Shoot	TN				

TP	-0.80**
OC	
C:N	
C:P	0.68*
N:P	0.68*

Note:* and ** ndicate the significant levels of p<0.05 and 0.01, respectively. BD, bulk density; *e* , total porosity; TN, total nitrogen; TP, total phosphorus; SOC, soil organic carbon.

Table4 RDA sequencing of soil properties affecting plant traits.

		TN	TP	SOC	N/P	C/N	C/P	BD	*e*	pH
Fe	Axis1	0.74	0.64	0.75	0.60	-0.28	0.63	-0.90	0.91	0.28
	Axis2	-0.29	-0.16	0.16	-0.41	0.38	0.49	-0.18	-0.07	-0.12
Ed	Axis1	0.56	0.48	0.61	0.42	-0.11	0.57	-0.98	0.79	0.05
	Axis2	0.28	0.30	0.56	0.15	-0.11	0.70	0.09	0.30	0.55
Ms	Axis1	0.01	-0.04	-0.22	0.14	-0.32	-0.35	0.89	-0.34	0.43
	Axis2	0.97	-0.74	-0.74	-0.92	0.68	-0.50	0.43	-0.91	-0.70
Fe+Ed	Axis1	0.92	0.77	0.87	0.80	-0.50	0.60	-0.69	0.95	0.52
	Axis2	0.30	0.20	0.03	0.39	-0.49	-0.17	0.71	-0.07	0.61
Fe+Ms	Axis1	0.76	0.65	0.79	0.60	-0.30	0.71	-0.87	0.93	0.33
	Axis2	0.61	0.46	0.41	0.62	-0.61	0.24	0.45	0.29	0.80
Ms+Ed	Axis1	-0.22	-0.24	-0.41	-0.06	-0.18	-0.47	0.96	-0.54	0.26
	Axis2	-0.91	-0.70	-0.78	-0.85	0.66	-0.64	0.17	-0.81	-0.90
Fe+Ms+Ed	Axis1	0.46	0.41	0.57	0.31	-0.04	0.57	-0.99	0.73	-0.04
	Axis2	-0.84	-0.67	-0.55	-0.83	0.70	-0.25	-0.04	-0.58	-0.75

Note: Fe, *Festuca elata* ; Ed, *Elymus dahuricus* ; Ms,*Medicago sativa* ; Fe+Ed, *Festuca elata plus Elymus dahuricus* ; Fe+Ms, *Festuca elata plus Medicago sativa* ; Ms+Ed,*Medicago sativa plus Elymus dahuricus* ;Fe+Ms+Ed, *Festuca elata plus Medicago sativa plus Elymus dahuricus* ; TN, soil total nitrogen; TP, soil total phosphorus; SOC, soil organic carbon; BD, bulk density; *e* , total porosity.

Figure captions

Fig 1 . The changes of total, shoot, root biomass and their ratio with gravel content for different plant species. Error bars refer to standard deviation. Different lowercase letters indicate significant differences among different gravel soils; different capital letters indicate significant differences among all treatments (p<0.05). Fe, *Festuca elata* ; Ed, *Elymus dahuricus* ; Ms, *Medicago sativa* ; Fe+Ed, *Festuca elata plus Elymus dahuricus* ; Fe+Ms, *Festuca elata plus Medicago sativa* ; Ms+Ed, *Medicago sativa plus Elymus dahuricus* ;Fe+Ms+Ed,*Festuca elata plus Medicago sativa plus Elymus dahuricus* .

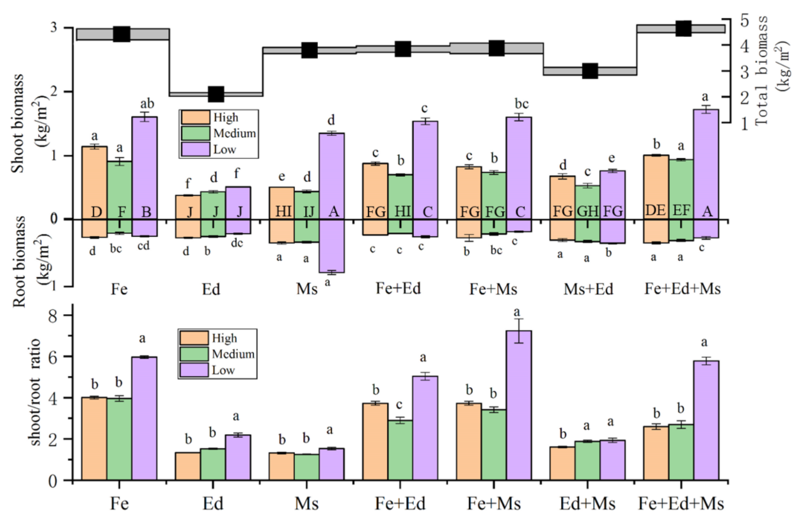
Fig. 2 The changes of plant height and coverage with gravel content for different plant species. (a), Total coverage; (b), Plant height; (c), Coverage of different plant species; (d), Height of different plant species. Error bars refer to standard deviation. Different lowercase letters indicate significant differences among different gravel soils (p<0.05). Fe, *Festuca elata* ; Ed,*Elymus dahuricus* ; Ms, *Medicago sativa* ; Fe+Ed,*Festuca elata plus Elymus dahuricus* ; Fe+Ms, *Festuca elata plus Medicago sativa* ; Ms+Ed, *Medicago sativa plus Elymus dahuricus* ;Fe+Ms+Ed, *Festuca elata plus Medicago sativa plus Elymus dahuricus* .

