Variation of plant CSR strategies across a precipitation gradient in the alpine grasslands on the northern Tibet Plateau

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HIGHLIGHTS

- S-strategy species dominate in the alpine grasslands.
- Higher water, nitrogen (N) and phosphorus (P) availability had significantly lower S-strategy values.
- Forbs and legumes adopted more flexible strategies compared with grasses and sedges.
- Water variability affected plant traits and CSR strategies through soil N and P availability and pH.

GRAPHICAL ABSTRACT
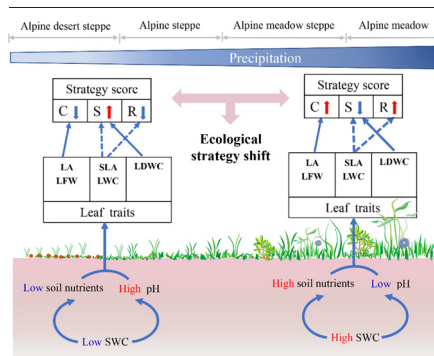
ABSTRACT

Identifying ecological strategies based on functional traits can help us better understand plants' adaptations and changes in ecological processes, and thus predict the impact of climate change on ecosystems, especially in the vulnerable alpine grasslands. Herein, we investigated the plant CSR strategies of four grassland types (alpine meadows, AM; alpine meadow steppes, AMS; alpine steppes, AS; and alpine desert steppes, ADS) and its functional groups (grasses, sedges, legumes, and forbs) along the east-to-west gradient of decreasing precipitation on the northern Tibetan grasslands by using Grime's CSR (C: competitor, S: stress tolerator, and R: ruderal) analysis. Although alpine grasslands were dominated by S-strategy, our results also indicated that AM with higher water, nitrogen (N) and phosphorus (P) availability had significantly lower S-strategy values and relatively higher C- and R-strategy values (C: S: R = 6: 63: 31 %) than those in AMS (C: S: R = 3: 94: 3 %,), AS (C: S: R = 3: 87: 10 %), and ADS (C: S: R = 1: 94: 5 %). The CSR strategy values of forbs and legumes showed greater variability compared with grasses and sedges in the environmental gradient. Furthermore, water variability on the precipitation gradient eventually affected plant traits and CSR strategies through soil N and P availability and pH. Our findings highlighted that plant CSR strategies were regulated by the availability of soil resources, and plants adopted more flexible adaptation strategies in relatively resource-rich environments. This study sheds light on the mechanisms of plant adaptation to the changing environment in the alpine grasslands.

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1. Introduction

Ecosystem properties are reflected by variations in the adaptive traits of plant species with their morphological and physiological features, i.e., functional traits (Diaz et al., 2016; Wright et al., 2004). Plant ecological strategies are specializations resulting from the trade-offs of different traits, which allow plants to cope with variable stresses and disturbances in order to achieve optimum fitness (Pierce et al., 2017; Pivovaroff et al., 2015; Rosado and de Mattos, 2017). Trait-based approaches have been the main foundation for constructing classifications to reflect plant resource acquisition and investment strategies influencing species distribution, community assembly and ecosystem functioning (Guo et al., 2018; Jung et al., 2010; Kraft et al., 2015). Therefore, understanding how plant traits respond to environmental change can contribute to explaining the ecological processes of plant adaptation to the environment.

The evaluation of plant ecological strategies based on plant traits, especially leaf traits, is an effective method to be widely used in ecological studies (Cross et al., 2015; Negreiros et al., 2014; Pierce et al., 2017). Grime (1977) conceived three main ecological strategies that species cope with the environment, namely competitor, stress-tolerator, ruderal (CSR plant strategies), as principal trade-offs among competitive ability (C: rapid investment in large size to allow resource preemption), stress-tolerance (S: maintain individual survival in variable and limiting environments), and ruderalism (R: investment in regeneration and reproduction). Based on this theory, numerous studies have showed that plants tend to adopt a conservative resource use strategy (S-strategy) in the resource-poor environments, with in lower specific leaf area (SLA) and higher leaf dry matter content (LDMC) (Chen et al., 2019; Pérez-Ramos et al., 2017). More recently, Pierce et al. (2017) used global trade-offs in SLA, LDMC and leaf area (LA) to develop a strategy calculator tool (StrateFy) for evaluating changes in CSR strategies. Although this approach has drawbacks (Rosado and de Mattos, 2017), the plant traits required by this method are widely available, applicable to a variety of lifeforms and represent a range of ecological strategies and plant functional trade-offs (Pierce et al., 2017). Currently, this approach to determining CSR strategies based on leaf size and economics traits is widely used to surrogate variations in other plant functional traits on various scales, such as species invasion (Escobedo et al., 2021), successional gradients (Barba-Escoto et al., 2019) and climatic zones (Han et al., 2021), evidencing how environment influences plant traits and CSR strategies.

The co-variation of plant traits with environmental gradients can lead to alternative ecological strategies, which is crucial to understanding the process of community dynamics (Araujo da Costa et al., 2020; Guo et al., 2018; Ordoñez et al., 2009). In resource-poor environments, ecological strategies tend to converge toward stress tolerance, but the phenotypic plasticity of plant traits allows ecological strategies to shift in response to environmental changes (Zhang and Wang, 2021). For example, plant strategies on the Tibetan Plateau show a trend from S to R strategies from non-degraded to severely degraded grasslands (Zhou et al., 2021). Warmer temperatures lead to the decrease of R and S components while increasing plant competitiveness (Rosenfield et al., 2019; Zhang and Wang, 2021). Similarly, the improvement of water and soil nutrient availability in habitats due to shading by shrub canopies would shift the community from pure S strategy species to less stress-tolerant species with higher C and R components (Butterfield and Briggs, 2011; Rosado and de Mattos, 2017). These studies have demonstrated that environmental changes, especially in water and nutrient availability, affect plant traits and CSR strategies, and to some extent can help explain the mechanisms of plant community assembly and environmental filtering. However, how environmental factors influence plant traits and further affect CSR strategies is still to be further explored, especially in the regional-scale environmental gradients (e.g., precipitation gradient). Such work can help better understand the generality of strategy dynamics across a wide range of environment change.

