



Patterns of carbon, nitrogen, and phosphorus stoichiometry of three life-form desert plants and responses to soil and microbial biomass factors in a hyper-arid desert ecosystem

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Abstract

Plant, soil, and microbial biomass ratios of carbon (C), nitrogen (N), and phosphorus (P) are crucial in maintaining stability of desert ecosystems. Nevertheless, variation in relations of elemental ratios between different life forms of plants and soil and microbial biomass in desert ecosystems remains unclear. In a hyper-arid desert ecosystem, C, N, and P concentrations and ratios were analyzed in the plant–soil–microbial biomass system of three perennial desert species (*Alhagi sparsifolia* Shap. [Herb, Fabaceae], *Karelinia caspica* Pall. [Herb, non-Fabaceae], and *Tamarix ramosissima* Ledeb. [Shrub]). Concentrations of N and P in *Alhagi sparsifolia* leaf, stem, and root were significantly greater than those in *Karelinia caspica* and *Tamarix ramosissima*, whereas plant C and soil organic C (SOC) were highest with *Tamarix ramosissima*. *Alhagi sparsifolia* and *Tamarix ramosissima* were P-limited, whereas *Karelinia caspica* was N-limited. According to correlation analysis, SOC rather than soil total P (STP) regulated plant N:P ratios, and microbial biomass C, N, and P rather than SOC, soil total N, and STP regulated plant C:N:P ratios. Soil water content also affected plant nutrient balance. Thus, in a hyper-arid desert ecosystem, the plant–soil–microbial biomass system and the balance of C, N, and P are closely related, and the role of soil microbial biomass in affecting plant nutrient balance should receive increased attention.

Keywords Desert ecosystem · Desert plant life forms · Ecological stoichiometry · Microbial biomass · Nutrient limitation · Soil nutrients · Plant–soil–microbial biomass system · C:N:P ratio

Introduction

Carbon (C), nitrogen (N), and phosphorus (P) are essential elements for plant growth, protein synthesis, energy storage and transmission, stress resistance, and cycling of other biogeochemicals (Elser and Hamilton 2007; Finzi et al. 2011). Compared with forest and grassland ecosystems, biogeochemical cycles in desert ecosystems are generally slow, resulting in barren soils and low net primary productivity (Yang et al. 2014). The slow cycling of elements is primarily attributed to the scarcity of water and low levels of soil nutrients (Hou et al. 2020). Various physiological and biochemical processes related to C, N, and P in desert species are likely to be constrained, including rate of soil organic matter decomposition, mineralization of soil N, and fixation and dissolution of soil P (Mackenzie et al. 2002). However, such processes are markedly influenced by the nutrient balance in soil and microbial biomass (Vitousek et al. 1997; Delgado-Baquerizzo et al. 2017). Therefore, exploring concentrations and stoichiometry of three major elements in

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plant–soil–microbial biomass systems can increase understanding of biogeochemical cycles in desert ecosystems.

The C:N:P ratios of plant leaves can provide insights into community structure and function and determine whether plants are restricted by nutrient availability (Sterner and Elser 2002). The C:N ratio often indicates nutritional status, whereas N:P and C:P ratios indicate balance of nutrients (Drenovsky and Richards 2004). Leaf N:P ratio is often used to determine whether a species is limited by N (N:P ratio < 14) or P (N:P ratio > 16) (Koerselman et al. 1996). To date, plant element ratios have been examined at global, regional, ecosystem, community, and individual plant scales (Yang et al. 2014; Yu et al. 2020). Leaf C:N:P ratio in grassland ecosystems is 440:17:1 (Yu et al. 2017), whereas in aquatic ecosystems, the ratio is 113:8:1 (Sardans et al. 2012). In the Taklimakan desert, the N:P ratio of herbs is 20:1 (Gao et al. 2022a), which is greater than the 17:1 of desert shrubs in Central Asia (Luo et al. 2021). Accordingly, plant element ratios are most likely controlled by heterogeneity of soil background elements, vegetation types, and differences in biogeography (Yu et al. 2017).

