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Response of aboveground organs of Woody plants in the Qaidam Basin in China to aridity via functional economic spectra

Siyu Liu[1†], Yiwen Kong[1†], Yue Fan[1] and Yanhong Liu[1*]

Abstract

Background Plant economic profiles involve trade-offs between many functional traits of a plant that are often used as indicators to characterize major adaptive strategies, thus providing insights into plant distribution, ecosystem processes, and function. However, research on plant economic profiles in extreme habitats is limited, and most studies on economic profiles have focused on single organs, with fewer studies on economic profiles among aboveground (leaf and stem) organs.

Methods Taking the desert area of Qaidam Basin as the research object, 8 leaf traits and 8 stem traits of 25 dominant woody plants accounting for more than 80% of biomass in 130 sample plots under different aridity gradients were quantitatively analyzed. The functional strategies and economic profiles of aboveground organs of desert plants adapted to arid environment were studied.

Results Traits of leaves and stems represent distinct resource strategies. Leaf traits emphasize resource acquisition, while stem traits highlight conservation. The leaf economic spectrum (LES) and stem economic spectrum (SES) strategies showed an inverse pattern, with leaf traits shifting from opportunistic to conservative strategies and stem traits shifting from conservative to stabilizing strategies as aridity intensified, revealing an integrated aboveground economic spectrum of the plant along the aridity gradient. Moreover, there was a significant negative correlation between leaf and stem function strategies and reflected significant leaf-stem trade-offs.

Conclusion The functional traits of plants can reflect plant responses to environmental changes, and the aboveground economics spectrum helps researchers understand the response of plants as a whole to environmental differences, thus deepening the knowledge of the economic spectrum of plants. The patterns of economic profiles embodied by plants in response to aridity were revealed in this study. The trade-off between the LES and SES demonstrated the existence of an aboveground economic spectrum, providing a scientific basis for understanding the survival mode and adaptive variation pattern of desert plants.

Keywords Qaidam basin, Shrub, Functional traits, Leaf, Stem, Aboveground, Economic spectrum, Aridity gradient

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[†] Siyu Liu and Yiwen Kong contributed equally to this work.

*Correspondence:
Yanhong Liu
liuyh@bjfu.edu.cn
[1] Beijing Key Laboratory of Forest Resource Ecosystem Processes, Beijing Forestry University, Beijing 100083, China

Introduction

Plant functional traits are a set of plant attributes that are related to the structure, processes, and functions of the environment, and ecosystems [1–2]. It can reflect the important life activities of plants, such as carbon acquisition, water transfer, and nutrient cycling, as well as the physiological and phenological characteristics of plants [3]. Plants adapt to changing and complex habitat conditions by changing their functional traits in response to external disturbances [4]. A range of changing functional characteristics constitute the economic spectrum, representing a trade-off between adaptations that promote resource acquisition and adaptations that promote resource conservation [5–7]. The leaf is the main organ of a plant for photosynthesis and other important physiological activities and is the organ most sensitive to the external environment [8]. Therefore, the leaf economic spectrum (LES) [8], is a broad spectrum of combinations of functional traits that trade off or synergize with each other [4], ranging from leaves that are cheap in terms of resources, have short lifespans, and employ a resource acquisition strategy (with a fast return on investment in carbon and nutrients) to those that are expensive in terms of resources, have long lifespans, and employ a resource conservation strategy (with a slow return on investment in carbon and nutrients) [9]. It can be used to quantify the trade-offs between plant resource access and resource conservation strategies [10–11]. The LES has been fully utilized in adaptive studies of plant functional strategies, providing a strong scientific basis for understanding the functions of trait combinations and the strategies represented by trade-offs or synergistic relationships between combinations of functional traits. Focusing on plant functional traits, whether at the species, community, or ecosystem scale, is a powerful method of addressing ecological problems [4].

With the introduction of LES, many scholars have extended the resource economic spectrum at the species level to the community level for leaves [12], stems [13–14], and roots [15–17]. LES has been extended to include properties of wood [18], and properties of plant organs other than leaves [17, 19]. Since the main function of leaves is to absorb aboveground resources, while the main function of roots is to obtain underground resources, the pattern of root economic spectrum (RES) is similar to that of LES [20]. In contrast to LES the stem economic spectrum (SES) (or wood economic spectrum) defines the trade-offs between water and nutrient transport [17, 21–22] and mechanical support and defense against biological attack [1, 18, 23]. However, in the global plant economic spectrum system, woody organs do not occur in all life forms of plants (such as herbaceous plants), so among the three economically significant plant organs (leaves, stems, roots), the stem economic spectrum is rarely studied [8]. At the same time, Reich et al. argue that in addition to carbon and nutrients, water is also extremely important, so multifunctional traits also need to be supplemented [24]. Moreover, the connection between leaves and roots in terms of plant wholeness has been emphasized by scholars, but little is known about the connection between aboveground organs. Second, stems, as aboveground organs, experience the same environmental stresses as leaves do, and the question of whether the same environmental selection causes leaves and stems to have similar adaptive variations or survival strategies should also be emphasized. Each plant organ contributes uniquely to ecological strategies and survival. The study of stems cannot be neglected if researchers want to construct a more complete economic spectrum of plants.

As resource acquisition becomes more difficult and given the environmental constraints on resource acquisition (i.e., carbon, water, and nutrient uptake) [25], the main functions of the different organs above ground should be coupled within the same framework to form a plant aboveground spectrum or a complete plant economic spectrum [20, 26–27]. For example, as the degree of aridity increases, there is a negative correlation between the place of physiological activity of the leaf (leaf area) and the mechanical support capacity of the stem (stem cross-sectional area) (Huber) [28]. Xu et al. also confirmed that Huber values decrease with increasing degree of aridity through predictive modeling [29]. Theoretically, the close linkage of these functions should lead to robust coordination of functional traits between organs, through a series of trade-offs or synergistic relationships that form an adaptive strategy for the plant part or its entirety. However, environmental stresses may cause trait variation to deviate from coordination among organs and thus the economics of plant parts or the whole system to converge, which may lead to the decoupling of resource economic strategies among organs. Organs can respond to the same environmental stresses in different ways [30–31], allowing plants to be free from environmental pressures and choices [32–34]. For example, leaves and stems show an inverse pattern of fast-slow economic spectra in the hyperarid environment of the Atacama Desert [12]; the leaf, stem, and root economic strategies of tropical trees are decoupled in water-logged environments in Amazonian forests [35–36]. Extreme environmental stress may be an important factor in the differences in the economic strategies of leaf and stem resources, implying that the influence of the environment on the overall strategy of a plant does not indicate that it has the same regularity for all organs. An in-depth exploration of the relationships that exist between functional traits and strategies by which organs respond to environmental stresses is helpful for improving the understanding of functional trait variation, plant adaptive variation, and functional strategy diversity.

