

# Biogeographic Patterns of Leaf Stoichiometry and Adaption Strategy of *Stellera Chamaejasme* L. in Degraded Grasslands Across Northern China

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## Research Article

**Keywords:** Biogeographic patterns, Leaf stoichiometry, Climatic variables, Soil factors, *Stellera chamaejasme* L.

**Posted Date:** December 7th, 2021

**DOI:** <https://doi.org/10.21203/rs.3.rs-1126970/v1>

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# Abstract

**Background:** Plant leaf stoichiometry reflect its adaptations to environments. Leaf stoichiometry variations across different environments have been extensively studied among grassland plants, but little is known about intraspecific leaf stoichiometry, especially for widely distributed species, such as *Stellera chamaejasme* L. We present the first study on the leaf stoichiometry of *S. chamaejasme*, and evaluate their relationships with environmental variables by collecting *S. chamaejasme* leaf and soil samples from 29 invaded sites in the two plateaus of distinct environments [the Inner Mongolian Plateau (IM) and Qinghai-Tibet Plateau (QT)] in Northern China. Leaf C, N, P, and K and their stoichiometric ratios, and soil physicochemical properties were determined, together with climate information from each sampling sites.

**Results:** Results showed that mean leaf C, N, P, and K concentrations were 498.60, 19.95, 2.15, and 6.57 g · kg<sup>-1</sup>, respectively; the C/N, C/P, and N/P ratios were 25.46, 246.22, and 9.84, respectively. Soil physicochemical properties of *S. chamaejasme* invaded area varied wildly, and few significant correlations between *S. chamaejasme* leaf ecological stoichiometry and soil physicochemical properties were observed. Except for C and N in leaves, the P and K had higher homeostasis than 1, between 4.17 and 13.21. Moreover, C and N content of *S. chamaejasme* leaves were unaffected by any climate factors. However, the correlation between leaf P and climate factors was significant in IM only, while leaf K in QT. Finally, partial least squares path modeling suggested that leaf P or leaf K were affected by different mechanisms in QT and IM regions.

**Conclusions:** Our results indicated that *S. chamaejasme* tend to be insensitive to variation in soil nutrient availability, resulting in their broad distributions in China grasslands. Moreover, *S. chamaejasme* adapt to changing environments by adjusting its relationships with climate or soil factors to improve their chances of survival and spread in degraded grasslands.

## Introduction

Ecological stoichiometry plays an important role in analyzing the composition, structure, and function of a concerned community and ecological system [1, 2]. Over the last few decades, a particular focus of ecological stoichiometry has been to document large-scale patterns of, and the driving factors for, plant carbon: nitrogen: phosphorus (C:N:P) stoichiometry [3-7]. The relationship between leaf stoichiometry, geographic patterns, and climate factors have been studied in both global and regional scale.

Geographical variation in foliar ecological stoichiometry is a challenging issue to plant ecologists [4, 8-10]. Meanwhile, homeostasis ( $H$ ) of element composition is one of the central concepts of ecological stoichiometry, and its strength is related to the ecological strategy and adaptability of the species [2, 11]. Stoichiometric homeostasis can help predict the strategies used by different plant species to cope with limited resources [2, 12]. The nutrient conservatism of high  $H$ -species could be an important mechanism contributing to their success, particularly in natural (unmodified) terrestrial ecosystems, where nutrient supply is often limiting and highly variable [13, 14]. Indeed, the stoichiometric homeostasis of plants varied with species, growth stages, and element types [15-18].

*Stellera chamaejasme* L., a toxic perennial weed, has been established and is now abundant in the alpine meadow on the eastern Tibetan Plateau and typical steppe on eastern Inner Mongolia Plateau of China [19, 20]. It has become one of the most serious weeds threatening a wide range of grasslands [21]. Much attention has been given to *S. chamaejasme* because of its potential hazards on the grassland ecological safety and its impact on animal husbandry sustainability [22-25]. Despite this, no similar phylogeographical study had ever been conducted on *S. chamaejasme*. Plant nutrient and stoichiometry are key foliar traits with great ecological importance, but existing publications provide limited insight into biogeographic leaf nutrient and stoichiometry patterns for *S. chamaejasme* [19, 20]. As habitat heterogeneity tends to increase with geographical distance, wide-ranging species can usually use a wide array of resources and tolerate broad environmental conditions or physiological stresses and flourish over a larger area [26, 27]. Recent studies have assumed that wide-ranging species always have stronger homeostasis or weak relationship in nutrient concentrations than narrow-ranging species in response to environmental factors (e.g. soil fertility)[14, 26]. Accordingly, we naturally associate the widespread of *S. chamaejasme* with its stoichiometric homeostasis and understand its distribution and invasiveness considering the stoichiometric homeostasis.

Several studies on a regional and global scale reported that changes of plant leaf N and P element stoichiometry are associated with many biotic and abiotic factors, including climate variables, soil properties, species, and plant functional groups [3, 5, 6, 9, 28-30]. However, species are commonly collected from a few individuals from one or a few populations and averaged at the population or species level, disregarding the intraspecific variability [31]. Investigating the geographic variation within species can help to uncover the mechanism of relationships between plant tissue nutrients and environments [32], which exclude the confounding effects of taxonomic and phylogenetic structure like those found to influence the geographic patterns in leaf nutrients, and their linkages to climate and soil. Since relationships between environment and plant traits along environmental gradients could be presented as evidence of environmental control over species distribution, examining plant-environment (e.g. climate and soil nutrient availability) interactions may provide some insights into the underlying mechanism of *S. chamaejasme* distribution in degraded grasslands. However, no studies have yet incorporated information on geographic patterns in leaf stoichiometry of *S. chamaejasme* in relation to environmental factors.

This study assesses the stoichiometry and patterns of *S. chamaejasme* leaves in degraded grasslands across northern China. The distinct habitats of Qinghai-Tibetan Plateau (QT) and Inner Mongolia Plateau (IM) provide a unique opportunity to test whether there are significant differences in leaf stoichiometry under different environmental conditions and to examine how and to what extent soil and climate modify leaf stoichiometry of *S. chamaejasme* across degraded grasslands. In general, most researchers focused on the roles of C, N, and P stoichiometry in the ecological process from individuals to ecosystems, but potassium (K) is an essential macronutrient that has been partly overshadowed by C, N, and P [4, 7, 33, 34]. Our study also showed the K concentration of *S. chamaejasme* leaves, which broadens the contents of ecological stoichiometry. We hypothesized that 1) *S. chamaejasme*, a wide-spread weed, would exhibit small variation in leaf stoichiometry and tolerate broad environmental conditions; in other words, *S.*

*chamaejasme* may have stoichiometric homeostasis, and, 2) due to QT and IM differ in their limiting factors to vegetation, the relationship between *S. chamaejasme* and environmental factors may be related to different factors in the two habitats. To test our hypotheses, we first explored the overall biogeographic patterns of C, N, P, and K stoichiometry of *S. chamaejasme* leaves from 29 sampling sites in two grassland ecosystems in northern China. We then disentangled the effects of climate and soil on the overall plant stoichiometry pattern and compared the difference between the two habitats.