Among many factors, soil and soil microbial biomass are two critical factors that affect plant element ratios (Bui and Henderson 2013). Notably, a robust link is found between soil and microbial biomass (Li et al. 2012). On one hand, the link is primarily attributed to soil microorganisms that adjust stoichiometries by absorbing and transforming soil nutrients (Kooijman et al. 2009). On the other hand, microbial community stoichiometry has certain plasticity because of changes in dominant microbial populations (Delgado-Baquerizzo et al. 2017; Yang et al. 2022). A similar close relation is also observed between soil element ratios and soil C, N, and P cycling in microbial populations and resistance (Luo et al. 2020). Nevertheless, soil microbial biomass is typically lower in desert ecosystems than in other ecosystems because of the strong influence of soil water content (SWC) (Gao et al. 2022a). Furthermore, changes in plant element ratios are also controlled by other soil properties (e.g., SWC, pH, and electrical conductivity) (Gong et al. 2017; Huang et al. 2018). According to Han et al. (2011), as annual average precipitation increases, plant N and P concentrations decrease, but the N:P ratio increases.

In the Taklimakan Desert, because of the water deficit and low levels of nutrients, the vegetation at its southern edge junction is mainly perennial xerophytic herbs, shrubs, and trees of different life forms, which dominate structure and function of the desert ecosystem (Liu et al. 2016; Li et al. 2021). For example, the shrub *Tamarix ramosissima* and the herbs *Alhagi sparsifolia* and *Karelinia caspica* are excellent desert species for wind protection and sand fixation (Zeng et al. 2013). Under the canopy of *Tamarix ramosissima* with relatively high aboveground biomass, nutrient cycling in soil is greater than that under *Alhagi sparsifolia* and *Karelinia*

caspica (Gao et al. 2022b). In the Taklimakan Desert, the focus has been on plant elemental ratios and basic soil properties (Li et al. 2015; Zhang et al. 2018). Nevertheless, relations between elemental ratios of different life forms of desert plants and soil and microbial biomass remain unclear. Therefore, in this study, three perennial species with different life forms were selected in a natural desert ecosystem, and changes in relations of plant–soil–microbial biomass C:N:P ratios were analyzed. Two hypotheses were tested in the hyper-arid and nutrient-poor soils of the Taklimakan Desert: (1) C:N:P ratios of the shrub *Tamarix ramosissima* would have stronger responses to soil and microbial biomass than those of the herbs *Alhagi sparsifolia* and *Karelinia caspica*; and (2) the dominant factor affecting variation in C:N:P ratios among three desert species would be the soil rather than microbial biomass C:N:P ratios.

Materials and methods

Study site

The field experiment was conducted in the Cele oasis and desert junction zone (37°56′N, 80°43′E) in the south of the Taklimakan Desert in Northwest China. Mean annual temperature is 15.85 °C, and mean annual precipitation is 42.62 mm. The site has an aeolian sandy soil with low organic matter but high salinity (Gao et al. 2022b). Natural vegetation is mainly several perennial phreatophytic species, including *Alhagi sparsifolia* Shap. (Fabaceae), *Karelinia caspica* Pall. (Compositae), *Calligonum mongolicum* Turcz. (Polygonaceae), and *Tamarix ramosissima* Ledeb. (Tamaricaceae) (Bruelheide et al. 2010; Zeng et al. 2013). The shrub *Tamarix ramosissima* and herbs *Alhagi sparsifolia* (Fabaceae), and *Karelinia caspica* were examined in this study. This study was performed four plots with an area of 2 hectares each. The three species were included in each plot, and the coverage of the same species was similar across the four plots. Any two plots were separated by at least two kilometers.