As environmental conditions deteriorate and plant access to water and nutrients becomes more difficult, plants should shift toward a slow conservative resource strategy according to the LES concept of Wright et al. [8]. However, in hyperarid areas, where the ability of all species to access resources is limited, the environmental impact on desert plants may change from a limitation on resources to a limitation on survival [37]. For the economic spectrum, the resource constraints of desert plants may be more manifested in water constraints, which is also the necessity of increasing the resource of water to the overall economic spectrum of plants [24]. In terms of the adaptation mechanisms of desert plants to water, the adaptation strategies of plants are diverse. For example, leaves may improve aridity tolerance by reducing transpiration and increasing water retention by reducing size, increasing thickness, and degrading assimilated branches [38]. The aridity tolerance characteristics of stems depend more on vessel characteristics, and a comparative study of 328 Compositae species revealed that vessel size decreases and vessel density increases during the progression from moderate habitats through dry to desert habitats [39]. However, it is undeniable that the economic spectrum of strategies for single organs to cope with the environment is hardly representative of the plant as a whole. It is equally likely that there are higher dimensional trade-off strategies between organs to maintain plant growth and reproduction while surviving. Particularly in desert ecosystems, severe water stress may lead to to decouple between organs on the economic spectrum or move toward opposite strategies to the overall economic spectrum. Therefore, exploring the multi-organ economic spectrum strategy of plants in desert ecosystems can help us further understand the overall economic spectrum characteristics of plants and deeply investigate the survival mechanism of desert plants. In contrast to semiarid steppe and grassland ecosystems, shrub species are considered the dominant plants in arid desert ecosystems [40–41]. Among the existing studies on the economic spectrum of plants, few have focused on hyperarid plants, which complicates the investigation of the main survival strategies of hyperarid plants through the traditional economic spectrum.

The Qaidam Basin is located in the northern part of the Qinghai–Tibetan Plateau in China and is characterized by high alpine, high salinity, strong winds, and rainfall less than evapotranspiration, with sparse vegetation, and the dominant species are basically all shrubs, which are typically hyperarid [42]. Aridity is a major factor affecting species in the Qaidam Basin, and few studies on the economic spectrum of plants have been conducted in hyperarid areas. The Qaidam Basin is an ideal study area for those who want to gain a deeper understanding of the economic spectrum of desert plants and their survival strategies. Moreover, much of the research on plant traits has focused on leaf traits and the interactions between leaf and root traits, whereas less research has focused on how aboveground organ (leaf and stem) traits interact with each other to adapt to the environment. In addition, scholars generally do not know whether the economic spectrum of aboveground organs is evident in extreme aridity habitats, nor is it clear how the economic spectrum of aboveground organs appears to change with increasing aridity severity and what relationships exist between the LES and SES. On this basis, the present study was conducted in the Qaidam Basin of the Tibetan Plateau (the study area), which has the dominant species of shrubs. The functional traits (morphological, economic, chemical and hydraulic traits) of the leaves and stems of desert plants under different aridity gradients were investigated, and the effects of environmental changes on the functional strategies of leaves and stems under different aridity gradients, as well as the harmonization between the LES and SES, were explored. This research proposes the following hypotheses: (1) there was a specific correlation between the functional traits of aboveground organs of desert plants, which could reflect their main functional strategies, and (2) there is a significant "fast-slow" economic spectrum between the aboveground organs of shrubs in the Qaidam Basin, which can well reflect the adaptability characteristics of plants in this area. This study aimed to elucidate the coordinated relationship of survival strategies among the aboveground organs of arid plants. In this manner, researchers can deepen their understanding of the adaptive variation patterns of functional traits in desert plants and their adaptive strategies and provide a scientific basis for the research and conservation of desert ecosystems.

Materials and methods

Study sites

The Qaidam Basin is located in Haixi Mongol and Tibetan Autonomous Prefecture, Qinghai Province, and is a typical inland arid area of China between the mountains and the fault basin, one of the three major inland basins in China [43], showing an irregular triangle spreading in a northwestern–southeastern direction, with the Qilian Mountains at the northern boundary, the Kunlun Mountains in the south, and the Arjinshan Mountains in the northwestern direction. The basin covers an area of approximately 250,000 km^2, and the altitude is between 2675 and 3350 m, with an average of 2800 m. The study area is located in the undisturbed natural area of the entire Qaidam Basin, a latitude between 35°00′ N and 39°20′ N, and a longitude between 90°16′ E and 99°16′ E [44]. The main climatic features of the

Qaidam Basin are arid and cold, and it has a temperate continental climate, with much less annual precipitation than evaporation [45]. In the study area, the mean annual relative humidity is between 30% and 40%, and the minimum can be less than 5%. The mean annual temperature is less than 5 °C, with an absolute annual temperature difference of more than 60 °C, a daily temperature difference of approximately 30 °C, and the temperature during summer nights can drop below 0 °C [46]. The number of windy days above grade 8 can reach 25–75 days per year, and strong winds of 40 m/s can even occur. The study area is ecologically fragile and one of the regions most significantly affected by global climate change [47].

The topography of the Qaidam Basin slopes from northwest to southeast, with saline desert soils and gypsum desert soils dominating the soil types, and the landscape types are mostly dominated by the Gobi Desert, wind-eroded residual mounds, salt lakes, salt crusts, deserts, and high mountains, which is a typical plateau desert ecosystem [48]. In terms of geomorphology, the vegetation type of the Qaidam Basin ranges from desertified grasslands and deserts in the east to extremely arid and bare areas, basically unvegetated desert areas in the west, with sparse vegetation, dominated by shrubs, semi-shrubs, and herbs with a high degree of aridity resistance, and more saline plants, which have a unique composition of flora and vegetation characteristics. Field surveys were conducted from August 2019 to September 2023. In the undisturbed natural desert area within the Qaidam Basin, sample plots were set up by selecting areas with obvious differences in natural vegetation, with a distance of more than 10 km between adjacent sample plots. A total of 130 sample plots of 100 × 100 m were set up, and the dominant species of shrubs within the sample plots were investigated and sampled (Fig. 1). All plants and plant material are naturally inherited and obtained from disturbed habitats, and there are no external sources such as anthropogenic cultivation. The biomass of the sample collection species within the 130 sample plots accounted for more than 80% of the community biomass, involving a total of 25 species (Table S1); the basic information is shown in Table S2. Thus, the community weighted means (CWMs) of the species traits within the sample plots can be used to represent the trait characteristics at the sample plot level [49]. The images of the acquired plants are detailed in Fig. S1. See Table S3 for details of the plots.

Sample collection and analysis

In each sample plot, good growth conditions for the established species were selected to set up sample plots. In each sample plot, all shrubs were surveyed and calculated biomass ratio, biomass ratio of more than 80% of all shrub species were surveyed and sampling, each selected three plants with good growth and consistent representative plants. Considering the fragility of the ecosystem in the region, we only collected aboveground samples, and aboveground biomass was also obtained by the calculation formula. Sampling disturbances were minimized to reduce the impact on the growth and survival of desert plants. The biomass calculation formula is [50]:

$M = a + b \times A_C$ (1).

$A_C = \Pi \times (L1 \times L2)/4$ (2).

