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ORIGINAL PAPER

Coordinated Patterns in the Allocation, Composition, and Variability of Multiple Elements Among Organs of Two Desert Shrubs Under Nitrogen Addition and Drought

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Abstract

Nutrient allocation closely correlates plant functional traits and development to ecosystem supply services. Desert shrubs maintain the stability of desert ecosystems, whereas the knowledge of how they coordinate nutrients among organs is still limited when responding to differing nitrogen (N) and water regimes. Here we investigated the allocation, composition, and variability of nine elements within organs of *Alhagi sparsifolia* and *Calligonum caput-medusae* seedlings under various N addition (0, 3, 6, and 9 gN m^{-2} $year^{-1}$) and water regimes (drought versus well-watered). Results showed that plant species identity, organ type, and nitrogen and water treatments significantly affected the concentrations of nine elements independently and interactively ($P < 0.05$). N addition significantly improved elemental allocation to roots of drought-stressed *A. sparsifolia* seedlings, whereas N addition of 9.0 gN m^{-2} $year^{-1}$ exerted adverse influence on *C. caput-medusae*. Photosynthetic organs contained more macronutrients, such as N and potassium (K), whereas trace metals accumulated in roots, such as iron (Fe) and manganese (Mn). Soil elemental concentrations were weakly correlated with those in plants. Macroelements in all organs show less variability (coefficient of variation). Coarse root Fe and stem K contents constituted hub traits in plant element networks (PENs) of *A. sparsifolia* and *C. caput-medusae* seedlings, respectively, and may play a key role in plant adaptation in desert environments. The looser PEN of *A. sparsifolia* implied its stronger adaptability than *C. caput-medusae*. Desert shrubs can coordinate the allocation of multiple elements within and among organs in response to changes in water and N in the environment.

Keywords Drought stress · Element composition · Network analysis · Nitrogen addition · Nutrient allocation pattern

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1 Introduction

The uptake, translocation, and accumulation of mineral nutrients across different tissues are crucial for plant physiology and biogeochemical cycling (Marschner 2012; Hogan et al. 2021; Pesacreta et al. 2021). Approximately 30 elements are involved in plant growth and development (Marschner 2012), divisible into macroelements, such as nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and microelements, such as manganese (Mn), iron (Fe), zinc (Zn), copper (Cu)—these all investigated in this study. The dynamic equilibrium between plants' metabolic requirements for these multiple elements and their availability in specific organs can help plants cope with multiple stresses, such as drought (da Silva et al. 2021; Liu et al. 2021). Accordingly, a better understanding of both the allocation and composition of manifold necessary elements across organs is critical for acquiring in-depth knowledge of plant adaptive strategies. Yet the focus has largely been on the allocation of multiple elements at the community level (Zhang et al. 2018b; Zhao et al. 2020; Ball et al. 2021), leaving its patterning at the individual or organ level mostly understudied.

Increasing anthropogenic nitrogen (N) deposition and drought are changing the biogeochemical cycles of bioavailable elements by altering soil properties and plant biological processes (Kou et al. 2018; Cleland and Goodale 2019). Improved soil N availability mediated by N deposition may directly mobilize positive ions in soil (Cusack et al. 2016), generating a nutrient imbalance across plant organs by influencing cation concentrations (Tafazoli et al. 2019). Additionally, drought can influence the stoichiometry of plants. Low-water availability can limit the mobility of elements in soil, thereby affecting their migration, uptake by roots, and translocation to other tissues (Pivovaroff et al. 2016), driving asymmetric changes in multiple nutrient concentrations between above- and below-ground organs (Cao et al. 2018). These findings are from tree or grass species and individual plant levels, however, the effects of N and water, two scarce resources in desert soils, on the nutrient allocation of desert shrubs were rarely simultaneously considered at the organ level.

Coordinated nutrient partitioning across organs of plants is crucial for their regular functioning and metabolic activity. For example, desert plants have higher foliar N concentration to improve water-use efficiency and light-capture ability (Yang et al. 2014; Castellanos et al. 2018; Huang et al. 2018). Woody organs, such as the stem and coarse roots, comprise a substantial proportion of shrub biomass, and function as a nutrient sink and transport apparatus (Cui et al. 2020). Being the absorptive organ, the fine root is a vital elemental source capable of stabilizing and removing toxic metals via rapid turnover (Hogan et al. 2021). Thus, the coordination of multiple elements across organs contributes to the plasticity of desert plants to a changing environment.

Desert plants are the main components of desert ecosystems, which control the nutrient cycle and affect the heterogeneous distribution of desert soil resources (Zhang et al. 2017). In recent decades, increased N deposition has drastically impacted desert ecosystems in drought-stricken northwest China (Li et al. 2015; Zhang et al. 2020; Zhou et al. 2016; Zhao et al. 2019). The planting of seedlings is widely used in vegetation restoration in arid areas, given that natural revegetation is challenging. Here we applied four N addition (0, 3, 6, 9 gN m^{-2} $year^{-1}$) and two water regimes (drought versus well-watered) to investigate the allocation, composition, and variability of nine elements (N, P, K, Ca, Mg, Mn, Cu, Zn, Fe) in organs (leaves/assimilating shoots (branchlets with reduced leaves), stems, coarse roots, fine roots) of two dominant desert shrubs' seedlings (*Alhagi sparsifolia* and *Calligonum caput-medusae*) in northwest China. To explore the ecological implications of multiple nutrient allocation patterns among and within organs, we used plant trait network (PTN) theory He et al. (2020). The present study can contribute to our understanding of the plasticity of desert plants under soil resource changing from the perspective of plant nutrient allocation strategies.

2 Materials and Methods

2.1 Experimental Design

The pot experiment was conducted in May–August 2019 in restoration ecology nursery field of the Cele National Station of Observation and Research for Desert-Grassland Ecosystem (37°00′56″N, 80°43′81″E), Chinese Academy of Sciences, at the southern edge of the Taklamakan Desert. Here, the aridity index (AI = mean annual precipitation/maximum evaporative potential) is 0.013, and the average yearly temperature is 11.9 °C (Zeng et al. 2012).