Plant and soil samples

Plant and soil samples were collected in August 2020. Three representative individuals of *Alhagi sparsifolia*, *Karelinia caspica*, and *Tamarix ramosissima* individuals with similar growth status were selected per plot. Individual plants were randomly selected such that all plants of each species in the four plots had similar crown width and height. The distance between any two individuals was greater than 10 m. Each individual selected had at least four representative branches that were fully mature and sun-exposed. All leaves on those branches were collected, the branches were cut with branch

shears into small, approximately 5-cm sections, and materials were placed into marked paper bags. Then, a soil profile (length, 100 cm; width, 100 cm; height, 100 cm) was excavated along the direction of the coarse root. After removing loose soil on the surface of the soil profile from top to bottom, soil samples were collected from three layers (surface, 0–30 cm; middle, 30–60 cm; and bottom, 60–100 cm) from bottom to top. A total of 36 soil samples were collected (three plant species \times four plots \times three soil layers). Then, the root system of the 0–100 cm soil layer was collected and put into a marked paper bag. Thus, a total of 36 plant samples were collected (three plant species \times four plots \times three plant organs). Fresh soil samples were passed through a 2-mm sieve and after thorough mixing, were divided into two sub-samples. One sub-sample was placed in a sealed bag and then immediately stored at 4 °C, and the other sub-sample was air-dried in the shade for further determinations.

Plant C, N, and P concentrations

Plant samples were washed with flowing water to remove sand and soil from the surface and then oven-dried at 75 °C for 2 days to constant weight. After drying, samples were pulverized, passed through a 0.15-mm sieve, and then digested in a mixture containing concentrated H₂SO₄, HClO₄, and HNO₃ (v:v:v, 1:2:7). Plant C, N, and P were analyzed using an inductively coupled plasma-atomic absorption spectrometer (ICP-ABS Hitachi Z-5000, Japan).

Soil organic C, total N, and total P concentrations and other soil properties

Soil organic C (SOC) concentration was analyzed by a wet-oxidation technique (Shaw 1959). Soil total N (STN) and soil total P (STP) concentrations were analyzed by Kjeldahl digestion and a Mo–Sb colorimetric method, respectively (Olsen and Sommers 1982). Soil water content was measured after oven-drying. A pH meter (Precision and Scientific Corp., China) was used to determine soil electrical conductivity (EC) and pH in mixtures with 1:5 (w/v) and 1:2.5 (w/v) soil-to-Nanopure water ratios, respectively.

Soil microbial biomass C, N, and P concentrations

A chloroform fumigation–extraction method was used to measure soil microbial biomass C (MBC), N (MBN), and P (MBP) concentrations (Dijkstra et al. 2012). First, 20 g of fresh soil was added to 150-mL triangle bottles and fumigated with chloroform at 25 °C for one day. In another set of 150-mL triangle bottles, 20 g of fresh soil was maintained in the same environment but was non-fumigated. Then, 80 mL of 0.5 M K₂SO₄ was added, and bottles were shaken for 60 min at 25 °C (150 rpm). After filtration,

concentrations of soil extractable C and N were measured in 10 mL of soil extract by a TOC analyzer (Multi N/C 2100 BU, Germany). To obtain the soil extracts used to measure MBP, 80 mL of 0.5 M NaHCO₃ was added to soils after incubations, followed by shaking for 60 min at 25 °C (150 rpm). After filtration, the concentration of extractable soil P was measured in 10 mL of soil extract using the method described by Murphy and Riley (1962).

Statistical analyses

Statistical analyses were conducted in SPSS 19.0 (SPSS Inc., Chicago, IL, USA). One- and two-way ANOVAs were conducted to interpret plant–soil–microbial biomass C, N, and P balance. Matrix test analysis was used to show pairwise comparisons of soil factors (soil and microbial biomass C, N, and P, SWC, pH, and EC) and that plant C, N, and P concentrations and ratios of each species were partially related to each soil factor. Correlations between C, N, and P concentrations and ratios in plant–soil–microbial biomass systems were analyzed using redundancy analysis (RDA). Mantel tests and RDA were conducted using the R project (R Development Core Team 2016).