Phenotypic plasticity in plant functional groups is important for species to respond to changes in a range of conditions and resources along environmental gradients (Davison et al., 2020). Spatial variabilities in

environmental conditions and corresponding stress gradients determine predictable variations in the functional composition of herbaceous layer plant communities (Catorci et al., 2011). Previous studies have demonstrated that different plant functional groups adopt obviously different ecological strategies (Behroozian et al., 2020; Zhou et al., 2021), which may allow species to exploit diverse niches in a complementary manner (Cerabolini et al., 2010). For instance, forbs with higher leaf water and nitrogen contents adopt more flexible SR strategies to capitalize on water and nutrient than grasses and sedges with S strategy in the degraded alpine meadows (Zhou et al., 2021). It is interspecific variability that allows different plant function groups to adopt flexible trade-offs of CSR strategies in order to adapt to different habitats or environmental changes (Dayrell et al., 2018; Silva et al., 2018). Therefore, addressing the relationships between plant CSR strategies of functional types and environmental variables can help predict the responses of plant communities to environmental changes, yet it has rarely been investigated in natural plant communities on the Tibetan Plateau.

The plant communities along a precipitation gradient provides an ideal platform for studying variations of ecological strategies and the underlying mechanisms, because soil nutrients generally change obviously with water availability. If soil water and nutrients are important growth-limiting factors, then trends in plant ecological strategies should be parallel to trends in adaptation to harsh environments (Vandvik and Birks, 2002). In other words, the variation in plant functional traits may be used to assess and reflect the relative importance of different environmental processes and key factors in structuring the patterns of CSR strategies in different grasslands. In the northern Tibetan grasslands where plant growth is limited by water and nutrients (Zong et al., 2020), exploring the functional trait plasticity and ecological strategy adjustment of different species and functional groups on the precipitation gradient is helpful to explain the mechanisms of plant community assembly. Herein, we investigated plant communities in a shift of vegetation sequence from alpine meadows (AM) to meadow steppes (AMS), steppes (AS), and desert steppes (ADS) across a precipitation gradient in the northern Tibetan grasslands ranging from >600 mm in the east to <100 mm in the west (Zhao et al., 2017). We measured key leaf traits and calculated CSR strategies of the different species and functional groups in the four grassland types on the precipitation gradient. The main objectives of this study are to (1) determine the patterns of variation in CSR strategies for different grassland types and functional group; (2) identify the key factors affecting plant CSR strategies in the alpine grasslands. We hypothesized that (1) Alpine grassland communities were dominated by species with S strategy, particularly in the western end with stressful water and nutrient availability; and (2) Compared with grasses and sedges, forbs and legumes might represent more flexible adaptation strategies in the alpine grasslands, i.e., ecological strategies might shift along the environmental gradient.

2. Materials and methods

2.1. Study area

Our study was conducted on the northern Tibetan Plateau, also known as the Changtang Plateau, with an average altitude of above 4500 m (Zong et al., 2020). Climate is characterized by alpine continental climate, with annual mean average temperature (MAT) below 0 °C, ranging from about −15 °C in the coldest month in January to 10 °C in the warmest month in July (Zhang et al., 2020). The MAT from east to west varies <2 °C (Table S1), but mean annual precipitation (MAP) decreases significantly (Table 1). Soils are characterized as alpine frost calcic soil and desert soil (Zhao et al., 2017). The vegetation in the study areas consist of four grasslands types, i.e., AM, AMS, AS and ADS, respectively from east to west (Fig. 1). The dominant species are *Kobresia pygmaea* and *Poa crymophila* Keng in AM, *Stipa purpurea* and *Carex moorcroftii* in AMS, *S. purpurea* and *Astragalus confertus* Benth. ex Bunge in AS, *S. purpurea* and *Oxytropis microphylla* in ADS. Herbaceous species can be mainly categorized into

Table 1
Variations of precipitation and soil properties in four alpine grasslands along the precipitation gradient.

Grassland types	MAP (mm)	SWC (%)	pH	NH_4^+-N (mg kg^{-1})	NO3$^-$-N (mg kg^{-1})	TN (g kg^{-1})	AP (mg kg^{-1})	TP (g kg^{-1})
AM	482.7 ± 7.2 a	26.4 ± 5.7 a	6.6 ± 0.7 c	12.4 ± 8.6 a	6.5 ± 2.0 ab	4.2 ± 1.2 a	8.7 ± 3.5 a	0.4 ± 0.1 a
AMS	400.7 ± 4.5 b	11.2 ± 0.7 b	8.3 ± 0.1 b	3.7 ± 2.4 b	7.4 ± 1.7 a	2.2 ± 0.4 b	2.0 ± 0.5 b	0.2 ± 0.03 c
AS	303.6 ± 4.6 c	14.1 ± 1.1 b	8.7 ± 0.1 ab	1.3 ± 0.6 b	4.7 ± 0.8 bc	0.8 ± 0.2 c	1.6 ± 0.7 b	0.3 ± 0.04 bc
ADS	208.6 ± 4.6 d	7.5 ± 2.1 b	8.9 ± 0.1 a	1.7 ± 1.2 b	4.2 ± 1.4 c	1.1 ± 0.2c	3.1 ± 1.0 b	0.3 ± 0.07 ab

Note: AM, alpine meadow; AMS, alpine meadow steppe; AS, alpine steppe; ADS, alpine desert steppe; MAP, mean annual precipitation; SWC, soil water content; TN, soil total N; AP, available phosphorus; TP, soil total P. Different letters indicate significant differences (Tukey's test, $P < 0.05$) among the four alpine grasslands.

four functional groups, including grasses, sedges, legumes, and forbs (see detail in Table S2).