A. sparsifolia and *C. caput-medusae* seeds were collected randomly from the nearby natural range the year before (August 2018). Before sowing, seeds were soaked at room temperature for 12 h. After watering the soil to the maximum field capacity (ca. 18%), at least 10 plump and uniform seeds of a given species were equably sown in the depth of 3–5 cm of 96 plastic pots (90-L volume). Each pot contained 100 kg of homogenized top-layer (0–30 cm) aeolian loamy sand taken from the nearby desert. Soil elemental status is summarized in Table S1. After 4 weeks, each pot retained a healthy and uniform seedling. We selected 48 pots of each species for the experimental treatments.

Water treatments were applied by controlling the amount of water delivered. For the first 30 days, 1.5 L of water per day was delivered to all pots, after which well-watered plants were still watered at 1.5 L/day, while thirsty plants were irrigated with 0.5 L/day. These watering regimes, 1.5 L vs. 0.5 L per day, generated a fourfold difference, on average, in soil moisture for well-watered (ca. 56%) vs. drought plants (ca. 14%), which could exert a distinct effect on their physiological performance (Zhang et al., 2020, 2021a, 2021b). Plastic trays were placed under individual pots to prevent material transfer among pots. A transparent plastic film covered plants when it rained, albeit little rain fell throughout the experiment. Rapid agricultural and industrial development is underway in Northwestern China, which will accelerate N deposition (2.5 gN m^{-2} $year^{-1}$) by 2030 (Liu et al. 2013). Galloway et al. (2008) suggested this atmospheric N deposition rate will double by the mid-twenty-first century. Additionally, we simulated the severe N deposition event (9.0 gN m^{-2} $year^{-1}$) occurring in the North China Plain (Liu et al., 2013). Overall, we conducted eight treatments, N0

(0 gN m^{-2} $year^{-1}$), N1 (3.0 gN m^{-2} $year^{-1}$), N2 (6.0 gN m^{-2} $year^{-1}$), and N3 (9.0 gN m^{-2} $year^{-1}$) under well-watered and drought stress regimes, with six pots per treatment combination. Monthly, from June through August 2019, the N (solid urea, 46% effective content of CH_4N_2O) was applied to the soil surface after watering it.

2.2 Plant and Soil Sampling

We sampled plants in late August 2019 when they were in the middle and late growth stages. The six individual plants per treatment were divided into two groups for the collection of plant and soil samples, respectively. After removing the above-ground parts, we washed away any soil with running water and tried to preserve the roots' integrity. Then all organ samples (i.e., leaves/assimilating shoots, stems, coarse roots, and fine roots) were classified and oven-dried at 60 °C for 72 h. Next, plant organ samples were weighed for their biomass and milled into fine powder (<0.15 mm) using a ball mill for their elemental analysis. Because washed soil cannot be analyzed for soil nutrients, soil samples from the other three pots were collected and air-dried at the indoor temperature and passed through a 0.25-mm sieve.

2.3 Elemental Analysis

N and P concentrations of plant or soil samples digested by concentrated H_2SO_4 were respectively determined with a Kjeldahl Nitrogen Analyzer (K1160, Jinan Hanon Instruments Co. Ltd., China) and an inductively coupled plasma optical emission spectrometer (iCAP 6300, Thermo Elemental, USA). After soaking the plant and soil samples in HNO_3 and $HF–HNO_3–H_2O_2$ overnight, respectively, all samples were digested and evaluated for K, Ca, Mg, Mn, Zn, Cu, and Fe contents using an inductively coupled plasma optical emission spectrometer (iCAP 6300, Thermo Elemental, USA).

2.4 Nutrient Allocation Calculation

Taking N for example, the N allocation to foliage was calculated according to Eqs. (1) and (2). The N allocation (N mass distribution ratios) to foliage was evaluated with the quotient of foliar N mass and the total N mass at the whole-plant level (Tsujii et al. 2020).

$$\text{Foliar } N \text{ mass} = \text{foliar } N \text{ concentration} \times \text{foliar biomass} \tag{1}$$

$$N \text{ allocation to foliage} = \text{Foliar } N \text{ mass/sum of } N \text{ mass in all organs} \tag{2}$$

2.5 Statistical Analyses

R software (version 4.0.3) was used for the statistical analyses (R Core Team, 2020). Four-way ANOVAs evaluated the effect of plant species, organs, and nitrogen and water treatments on each mineral element concentration (Table S2). One-way ANOVA was used to evaluate the effect of N addition upon nutrient allocation among organs under each water regime (drought and well-watered). If differences among groups were significant, the LSD method was used for the multiple pairwise comparisons of means. P values were corrected by the False Discovery Rate (FDR) method (Benjamini et al. 2006). To assess the plasticity and variability of various elements in different organs in the context of nitrogen and water changes, we averaged the concentration values with replicates of these elements in all treatments and calculated their coefficients of variation (CVs). An element with a lower CV value was deemed less variable, and vice-versa. The effects of soil element concentrations (N, P, K, Ca, Mg, Mn, Zn, Cu, Fe) were tested with linear regression, with each corresponding element in the specific organ as the dependent variables (Fig. S1, S2). A Pearson correlation matrix of element concentration between above- and below-ground organs was conducted using the "corrplot" package (Taiyun and Viliam 2017) (Table S3). Given that many elements among organs are intercorrelated, network theory provides an effective method to resolve these relationships among these traits and their significance (Flores-Moreno et al. 2019; Kleyer et al. 2019; He et al. 2020). We used network theory to explore the relationships among elemental concentrations across organs. Firstly, we calculated the matrix of trait–trait relationships and quantified the correlation coefficient (r) using Spearman's method in the 'psych' package (Revelle 2018). Secondly, to remove spurious correlations among traits, we set the threshold of the adjacency matrix to $|r| > 0.5$ and $P < 0.05$ (Kleyer et al. 2019). Finally, we visualized the elemental networks and topological parameters of these two plants using the "igraph" package (Csardi and Nepusz 2006) (Fig. 5; Tables 1 and S4). The 'ggplot2' package was used to draw the figures.