Results

Plant C, N, and P concentrations and stoichiometry

Carbon concentration of roots and stems was 6.1% and 14.2% greater, respectively, in *Tamarix ramosissima* than in *Karelinia caspica* (Table 1). However, N concentrations of roots, stems, and leaves of *Alhagi sparsifolia* were 178.6%, 155.2%, and 715.5% higher, respectively, than those of *Karelinia caspica*, and 151.9%, 116.7%, and 60% higher, respectively, than those of *Tamarix ramosissima*. Phosphorus concentrations of stems and leaves of *Alhagi sparsifolia* were 27.8% and 25.6% higher, respectively, than those of *Karelinia caspica* and 97.1% and 77% higher, respectively, than those of *Tamarix ramosissima*. In addition, C:N ratios of *Tamarix ramosissima* and *Karelinia caspica* were significantly higher than those of *Alhagi sparsifolia* (Fig. 1)A and B. The C:N ratio of *Karelinia caspica* leaves was significantly greater than that of *Tamarix ramosissima* and *Alhagi sparsifolia* leaves ($p < 0.001$). However, the C:P ratio of *Tamarix ramosissima* was significantly greater than that of *Karelinia caspica* and *Alhagi sparsifolia* (Fig. 1C, D). The N:P ratio of *Alhagi sparsifolia* was 18.2 and that of *Tamarix ramosissima* was 17.2, which were significantly higher than the ratio of *Karelinia caspica* (Fig. 1E, F).

Table 1 Carbon (C), nitrogen (N), and phosphorus (P) concentrations of plants, soil, and soil microbial biomass

			Concentration (g kg ⁻¹)	Organs/soil layers (cm)	<i>Alhagi sparsifolia</i>	<i>Karelinia caspica</i>	<i>Tamarix ramosissima</i>	p value
Plant	C	Root	446.66±11.20a		424.98±12.43a	450.86±16.90b	<0.05	
		Stem	446.41±3.52a		420.55±8.79a	480.12±10.00a	<0.05	
		Leaf	419.49±15.99b		398.26±20.29b	379.44±20.21c	<0.05	
	N	Root	11.31±2.33b		4.06±0.47b	4.49±1.14b	<0.001	
		Stem	10.64±2.52b		4.17±0.24b	4.91±0.52b	<0.001	
		Leaf	20.53±1.64a		11.97±1.28a	12.83±1.27a	<0.001	
	P	Root	0.61±0.16b		0.69±0.23b	0.28±0.08b	<0.01	
		Stem	0.69±0.11b		0.54±0.09c	0.35±0.03b	<0.01	
		Leaf	1.08±0.18a		0.86±0.09a	0.61±0.11a	<0.01	
	Soil	C	0–30	3.00±0.22a		2.76±0.29a	3.50±0.30a	< 0.01
			30–60	1.85±0.08b		1.74±0.11b	2.80±0.30b	< 0.01
			60–100	1.78±0.09b		1.67±0.08b	2.15±0.23c	< 0.01
		N	0–30	0.32±0.05b		0.34±0.05a	0.34±0.05a	> 0.05
			30–60	0.35±0.02a		0.32±0.04a	0.33±0.04a	< 0.05
			60–100	0.32±0.03b		0.33±0.04a	0.37±0.06a	< 0.05
P		0–30	0.58±0.03c		0.59±0.02b	0.60±0.02a	< 0.05	
		30–60	0.61±0.02b		0.62±0.03a	0.61±0.04a	> 0.05	
		60–100	0.65±0.02a		0.63±0.02a	0.61±0.04a	< 0.05	
Soil microbial biomass		C	0–30	52.98±7.17a		71.75±18.32a	55.23±15.12a	< 0.01
			30–60	49.86±8.17a		71.42±15.66a	52.60±14.87a	< 0.001
			60–100	53.14±7.44a		67.07±17.69a	50.41±15.51a	< 0.01
	N	0–30	2.41±0.26a		2.75±0.22b	4.36±1.95a	< 0.01	
		30–60	2.23±0.26b		2.93±0.29ab	4.30±1.53a	< 0.01	
		60–100	2.22±0.14b		2.98±0.18a	4.40±1.78a	< 0.01	
	P	0–30	0.20±0.03a		0.65±0.15a	0.25±0.05a	< 0.01	
		30–60	0.18±0.02a		0.67±0.16a	0.26±0.05a	< 0.01	
		60–100	0.15±0.02b		0.67±0.16a	0.25±0.04a	< 0.001	