2.2. Community survey and sample collection

In mid-August 2021, during the peak of the growing season, 16 sites and 64 quadrats (four grassland types × four plots in each type × four quadrats in each plot) along the precipitation gradient were randomly selected in the fenced grasslands to investigate community structure and species composition. To avoid grazing, all plots has been fenced off for about 13 years since the implementation of project "Returning Grazing Land to Grasslands" in Tibet. The sampling sites with similar bedrock material were selected for plant community investigation in the places with flat and open terrain, avoiding low-lying areas. Each quadrat is 1.0 m × 1.0 m, with a distance at least of 100 m. After investigating the community structure and species composition of each quadrat, the aboveground of each plant species was separately cut and packed in paper bags. Soil samples (0–15 cm) at each plot were collected after mixing three drills of soil cores. All soil samples were passed through a 2-mm sieve in the field in a fresh state after the visible roots were removed, then each soil sample was divided into two subsamples. One subsample was immediately put in plastic bag and stored at 4 °C in small refrigerator for soil water content measurement, and the other subsample was air-dried for analyzing physicochemical properties.

2.3. Functional traits and CSR classification

Ten fresh and fully expanded leaves from each species were randomly selected to determine functional traits (the mean value of 10 replicates represents the value of the respective species) in each quadrat. When measuring tiny leaves, we increased the number of leaves to reduce the error. LA was determined using a digital leaf area meter (LI-3000; LI-COR, Lincoln, NE, USA). Leaf fresh weight (LFW) was obtained from water-saturated leaves, and leaf dry weight (LDW) was determined after drying for 48 h in an oven at 65 °C until leaves reached constant weight. Moreover, leaf succulence index (LSI), leaf water content (LWC), leaf mass per area (LMA), LDMC and SLA were calculated. The C, S and R percentages for each species were calculated based on three leaf traits (LA, LDMC and SLA) in the "StrateFy" spreadsheet, which is available from the supporting information in Pierce et al. (2017) (https://besjournals.onlinelibrary. wiley.com/doi/ 10.1111/1365-2435.12722). The StrateFy calculated plant CSR strategy values by regressing leaf trait values against the principal component analysis axes derived from a multivariate analysis of global plant leaf traits (Pierce et al., 2017). The StrateFy CSR ordination method classifies species into 19 tertiary ecological strategy categories (C, S, R, CSR, S/CR, S/SR, etc.) based on the proportion of CSR (see detail in Table S3). The mean values of traits and CSR strategies for each species in the four alpine grassland types are shown in Table S2. We also selected four common species in the four grassland types, including *A. confertus* Benth. ex Bunge (legume),
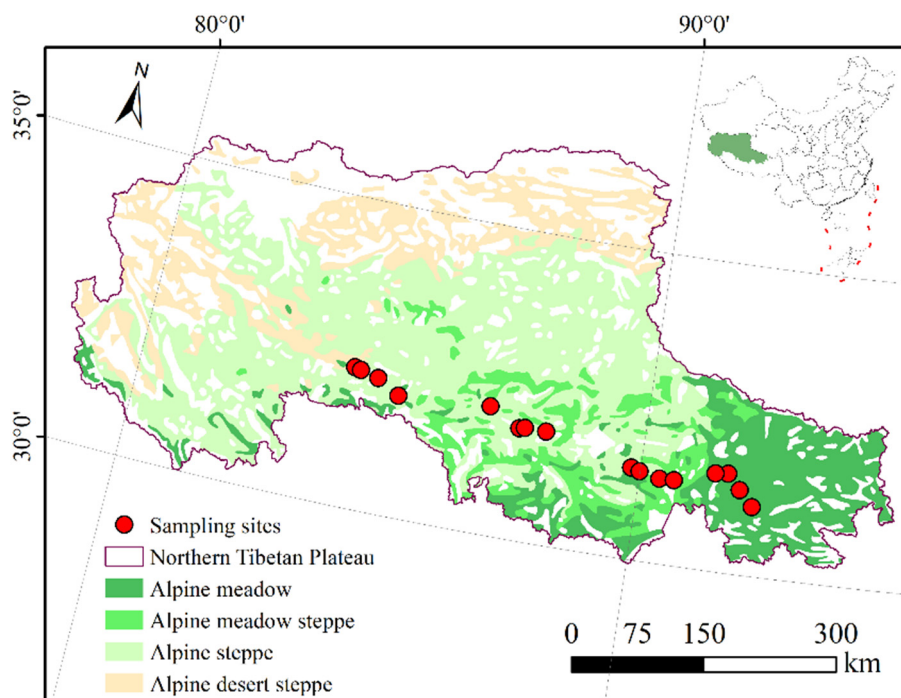

Fig. 1. Locations of the study sites across the northern Tibet Plateau.

C. moorcroftii (sedge), *Potentilla bifurca* Linn. (forb) and *S. purpurea* (grass), to compare their CSR strategies (*P. bifurca* was absent in ADS). In addition, we calculated community-weighted means (CWM) for each trait, which was the community-level mean of trait values weighted by the relative abundance of each species (Garnier et al., 2004). We used the relative aboveground biomass of species to represent relative abundance. The CWM values for CSR scores were calculated for each site using species' mean CSR score weighted by their biomass.

2.4. Soil analysis

Soil water content (SWC) was determined by oven-drying 20 g of fresh soil at 105 °C for 48 h. Soil pH was measured using a glass electrode meter (InsMark™ IS126, Shanghai, China) in a 1: 2.5 soil: water (w/v) mixture. The total nitrogen (TN) was measured using the Kjeldahl method (Bremner and Mulvaney, 1982). Soil total phosphorus (TP) was measured using an ultraviolet spectrophotometer after digestion with H_2SO_4 and $HClO_4$ (Parkinson and Allen, 1975). Soil NH_4^+-N and NO_3^--N contents were determined using a Seal Auto Analyzer after extraction with 2 M potassium chloride (KCl). Available phosphorus (AP) content was determined via 0.5 M NaHCO₃ extraction, and then determined by the molybdenum blue method using an ultraviolet spectrophotometer (Hitachi UV2300) at 700 nm.