Table 1 The parameters describing plant trait networks of *A. sparsifolia* and *C. caput-medusae* seedlings

Topology	Parameters	*A. sparsifolia*	*C. caput-medusae*
Tightness	Edge density	0.208	0.260
	Diameter	4	3
	Average path length	2.140	1.981
Complexity	Average clustering coefficient	0.480	0.570
	Modularity	0.369	0.379

3 Results

3.1 Concentrations and Variability of Mineral Elements among Organs

Average concentrations of nine mineral elements varied in the two desert shrubs' seedlings and organs (Fig. 1; Table S2). For *A. sparsifolia*, concentrations in leaves ranged from 36,867 mg kg^{-1} for N to 6.86 mg kg^{-1} for Cu; in stems from 20,896 mg kg^{-1} for K to 22.21 mg kg^{-1} for Mn; in coarse roots from 18,799 mg kg^{-1} for N to 11.59 mg kg^{-1} for Cu; in fine roots from 47,661 mg kg^{-1} for Ca to 39.39 mg kg^{-1} for Cu. The N concentrations were significantly higher in leaves than the other elements across all organs of *A.* seedlings, while Ca, Mg, Fe, and Mn concentrations were noticeably higher in fine roots than other organs ($P < 0.001$, Table S2; Fig. 1a–c).

For *C. caput-medusae* seedlings, concentrations in assimilating shoots ranged from 31,525 mg kg^{-1} for K to 5.27 mg kg^{-1} for Cu; in stems from 11,496 mg kg^{-1} for Ca to 9.43 mg kg^{-1} for Cu; in coarse roots from 16,686 mg kg^{-1} for Ca to 12.69 mg kg^{-1} for Cu; in fine roots from 12,443 mg kg^{-1} for N to 18.02 mg kg^{-1} for Zn. The concentrations of the nine mineral elements varied among organs ($P < 0.001$, Table S2; Fig. 1). The concentrations of macroelements (N, K, Ca, and Mg, except P) and Zn were higher in assimilating shoots, while P, Mn, and Fe concentrations mainly accumulated in coarse roots. The Cu concentration was maximal in fine roots ($P < 0.001$, Table S2; Fig. 1d–f).

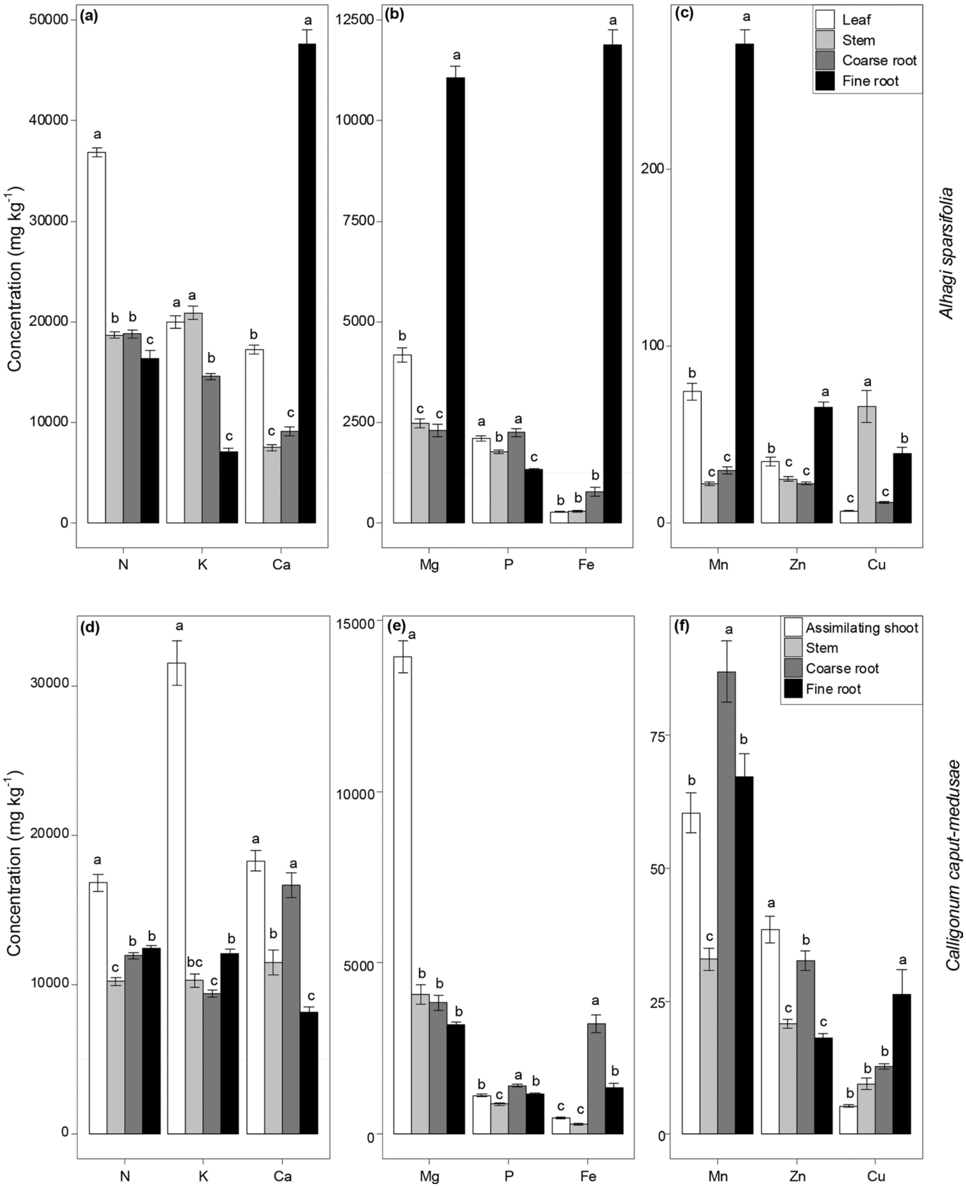


Fig. 1 The average concentration of 9 mineral elements (N, P, K, Ca, Mg, Mn, Zn, Cu, Fe) among organs of *Alhagi sparsifolia* and *Calligonum caput-medusae* seedlings. Different letters above indicate significant differences (FDR adjusted-$P < 0.05$) among organs with the least significant difference (LSD) test