Values are the mean ± standard deviation ($n = 12$). A distance-based linear regression model was used to assess significant differences in C, N, and P concentrations of plant, soil, and microbial biomass among three desert species, expressed by p -values. Soil C: soil organic C; Soil N: soil total N; Soil P: soil total P. Different lowercase letters indicate significant differences between different plant organs and between soil and soil microbial biomass in different soil layers ($p < 0.05$)

Soil total N, P, and organic C concentrations and stoichiometry

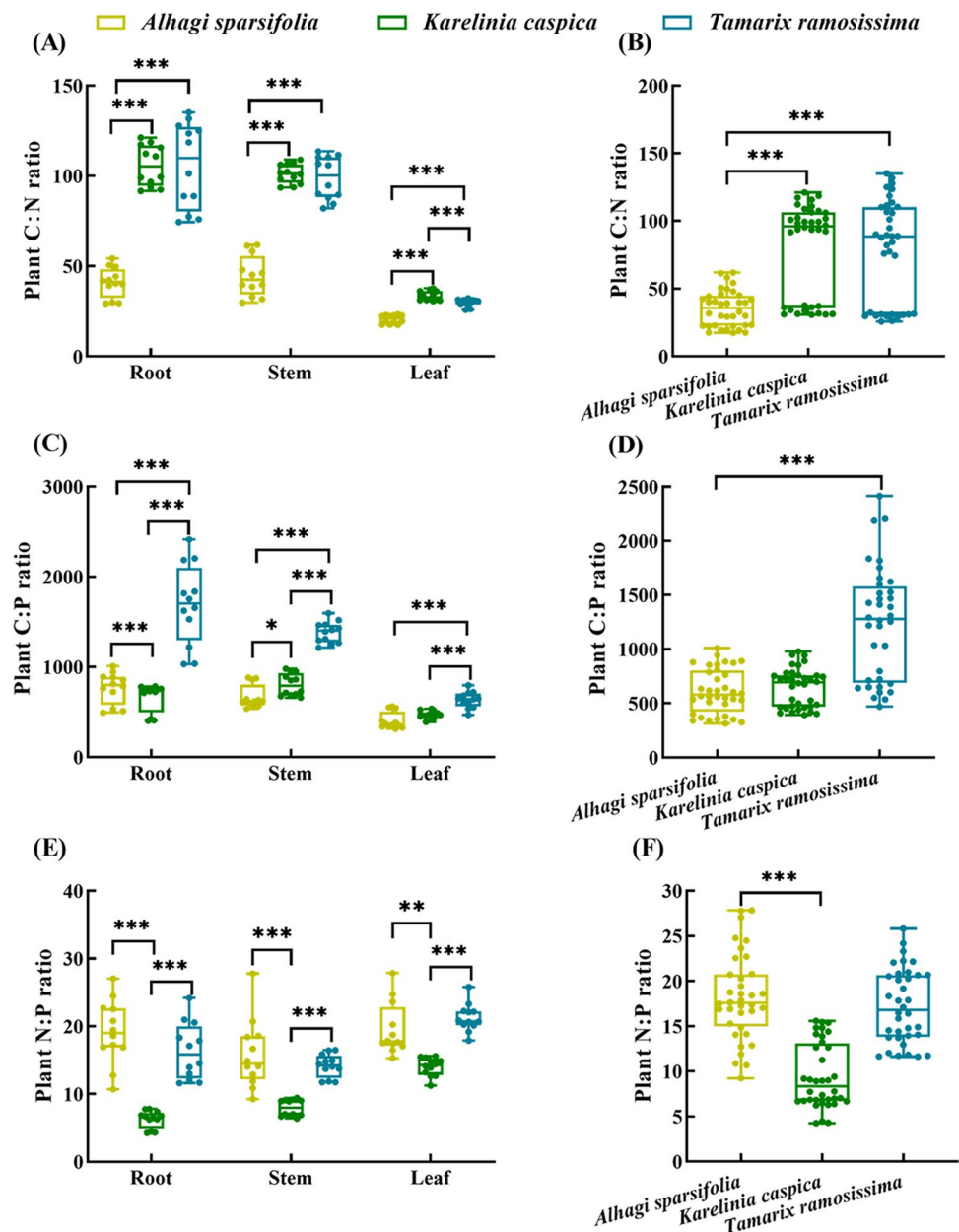
The SOC concentration of topsoil was significantly greater than that in other soil layers (Table 1). The SOC concentrations of the three soil layers under *Tamarix ramosissima* were 26.8% (surface), 60.9% (middle), and 28.7% (bottom) higher than those under *Karelinia caspica* and 16.7% (surface), 51.4% (middle), and 41.0% (bottom) higher than those under *Alhagi sparsifolia*. In addition, the bottom soil layer contained the highest STN concentration under *Tamarix ramosissima* and the highest STP concentration under *Alhagi sparsifolia*. Soil total N in the bottom soil layer under *Tamarix ramosissima* was significantly higher by 15.6% than that under *Alhagi sparsifolia*. Furthermore, soil C:N ratio under *Tamarix ramosissima* was significantly higher than that under *Alhagi sparsifolia* and *Karelinia caspica* (Fig. 2A,