2.5. Statistical analysis

The data were analyzed with a one-way analysis of variance (ANOVA) using the SPSS 20.0 statistical software package (SPSS Inc., Chicago, USA). Tukey's test was used for multiple comparisons ($P < 0.05$) to assess the significance of differences among the different sampling sites. All graphs and box-and-whisker plots were drawn using Origin 2021. Variation partitioning analysis was applied to quantify the individual contribution of climate and soil to the plant CSR strategies using the "vegan" package in R (Cui et al., 2019). To quantify the relative importance of predictor variables to the CSR strategy, we conducted the relative importance of predictor variables in linear models using the "relaimpo" package (Zhou et al., 2021). Meanwhile, a partial Mantel test was used to reveal the relationships between the CSR strategy and explaining factors, including climate, soil properties and plant traits by using the vegan R software package (Sunagawa et al., 2015). Furthermore, partial least squares path modeling (PLS-PM) was used to identify the possible pathways of various factors affecting the CSR strategies. Plant traits selected in the model were mainly based on relative importance (Fig. 4) and redundancy analysis (Fig. S2), and backward stepwise regression model was used to select variables satisfied with the requirement of variance inflation factor (VIF) <5 in order to prevent covariance (Table S4). The total effects of climate, soil properties, and plant traits on plant CSR strategies in PLS-PM were shown in Fig. S4. The models were constructed using the "innerplot" function of the R package "plspm" (Sanchez et al., 2017). All these analyses were performed using R (v.4.1.2).

3. Results

3.1. Variations of environmental factors, plant traits and CSR strategies

From AM to ADS, MAP and soil moisture decreased significantly and thereby resulted in gradual changes in soil properties along the precipitation gradient (Table 1). Soil pH values increased but TN decreased significantly ($P < 0.05$) from AM to ADS. SWC, NH_4^+-N, NO_3^--N, AP, and TP were significantly ($P < 0.05$) higher in AM than in the other grassland types. Variations of plant community properties and leaf traits are shown in Table 2. LDMC was significantly lower in AM than in AMS and ADS, while SLA in AM was 2.2, 2.1 and 1.9 times higher than those of AMS, AS and ADS, respectively.

Most species were ordinated within the same multidimensional space of the CSR triangle. Plant species in the AMS, AS and ADS were primarily concentrated in the S-strategy, with the mean C: S: R = 3: 94: 3 %, 3: 87: 10 % and 1: 94: 5 %, respectively (for detailed CSR strategies of each species see in Table S2). Although the species in AM were also dominated by S-strategy (C: S: R = 6: 63: 31 %), the value of S-strategy was significantly lower than those of other grassland types, accompanied by a significant increase in the proportion of R-strategy value (Fig. 2).

In different functional groups of the grassland communities, the CSR strategy values of forbs and legumes showed greater variability compared with grasses and sedges across the environmental gradient (Fig. 2). Specifically, the C-strategy values of grasses and sedges showed no difference among the four grassland types, while the C-strategy values of legumes and forbs were significantly higher in AM than in other grasslands. The S-strategy values of grasses, legumes, and forbs were significantly lower, while the R-strategy values of them were significantly higher in AM than in other grassland types ($P < 0.05$). In addition, the CSR strategies of common species differed and indicated similar trend with functional groups in four grassland types along the precipitation gradient (Fig. S1). *A. confertus* and *C. moorcroftii* in AM had significantly lower S-strategy but higher R-strategy values than those of other grassland types. In addition, the CSR strategies of *P. bifurca* showed large intraspecific variation, whereas *S. purpurea* exhibited insignificantly intraspecific variation in all four grassland types.