The variability of the nine mineral elements was substantial (Fig. 2a–h). For *A. sparsifolia*, the lowest CVs were obtained for leaf N (5.8%), stem N (7.6%), and coarse root N (10.0%), and the highest CVs were 34.8% for leaf Zn, 66.5% for stem Cu, and 65.0% for coarse root Fe. The CVs increased from 12.5% for P to 42.6% for Cu in fine roots (Fig. 2d). Notably, the CVs of all foliar elements were markedly negatively correlated with their concentrations ($R^2 = 0.50$, $P < 0.05$; Fig. 2a); elemental variability diminished considerably with an elevated elemental concentration in leaves of *A. sparsifolia* seedlings. For *C. caput-medusae* seedlings, the CVs increased from 16.3% for assimilating shoot Mg up to 31.7% for assimilating shoot Zn (Fig. 2e). The lowest CVs were for stem N (12.9%), coarse root N

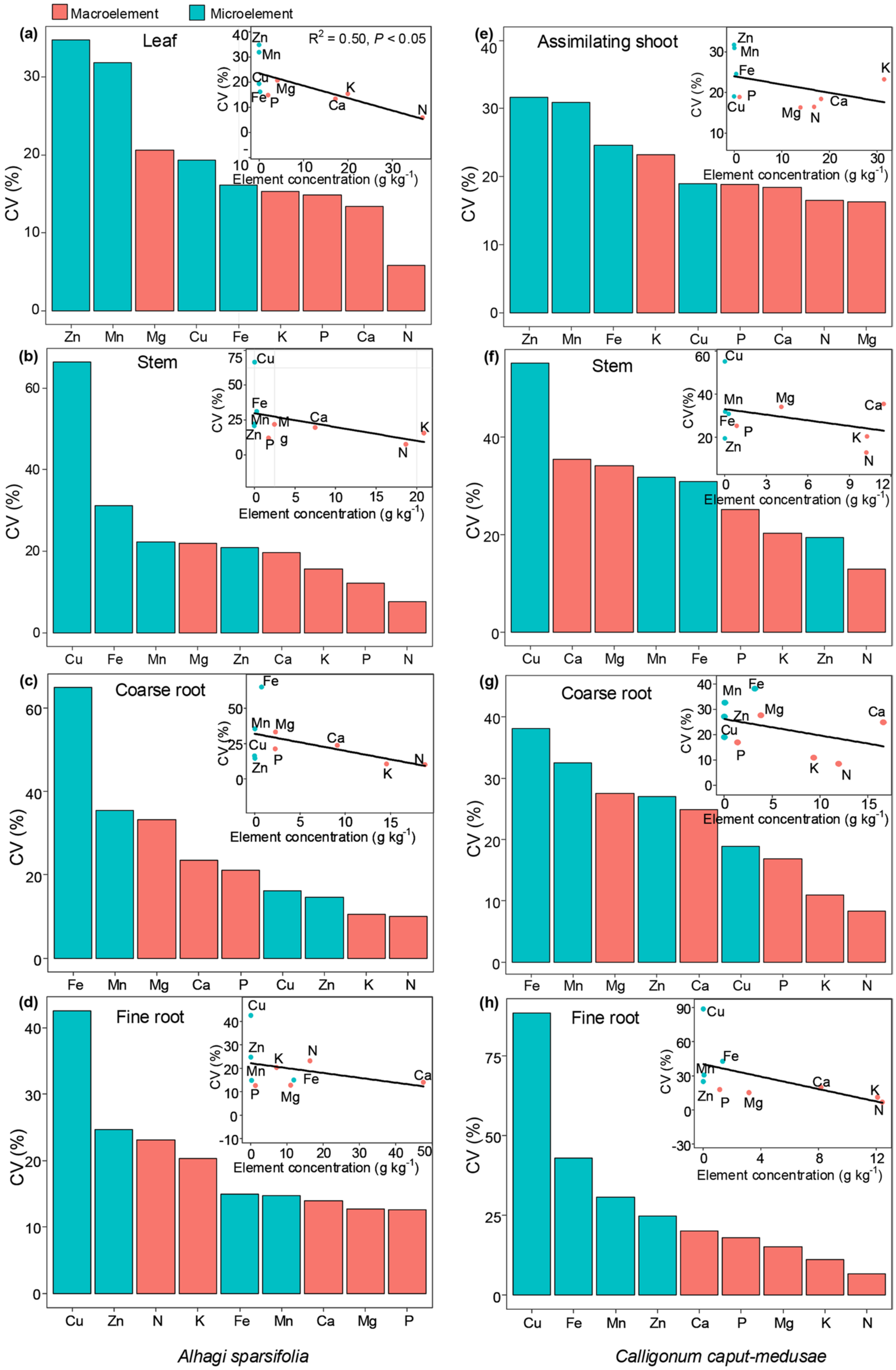


Fig. 2 The coefficient of variation (CV) of the 9 elements among organs, and the relationship between elemental concentration and CV

(8.3%), and fine root N (6.6%), whereas the highest CVs were 55.2% for stem Cu, 38.1% for coarse root Fe, and 88.5% for fine root Cu, respectively (Fig. 2e–h).

3.2 Allocation Patterns of Elements Among Organs Under Different Nitrogen Addition and Water Regimes

The interaction of plant species identities, organs, and nitrogen and water treatments had a significant effect on the concentrations of these nine elements (Table S2). Among these factors, differing plant species identity and water conditions did not significantly affect certain elements. Specifically, the K content was similar between the two shrubs. The difference in water regimes had little effect on P, K, Mg, or Cu.