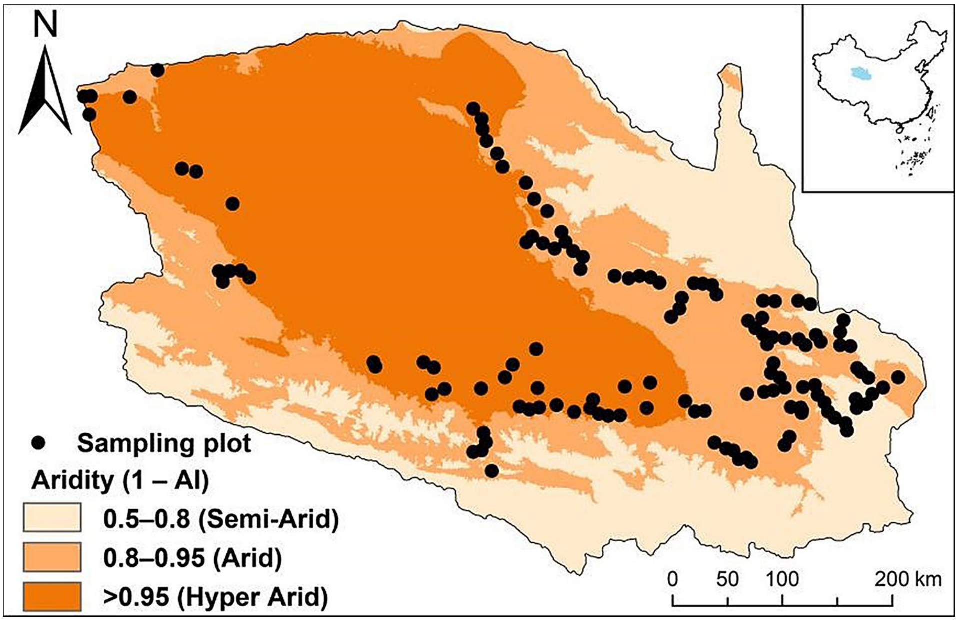

Fig. 1 Location of the Qaidam Basin and sampling sites (The map is open sourced from [45]). The base map shows the degree of aridity (1-AI) converted from the Aridity Index (AI)

M is the aboveground biomass of plants on the Tibetan Plateau, a and b are model coefficients, a = 0.1375 and b = 0.2029, A_C is the projected area of the canopy, L1 is the length of the long axis of the canopy, and L2 is the length of the short axis of the canopy. The biomass ratio is the proportion of biomass per species in the sample plot.

Three to four whole branches per plant were collected from the periphery of the canopy in the upper-middle layer of the tree, which has uniform growth and is healthy and mature. A total of 25 species of representative woody perennials were collected (Table S2), and the distributional habitat information of the species was obtained from the Flora of China [51]. A total of 16 functional traits, including eight leaf traits and eight stem traits, were selected for this study. Leaf traits included single leaf area (LA), leaf thickness (LT), specific leaf area (SLA), leaf dry matter content (LDMC), leaf carbon content (LCC), leaf nitrogen content (LNC), leaf phosphorus content (LPC), and the carbon nitrogen content ratio (LCN). The stem traits included stem cross-sectional area (SA), wood density (WD), specific stem area (SSA), stem dry matter content (SDMC), wood carbon content (WCC), wood nitrogen content (WNC), wood phosphorus content (WPC), and the carbon nitrogen content ratio (WCN). The specific descriptions of these parameters are shown in Table S4.

Leaf and stem traits were determined as follows. LT and SA were determined directly by vernier calipers. LA was scanned into images using a scanner (CanoScan LiDE 200, Canon, Inc., Japan). SD and SL were scanned into images using a scanning electron microscope. VD and VL were made into sections by a slicer (MTH-1, DL Nature Gene Life Science, Inc., Japan) and scanned into images using an optical microscope. All images were measured using ImageJ software (National Institutes of Health, NIH, USA) [52]. The leaf and stem carbon and nitrogen contents per unit mass (C and N mass, ‰) were determined via an element analyzer (VARIO EL III Element Analyzer, Elementar). The leaf and stem phosphorus contents per unit mass (P mass, ‰) were measured via a continuous flow analyzer (San++, Skalar) after H_2SO_4-$HClO_4$ (4:1, v: v) digestion. All other traits were obtained by the formula. Leaf and stem traits were measured following standard protocols (detailed in Table S5).

Environmental factor data

A total of 11 environmental factors were selected in the study area, including one aridity index, five soil indices, and five climate indicators (Table S6). The aridity index (AI) was derived from the Global Aridity Index and Potential Evapo-Transpiration (ET0) Climate Database v2 [53] and the climate indicators were obtained from the interpolated raster data of meteorological stations provided by the "National Geosystems Science Data Center" which include mean annual precipitation, mean annual evaporation, mean annual humidity, mean annual air temperature, and mean annual speed. Raster data acquisition was performed using ArcGIS 10.2 (Environmental Systems Research Institute, Inc., USA) [54].

The soil data used for field measurements included the pH of the soil (pH), soil electrical conductivity (EC), soil moisture content (SM), soil bulk density (BD), and soil organic matter (SOM). The top 0–20 cm of the soil was sampled at three different locations within each large sample plot, and each soil sample was divided into two parts for experiments on the soil water content and soil physical and chemical properties. One of the soil samples was weighed immediately for fresh weight, after which it was returned to the laboratory for drying (105 °C, 24 h) and weighed for dry weight, and the SM was calculated. BD was determined via the ring knife method, and pH was measured via the potentiometric method [55–56]. The other soil samples were naturally air-dried. Each sample was air-dried and crushed using a 100-mesh sieve. The EC was expressed by measuring the soil conductivity via the conductivity method [57]. SOM was determined by dichromate oxidation [58].

Statistical analysis

The effects of environmental factors on plants in natural desert areas were integrated, and correlation analyses were conducted between the AI and the full range of environmental factors, using AI instead of the overall environmental trend. The 1-AI was used to classify the aridity gradient across the Qaidam Basin via the following criteria [59]: >0.95 (hyperarid), 0.80–0.95 (arid), and 0.50–0.80 (semiarid). The CWMs were calculated to investigate the shifts and variations in fast-slow ecological strategies at the community level. CWMs represent the total traits of plant traits, which reflect the metrics of the desired function in any group sample. Therefore, CWM values were used for both leaf and stem traits in each sample plot. The community trait CWM was calculated as follows:

$$CWM = \sum_{i=1}^{n} Pi \times trait_i \quad i = 1, 2, 3... n \tag{3}$$

where *Pi* is the relative biomass of species *i* in the community, *n* is the total number of species in the community, and *trait* is the trait value of species *i* [60]. The plant aboveground biomass was used in this study as a measure of the relative abundance of each species in each community.

The community-level plasticity index (PI) and coefficient of variation (CV) were calculated using the average value (AV), standard deviation (SD), maximum (MAX), and minimum (MIN) of community traits at different aridity gradients to determine the possible strategies for determining the relative occurrence of plant traits in the study area. PI and CV were calculated to assess trait variability and adaptive strategies across aridity gradients. High plasticity and variability constitute the basis for the emergence of "fast-slow" strategies in the study area [4].

PI=(MAX-MIN)/MAX (4).

CV = SD/AV (5).

The PI can be used to measure the degree of response of plant functional traits, and the CV can be used to quantify the degree of variation in plant traits. See Table S7 for detailed information.