B). In surface and middle soil layers, soil C:N ratios under *Tamarix ramosissima* were significantly higher than those under *Karelinia caspica*. Differences in soil C:P ratios were similar to those in soil C:N ratios (Fig. 2C, D), but there were no significant differences in soil N:P ratios in different soil layers under different plant species (Fig. 2E, F).

Soil microbial biomass C, N, and P concentrations and stoichiometry

Concentrations of topsoil MBN and MBP under *Alhagi sparsifolia* were significantly greater than those in bottom soil, but MBN concentration in bottom soil under *Karelinia caspica* was significantly greater than that in topsoil (Table 1). Soil microbial C:N ratios under *Alhagi sparsifolia* and *Karelinia caspica* were significantly greater than those under *Tamarix ramosissima* (Fig. 3A, B). Soil

Fig. 1 Plant carbon (C), nitrogen (N), and phosphorus (P) stoichiometry. Asterisks indicate significant differences among different organs or plant species. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

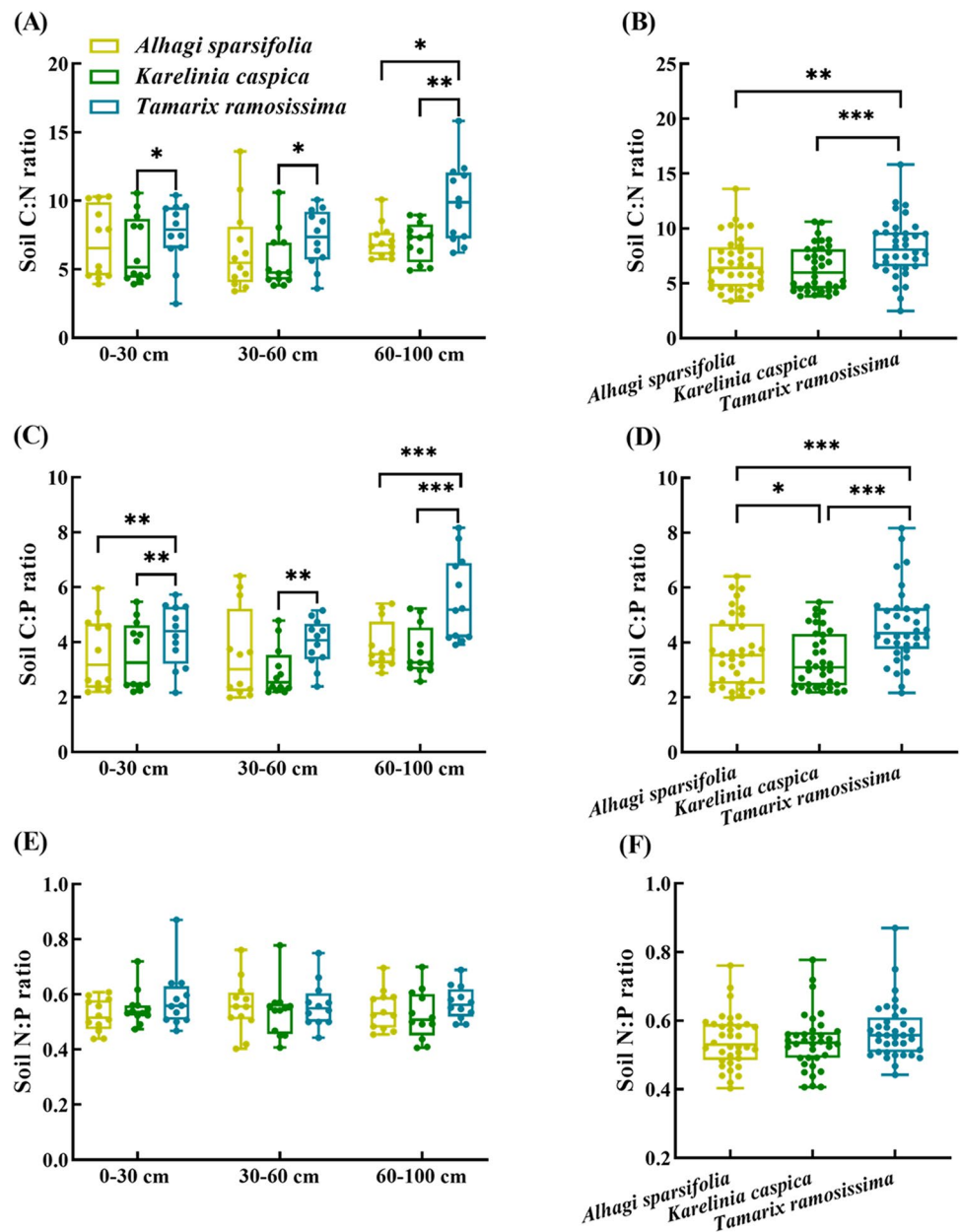


microbial C:N ratio in topsoil was significantly higher under *Karelinia caspica* than under *Alhagi sparsifolia* ($p < 0.001$). Soil microbial C:P ratio under *Alhagi sparsifolia* was significantly higher than that under *Karelinia