N addition and water regimes significantly changed elemental allocation patterns (Figs. 3 and 4). For *A. sparsifolia*, in general, drought stress improved the distribution of these nine elements to its above-ground parts, especially stems (Fig. 3). Under drought, N addition significantly amplified the relative allocation of nutrients to roots, especially fine roots. The distribution of these nine elements (except Cu)

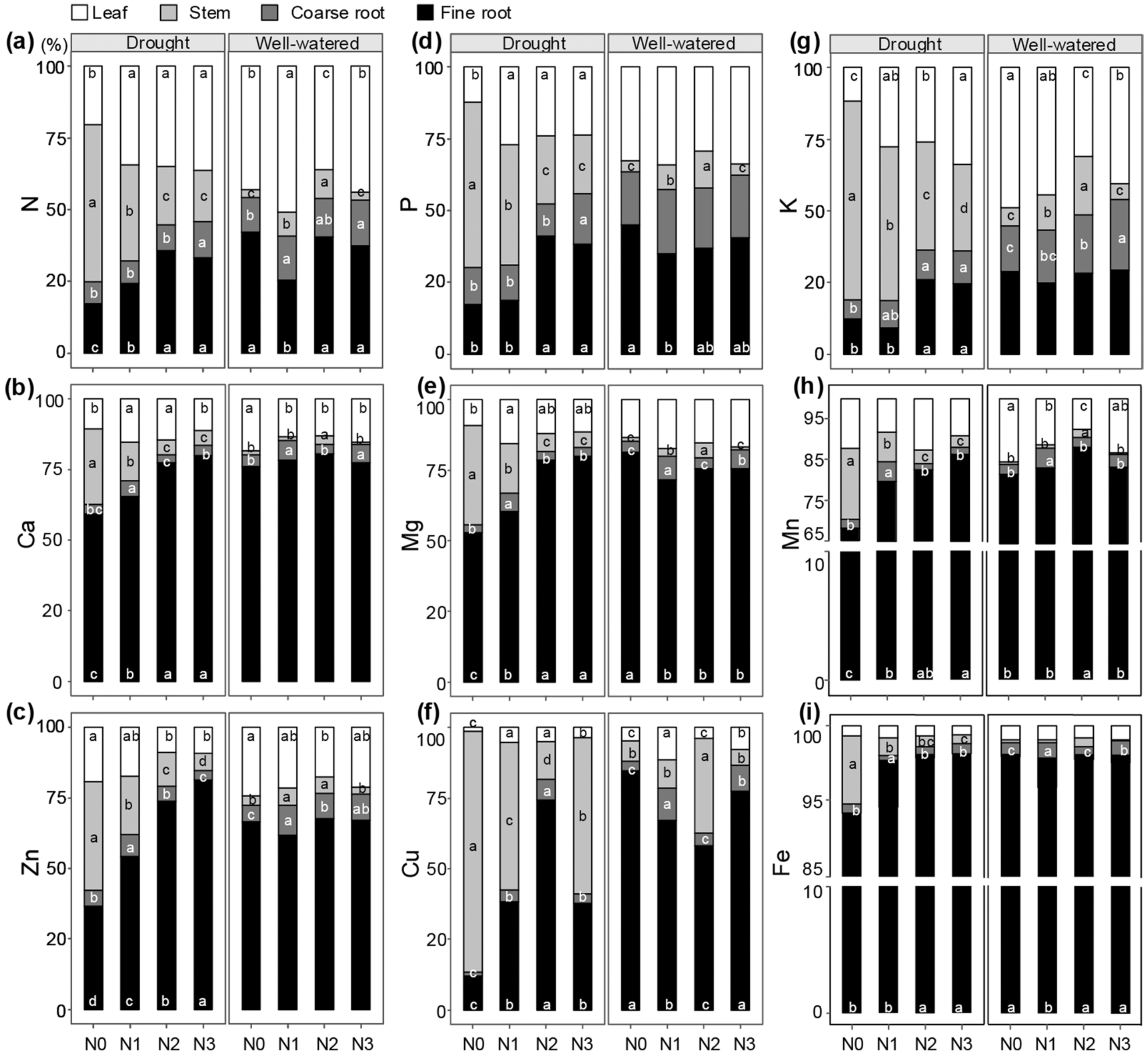


Fig. 3 The effects of nitrogen addition and water regimes on nine elemental allocations among organs of *Alhagi sparsifolia* seedlings. Nitrogen deposition treatments: ambient deposition with no addition (N0, control), 3 gN m^{-2} year^{-1}(N1), 6 gN m^{-2} year^{-1} (N2), 9 gN m^{-2} year^{-1} (N3). Different letters above indicate significant differences (FDR adjusted-$P < 0.05$) among N addition treatments under drought or well-watered regimes with the LSD test