The trend of variation in leaf and stem functional traits with increasing degree of aridity was elucidated using linear fit analysis. Correlation analyses were performed for all traits to verify the existence of correlations or composite relationships between traits in different organs, thereby advancing the understanding of the relationships between traits. Before correlation analysis we tested all traits for normality and log transformed all data to make them closer to normal distribution. In the end, 18 of the 20 traits were transformed to conform to normal distribution, and the other two traits belonged to bimodal distribution, which could not be fully transformed into normally distributed traits, but the transformed values of the traits were closer to normal distribution. The correlation analysis was performed using Pearson correlation analysis, and the data were analyzed using the normally transformed trait values. Strategic patterns of variation in leaves, stems, and aboveground parts were searched for at the community level via principal component analysis (PCA). Leaf PCA (PCA-Leaf) analysis was performed via CWM values for eight leaf traits, stem PCA (PCA-Stem) analysis was performed using CWM values for eight stem traits, and above-ground PCA (PCA-Aboveground) analysis was performed using CWM values for all the traits. Due to the high coefficient of variation of CWM values for most traits, we defined the first principal axis as an arid zone economic spectrum strategy similar to the traditional economic spectrum characterization by the distribution of functional traits in PCA. For the scores of the first principal axis of the different principal component analyses, the relationship with aridity was assessed using linear fitting. All statistical tests were considered significant at the $P < 0.05$ level. In terms of evaluating the organization of plant variation in response to aridity degree, linear fitting was used to explore the fitted relationships between leaf, stem, and aboveground first principal axis scores. This was to show more clearly the trade-offs between the different principal component scores. For the pattern of variation of individual traits on the AES, bivariate correlations of each trait with PCA axis 1 (PC1) and axis 2 (PC2) were assessed using Pearson correlation coefficient (r) to determine the relative contribution of each trait to PC1 and PC2. The most dominant and variable functional traits were identified and key environmental factors were explored through correlation analysis with various environmental factors.

For the analysis of the abovementioned data, PCA was performed using the ggbiplot package [61] and the factoextra package [62] of R 4.2.1 (GNU General Public License, version 2) [63]. Correlation analysis was performed using the psych package [64] and ggplot2 package [65]. Linear fit analysis was performed using Origin (2023b, OriginLab, Inc., USA) [43].

Results

Trends in adaptive variability of functional traits with aridity

Figure 1 shows a clear division of aridity gradients, with hyperarid, arid, and semiarid zones distributed across the Qaidam Basin. The results of the correlation analysis between the 1-AI and all the environmental factors are shown in Fig. S2. The results of the linear fit analysis between all functional traits and aridity are shown in Fig. 2. With increasing aridity, only LDMC, LCC, LCN and SL changed significantly in leaves, while no significant relationship existed for all other traits. Among the traits for which significant relationship existed, SL increased significantly and the other three traits decreased significantly, with LCC having the highest degree of variability. Stem only WD and SSA showed insignificant degree of variation, all other traits showed significant relationship. Among them only WNC and WPC were significantly decreased and all other traits were significantly increased with WCC having the highest degree of variation.

Relationships between aboveground organ (leaf and stem) traits

The results of the correlation between functional traits are shown in Fig. 3. Significant relationships existed in 18 groups of leaf trait combinations and 40 groups of stem trait combinations. The correlations between leaf traits were weaker than the correlations between stem traits. Among the significantly correlated leaf trait combinations, there were 6 sets of positively correlated combinations and 12 sets of negatively correlated combinations. Significant relationships existed between all types of leaf traits. Among the significantly correlated stem trait combinations, the positively correlated combinations22 totaled 22 groups and the negatively correlated combinations totaled 18 groups. Only 5 groups of stem traits were not significantly related to each other. There were mostly positive correlations between stem and C-related traits and other types of stem traits, and mostly negative correlations between other types of traits. This was in contrast

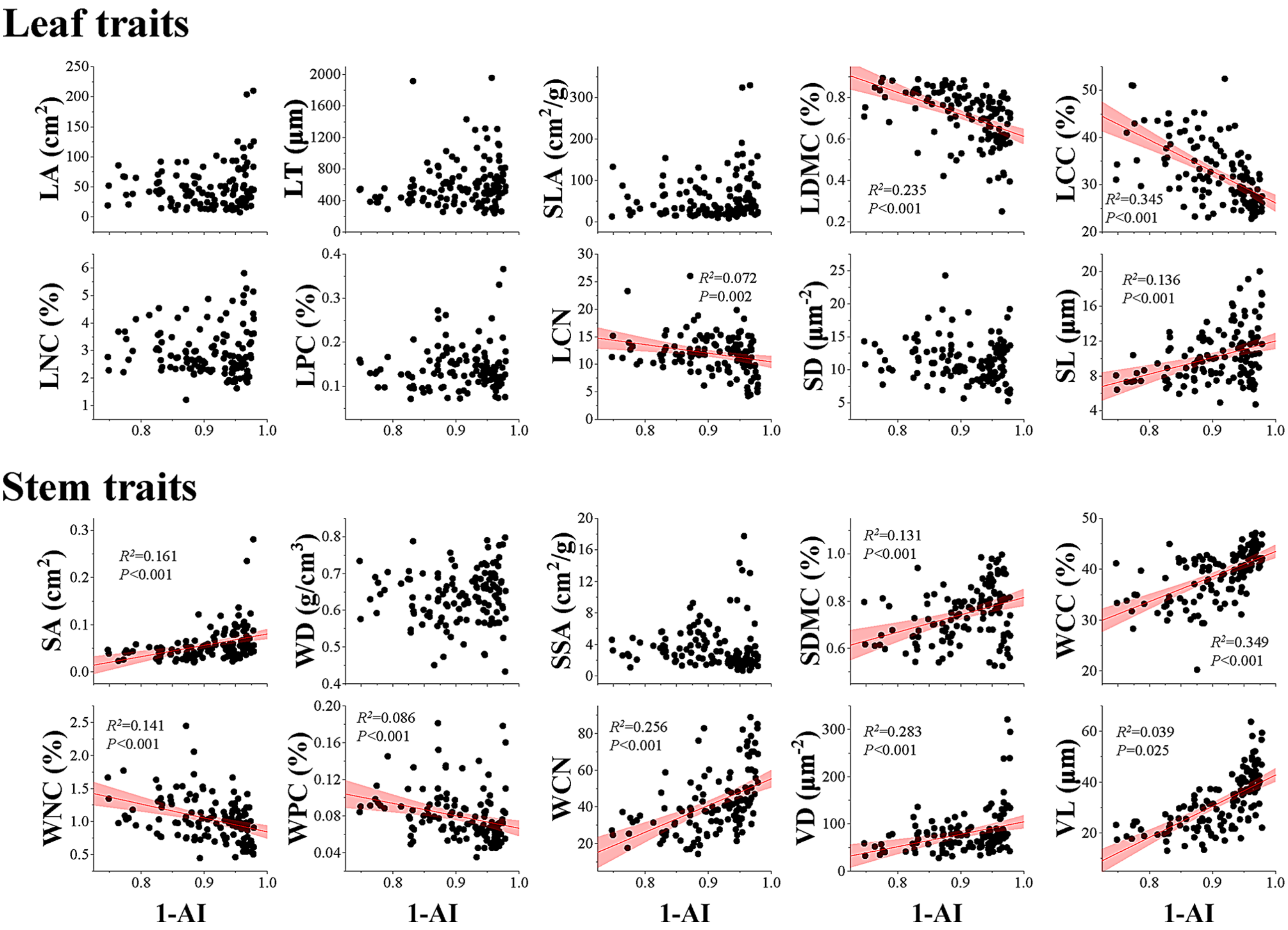

Fig. 2 Linear fitting relationship between functional traits and aridity. Combinations with significant relationships show a line of fit with a 95% confidence interval (red)

to leaf traits, which were mostly positively correlated between C-related traits but mostly negatively correlated with other types of traits. The other types of traits were also mostly negatively correlated with each other.