Fig. 3 Content and stoichiometric characteristics of organic carbon, total nitrogen, and total phosphorus in plant root and shoot fractions and rhizosphere soils with different gravel contents. Error bars refer to standard deviation Different lowercase letters indicate significant differences among different gravel soils (p<0.05).

Fig. 4. Content and stoichiometric characteristics of organic carbon, total nitrogen, and total phosphorus in plant root and aboveground fractions and rhizosphere soils for different plant species. Error bars refer to standard deviation; respectively. Different lowercase letters indicate significant differences among different plant species ($p<0.05$). Fe, *Festuca elata* ; Ed, *Elymus dahuricus* ; Ms, *Medicago sativa* ; Fe+Ed, *Festuca elata plus Elymus dahuricus* ; Fe+Ms, *Festuca elata plus Medicago sativa* ; Ms+Ed, *Medicago sativa plus Elymus dahuricus* ;Fe+Ms+Ed,*Festuca elata plus Medicago sativa plus Elymus dahuricus* .

Fig. 5 RDA of the relationships among plant traits, soil properties, and their stoichiometric characteristics for different plant species. TN, soil total nitrogen; TP, soil total phosphorus; SOC, soil organic carbon;S-C/N, soil C/N ratio; S-C/P, soil C/P ratio; S-N/P, soil N/P ratio; PH, soil pH; BD, bulk density; *e* , total porosity; PTN, plant total nitrogen; PTP, plant total phosphorus; POC, plant organic carbon; P-C/N, plant C/N ratio; P-C/P, plant C/P ratio; P-N/P, plant N/P ratio; RTN, root total nitrogen; RTP, root total phosphorus; ROC, root organic carbon; R-C/N, root C/N ratio; R-C/P, root C/P ratio; R-N/P, root N/P ratio; H, Plant height; Tc, total coverage; Ab, aboveground biomass; Rb, root biomass; B, total biomass.

Fig 1 . The changes of total, shoot, root biomass and their ratio with gravel content for different plant species. Error bars refer to standard deviation. Different lowercase letters indicate significant differences among different gravel soils; different capital letters indicate significant differences among all treatments ($p<0.05$). Fe, *Festuca elata* ; Ed, *Elymus dahuricus* ; Ms, *Medicago sativa* ; Fe+Ed, *Festuca elata plus Elymus dahuricus* ; Fe+Ms, *Festuca elata plus Medicago sativa* ; Ms+Ed, *Medicago sativa plus Elymus dahuricus* ;Fe+Ms+Ed,*Festuca elata plus Medicago sativa plus Elymus dahuricus* .



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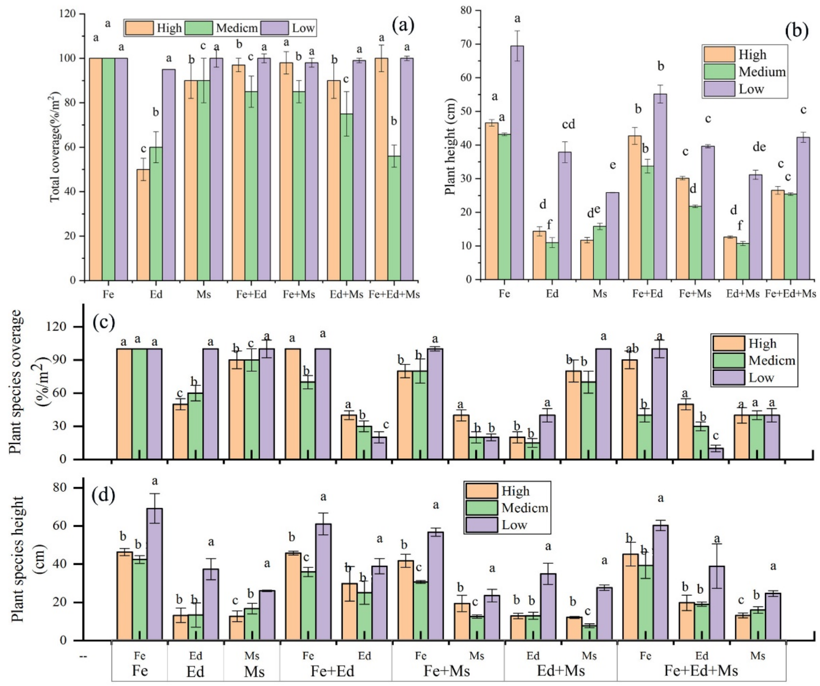