## Results

### Pattern of leaf ecological stoichiometry and soil physicochemical properties of *S. chamaejasme*

The mean value (mean), standard deviation (SD), and coefficients of variation (CV%) of leaf ecological stoichiometry of *S. chamaejasme*, and soil chemical and physical properties were listed in Table 1, and a comparison was made between two main habitats of *S. chamaejasme* (Fig. 2). Leaf C, N, P, K and C:N, C:P, N:P of *S. chamaejasme* varied gently across all study sites. The mean leaf C, N, P, and K were  $498.60 \text{ g} \cdot \text{kg}^{-1}$ ,  $19.95 \text{ g} \cdot \text{kg}^{-1}$ ,  $2.15 \text{ g} \cdot \text{kg}^{-1}$ , and  $6.57 \text{ g} \cdot \text{kg}^{-1}$ , respectively, and CV% of leaf P was the largest. Moreover, the mean leaf C:N ratio was 25.46, C:P ratio 246.22, N:P ratio 9.84. Inconsistent with the pattern of leaf results, soil physicochemical properties of *S. chamaejasme* invaded area varied wildly. Soil C, N, P, and K exhibited large variations, primarily ranging c.  $5.87 - 84.74 \text{ g} \cdot \text{kg}^{-1}$  for C;  $0.24 - 7.43 \text{ g} \cdot \text{kg}^{-1}$  for N,  $0.20 - 0.82 \text{ g} \cdot \text{kg}^{-1}$  for P, and  $0.95 - 30.55 \text{ g} \cdot \text{kg}^{-1}$  for K. Variation in soil K content across all study sites was about 32 times (Maximum / Minimum), which was the most variable element among the four total elements. Soil mean C:N, N:P, and C:P ratios were 13.99, 77.50, and 6.34, respectively. For available soil nutrients, soil NN variation was considerably larger than that for the AP, AK, and AN content, as evidenced by coefficients of variation (CVs) (Table 1). Similarly, soil WC, pH, and Ec showed a greater variation throughout the sampling areas.

When compared leaf element contents of *S. chamaejasme* in QT and IM, we found that only leaf K concentrations were significantly different between the two habitats, which was greater in QT (Fig. 2). Moreover, most soil physicochemical properties were higher in QT than those in IM, except soil AN, NN, and Ec. Specifically, soil P (Fig. 2h), K (Fig. 2i), AP (Fig. 2m), WC (Fig. 2e), and pH (Fig. 2j) were significantly higher in QT than IM, but soil Ec was significantly lower in QT (Fig. 2o).

### Ecological stoichiometry homeostasis of *S. chamaejasme* in degraded grassland

*Pearson* correlations analysis indicates that there are only weak or no correlations between leaf ecological stoichiometry and soil physicochemical properties (Table 2). Furthermore, when analyzed the relationships between leaf elements of *S. chamaejasme* and soil by using the homeostasis model, we got a very interesting result. In Fig. 3, the homeostasis index ( $H$ ) of C and N were 0, indicating that the leaf of *S. chamaejasme* could not retain carbon and nitrogen. The  $H$  of AN and NN were 0, showing the stronger effect of both forms of soil inorganic nitrogen on leaf nitrogen of *S. chamaejasme*. Additionally,  $H$  of P and K were higher than 1, and  $H_K$  (13.16) was greater than  $H_P$  (4.17). Likewise,  $H_{AP}$  (4.17) was smaller

than  $H_{AK}$  (13.21) in *S. chamaejasme* leaves. In summary, the  $H$  index of *S. chamaejasme* changed between 4.17 and 13.21.

### **Spatial variation of leaf elements of *S. chamaejasme* in relation to climatic factors**

No significant relationships among leaf C and N content and climatic factors (MAT and MAP) were found using data for all sample sites or regions. For all study sites, only leaf K content was correlated with climate factors ( $P < 0.001$ ) with greater K with increasing MAT (Fig.4). For the regions, it should be noted that in IM, the relationship between leaf P and climatic factors was significant, but K was not; on the contrary, the K content of *S. chamaejasme* leaves was related to climatic factors but P was not in QT. To be specific, leaf P concentration increased with increasing MAT and MAP in IM. Moreover, with increasing MAT, leaf K had an increasing trend, but increasing MAP showed an opposite trend in QT.

### **Relative roles of soil and climatic factors in leaf P or K contents of *S. chamaejasme***

Both P and K content of *S. chamaejasme* leaves were affected by soil and climatic factors simultaneously. Thus a more in-depth analysis using partial least squares path modeling revealed direct and indirect effects of the environmental drivers on leaf P and K content of *S. chamaejasme* in different regions (Fig. 5). The standardized direct, indirect, and total effects of soil and climate variables on the leaf P and K in QT and IM are presented in Table 3. Firstly, the influence of climatic factors on soil were bigger in IM than that in QT, and the effect of climatic factors on soil was significant on LP in IM. Secondly, we found that soil factors had significant effect only on leaf P in QT only. Thirdly, the effect of climate factors on leaf P was significant in IM, but the direct effect of climate factors on leaf P or leaf K in IM and QT were greater than the indirect. These results suggest that leaf P or leaf K were affected by different mechanisms in QT and IM regions. Moreover, the goodness of fit (GOF) was 0.3205 and 0.3556 for LP and LK in QT, respectively, and 0.5490 and 0.4431 in IM. The relatively low predictive power of the model of QT suggested that most variation remained unexplained.

## **Discussion**

### **Overall patterns of leaf ecological stoichiometry and soil physicochemical properties of *S. chamaejasme* across northern China**

The patterns of N and P status in plant biomass, and especially in leaves, have been intensely studied [4-6, 35-38], but few studies have attempted to document intraspecific leaf stoichiometry, especially for poisonous weeds in grasslands. This study presents, to our knowledge, the first analysis of leaf element concentrations (C, N, P, K) and ratios (C:N, C:P, N:P) of *S. chamaejasme* across degraded grassland in northern China. Our results show that leaf C ( $498.60 \text{ g} \cdot \text{kg}^{-1}$ ), N ( $19.95 \text{ g} \cdot \text{kg}^{-1}$ ), and P ( $2.15 \text{ g} \cdot \text{kg}^{-1}$ ) of *S. chamaejasme* were higher than the mean value of all species in the China Grassland Transect [38], and there was no obvious difference between two habitats of *S. chamaejasme*. N and P are the most important limiting nutrients for primary productivity in terrestrial ecosystems [39], and a high concentration of N and P in *S. chamaejasme* leaves means high nutrient uptake efficiency of *S.*

*chamaejasme* in degraded grasslands, which could facilitate *S. chamaejasme* outcompete other species in nutrient-poor environments. Moreover, K is one of the essential macronutrients that play critical roles in various metabolic processes, but it has been partly overshadowed in ecological stoichiometry by nitrogen and phosphorus [40, 41]. Although most studies did not involve the K content in plant leaves, it is worth noting that K concentrations of *S. chamaejasme* were significantly greater in QT than that in IM. The reason may be that the content of nutrients in plants can be constrained by nutrient supply in the soil, and the content of soil K is significantly higher in QT, therefore generating this difference. The leaf C:N ratio of *S. chamaejasme* was 25.46, C:P ratio 246.22, N:P ratio 9.84. Generally, it is not uncommon that using N:P ratios of plant biomass as indicators of N or P limitation in various studies [35, 42]. The low N/P ratio in *S. chamaejasme* might imply that its growth is restricted by N, which was consistent with the results reported by Guo et al [20].