The total number of trait combinations with significant relationship between leaf and stem traits was 37, of which 14 combinations were positively correlated and 23 were negatively correlated. There were relatively few combinations of traits with significant relationships between leaf and stem, with significant relationships between LDMC and LCC and all stem traits, and all combinations of traits were negatively correlated except for positive correlations with SSA and stem nutritional traits. The relationships between leaf stomatal traits and stem traits were also more significant, but there was no clear pattern.

PCA and principal component scores of leaves, stems and aboveground in relation to aridity

The results of the PCA are shown in Fig. 4. The first principal axis of PCA-Leaf explained 26.22%, and the second principal axis explained 22.04%. The traits contributing more in the positive direction in the first major axis (Leaf) were LCN, LDMC and LCC, whereas the traits contributing more in the negative direction were SLA, SL, LPC and LT. The first principal axis of PCA-Stem explained 37.51%, and the second principal axis explained 15.43%. The traits that contributed more in the positive direction in the first major axis (Stem) were WD, SDMC, SA, VL, WCC, and WCN, and the traits that contributed more in the negative direction were WNC, WPC, and SSA. The first principal axis of PCA-Aboveground explained 27.02%, and the second principal axis explained 13.94%. The traits that contributed more in the positive direction of the first major axis (Aboveground) were WCC, SDMC, VL, WCN and SA, and the traits that contributed more in the negative direction of the first major axis were LCN, WNC, LDMC and LCC. See Table S8-S10 for details such as the explanatory rate, eigenvalues, and principal component dimensionality reduction values.

The results of the linear fit analysis of the first principal axis of PCA to aridity are shown in Fig. 5. All three linear fits showed significant relationships. Among them, leaf principal component scores decreased with increasing aridity, stem principal component scores increased

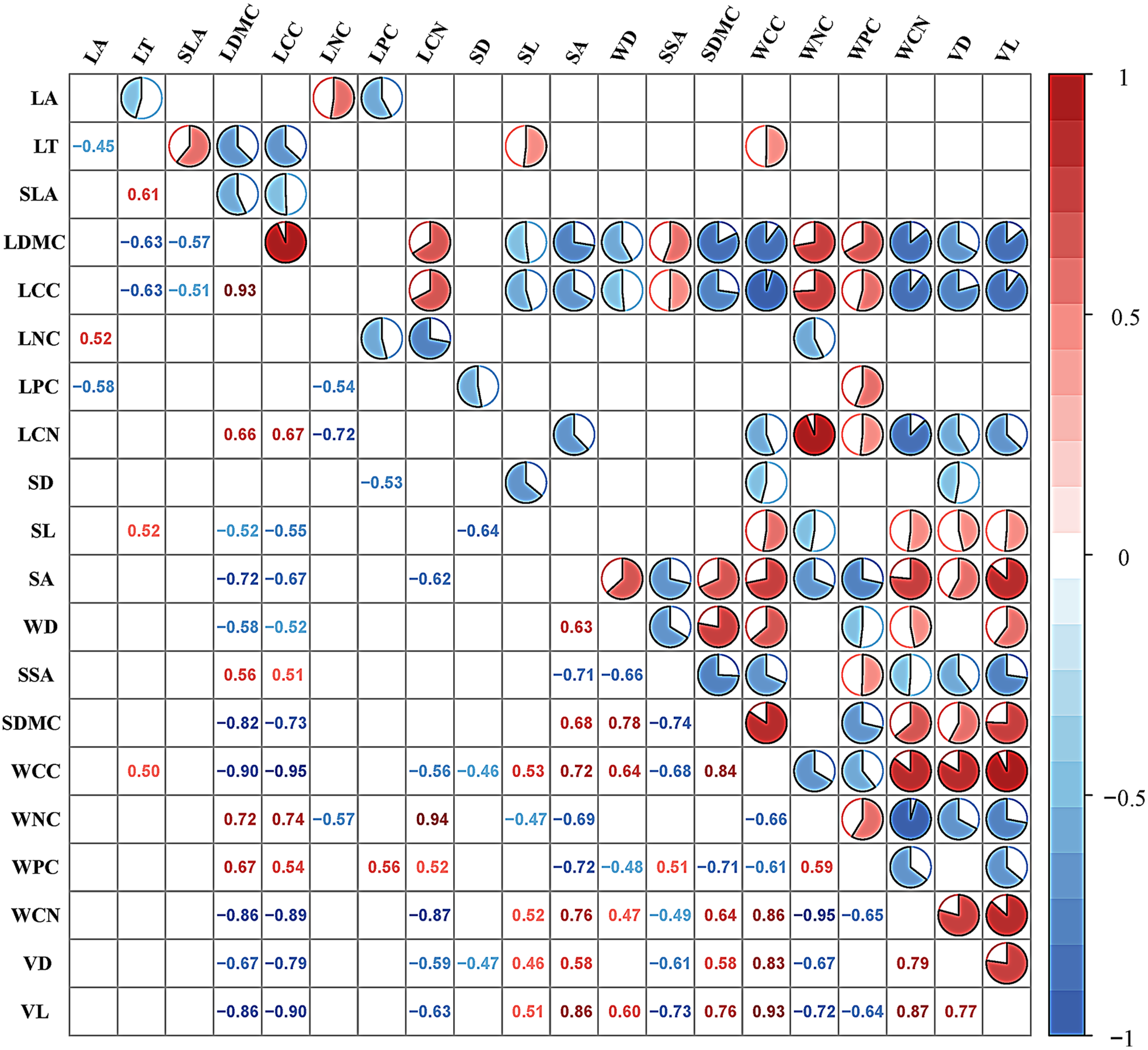

Fig. 3 Relationship between aboveground functional traits. The pie chart shows the combination of traits with significant relationships, and the number is the correlation coefficient with significant combinations. Red is a positive correlation, and blue is a negative correlation

with increasing aridity, and above-ground principal component scores increased with increasing aridity. The linear fit between the three principal component scores is shown in Fig. S3. The full PCA dimensionality reduction results are shown in Table S11.