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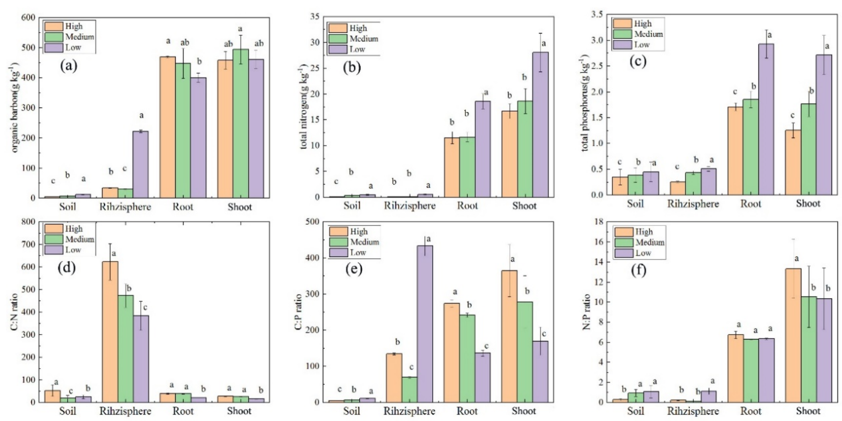

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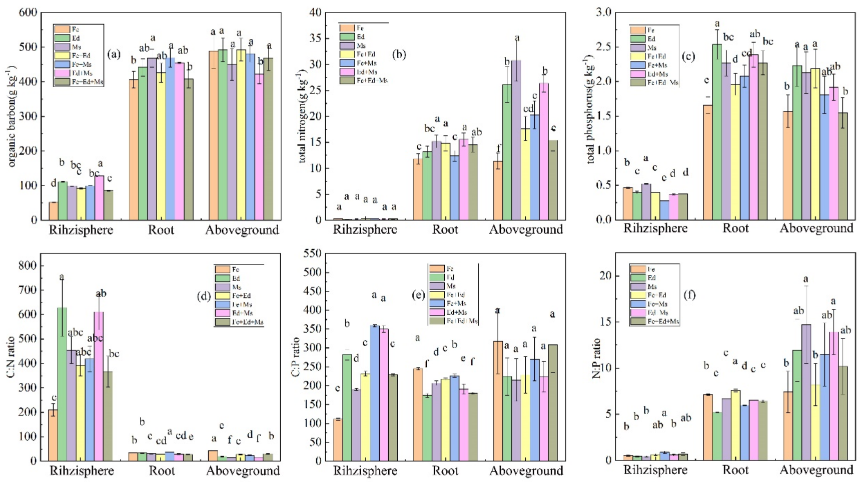