3.2. The relationship between CSR strategies and plant traits and environmental factors

The variation-partitioning analysis indicated that climate and soil factors jointly explained 19.7 %, 43.40 % and 41.6 % of C-, S- and R-strategy variation, respectively (Fig. 4). In addition, to better understand the key factors of plant traits that regulated CSR strategies, a partial (geographic distance-corrected) Mantel test of the relative importance of regressors in the linear models showed that LA and LFW, LWC and LDWC and SLA were identified as the most important plant traits for C-, S- and R-strategy, respectively (Figs. 4 and S2). Furthermore, PLS-PM analysis results indicated that changes in climate (mainly MAP) affected pH, soil nutrient availability and plant traits, and consequently resulted in plant ecological strategies (Fig. 5). Specifically, plant traits (0.85), including LA and LFW,
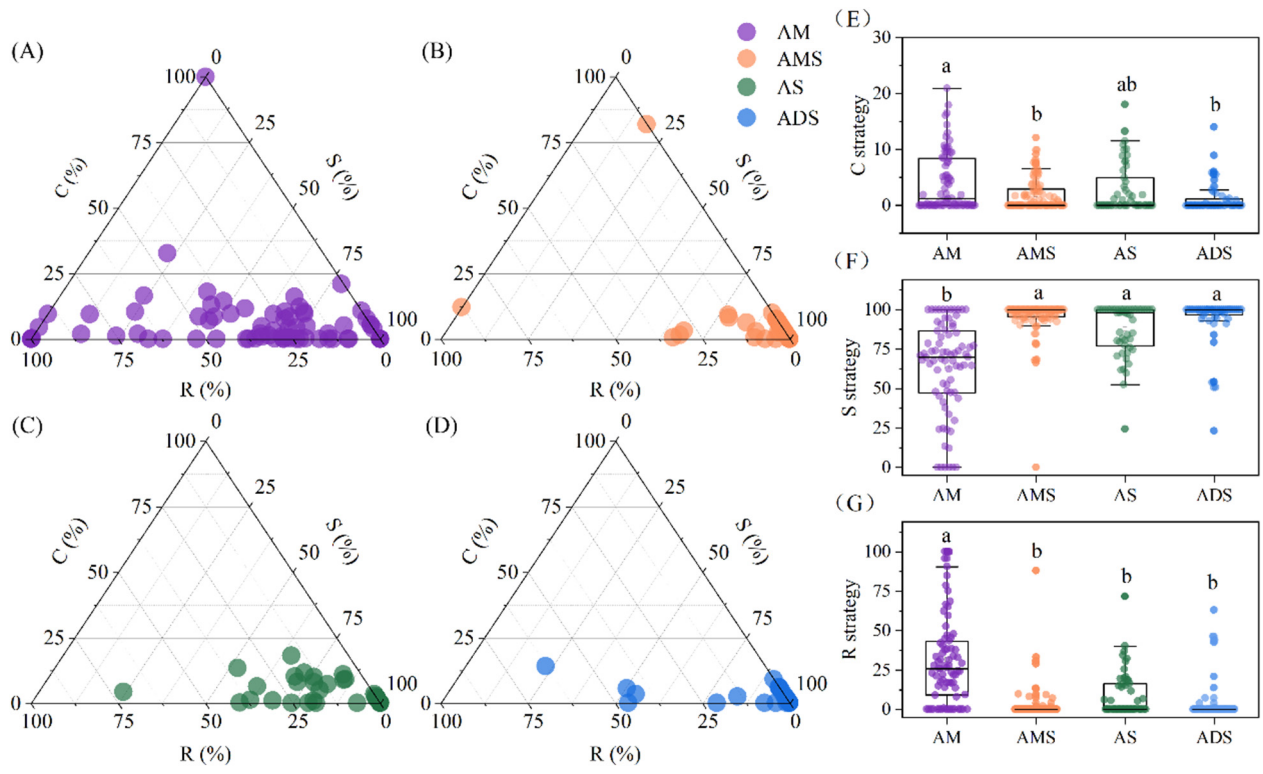
Table 2
The leaf traits of plant functional groups in four alpine grasslands along the precipitation gradient.

Grassland types	Coverage (%)	Biomass (g)	MI	LA (mm²)	LFW (mg)	LDW (mg)	LSI (g water dm⁻²)	LWC (% of LFW)	LMA (g m⁻²)	LDMC (%)	SLA (mm² mg⁻¹)
AM	80.2 ± 7.2 a	142.9 ± 18.3 a	1.6 ± 0.12 a	27 ± 4.7 a	8.9 ± 1.6 a	2.5 ± 0.5 a	2.7 ± 0.9 a	53.7 ± 6.4 a	115.6 ± 44.6 a	22.4 ± 2.8 b	10.2 ± 1.7 a
AMS	30.9 ± 1.8 b	56.0 ± 8.8 b	1.8 ± 0.08 a	19.1 ± 2.7 a	10.5 ± 0.7 a	3.7 ± 0.2 a	8.2 ± 1.8 a	61.5 ± 0.7 a	482.2 ± 92.7 a	37.3 ± 0.8 a	4.6 ± 0.6 b
AS	28.7 ± 1.3 b	38.7 ± 5.2 bc	0.9 ± 0.03 b	35.2 ± 11.7 a	13.8 ± 3.3 a	4.5 ± 1 a	6.3 ± 2.0 a	60.2 ± 1.8 a	325.6 ± 60.7 a	33.3 ± 3.3 a	4.9 ± 0.6 b
ADS	24.0 ± 1.1 b	22.3 ± 2.3 c	1.0 ± 0.05 b	36.1 ± 11.8 a	12.2 ± 2.2 a	4.4 ± 0.8 a	5.1 ± 1.3 a	54.9 ± 4.4 a	346.5 ± 77.5 a	32.6 ± 3.6 ab	5.5 ± 1.6 b

Note: MI, the species diversity index of Margalef Index; LA, leaf area; LFW, leaf fresh weight; LDW, leaf dry weight; LSI, leaf succulence index; LWC, leaf water content; LMA, leaf mass per area; LDMC, leaf dry matter content; SLA, specific leaf area. Different letters indicate significant differences among the four alpine grasslands (Tukey's test, $P < 0.05$).

Fig. 2. Relative proportions (%) of C-, S- and R-strategy for plant species in four types of alpine grasslands. (A) alpine meadows (AM); alpine meadow steppes (AMS); alpine steppes (AS); and alpine desert steppes (ADS). Box-and-whisker plots showing changes in C-, S- and R-strategy in AM, AMS, AS and ADS. (E) C-strategy; (F) S-strategy; and (G) R-strategy. Different letters indicate significant differences amongst the four alpine grasslands (Tukey's test, $P < 0.05$). The values of C-, S-, and R-strategy was calculated using the globally calibrated CSR analysis tool 'StrateFy'.

and pH (-0.75) had the highest positive and negative total effects on C-strategy, respectively. The total effects of SLA and LWC, and soil nutrients on S-strategy were -0.73 and -0.54, respectively. The total effects of pH and soil nutrients on R-strategy were -0.93 and -0.44, respectively (Fig. S4).

4. Discussion

4.1. Distribution patterns of CSR strategies in different grasslands

We found that plant species in the alpine grasslands along a precipitation gradient were dominated by S-strategy (Fig. 2), which was consistent with our hypothesis. Environmental filtering led to convergence in leaf functional traits within biomes and divergence among biomes across a global scale (Bernard-Verdier et al., 2012; Ordoñez et al., 2009; Steinbauer et al., 2022). Despite different environmental conditions in the four types of grasslands in our study, they still belong to the same biome. The S-strategy species generally occur in resource-poor environments through investing in the capacity to retain resources in durable and well-defended structures (Araujo da Costa et al., 2020). The S-strategy of different grassland communities may be closely related to the cold and arid environment on the Tibetan Plateau. Previous studies also indicated that species with strong S-strategy dominated the alpine grasslands on the Tibetan Plateau (Wang et al., 2018; Zhou et al., 2021). Alpine ecosystems are characterized by low temperatures, low nutrient availability and short growing seasons that render the stress-tolerant species to make functional trade-offs, invest more carbon on a per-leaf basis and form a resource conservative trait syndrome, such as lower SLA and larger LDMC (Pierce et al., 2007; Negreiros et al., 2014; Rosbakh et al., 2015; Stanisci et al., 2020).