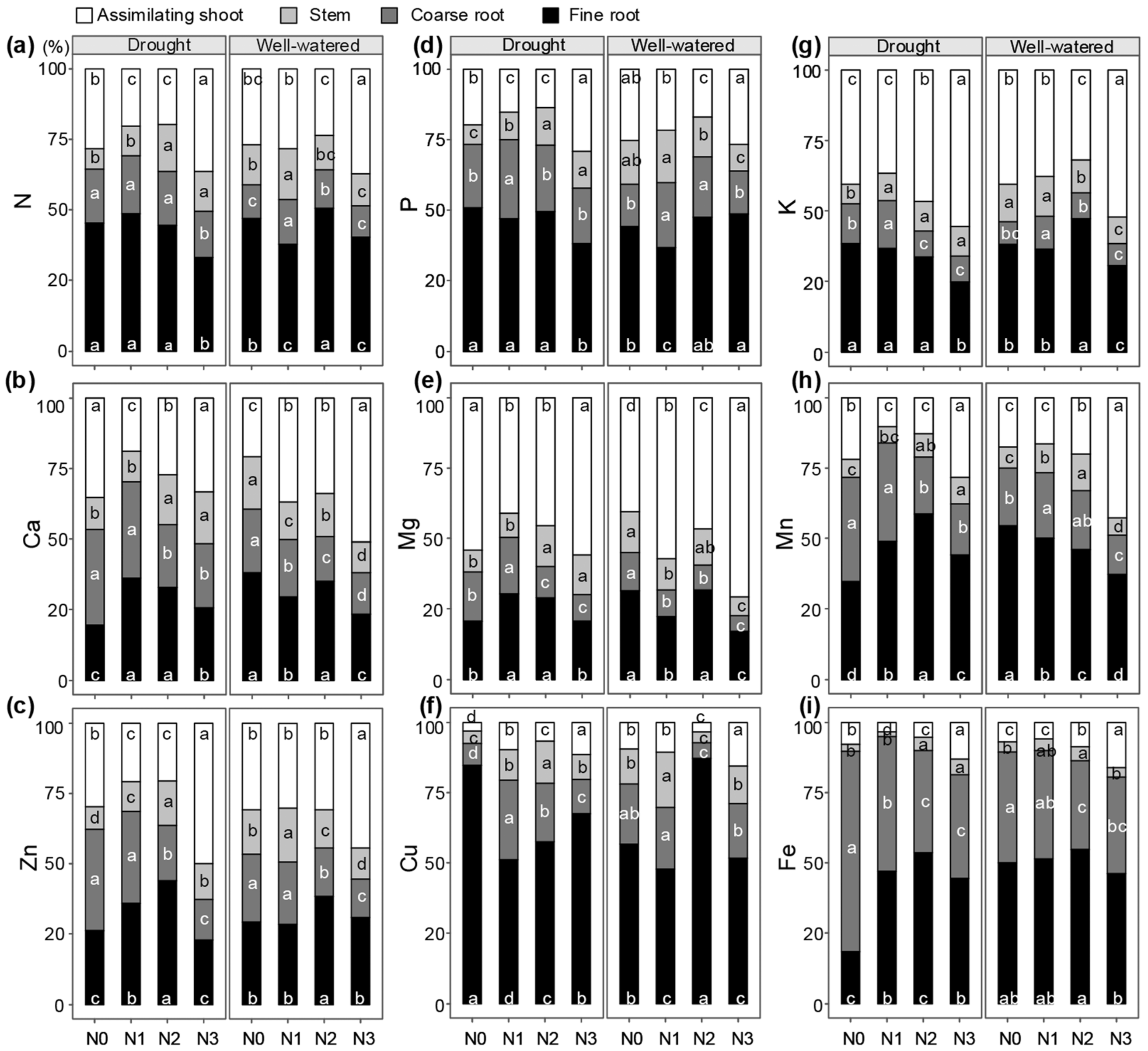


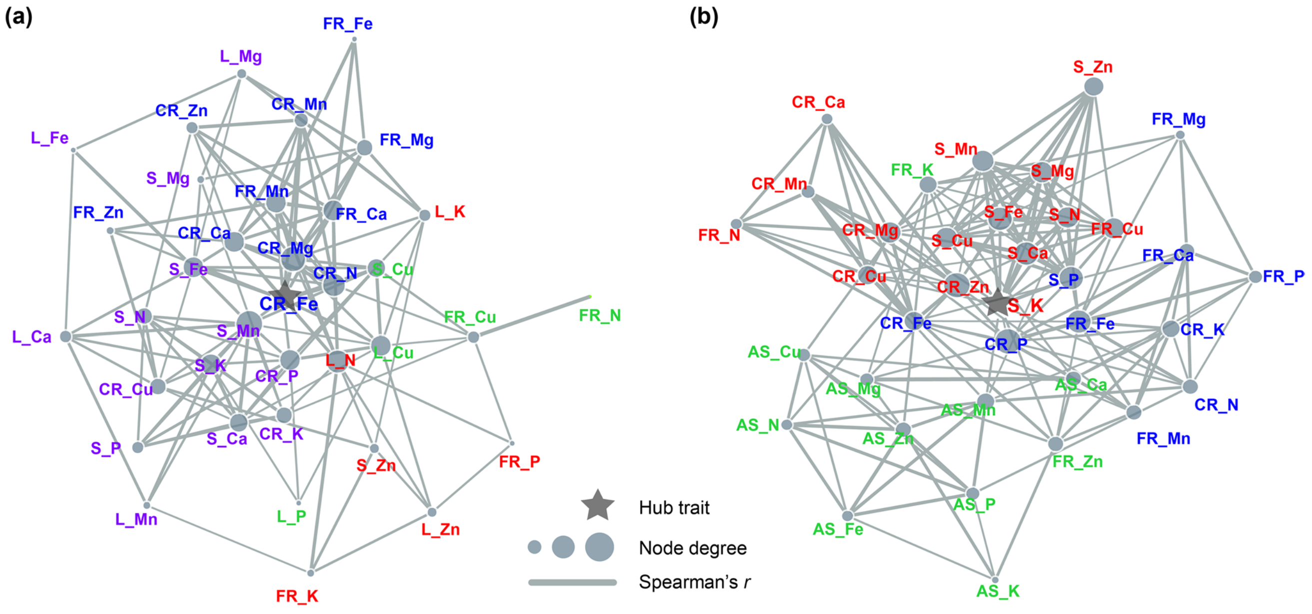
Fig. 4 The effects of nitrogen addition and water regimes on nine elemental allocations among organs of *Calligonum caput-medusae* seedlings. Nitrogen deposition treatments: ambient deposition with no addition (N0, control), 3 gN m^{-2} year^{-1}(N1), 6 gN m^{-2} year^{-1} (N2), 9 gN m^{-2} year^{-1} (N3). Different letters above indicate significant differences (FDR adjusted-$P < 0.05$) among N addition treatments under drought or well-watered regimes with the LSD test

to stems tended to decrease with an increasing N addition under water deficit conditions.

For *C. caput-medusae*, drought stress increased the distribution of N, P, K, Zn, and Cu to its below-ground parts, especially fine roots (except Zn), while improving the relative allocation of Ca, Mg, and Mn to above-ground parts, especially assimilating shoots (Fig. 2). N addition significantly improved the distribution of Ca and Mn to fine roots under drought. Relatively reduced allocations of N, P, K, Ca, Mg, Zn, and Fe to assimilating shoots were observed in low or medium N input (N1 and N2 addition) under drought stress. In the drought regime, high N addition (N3) considerably reduced the relative allocation of macronutrients (i.e., N, P, K) to fine roots, yet markedly augmented their allocation to assimilating shoots.