We found that *S. chamaejasme* could survive in a soil environment with considerable variation, which is consistent with the fact that *S. chamaejasme* is wide-ranging species with a wide geographic range in China grassland [43]. The soil condition for *S. chamaejasme* growth varies considerably from site to site. Soil physicochemical properties varied with a difference of more than 10 times between the maximum and the minimum included C (14.43 times), N (30.94 times), K (32.27 times), NN (26.66 times), WC (10.60 times), Ec (21.86 times). Moreover, one sampling site (Haiyan in QT) showed the greatest soil physicochemical properties. For example, the content of soil P was lowest ( $0.20 \text{ g} \cdot \text{kg}^{-1}$ ), and soil WC was the minimum (0.03), but pH reached a maximum (8.81), indicating *S. chamaejasme* could tolerate an extreme environment. This may provide a competitive advantage for *S. chamaejasme* against other plant species and help explain its rapidly expansion in degraded grasslands. Additionally, we also found that the CV of NN was 100.57%, greater than for AN (41.16 %), indicating that *S. chamaejasme* was less sensitive to the NN variation.

Generally, Tibetan alpine grasslands and Inner Mongolian temperate grasslands, which have different limiting factors, are both zonal grassland types in China [44]. Alpine grasslands are mainly limited by low temperatures in the growing season, while temperate grasslands are affected by drought [38]. Accordingly, our analysis indicated that some soil physicochemical properties of *S. chamaejasme* for the regions were significantly different. Soil WC and pH for Qinghai-Tibet were significantly higher, and Ec lower than those for Inner Mongolia. However, apart from SP, SK and SAP, soil C and N concentrations and other soil available nutrients (AN, NN, AK) for the regions were insignificantly different. These findings suggest that climate imposes important controls on soil nutrients.

### **Relationships between leaf ecological stoichiometry and environmental variables**

Plant nutrient concentrations and their correlations with soil nutrient conditions are considered effective tools for exploring plant adaptation and resource utilization strategies in a severe environment [28, 45]. In our study, few significant correlations between *S. chamaejasme* leaf ecological stoichiometry and soil physicochemical properties were observed, implying insensitive response to the changes in soil nutrient supply of *S. chamaejasme*. This supports the finding of Geng et al. [26], and provides confirmation that

wide-ranging species are usually able to use a wide array of resources and to tolerate broad environmental conditions or physiological stresses, and hence flourish over a larger area. The poor synchronization with local edaphic conditions demonstrates a capacity of *S. chamaejasme* to maintain a high level of function at both high and low resource levels, resulting in their broad distributions in China grasslands. Further, stoichiometric homeostasis is the ability of plants to maintain their element composition relatively stable regardless of changes in nutrient availability via various physiological mechanisms [2, 11], and the degree of stoichiometric homeostasis can be indicated by the homeostatic coefficient ( $H$ ) [12, 46, 47]. It is well known that stoichiometric homeostasis had been reported in many dominant palatable species [15, 18, 48] in grasslands. However, this has not been established in unpalatable species. Since poisonous plants represent the majority of the plant species detected after grasslands have been degraded, reveal the eco-physiology characteristics of poisonous weeds will help us better understand how the communities dominated by poisonous weeds form. We found  $H_C$  and  $H_N$  of *S. chamaejasme* were 0, indicating that *S. chamaejasme* could not maintain carbon and nitrogen internally. Compared with other grassland species, *S. chamaejasme* had no  $H_N$ , which was different from previously reported results for other species [17, 49]. Our data clearly show that the stoichiometric homeostasis coefficient of P ( $H_P$ ) of *S. chamaejasme* was higher than  $H_N$ , indicating *S. chamaejasme* was relatively less sensitive responses to soil P than soil N. However,  $H_N$  was consistently higher than  $H_P$  at the levels of community, family, and species in China reported by previous studies [15, 18]. Like many other terrestrial ecosystems, grassland ecosystems face an ongoing increase of atmospheric nitrogen deposition in recent decades [50]. The increase of N availability in the soil leads to ecosystems limited by N have gradually transformed to P-limitation or other elements [51, 52]. Thus *S. chamaejasme* with  $H_P$  could survive outstandingly than species without  $H_P$  in the future P-limited surroundings. Moreover, although globally N and P are considered of paramount importance to plant function, it is widely known that many other elements are also important in specific contexts or regions [33]. We also found that  $H_K$  was greater than  $H_P$ , implying K could be used as another important element that indicates the degree to which an organism maintains homeostasis.

Our results indicate that in the macro scale, leaf C and N do not directly correlate with meteorological factors (MAT and MAP), which is in agreement with previous studies conducted in the grassland biomes of China [6]. The weak relationships observed between leaf C, N, and climatic variables may result from plant growth, development, metabolism, phenological and life-history traits rather than from the specific geographic environment. On the contrary, there were close relationships between leaf P and K and climatic factors (Fig. 4). The relationship between leaf P and climate factors was significant only in IM, and the K content of *S. chamaejasme* leaves was significantly related to climate factors only in QT. We noticed that the correlation of leaf P and MAP ( $R^2 = 0.5523$ ) was greater than the relationship between P and MAT ( $R^2 = 0.4886$ ) in IM, and the relationship between K and MAT ( $R^2 = 0.3338$ ) was greater than that with MAP ( $R^2 = 0.2920$ ) in QT. These again reflect the different limiting factors of plant growth in different regions [38]. It is a reasonable assumption that precipitation is a more important limiting factor than the temperature for vegetation growth in arid and semi-arid regions like Inner Mongolian Plateau

temperate grasslands. In contrast, the temperature is more likely to have a greater effect on leaf element concentrations than precipitation in Qinghai Tibet Plateau alpine grasslands with high-altitude and low temperature. We also found that only leaf K was negative related with MAP in QT. In fact, K leaches more easily from leaves than N and P [34]; hence it is easy to ascertain the increasement of MAP in the studies leading more leaf leaching of K in *S. chamaejasme*.