In addition, it is worth noting that although stronger plant S strategies were dominant in all alpine grasslands, the scores for S-strategy were lower in the eastern alpine meadows than in other western steppes, in

contrast, the scores for R- and C-strategy were higher in the meadows. Precipitation gradient reflects the environment change from semi-humid to arid, accompanied by a significant decrease in soil water and nutrient availability (Table 1). SLA has been found to be dependent on differences in soil fertility, water supply and disturbance (Garnier et al., 2004; Rosbakh et al., 2015). Plants in relatively stable environments with high resource availability can invest more in growth and rapid uptake of resources, thus show higher C-strategy (Negreiros et al., 2014; Pierce et al., 2017). In AM with a relatively benign environment, the growth of species was less stressed by water and nutrients, resulting in larger SLA, lower LDMC and higher C-strategy through trade-offs between functional traits (Table 1). Both stress tolerance and competitiveness of species are strongly associated with the environmental gradient. Previous studies indicated that the improvement of water and soil nutrient availability in habitats due to shading by shrub canopies would result in a shift in community composition from pure S-strategy species to less stress-tolerant species with higher C and R components (Butterfield and Briggs, 2011; Rosado and de Mattos, 2017). Therefore, the co-variation of environmental resources and plant functional traits eventually leads to a shift in CSR strategies as a result of plant adaptation to environmental changes.

Ruderalism is commonly related to the disturbance regime (Negreiros et al., 2014). According to the theory of CSR strategy, the grasslands in the west with limited resources might be more frequently disturbed because of their low vegetative coverage, leading to a stronger R-strategy for the species. Contrary to imagination, the value of R-strategy in AM was, in fact, higher than those of other western grasslands (Fig. 2). The possible explanation is that although the western grasslands were greatly disturbed, the scarcity of water and nutrient resources led to the difficulty of community recovery after disturbance (Matos et al., 2019; Escobedo et al., 2021), thus abating the growth of R-strategy species, such as annual plants. In contrast, AM with a relatively relaxed environment has a stronger resilience, and thus can recover after disturbance, which is conducive to

developing the R-strategy of plant species (Zhou et al., 2021), especially the forbs with higher phenotypic plasticity.

4.2. The changes in the ecological strategies with functional groups

The interspecific variations of plant functional groups are conducive to flexible trade-offs of CSR strategies to adapt to environmental changes. Our results indicated that forbs and legumes in AM had relatively higher C- and R-strategy values and lower S-strategy values than other grasslands, whereas the CSR strategy of sedge showed no significant change in precipitation gradient (Fig. 3). Similarly, at the species level, common species *A. confertus* (legumes) had significantly lower S-strategy than those of other grassland types, which *S. purpurea* (grasses) had no significant difference in CSR strategies among different grasslands (Fig. S1). Different species groups occupy different fundamental niches in the community and have distinct adaptation strategies to cope with environmental changes so as to maintain community stability (Loreau and de Mazancourt, 2013; Valencia et al., 2020). Previous studies have demonstrated that forbs in cold and arid environments can show a stronger competitive capacity for resources (Silva et al., 2018; Zhou et al., 2021). Forbs and legumes are commonly identified as pioneers due to well-developed acquisitive strategies in the early stages of succession (Caccianiga et al., 2006; Chelli et al., 2019). However, in this study, the species of all four functional groups showed more conservative strategies with lower C- and R-strategy and higher S-strategy values in western grasslands. In these water and nutrient-poor environments, even forbs and legumes with flexible strategies had evolved conservative strategies to cope with the harsh environment, and C- and R-strategy species were filtered out.

The difference in the variation of strategies between AM and the other grassland types was mainly due to the roles of forbs and legumes. First, forbs and legumes have strong phenotypic plasticity and often adopt a more acquisitive strategy in the face of limited resources. Nutrient acquisitive species can translate high production of biomass into quick regeneration after disturbance events through flexible responses to nutrient availability (Busch et al., 2019; Cruz and Lasso, 2021). Generally, forbs are characterized by higher N content, LWC, and SLA, coupled with greater variations in leaf traits to adapt to resource deficient and disturbed environments. Legumes can acquire nutrients through a symbiosis with mycorrhizae and, thus, enhance their ability to alleviate environmental stress (Ma et al., 2021). Second, the high vegetation coverage (Table 2), and possible overlap of species niches in AM could increase the competition of community species for resources such as light, water and soil nutrients, which may favor forbs and legumes with a more competitive acquisition strategy.

In addition, it is worth noting that the CSR strategies of sedges were not different along the precipitation gradient at the functional group level, however, *C. moorcroftii* (sedges) in AM had significantly lower S-strategy and higher R-strategy values than those of other grassland types (Fig. S1). The main reason is that the dominant species in AM is *K. pygmaea* (C: S: R = 0: 96: 4 %), while the relative abundance of *C. moorcroftii* is low in AM community, resulting in strong stress-tolerance in AM.