3.3 Plant element Networks Among Organs

Given that desert plants can adapt to dry environments by coordinating multiple elements and their relationships, we examined plant element networks (PENs) among organs of both shrub species (Fig. 5; Table 1). The ratio of actual



Alhagi sparsifolia

Calligonum caput-medusae

Fig. 5 The plant element networks (PENs) of *Alhagi sparsifolia* (**a**) and *Calligonum caput-medusae* seedlings (**b**). In each panel, circles denote different element concentrations among organs (nodes), and node size shows its degree, and pentacles represent hub traits. Based on the greedy module algorithm, PENs are divided into three (in *C. caput-medusae* PEN) or four modules (in *A. sparsifolia* PEN), which are distinguished by different color fonts. The width of the line indicates the strength of Spearman's association. Organs: L, leaves; AS, assimilating shoots; S, stems; CR, coarse roots; FR, Fine roots

connections between nodes (traits) to all possible connections is defined as edge density. PENs with a higher diameter and average path length had greater overall independence among traits. The modularity of the network measures the separation of trait clusters within the network and quantifies the complexity of PENs. PEN with a higher average clustering coefficient is usually divided into several different components. Our result showed that the PEN of *C. caput-medusae* exhibited a higher edge density, higher average clustering coefficient, higher modularity, and lower diameter and average path length (Table 1). The PEN of *A. sparsifolia* differentiated more into clusters, in that it had more modular constructures PENs (Fig. 5a). Generally, the PEN of *C. caput-medusae* was clustered according to the different organs (Fig. 5b). Coarse root Fe and stem K emerged as the hub trait in PENs of *A. sparsifolia* and *C. caput-medusae* seedlings, respectively; each had the highest degree (Table S4), indicating more connections existed between these two elements and the others.

4 Discussion

Shrubs are an important vegetation type in desert ecosystems, which are susceptible to environmental changes (Jiang et al. 2017). Coordinated nutrient allocation among organs or maintaining a proper elemental composition within a specific organ is vital for desert plants to plastically modify their growth, as available resources (e.g., N and water) in arid land are generally limited (Huo et al. 2021). An intriguing question is how desert shrubs allocate nutrients within and among organs in response to different N and water availabilities.

The different responses of nutrient allocation to nitrogen and water changing in desert plants were related to plant species identities and organ types. Take *A. sparsifolia* for example, in contrast to its drought-stressed seedlings, well-watered ones showed better relative allocation of the nine elements to below-ground parts, especially fine roots (Fig. 3). This may be due to increased water availability stimulating root growth to improve multiple nutrients' uptake (Zhang et al. 2020). Conversely, drought stress enhanced the distribution of elements to above-ground parts, especially stems, suggesting a greater investment there to cope with harsh conditions and increase resource acquisition, for which stems may function as nutrient pools (Sergeeva et al. 2021). Under drought stress, compared to stems and roots, the lower distribution of elements to short-lived leaves may indicate that *A. sparsifolia* seedlings employ an adaptive strategy to prolong multi-elements' residence time for future usage. Interestingly, N addition modified nutrient utilization strategies of drought-stress *A. sparsifolia* seedlings. The reduced nutrient (except Cu) in stems were transferred into fine roots and leaves by N addition, suggesting a weakened nutrient storage function of stems and enhanced activities in leaves and fine roots. As the resource-exploring organs of plants, both leaves and fine roots are sensitive to environmental changes (Kou et al. 2018). N addition could largely promote the allocation of nutrients to fine roots (Fig. 3). However, drought-stressed *A. sparsifolia* foliage may respond weakly to Fe and Mn. We speculate these two elements are immobilized into fine roots during their translocation among organs, as some related rate-limiting steps are involved in the specific translocations of elements to leaves (van der Heijden et al. 2015). Therefore, the nutrient allocation patterns of desert plants are coupled to the function of their organs.

From 10 nutrient (N, K, Ca, Mg, S, P, Mn, Zn, Cu, and Ni) scaling relationships, Zhao et al. (2020) argued plants employ a conservative allocation strategy among organs of different plant functional groups. However, we uncovered a species-specific difference in elemental relative allocation strategy. Drought stress improved the distribution of N, P, and K in roots of *C. caput-medusae* seedlings, implying stronger requirements of macroelements in below-ground parts (Fig. 4). Ca, Mg, and Mn are associated with cell wall formation, buffering toxic metals, chlorophyll synthesis, and enzyme activation (Kou et al. 2018; Zhao et al. 2018). More allocation of these elements to assimilating shoots may improve the resistance of *C. caput-medusae* seedlings under drought stress. However, different N addition levels had different effects on the nutrient status of different organs. For instance, low and/or moderate N additions (N1 and/or N2) fostered the transfer of nutrients to stems and roots, whereas these processes were reversed by high-level N addition (N3) (Fig. 4). N3 likely suppressed the nutrient exploration of fine roots by influencing soil nutrient mineralization, increasing soil acidity, and decreasing soil P availability via binding to metal ions (Averill and Waring 2018; Penuelas et al. 2020). Interestingly, in contrast to *C. caput-medusae*, thirsty *A. sparsifolia* showed a positive response to soil N enrichment by enhancing the absorption capacity of fine roots and impairing the nutrient storage function of stems. Their different responses to soil resources changing can help us predict the succession direction of desert vegetation.