Relationships between the economic spectrum and the contribution of each trait to the economic spectrum

The results of the correlation analysis between the traits and the principal component scores are shown in Table 1. Significant correlations were found between all leaf traits and the first principal axis of leaf principal components except LNC, but the correlations were lower for LA and SD. no significant correlations were found between LDMC, LCC and the second long axis. All other leaf traits were significantly correlated with the second major axis. Significant correlations were found between all stem traits and the first principal axis of SES.VL, WCC, WPC were not significantly correlated with the second principal axis. All other stem traits were significantly correlated with the second longest axis of stem. Among all the traits, there was no significant correlation between LA, LNC, LPC, SD and first long axis of aboveground; all other traits were significantly correlated with first main axis of aboveground.SLA, SA, WPC, WCN, VL were not significantly correlated with second main axis of aboveground; all other traits were significantly correlated with second main axis of aboveground.

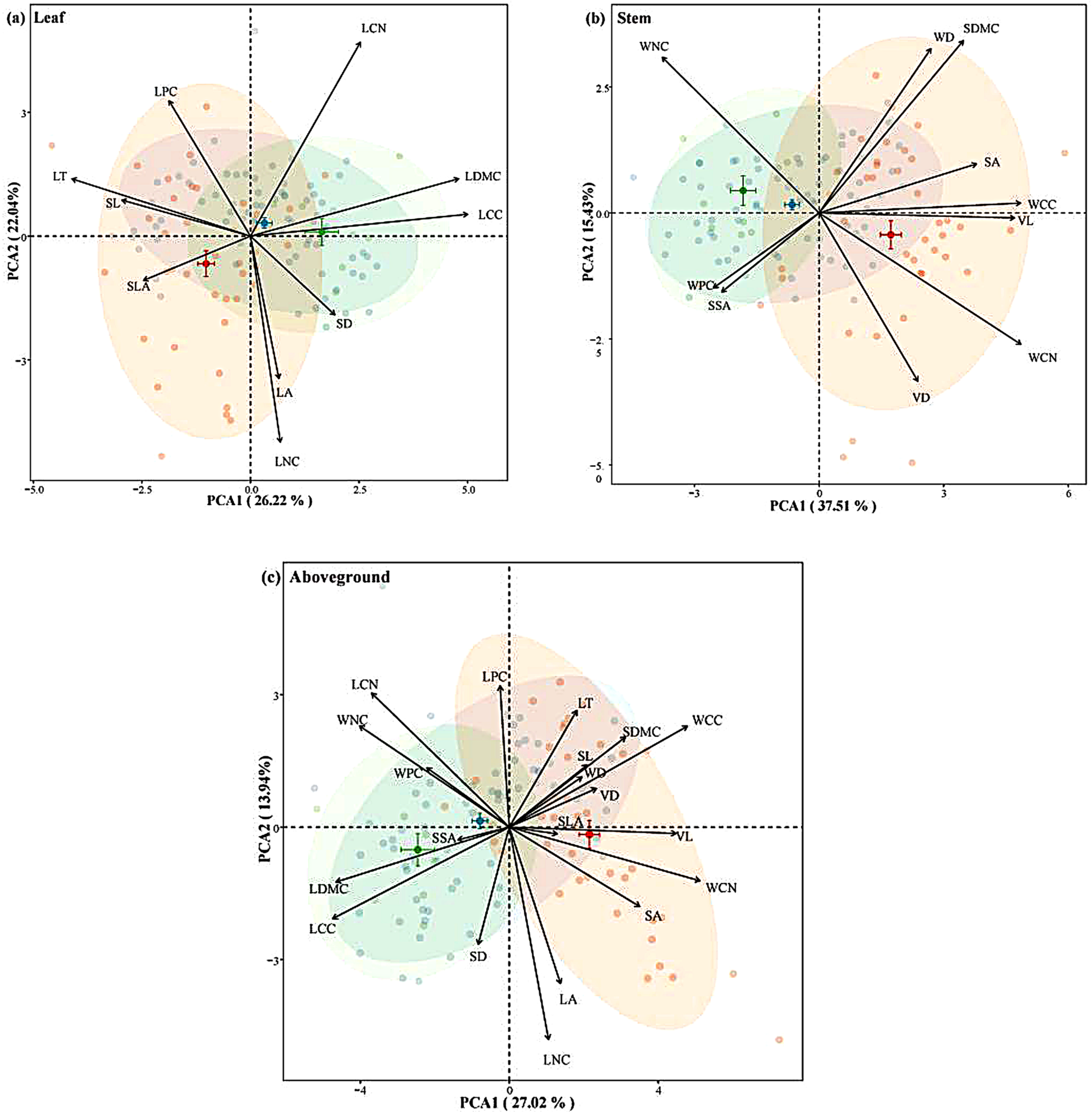

Fig. 4 Principal component analysis of leaves (**a**), stems (**b**), and aboveground (**c**) traits. Among them, the green points and areas are semi-arid, the blue points and areas are arid, and the red points and areas are hyper arid

Discussion

Functional traits of aboveground organs and their relationships with functional strategies under aridity limitation

As the degree of aridity increased, functional traits in the above-ground parts of the plant showed some degree of adaptive variation, and these traits were closely related to each other with a series of relationships reflecting synergy or trade-offs. Overall, stem traits showed a higher degree of plastic variation and closer relationships among stem traits, which may explain the greater importance of stems than leaves in arid regions. In addition, the correlations between aboveground organ traits were mainly in carbon sequestration, nutrients and water, which corresponds to the main resource exploration directions in the economic spectrum strategy [24]. Resource acquisition among organs showed significant trade-offs, which demonstrated that stems were more capable of sustaining the plant under aridity conditions and inhibited leaf

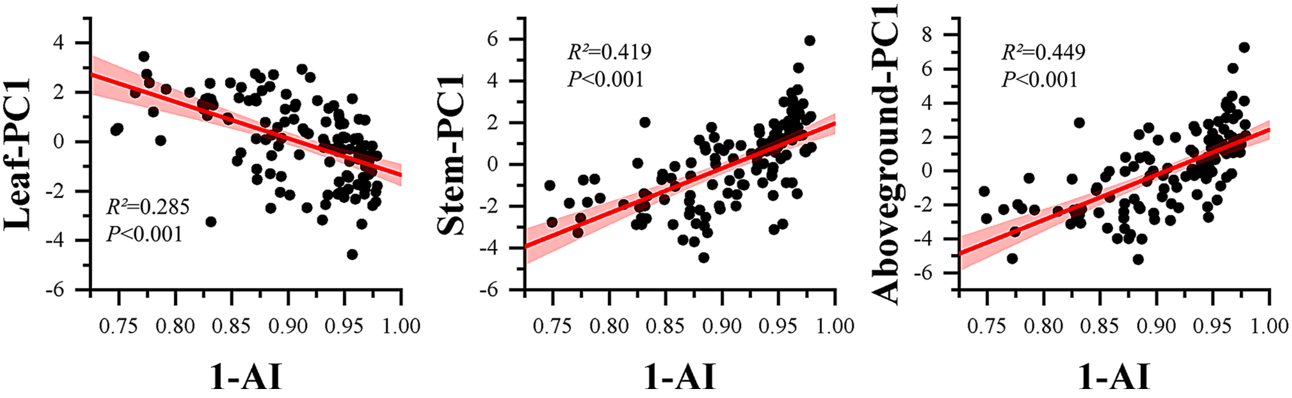

Fig. 5 Linear relationship between the dimensionality reduction value of leaves, stems and aboveground on the first principal axis of PCA and aridity