To explore complex relationships between soil and climatic factors on leaf P and K contents of *S. chamaejasme*, we conducted a PLS-PM analysis. We found soil exerted a significant effect on leaf P and climate affected leaf K directly in QT, while leaf P appeared to be limited mainly by climatic factors and leaf K was not affected significantly by any environmental factors in IM. This was contradicting our knowledge that climate factors often affect leaf elements through their influence on soil nutrient status [53]. The arid conditions of the Inner Mongolia Plateau (Arid and Semi-Arid Areas) have no doubt restricted grassland plants growth by insufficient water, but the results of our previous study [20] have proved that high water use efficiency plus high nutrient uptake efficiency of *S. chamaejasme* ensure its competitive advantage on degraded grasslands in Inner Mongolia Plateau, which makes the relationship between leaf P or K of *S. chamaejasme* and the soil factors was insignificant in IM region. However, the leaf P content was significantly positively correlated with soil factors (soil P, available P, nitrate N and pH), which was not entirely consistent with the result obtained in IM. The negative influence of climatic variables on leaf K was significant in QT may be the result of the negative relationship between MAP and leaf K, because K shows a greater loss from the plant canopy by foliar leaching than other nutrients such as N and P [34, 54]. Our model suggests that underlying mechanisms behind the leaf P or leaf K content of *S. chamaejasme* were different in two habitats studied, which means *S. chamaejasme* developed adjustable relationships with environmental factors to adapt to different growth conditions, thus facilitating the spread of *S. chamaejasme* in degraded grasslands.

In addition, species natural habitats will be subject to more disturbances in the future due to climate change and habitat degradation caused by intensive anthropogenic activities [55, 56]. In future works, continuing wide-scale sampling and considering the influence of human activities are required to further develop a deeper understanding of the geographic patterns in *S. chamaejasme*.

## Conclusion

Our study is, to our knowledge, the first to comprehensively document the chemistry of multiple mineral elements (C, N, P, K) and ratios of *S. chamaejasme* leaves and its surrounding soil physiochemical properties and quantify the potential controls and variability at a large scale. We found that there was no obvious difference leaf C, N, and P content of *S. chamaejasme* between the QT and IM, but K concentrations were significantly greater in QT than that in IM. Inconsistent with the pattern of leaf results, soil physiochemical properties of *S. chamaejasme* invaded area varied wildly, and most of them were greater in QT. our result clearly show that there were few significant correlations between *S. chamaejasme* leaf ecological stoichiometry and soil physicochemical properties, and the stoichiometric

homeostasis of P and K across north China was observed based on the homeostasis model, which supported the fact that wide-ranging species tend to be insensitive to variation in soil nutrient availability.

In addition, leaf P and K were affected by climatic variables. We found the relationship between leaf P and climate factors was significant only in IM, while the K content was related significantly to climate factors only in QT. In sum, both C and N content of *S. chamaejasme* leaves were unaffected by any environmental factors, but leaf P or leaf K were affected by different mechanisms in QT and IM regions by conducting a PLS-PM analysis, suggesting that *S. chamaejasme* adapt to changing environments by adjusting its relationships with climate or soil factors to improve their chances of survival and spread in degraded grasslands. This study contributes to the understanding of biogeographic patterns and adaptation strategy of *S. chamaejasme* in the degraded grasslands in China.

## Methods

### Study area

*Stellera chamaejasme* is a poisonous plant widely distributed in degraded grasslands in China. The typical grassland of the Inner Mongolia Plateau (IM) and the alpine steppe of Qinghai-Tibetan Plateau (QT) are the two main grassland types and present a wide *S. chamaejasme* distribution. Twenty-nine sites were selected (10 sites in IM, 19 sites in QT, Fig. 1), extending from longitude 99.68 to 118.16 °E and latitude 33.35 to 44.77 °N, along with altitudes ranging from 1060 to 3500 m (Supplementary 1). The mean annual temperature (MAT) and mean annual precipitation (MAP) ranged from 1.29 to 8.19 °C and 143.84 to 587.53 mm, respectively.

### Plant and soil sampling

Field measurements were conducted in June-July 2019, which was the vigorous growth stage for *S. chamaejasme*. At least 30 *S. chamaejasme* plants were randomly collected in each sampling site, then were subdivided into three subsamples, and the leaves of the subsamples were mixed into a composite sample. The samples were ground into fine powder for testing the content of elements (carbon, nitrogen, phosphorus, potassium). Concentrations of total C and total N of the *S. chamaejasme* leaves were determined sequentially by a FLASH 2000 elemental analyzer (Thermo Fisher Scientific, MA, USA). Total leaf P and K content were determined by using an AA-6300 Atomic absorption spectrophotometer (Shimadzu, Japan).

Three soil samples (0-15 cm in depth) were collected from each sample site, and each sample was thoroughly mixed with three subsamples and air-dried. Roots in the soil were removed by hand and passed through a 100-mesh sieve. Then, the soil was analysed for soil carbon (C), nitrogen (N), phosphorus (P), potassium (K), ammonium nitrogen (AN), nitrate nitrogen (NN), available potassium (AK), available phosphorus (AP), the potential of hydrogen (pH), electrical conductivity (Ec), and water content (WC). Soil physicochemical properties were measured as by Bao [57], soil C and N by the FLASH 2000 elemental analyzer, K by NaOH fusion-flame photometry, P by NaOH fusion-Mo/Sb colorimetry, soil AN

and NN by Auto Discrete analyzer, and soil AK were determined by the flame atomic absorption spectrophotometer. To measure soil AP, air-dried and pre-weighed soil was extracted using 0.5 mol L<sup>-1</sup> NaHCO<sub>3</sub> and P concentration in the extract was determined by the ammonium molybdate method. Soil pH was measured in a 1:2.5 soil:water suspension, and soil Ec was measured using a conductivity meter. Soil water contents were determined gravimetrically by oven-drying subsamples at 105 °C for 24 h.

## Data Analysis

The means, standard deviations (SD), and coefficients of variation (CV) of leaf element concentrations and their ratios, and soil physicochemical properties were calculated for all sites, regions (IM and QT). The data exhibited significant heteroscedasticity and non-normal distributions. Thus, these variables were transformed using the natural logarithm before analysis to eliminate outliers or homogeneity of variances. Differences between QT and IM were evaluated by Independent-Samples T Test. *Pearson* correlations analysis was evaluated the relationship between *S. chamaejasme* leaf ecological stoichiometry and soil physicochemical properties across 29 sampling sites in Northern China.

We calculated  $H$  according to the homeostasis model:  $y = cx^{1/H}$ , where  $y$  is the leaf element concentration of *S. chamaejasme*,  $x$  is the total nutrient contents or available nutrients in the soil, and  $c$  is a constant. The values of  $H$  and  $c$  were obtained when we analyzed the relationship between  $y$  and  $x$  using regression analysis. A high value of  $H$  indicates strong stoichiometric homeostatic regulation.