caspica* and *Tamarix ramosissima* ($p < 0.001$), whereas soil microbial C:P ratio under *Tamarix ramosissima* was significantly greater than that under *Karelinia caspica* (Fig. 3C, D). In addition, soil microbial N:P ratio under *Tamarix ramosissima* was significantly greater than that under *Alhagi sparsifolia* and *Karelinia caspica* ($p < 0.001$), whereas the ratio under *A. sparsifolia* was significantly greater than that under *Karelinia caspica* (Fig. 3E, F).

Correlations between plant, soil, and microbial biomass C, N, and P stoichiometry

Soil EC significantly affected soil C, N, and P balance, especially under *Alhagi sparsifolia* (Fig. 4A). In contrast to *Alhagi sparsifolia*, SOC, soil C:N ratio, and soil C:P ratio under *Karelinia caspica* were negatively correlated with MBN (Fig. 4B). Soil organic C, soil C:N ratio, and soil C:P ratio under *Tamarix ramosissima* were significantly negatively correlated with MBC and MBN (Fig. 4C). However, soil microbial biomass under the three desert species was positively correlated with SWC. In *Alhagi sparsifolia*, plant C was influenced primarily

Fig. 2 Soil carbon (C), nitrogen (N), and phosphorus (P) stoichiometry. Asterisks indicate significant differences among different soil layers or plant species. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