Table 1 The relationship between the first two axes and traits in the economic spectrum of leaves, stems and aboveground of Woody plants in the Qaidam basin

	Leaf		**Stem**		**Aboveground**	
	PC1	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**
LA	0.273^{**}	-0.411^{***}			-0.023	-0.565^{***}
LT	-0.639^{***}	0.186^{*}			0.315^{***}	0.427^{***}
SLA	-0.448^{***}	-0.223^{*}			0.291^{***}	-0.050
LDMC	0.838^{***}	0.066			-0.797^{***}	-0.344^{***}
LCC	0.857^{***}	0.054			-0.821^{***}	-0.339^{***}
LNC	0.155	-0.828^{***}			0.020	-0.800^{***}
LPC	-0.296^{***}	0.504^{***}			0.013	0.516^{***}
LCN	0.431^{***}	0.731^{***}			-0.525^{***}	0.407^{***}
SD	0.272^{**}	-0.294^{***}			-0.121	-0.375^{***}
SL	-0.435^{***}	0.252^{**}			0.334^{***}	0.259^{**}
SA			0.647^{***}	0.199^{*}	0.548^{***}	-0.117
WD			0.457^{***}	0.573^{***}	0.335^{***}	0.206^{*}
SSA			-0.510^{***}	-0.364^{***}	-0.365^{***}	-0.223^{*}
SDMC			0.603^{***}	0.575^{***}	0.547^{***}	0.367^{***}
WCC			0.804^{***}	0.077	0.786^{***}	0.382^{***}
WNC			-0.598^{***}	0.558^{***}	-0.648^{***}	0.283^{***}
WPC			-0.529^{***}	-0.104	-0.452^{***}	0.094
WCN			0.815^{***}	-0.379^{***}	0.866^{***}	-0.018
VD			0.566^{***}	-0.202^{*}	0.508^{***}	0.203^{*}
VL			0.783^{***}	0.043	0.733^{***}	0.119

function. These results support our first hypothesis that aboveground parts of plants are closely related to each other in arid ecosystems and reflect some major functional strategies.

As the degree of aridity increased, the carbon sequestration efficiency of leaves decreased significantly (LDMC and LCC decreased), but their physiological activity appeared to be enhanced (SL increased), implying that the security and water retention capacity of leaves decreased with the increase of aridity, which contradicts the results of most of the existing studies [66]. Micco & Aronne summarized the aridity-tolerance modes of leaves of desert plants as being mainly a combination of reduced transpirational water loss and increased water retention capacity [38]. However, under extreme aridity conditions, the leaf morphology takes the form of a smaller globular or encapsulated stem or even degenerates into assimilated branches to ensure its own survival and greater ability to retain water and to maintain a healthy diet. survival and greater ability to retain water and reduce evaporation [38]. The increase in LT and LPC further corroborates this speculation, as smaller and thicker leaves largely increase the security of this organ, and P, which plays a key role in plant physiology and biochemistry, ensures the supply of resources to the leaf, and overall improves its aridity tolerance. However, the reduction of leaf morphology increases the difficulty of leaf physiological activity (the reduction of single leaf area causes the lack of physiological activity sites), while the increase of SL may have played a role in improving leaf physiological activity. Overall, in the desert ecosystem of the Qaidam Basin, shrub leaves responded to increased aridity mainly through the strategy of reducing morphology.

As an important woody organ, stems respond to increased aridity by enhancing their support capacity and water transport capacity, which is crucial for the survival of desert plants [67]. As the degree of aridity increased, the carbon sequestration efficiency of stems showed a trend of variation that was diametrically opposed to that of leaves, reflecting the increased mechanical support capacity and security of stems. While enhancing their security, stems prioritized the upward supply of more water (increase in VD and VL) and nutrients (decrease in WNC and WPC) to maintain the N balance in leaves (LNC was insignificant and contributed little in the first major axis of leaf PCA), and to maintain leaf survival as well as normal physiological activities [68]. Overall, stems enhanced aridity tolerance and supported leaf survival by increasing support capacity and improving resource transportation efficiency.

The results of the three analyses (linear relationship, correlation, and principal component analysis) responded to the functional strategies of above-ground single organs in adapting to the aridity environment. In comparison, leaves were prioritized lower than stems in the overall plant response to aridity habitats. Even in terms of the characterization of functional strategies, many of the functional strategies of leaves were dominated by stems, which indicates the important value of studying stem functional strategies in arid ecosystems. The significant trade-off between leaves and stems in water and nutrient utilization proves that there is a strong synergistic aridity tolerance between above-ground organs in desert ecosystems. Arid shrubs have highly adaptive aboveground characteristics that work together to enhance aridity tolerance. Leaf organs increase their security and aridity tolerance through morphological reduction and maintenance of nutrient uptake. Stem organs support aridity tolerance by providing mechanical strength and ensuring efficient transportation of water and nutrients, which helps maintain the physiological activity of leaf organs. This cooperation between different organs enhances the plant's ability to survive under aridity conditions.

Economic spectrum strategies for aboveground organs and the whole in arid areas

In this study, we explored the relationships among multiple plant traits using principal component analysis (PCA), and the traits reflected certain synergistic and trade-off relationships. Synergistic traits collectively indicate the plant's functional strategy, while trade-off relationships reflect trade-offs between different strategies. The trade-off relationships among traits shown by principal component analysis were similar to the traditional economic spectrum, revealing the economic spectrum strategies of leaves, stems and aboveground, and also reflecting their trends under different degrees of aridity, supporting the existence of a significant economic spectrum of shrubs in the desert ecosystems of the Qaidam Basin, validating our second hypothesis.

Despite the arid ecosystem nature of the study area, the leaf functioning strategy of desert shrubs can be understood through the high-resource acquisition capacity of exploitative species (high SLA and low LDMC) and the high-resource conservation capacity of conservative species (high LDMC and low SLA) [6, 8, 69]. However, contrary to the traditional economic spectrum, leaves are on the conservative strategy side in areas with a low degree of aridity, while extreme aridity areas are characterized by an exploitative strategy. To be sure, this result does not mean that plant leaves in extreme arid zones carry out high resource acquisition strategies. In the discussion in the previous section, we have clarified that leaves in the extreme arid zone respond to severe habitats with reduced morphology strategies. In contrast, in the semi-arid zone, large and thin leaves are the main functional strategy as a way to maximize the use of resources in a resource-limited situation (increase in LDMC and LCC). The emergence of this strategy may be related to the more relaxed environmental and resource conditions in semi-arid regions, where plants are able to acquire more resources in a short period of time through normal physiological activities. On this basis again, stomata limit excessive water dissipation from leaves due to physiological activities (SD increases and SL decreases) to maintain the overall water balance of the plant. During the increase in degree of aridity, we have been emphasizing the reduction of leaf morphology as the main way for leaves to cope with aridity, but LA did not show a significant contribution on the economic spectrum axis. Combined with the actual sampling situation (Fig. S1), we found that the number of leaves increased significantly as leaf morphology decreased, which may be the reason for the insignificant change in LA in the overall. Overall, as the degree of aridity increased, the trend of leaf functional traits changed significantly, specifically from a low-security, high-resource-acquisition, low-water-utilization strategy to a high-security, low-resource-acquisition, high-water-utilization one.