In order to determine the influence of climate factors, we obtained raw daily precipitation and temperature data (2010-2019) from the China Meteorological Administration and calculated annual precipitation and temperature using the Kriging interpolation method in ArcGIS (ESRI (Environmental Systems Research Institute), Redlands, CA, USA). Therefore, climate data for mean annual temperature (MAT) and mean annual precipitation (MAP) for the sample sites were obtained. Regression analyses were performed to determine the correlation of leaf element contents and climate factors (MAT, MAP). Scatter plots were used to visualize the relationships among leaf element contents and climate factors (MAT, MAP), and appropriate regression equations were developed.

Partial least squares path modeling (PLS-PM) was employed to explore the direct, indirect, and interactive effects between all environmental variables for leaf element contents (The R package *pls* *pm* (0.4.9)). The model included the following variables: Leaf elements (P, K), climate factors (MAT, MAP), and soil factors (K, AK, NN, and pH for leaf P in IM, P, AN and NN for leaf K in IM, P, AP, NN and pH for leaf P in QT, C, K, AP, WC, and pH for leaf K in QT), after testing for collinearity of soil factors with the multivariate analog of Levene's test using the "betadisper" function in the *vegan* package. Indirect effects are defined as multiplied path coefficients between predictor and response variables, including all possible paths excluding the direct effect. The final model was chosen among all constructed models based on the Goodness of Fit (GOF) statistic according to the model's overall predictive power.

## Abbreviations

C: carbon; N: nitrogen; P: phosphorus; K: potassium; AN: ammonium nitrogen; NN: nitrate nitrogen; AK: available potassium; AP: available phosphorus; pH: the potential of hydrogen; Ec: electrical conductivity; WC: water content; MAT: mean annual temperature; MAP: mean annual precipitation; IM: Inner Mongolia Plateau; QT: Qinghai-Tibetan Plateau; PLS-PM: Partial least squares path modeling; GOF: goodness of fit; *H*: homeostatic index.

## Declarations

### Ethics approval and consent to participate

The sampling of plant and soil did not require permission from any local or national authority as sampled. The sampled species are not classified as endangered and are not under any protection in the sampled area.

### Consent to publish

Not applicable

### Availability of data and materials

All the data are summarized in the manuscript itself. Please contact the corresponding author regarding any additional queries related to the dataset generated and analyzed during the current study. The datasets in this study are available from the corresponding author on reasonable request.

### Competing interests

The authors declare that they have no competing interests.

### Funding

This study was financially supported by Beijing Science and Technology Project (Z181100009618031), Special Aid Fund for Qinghai Province (2020-QY-210), International Collaboration Fund of Department of Science and Technology of Shaanxi Province (2020KW-030).

### Authors' contributions

LZG and DH conceived the ideas and designed methodology; LL, HZM, LZ, and WH collected the data; LZG and KW analysed the data; LZG and DH led the writing of the manuscript; WH and VJS reviewed and edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Tables

**Table 1** Descriptive statistics for regional *S. chamaejasme* leaf ecological stoichiometry and soil physicochemical properties in Northern China. SD is standard deviations and CV is coefficient of variation.

Overall (n=29)	Soil		Leaf	
	Mean $\pm$ SD	CV (%)	Mean $\pm$ SD	CV (%)
C (g kg <sup>-1</sup> )	46.11 $\pm$ 21.63	46.91	498.60 $\pm$ 22.07	4.43
N (g kg <sup>-1</sup> )	3.75 $\pm$ 1.70	45.24	19.95 $\pm$ 2.09	10.48
P (g kg <sup>-1</sup> )	0.57 $\pm$ 0.17	29.82	2.15 $\pm$ 0.52	24.19
K (g kg <sup>-1</sup> )	20.80 $\pm$ 5.86	28.17	6.57 $\pm$ 1.18	17.96
C:N	13.99 $\pm$ 8.08	57.70	25.46 $\pm$ 2.51	9.86
C:P	77.50 $\pm$ 25.49	32.89	246.22 $\pm$ 61.75	25.08
N:P	6.34 $\pm$ 2.17	34.15	9.84 $\pm$ 2.61	26.52
AP (mg kg <sup>-1</sup> )	5.29 $\pm$ 1.96	37.00		
AK (mg kg <sup>-1</sup> )	175.91 $\pm$ 96.39	54.80		
AN (mg kg <sup>-1</sup> )	19.17 $\pm$ 7.89	41.16		
NN (mg kg <sup>-1</sup> )	14.12 $\pm$ 14.20	100.57		
WC	0.18 $\pm$ 0.09	50.00		
pH	7.90 $\pm$ 0.51	6.46		
Ec ( $\mu$ s cm <sup>-1</sup> )	247.21 $\pm$ 221.21	89.48		

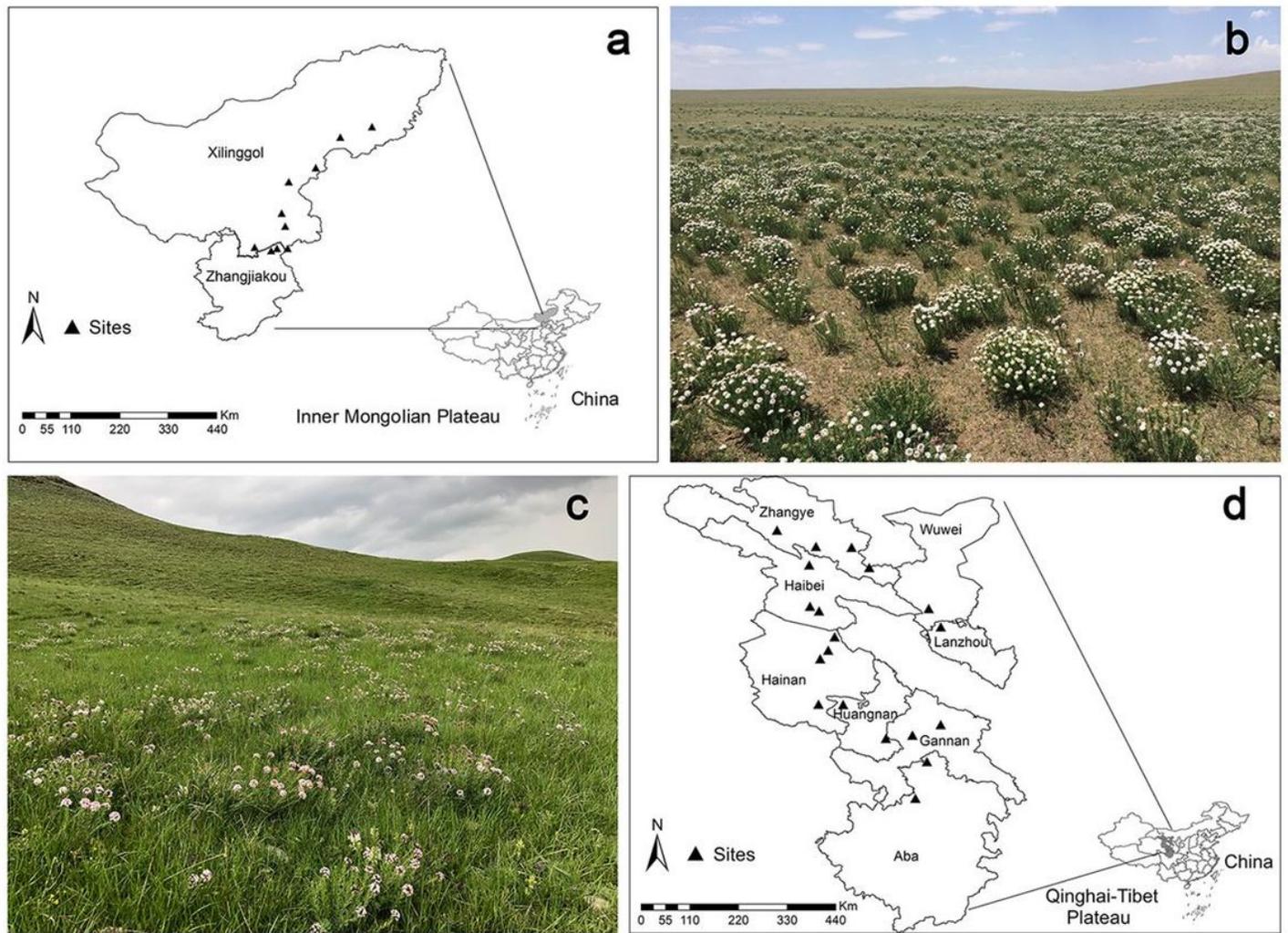
**Table 2** Relationship between *S. chamaejasme* leaf stoichiometry and soil physicochemical properties in Northern China (n = 29 sites, Pearson correlations ). Significant correlation is indicated by an \* (P < 0.05).