Above-ground and below-ground organs of both species had different elemental compositions. Macronutrients tend to accumulate in leaves or assimilating shoots (Figs. 1 and 2; Table S2), which agrees with previous studies (Pandey et al. 2017; Zhao et al. 2020). High contents of macronutrients in photosynthetic organs can ensure the performance of multiple physiological functions and nutritional status in photosynthetic organs is positively correlated with plant productivity and drought resistance (Mansour et al. 2021). Desert plants invest a lot of carbon in their roots to absorb soil resources (Ma et al. 2021; Stock et al. 2021). High root-mass fraction is a diluting factor, reducing elemental concentrations in below-ground tissues (He et al. 2016); even so, roots did concentrate more trace metals (Fe, Zn, Mn, Cu). Some trace metals (e.g., Mn, Fe, Cu, Zn) have strong bonds in root cells (Kabata-Pendias 2011), causing them to accumulate in roots, which are mainly determined by the absorption and transport of specific elements within the plant (Zhao et al. 2016). Intriguingly, two shrubs in the present study exhibited different nutrient composition patterns (Fig. 1). Some elements such as Ca, Mg, and Zn were abundant in different resource-acquisition organs of *A. sparsifolia* (fine roots) and *C. caput-medusae* (assimilating shoots), respectively, reflecting their different survival strategies to environmental stresses and genetic evolutions (Zhang et al. 2021a, 2021b). In the non-growing season, *C. caput-medusae*'s above-ground parts are still physiologically active, whereas all those of *A. sparsifolia* are withered (Zeng et al. 2006). Plants can withdraw nutrients from senesced tissues and transport them to other live parts, which could reduce costs associated with soil nutrients' uptake (Zhang et al. 2018a).

Elemental variability increased with decreasing elemental concentration. Microelements were more variable than macroelements, with similar patterns of elemental variability observed in all tissues (Fig. 2). The co-variation of multiple elements reflects their coordinated allocation pattern among above- and below-ground organs (Table S3). A close relationship in nutrient acquisition underpins the coordinated patterning of elemental variation between those tissues, consistent with previous works on Chinese forest biomes (Zhao et al. 2016), terrestrial plant leaf elements across China (Zhang et al. 2012), and the interconnectedness among 25 foliar elements in 24 plant species in Japan (Zhang et al. 2021a, 2021b). During plant growth, elements in high demand (needed at higher concentrations) undergo fewer changes and are less sensitive to environmental alterations, which might explain why macroelements are less variable than microelements (Stability of Limiting Elements Hypothesis) (Han et al. 2011). Therefore, elements' variability is closely associated with plant physiological requirements. However, the range of CVs in our study (5.8 – 88.5%) was noticeably lower than those (35 – 120% and 44 – 240%) reported by Zhao et al. (2016) and Zhang et al. 2021a, 2021b), respectively. These discrepancies imply sample size, species, and geographical factors can exert a considerable influence on elemental variability.

Although elements in plants primarily originate from soil, in our study, the current element concentration in soil may not reliably indicate the degree of soil element transfer to plants. Few elements in leaf/assimilating, shoots stems, and fine roots were positively or negatively correlated with their respective soil content, whereas other plant elements failed to show such clear relationships (Fig. S1, S2), implying a weak coupling between plant and soil nutrient concentrations. The contribution of litter nutrients and environmental factors (e.g., soil moisture, temperature, latitude, and precipitation) might blur the co-variation between plant and soil element concentrations to some extent (Zhao et al. 2016; Pang et al. 2021; Zhang et al. 2021a, 2021b).

Given that many elements among organs are intercorrelated, applying network theory to these relationships could contribute to better understanding plant adaptation strategies and their environmental responses (He et al. 2020). Under this theory, our study identified coarse root Fe and stem K as the hub trait in PENs of *A. sparsifolia* and *C. caput-medusae* seedlings, respectively (Fig. 5). Coarse roots are multifunctional organs providing basic functions, such as storage of nutrients, and transportation of water and photosynthetic products, and biochemical stability (Akburak 2020). Fe is an essential trace element for plant growth when below the critical value. K is involved in enzyme activation, osmotic regulation, and phloem transport (Sardans and Peñuelas 2015). The essential functioning of both two elements in coarse roots and stems ensures the transport of nutrients and water from below- to above-ground. Consistent with Liebig's law of the minimum (Liebig 1840), the hub trait interacts with many other traits and may play a central regulatory role affecting the entire plant phenotype. Theoretically, the deformity of ionomic networks caused by shifting hub traits could reflect changes in limiting resources (He et al. 2020). Hence, we speculate coarse root Fe and stem K plays a vital role in enhancing the adaptive capacity of *A. sparsifolia* and *C. caput-medusae* seedlings to desert environments, respectively. Alterations to either element in corresponding organs might have distinct functional consequences for plant adaptions in deserts.

Although elements among organs can be biologically or statistically intercorrelated, not all traits are aimlessly connected in PENs. The PEN of *C. caput-medusae*, with its shorter average path length, smaller diameter, and higher edge density implied closer coordination among tissue nutrients than in *A. sparsifolia* seedlings, whose coordination is primarily exhibited at the intra-organ level, as reflected by different modules (Fig. 5). Plants adapted to stressful habitats are generally restricted in a peripheral trait usually unconnected to other traits in the plant trait network, yielding a looser overall network (He et al. 2020). In this regard, *A. sparsifolia* seedlings showed stronger adaptability in the study area; further, the PEN of *A. sparsifolia* featured more inter-organ element connections, implying greater coordination between multiple elements and multiple organs (Fig. 5a).

5 Conclusions

The present study examined the distribution patterns among multiple organs of *A. sparsifolia* and *C. caput-medusae* seedlings under different N addition and water regimes. In summary, the above- and under-ground organs of both shrub species were enriched with relatively high concentrations of macroelements and trace elements, respectively. Yet, the uptake of the two plants for macroelements was more stable than that for trace elements. Under drought stress, two species adopted different nutrient allocation strategies in response to N addition. Using plant trait network theory, we identified hub elements (coarse root Fe for *A. sparsifolia* and stem K for *C. caput-medusae*) that play key roles in two plant ionomic networks, and their concentrations may be quick indicators of desert plant adaptation to environmental stress, which would provide the possibility for efficient and targeted management of vegetation nutrients in desert ecosystems. Therefore, our study offered new prospects for further research on ionomic responses of different desert plant shrubs to environmental changing perturbations and adaptive evolutions.

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Declarations

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