As important organs for support and resource transportation [67], stems also form an economic spectrum with trade-offs. In regions with a relatively low degree of aridity (the positively oriented portion of PCA1), the nutrient levels of the stems were relatively high, and most of the nutrient elements were anchored by the stems to themselves rather than being transferred upwards. The researchers of this study believe that the reason for this situation is twofold. First, at this time, the leaf is in the stage of maintaining normal physiological activities, the plant as a whole is not short of nutrients, the stem organs can experience normal growth, and more nutrient elements are needed, leading to this phenomenon. Second, the excessive physiological activities of the leaf may lead to excessive water loss from the plant, and the stem, as the main organ of resource transportation, reduces its own transport efficiency to inhibit excess water loss from leaves. A lower SA and WCC imply that stems reduce the area of water transportation channels. The underlying mechanism was explained in this study. In contrast, in the hyperarid zone (the negatively oriented portion of PCA1), the area of water transport channels in the stem increased, increasing its own carbon sequestration efficiency and sequestration to maintain its security and mechanical support capacity while increasing the efficiency of upward resource transport, leading to a decrease in its own nutritional value. This strategy corresponds to the conservation strategy of leaf organs in hyperarid zones to ensure their survival. Overall, stem organs in arid regions also present significant economic strategies and synergistic effects on leaf organs. As the degree of aridity increased, the stem economic spectrum shifted from a conservative strategy of limiting upward resource (water and nutrient) transport to prevent excessive water dissipation to a stabilizing strategy of increasing the capacity of upward resource (water and nutrient) transport to sustain leaf organ survival.

Although confirming the existence of a significant economic spectrum of strategies for all aboveground organs (leaves and stems), leaf and stem strategies are mutually inhibitory, trade-off relationships that jointly maintain the viability of desert plants. When the leaf water use is high, the stem lowers the water supply to maintain overall plant water security. When leaf water use is low, the water supply to the stem increases to maintain the physiological security of the leaf for plant survival. Strategic trade-offs between organs demonstrate the existence of a holistic economic spectrum in the aboveground areas of extreme desert zones, and that this integrated economic spectrum is better able to sustain the survival and growth of desert plants. However, it is undeniable that this relationship is more complete only between stems and aboveground, that the relationship between leaves and aboveground disappears in the hyper-arid zone, and that the economic spectrum of the relationship between leaves and stems exists only in the arid zone. The researchers of this study believe that this characteristic occurs because the stem is the most important organ of the desert plant for its own survival; furthermore, given its "expensive" woody nature, it guarantees carbon sequestration and a slow response to changes in the external environment, increasing the stability of its own strategy. Although the leaf is the most sensitive organ of the plant to cope with the external environment, the harsh and diverse stress conditions in the desert region may lead to diverse characteristics of leaf organ morphological features and nutrient partitioning [38], and although its main strategy presents the characteristics of the economic spectrum, the diversity of adaptive capacity of traits at the community level may lead to the destabilization of the economic spectrum of strategies. The LES and SES strategies of dominant species under extreme aridity conditions, which are generally stable at regional scales, may be biased or even decoupled in the overall aboveground characterization of the strategic trade-offs between leaves and stems [9].

It should be emphasized that the trade-off relationship between above-ground organ economic spectra obtained in this study may be more applicable to arid ecosystems. In studies in other habitats, this result may appear decoupled or even opposite. For example, Liu et al. found a positive correlation between leaf and stem economic spectra of Artemisia at large scales in China. This may be due to the special arid habitat of deserts. On this basis, species-level economic profiles emphasize more on the characteristics of intraspecific variation caused by the environment, whereas community-level economic profiles emphasize the characteristics and stability of ecosystems or communities in which multiple plants exhibit common characteristics. We prefer to explore whether there is a stable system of overall plant functional strategies in fragile desert ecosystems. Based on this, we obtained the aboveground economic spectrum strategy of shrubs in the desert ecosystem of the Qaidam Basin. With the increase of degree of aridity, leaves changed from low to high in security, from high to low in resource acquisition, from low to high in water utilization, and the overall traits showed a change from opportunistic to conservative strategies; stems changed from low to high in security, from high to low in resource utilization, from low to high in water transport efficiency, and the overall traits showed a change from conservative to stable strategies.

Conclusion

Adaptive variation in plant functional traits to adapt to the external environment results in different functional strategies, and the trade-offs between functional strategies exhibit an economic spectrum model. The aboveground organ traits are correlated and integrated, and the correlated traits characterize the most important functional strategies of leaves and stems in arid environments. In particular, the safety and aridity resistance of leaf organs can be improved by reducing their morphology, increasing their number, and maintaining nutrient acquisition. Stem organs play an overall role in aridity resistance by improving their mechanical support and safety and increasing the efficiency of the upward transportation of resources (water and nutrients) to ensure normal physiological activities and the survival of leaf organs. As the degree of aridity increased, shifts in functional strategies shaped economic spectrum patterns, with LES strategies shifting from opportunistic to conservative and SES strategies shifting from conservative to stable. The trade-offs presented by the LES and SES demonstrate the existence of a holistic economic spectrum strategy in the aboveground part of the plant, providing new insights into furthering the understanding of desert plant survival and aridity tolerance patterns. These findings can help researchers gain a deeper understanding of the adaptive variation patterns of functional traits in desert plants and their adaptive strategies and provide a scientific basis for the study and protection of desert ecosystems.

Supplementary Information

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Supplementary Material 1

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Author contributions

Siyu Liu and Yiwen Kong wrote the main manuscript text and prepared the main figures. Yue Fan put forward valuable suggestions for revision. All authors reviewed the manuscript.

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Data availability

All trait data are collected and experimented by the authors, and there is no conflict of interest. All plant data are measured and publicly available and uploaded with attachments. Meteorological data from the global high-resolution climate data-sharing platform "WorldClim" (http://worldclim.org) and the "National Earth System Science Data Center" (http://www.geodata.cn/data/index.html?publisherGuid=126744287495931%26;categoryId=4).

Declarations

Ethics approval and consent to participate

Our research does not contain any clinical trial content, and all experimental content and data are obtained in an ethical manner. All experiments in the study area were approved by the person in charge of the trial area, and there was no controversy. The investigation and sampling of plant material is carried out on the basis of "the Second Tibetan Plateau Scientific Expedition and Research Program (2019QZKK0305)", which gives us permission to collect plants on public land without the need to submit additional documentation. Our research was based on field visits and all data were measured. During the work, there was no damage to plants and ecosystems, and no impact on local economic construction and life safety. We recognize that studies of shrub adaptation strategies and economic spectrum strategies in the Qaidam Basin of the Tibetan Plateau can provide a basis for research on survival responses of plants. We are planning to address these caveats in future research.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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