	Leaf C	Leaf N	Leaf P	Leaf K	Leaf C:N	Leaf C:P	Leaf N:P
<b>Soil C</b>	-18.27%	-7.46%	32.91%	20.65%	-3.28%	-41.17%*	-41.85%*
<b>Soil N</b>	-6.84%	1.42%	33.63%	26.88%	-8.80%	-39.62%*	-38.46%*
<b>Soil C:N</b>	10.07%	3.89%	-13.77%	9.47%	3.94%	14.38%	15.42%
<b>Soil C:P</b>	-10.30%	-1.92%	35.45%	22.29%	-7.50%	-45.65%*	-44.92%*
<b>Soil N:P</b>	2.58%	8.14%	28.96%	18.19%	-14.05%	-35.31%	-33.07%
<b>Soil P</b>	-18.04%	-3.07%	36.04%	26.50%	-4.06%	-39.10%*	-37.14%*
<b>Soil K</b>	13.94%	5.49%	27.48%	15.60%	-2.74%	-33.05%	-34.20%
<b>Soil available P</b>	10.11%	7.57%	51.31%*	55.79%*	-2.06%	-49.69%*	-45.29%*
<b>Soil available K</b>	-12.79%	-23.16%	-0.63%	29.47%	23.93%	-0.49%	-8.77%
<b>Soil ammonium N</b>	-31.40%	-22.06%	-0.05%	11.19%	13.27%	-4.53%	-8.86%
<b>Soil Nitrate N</b>	-33.42%	-36.38%	-16.41%	-1.30%	29.24%	14.31%	0.73%
<b>Soil WC</b>	-2.70%	4.86%	36.81%*	40.87%*	-8.06%	-40.80%*	-36.77%*
<b>Soil pH</b>	24.92%	16.07%	2.61%	20.08%	-1.61%	1.84%	6.53%
<b>Soil Ec</b>	-6.50%	-2.94%	3.03%	-23.17%	0.76%	-6.22%	-9.46%

**Table 3** Summary of the total effects on the leaf P and K of *S. chamaejasme* in Qinghai Tibet Plateau (QT) and Inner Mongolia Plateau (IM). Significant effect is indicated by an \* ( $P < 0.05$ ).

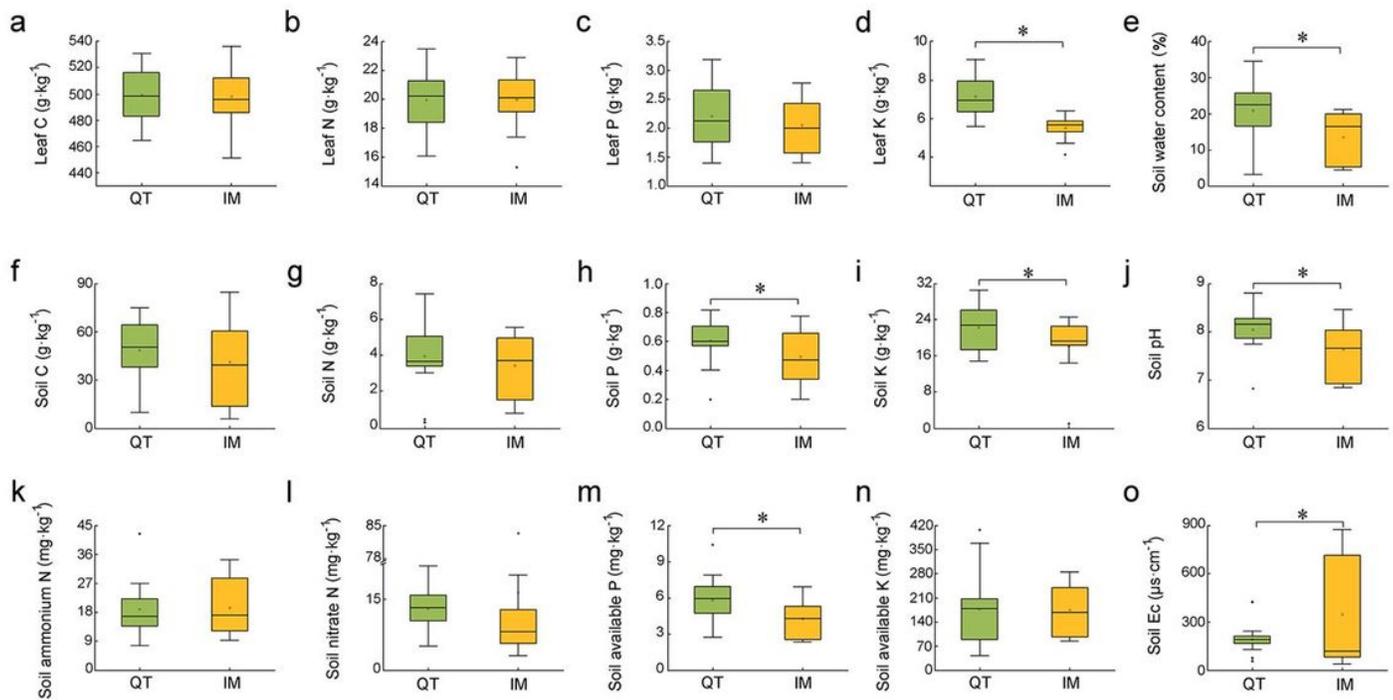
Leaf elements	Relationships	QT			IM		
		Direct	Indirect	Total	Direct	Indirect	Total
P	Climate → Soil	0.369	0	0.369	0.682*	0	0.682
	Climate → Leaf P	-0.456	0.192	-0.264	0.665	0.123	0.788
	Soil → Leaf P	0.519*	0	0.519	0.180	0	0.180
K	Climate → Soil	0.331	0	0.331	0.590	0	0.590
	Climate → Leaf K	-0.476*	-0.127	-0.604	0.248	0.181	0.428
	Soil → Leaf K	-0.385	0	-0.385	0.306	0	0.306