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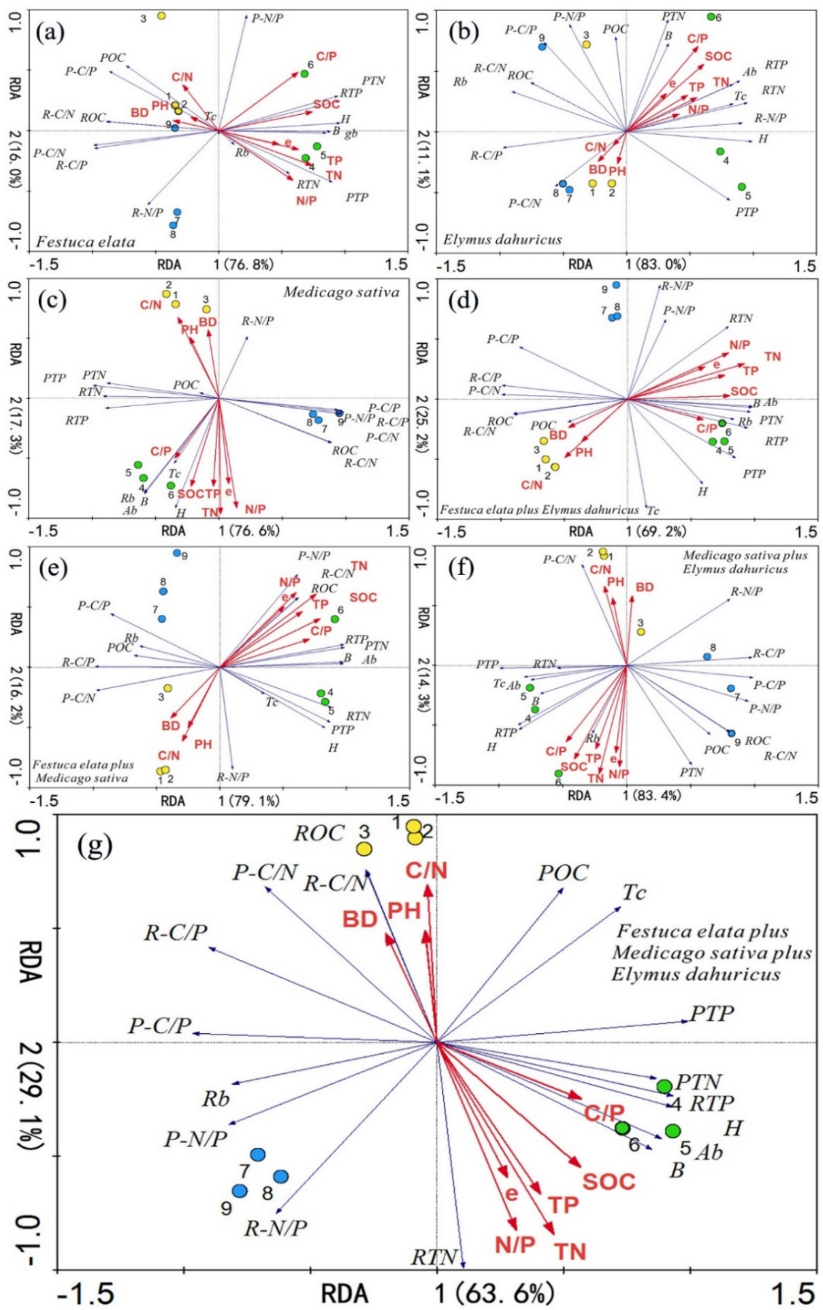
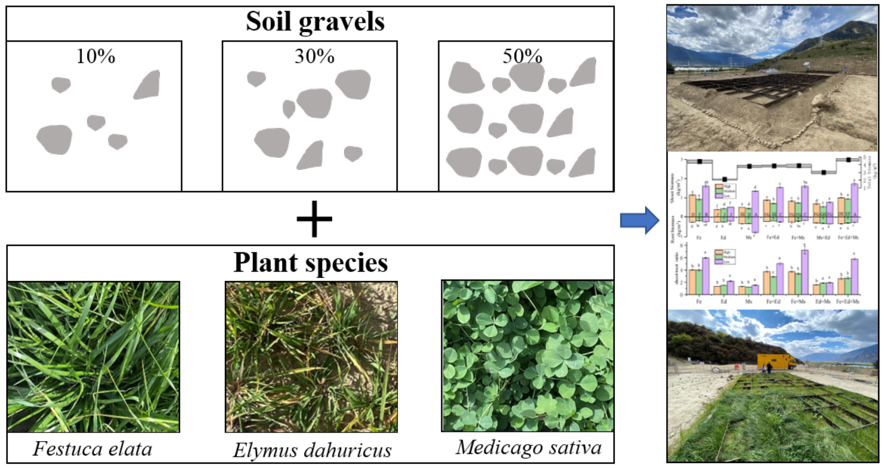

(a)
Festuca elata
RDA 1 (76.8%)
RDA 2 (16.0%)
(b)
Elymus dahuricus
RDA 1 (83.0%)
RDA 2 (11.1%)
(c)
Medicago sativa
RDA 1 (76.6%)
RDA 2 (17.3%)
(d)
Festuca elata plus Elymus dahuricus
RDA 1 (69.2%)
RDA 2 (25.2%)
(e)
Festuca elata plus Medicago sativa
RDA 1 (79.1%)
RDA 2 (16.2%)
(f)
Medicago sativa plus Elymus dahuricus
RDA 1 (83.4%)
RDA 2 (14.3%)
(g)
Festuca elata plus Medicago sativa plus Elymus dahuricus
RDA 1 (63.6%)
RDA 2 (29.1%)
ROC
P-C/N
R-C/N
R-C/P
P-C/P
Rb
P-N/P
R-N/P
RTN
POC
Tc
PTP
PTN
RTP
H
Ab
B
C/N
BD
PH
C/P
SOC
e
TP
N/P
TN


Soil gravels
10%
30%
50%
+
Plant species
Festuca elata
Elymus dahuricus
Medicago sativa