4.3. Factors regulating the plant CSR strategies

Climate and soil properties may modify plant traits via phenotypic plasticity which shifts from conservation to a little more acquisition in more fertile soil (Semchenko et al., 2018). In our study, environmental changes modulated the functional traits of plants, which in turn affected the plant's ecological strategy. Further, PLS-PM confirmed that LA and LFW had a positive effect on C-strategy under the influence of environmental factors, while SLA and LWC had a negative effect on S-strategy and a positive effect on R-strategy (Fig. 5). This pattern is consistent with other studies that the improvement of water and soil nutrient availability
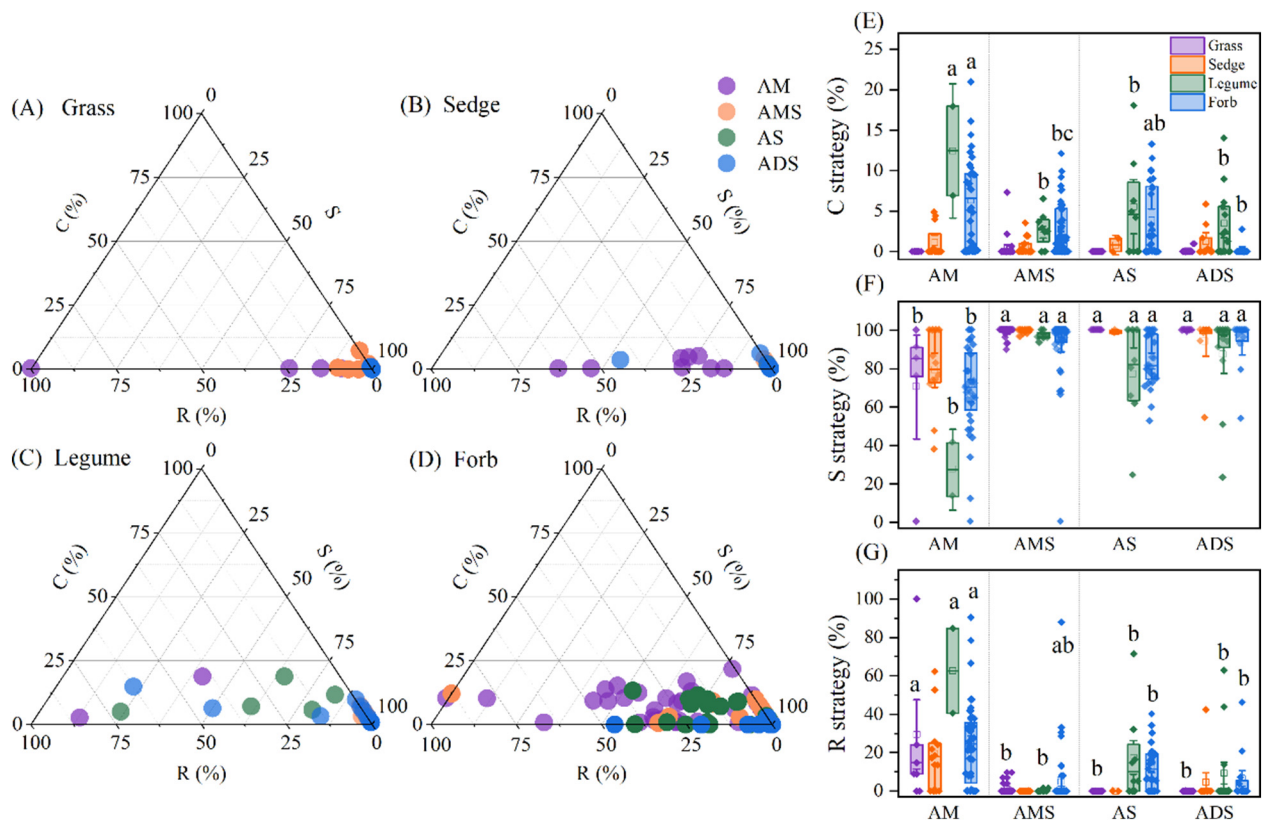