# Figures



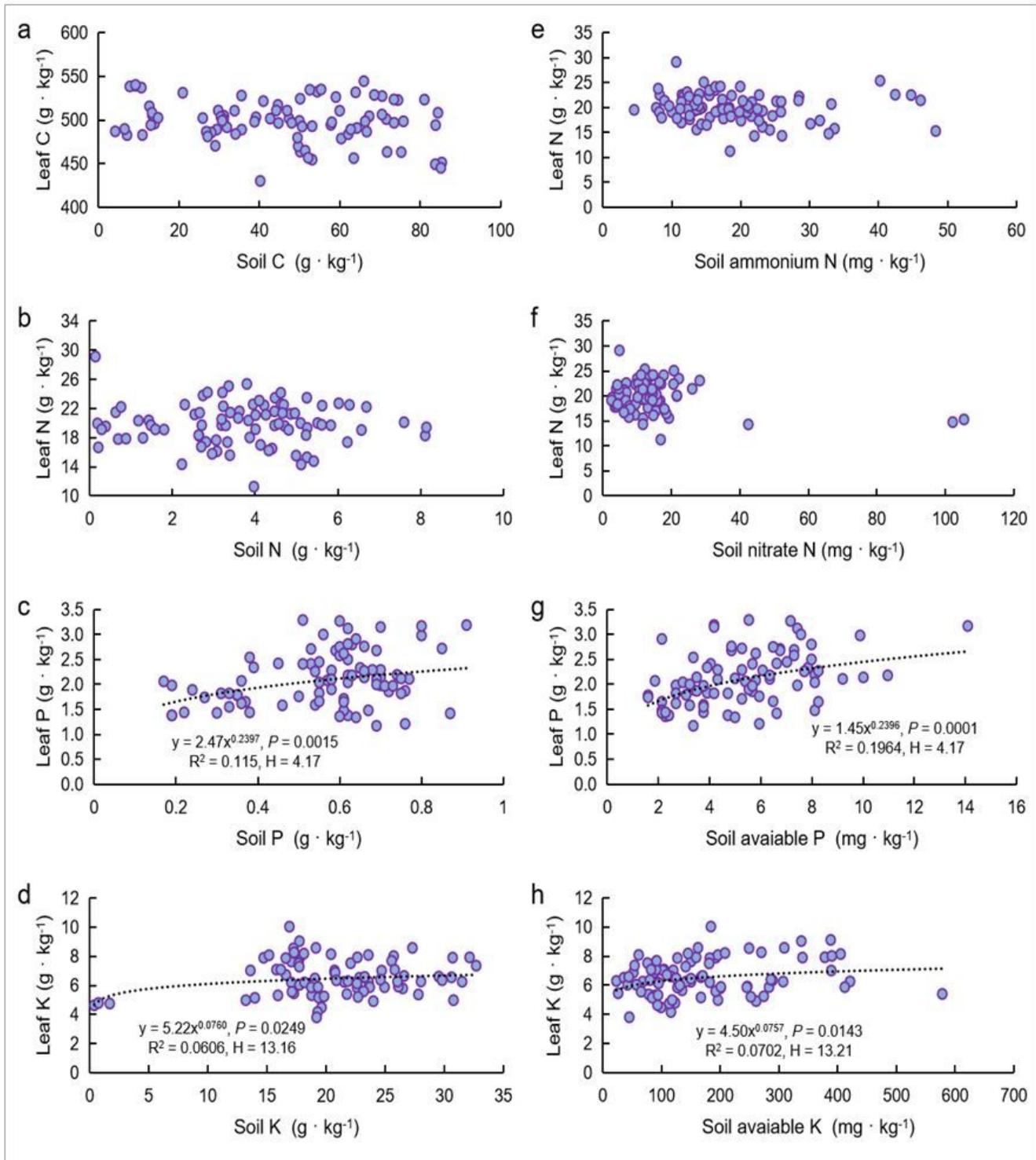
**Figure 1**

Location of the study and sampling sites. (a) Sampling sites on Inner Mongolia Plateau; (b) *S. chamaejasme* coverage in Taipusi Banner on Inner Mongolia Plateau; (c) Sampling sites on Qinghai-Tibetan Plateau; and (d) *S. chamaejasme* coverage in Qilian County on Qinghai-Tibetan Plateau.



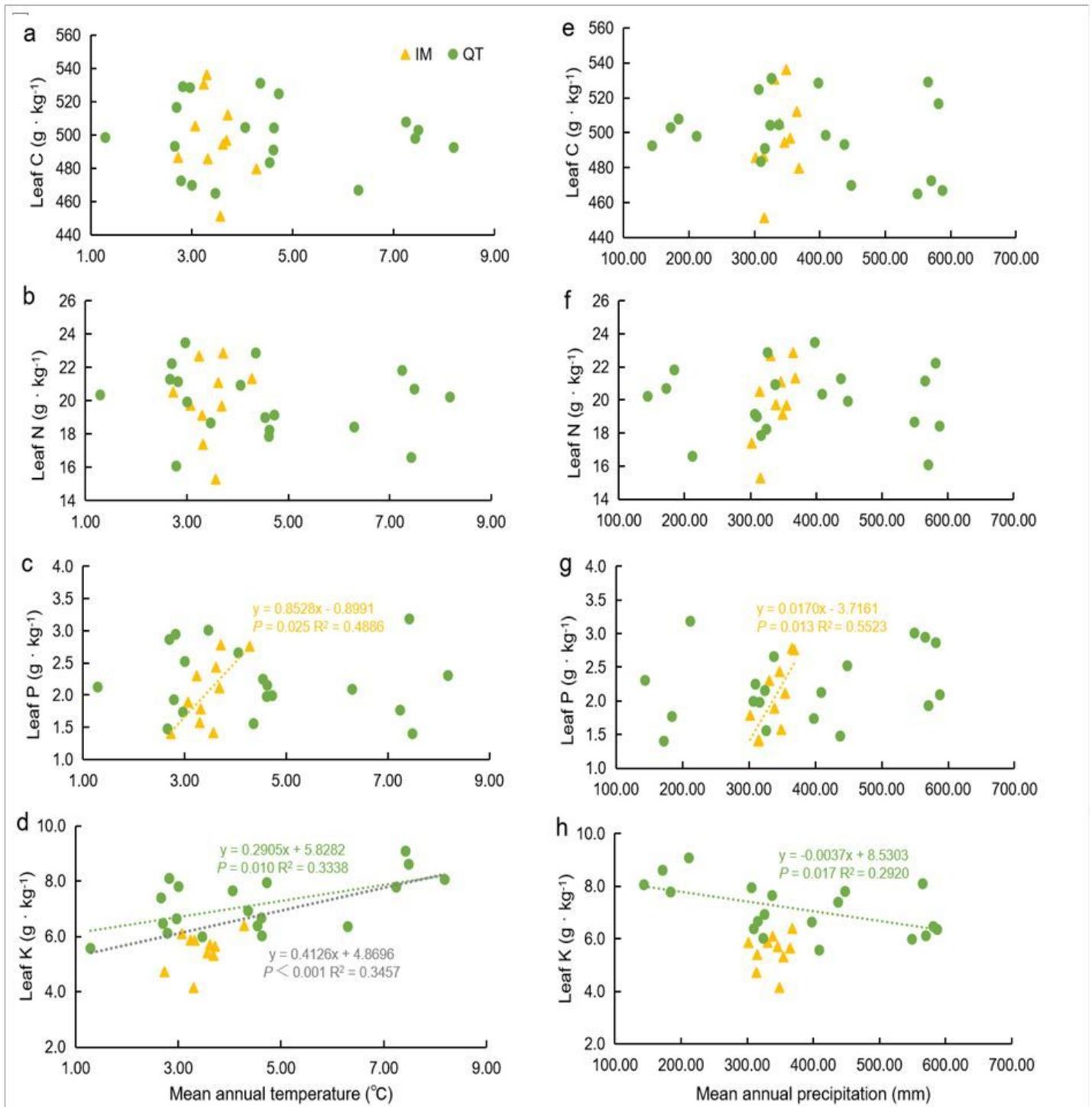
**Figure 2**

Comparison of leaf element contents and soil physiochemical properties in Qinghai Tibetan Plateau (QT, n=19) and Inner Mongolian Plateau (IM, n=10). Significant differences ( $P < 0.05$  on the basis of t-test) between the QT and IM were indicated by \*.



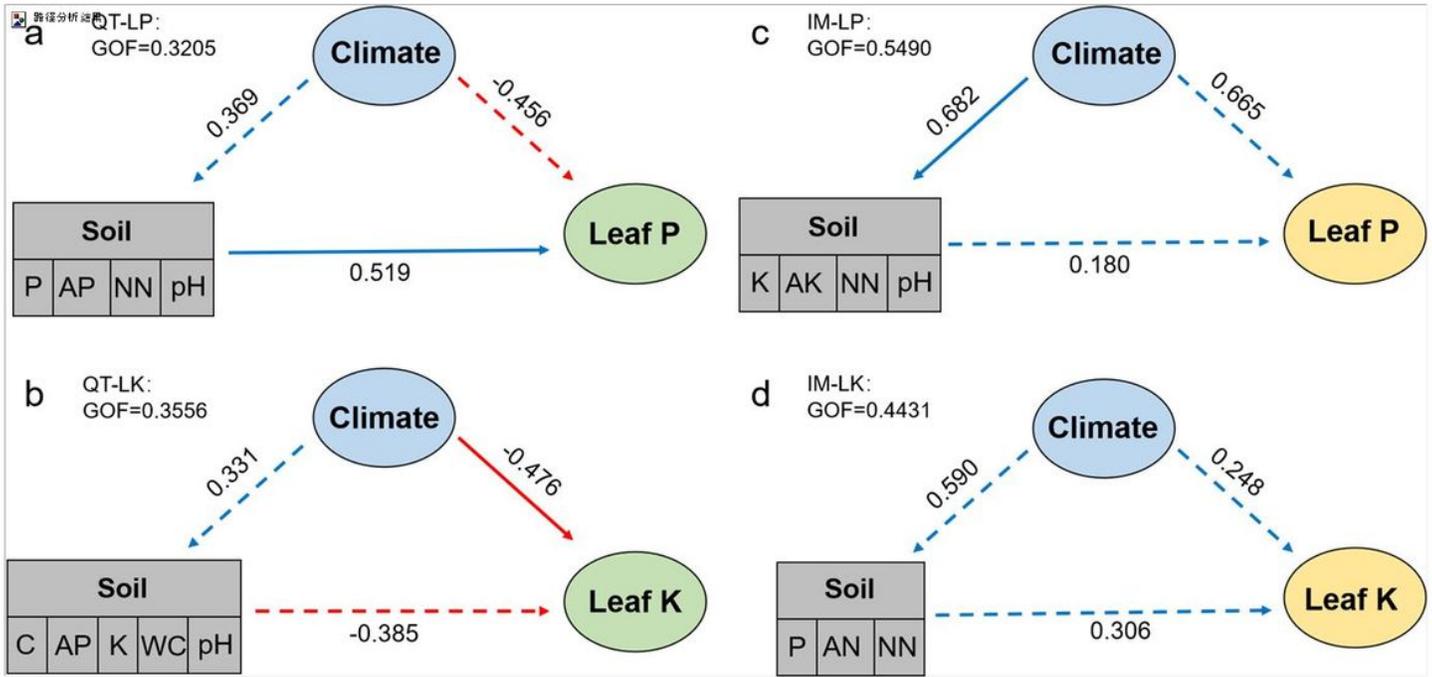
**Figure 3**

Relationship between the content of C, N, P, K elements in *S. chamaejasme* leaves and soil nutrient, however, significant relationships only found in leaf P and K. Power function regression were utilized. (a) soil C vs leaf C; (b) soil N vs leaf N; (c) soil P vs leaf P; (d) soil K vs leaf K; (e) soil ammonium N vs leaf N; (f) soil nitrate N vs leaf N; (g) soil available P vs leaf P; (h) soil available K vs leaf K.



**Figure 4**

Relationship of leaf C, N, P, K content of *S. chamaejasme* and climate factors (MAT & MAP) in Qinghai Tibet Plateau (green circles) and Inner Mongolia Plateau (yellow triangles), however, significant relationships only found in leaf P and K. Linear regression model analyses were utilized. Colored dotted lines represented significant relationships ( $P < 0.05$ ) in different region (yellow, IM; green, QT; grey, all sampling sites). (a) MAT vs leaf C; (b) MAT vs leaf N; (c) MAT vs leaf P; (d) MAT vs leaf K; (e) MAP vs leaf C; (f) MAP vs leaf N; (g) MAP vs leaf P; (h) MAP vs leaf K.



**Figure 5**

Effects of different variables (soil and climatic variables) on the leaf P and K of *S. chamaejasme* in Qinghai Tibet Plateau (QT) and Inner Mongolia Plateau (IM) based on. The blue arrows represent positive pathways, and the red arrows indicate negative pathways. The standard path coefficients are showed on the arrow. GOF, goodness of fit of the statistical model. (a) and (b) PLS-PM describing the relationships in QT; (c) and (d) PLS-PM describing the relationships in IM.

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