Fig. 3. The C-, S-, and R-strategy values of plant functional groups in four types of alpine grasslands. (A) grass; (B) sedge; (C) legume; (D) forb. (A) alpine meadows (AM); alpine meadow steppes (AMS); alpine steppes (AS); and alpine desert steppes (ADS). Box-and-whisker plots showing changes in C-, S- and R-strategy of plant functional groups in the communities of AM, AMS, AS and ADS. (E) C-strategy; (F) S-strategy; and (G) R-strategy. Different letters indicate that the same functional group is significantly different in different grasslands (Tukey's test, *P* < 0.05).
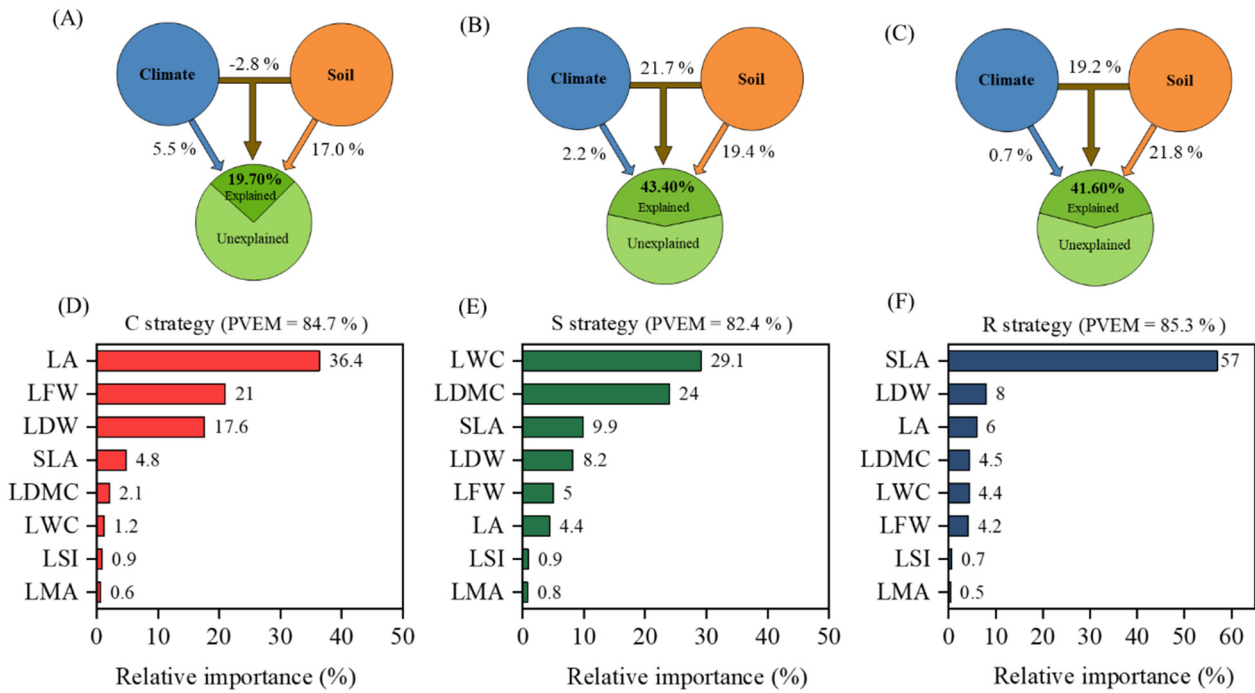
Fig. 4. Variation partitioning analysis showing the percentages of the variance in the C, S and R strategy scores (A, B and C, respectively) explained by the climate and soil, and the relative importance of leaf traits in explaining the variations in C, S and R strategy scores (D, E and F, respectively). LA, leaf area; LFW, leaf fresh weight; LDW, leaf dry weight; LSI, leaf succulence index; LWC, leaf water content; LMA, leaf mass per area; LDMC, leaf dry matter content; SLA, specific leaf area.
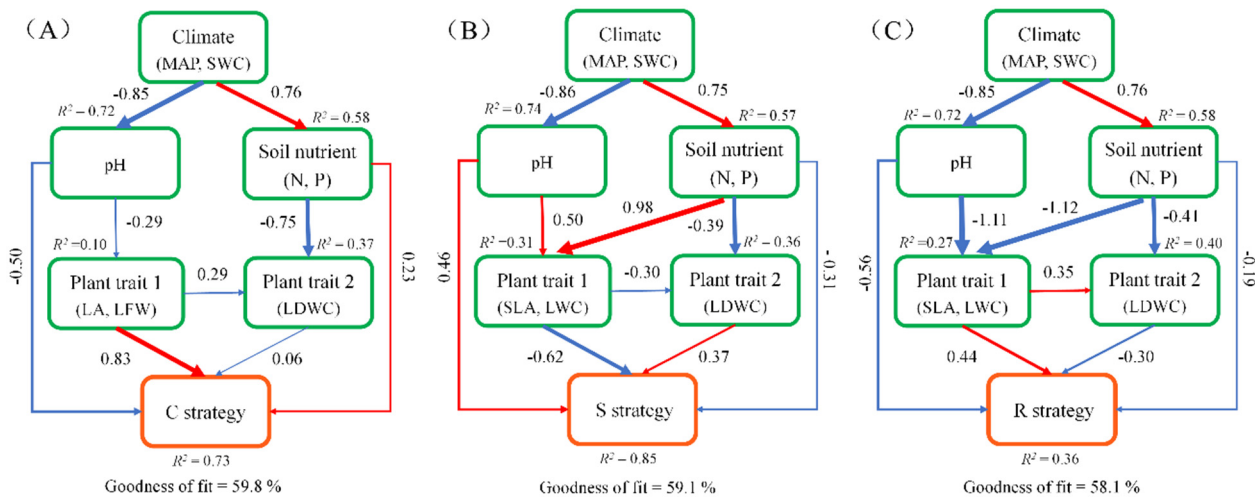

Fig. 5. Cascading relationships of C, S and R-strategy with climate, soil properties, and plant traits. Partial least squares path modelling (PLS-PM) disentangling major pathways of the effects of climate, soil properties, and plant traits on plant strategy. The red and blue arrows indicate positive and negative flows of causality, respectively.

would shift species composition of communities from pure S-strategy species to less stress-tolerant species with higher C and R components (Butterfield and Briggs, 2011; Rosado and de Mattos, 2017). Low soil moisture limits the mineralization of organic nutrients that may represent somewhat stressful conditions for plant growth (Escobedo et al., 2021). In this study, the water variability along the precipitation gradient eventually affected plant traits and CSR strategies by affecting soil nutrients and pH (Fig. 5). Compared with sites with lower water and soil nutrients, species have higher C- and R-strategies and lower S-strategy values in AM. Moreover, pH plays a crucial role in soil nutrient availability, microbial activity, and plant growth (Ma et al., 2021), which may indirectly affect the CSR of plants. Previous studies have shown that challenges in habitats with

alkaline soil conditions are thought to be low availabilities of phosphorus and iron, and the predominant form of available nitrogen is dependent on soil pH (Bartelheimer et al., 2015). Consequently, the co-variation of plant traits and the environment along the precipitation gradient regulates the CSR of alpine plants. Understanding the responses of plant traits and ecological strategies to environmental variability helps predict alpine grassland community dynamics under environmental change.

5. Conclusions

Although the alpine grasslands showed a prevalence of S-strategies, the eastern alpine meadows with higher soil water and nutrients had lower

S-strategy values and higher C- and R-strategy values than the other types of grasslands. Compared with grasses and sedges, forbs and legumes showed more flexible ecological strategies along the precipitation gradient. In addition, plant traits and ecological strategies presented covariance with environmental gradients. Water variability eventually regulated plant traits and CSR strategies by affecting soil nutrients and pH. Our study contributes to understanding the mechanism of plant adaptation to environment and helps to predict community dynamics under environmental change in the alpine grasslands.

CRediT authorship contribution statement

Jialuo Yu: Investigation, Data curation, Methodology, Software, Writing – original draft. **Ge Hou:** Investigation, Data curation, Writing – review & editing. **Tiancai Zhou:** Methodology, Software, Writing – review & editing. **Peili Shi:** Conceptualization, Writing – review & editing, Supervision. **Ning Zong:** Investigation, Data curation. **Jian Sun:** Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.156512.

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