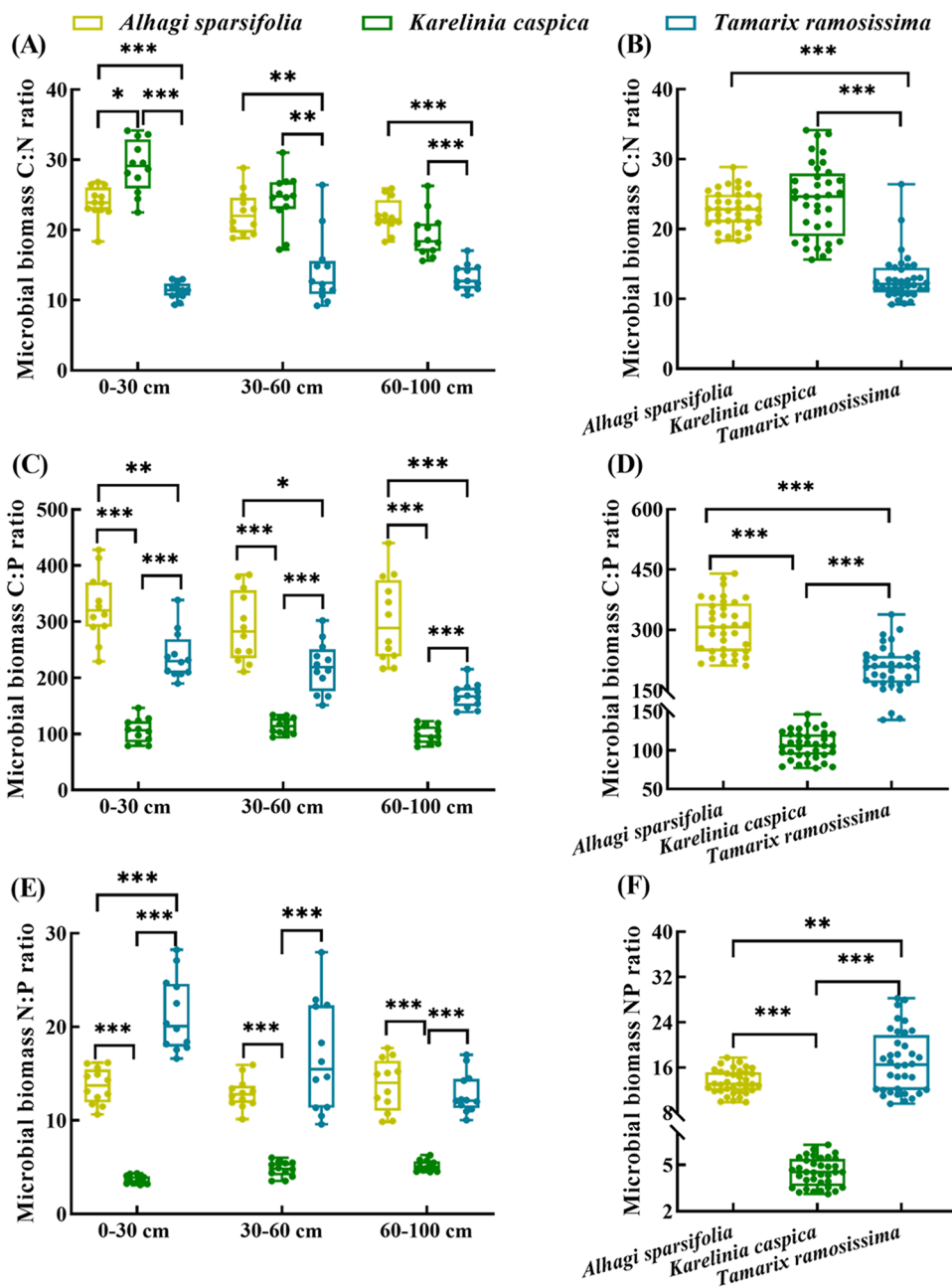


by MBC; plant N was influenced by SOC and MBC; and plant P was influenced by MBN. The C:N and C:P ratios of *Alhagi sparsifolia* were primarily affected by MBC, whereas plant N:P ratio was regulated by SOC and soil C:N ratio. Notably, MBC and MBP affected N and P concentrations and C:N:P ratios in *Karelinia caspica*. Similarly, SOC, MBC, soil C:P ratio, MBP, and MBN affected concentrations and ratios in *Tamarix ramosissima*.

Responses of C, N, and P stoichiometry in different desert species to soil and microbial biomass C, N, and P stoichiometry

Compared with *Karelinia caspica* and *Alhagi sparsifolia*, nutrient concentrations and stoichiometry in *Tamarix ramosissima* were more tightly interrelated with soil factors (Fig. 5A, C, E). In *Alhagi sparsifolia*, soil MBC

Fig. 3 Soil microbial biomass carbon (C), nitrogen (N), and phosphorus (P) stoichiometry. Asterisks indicate significant differences among different soil layers or plant species. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$



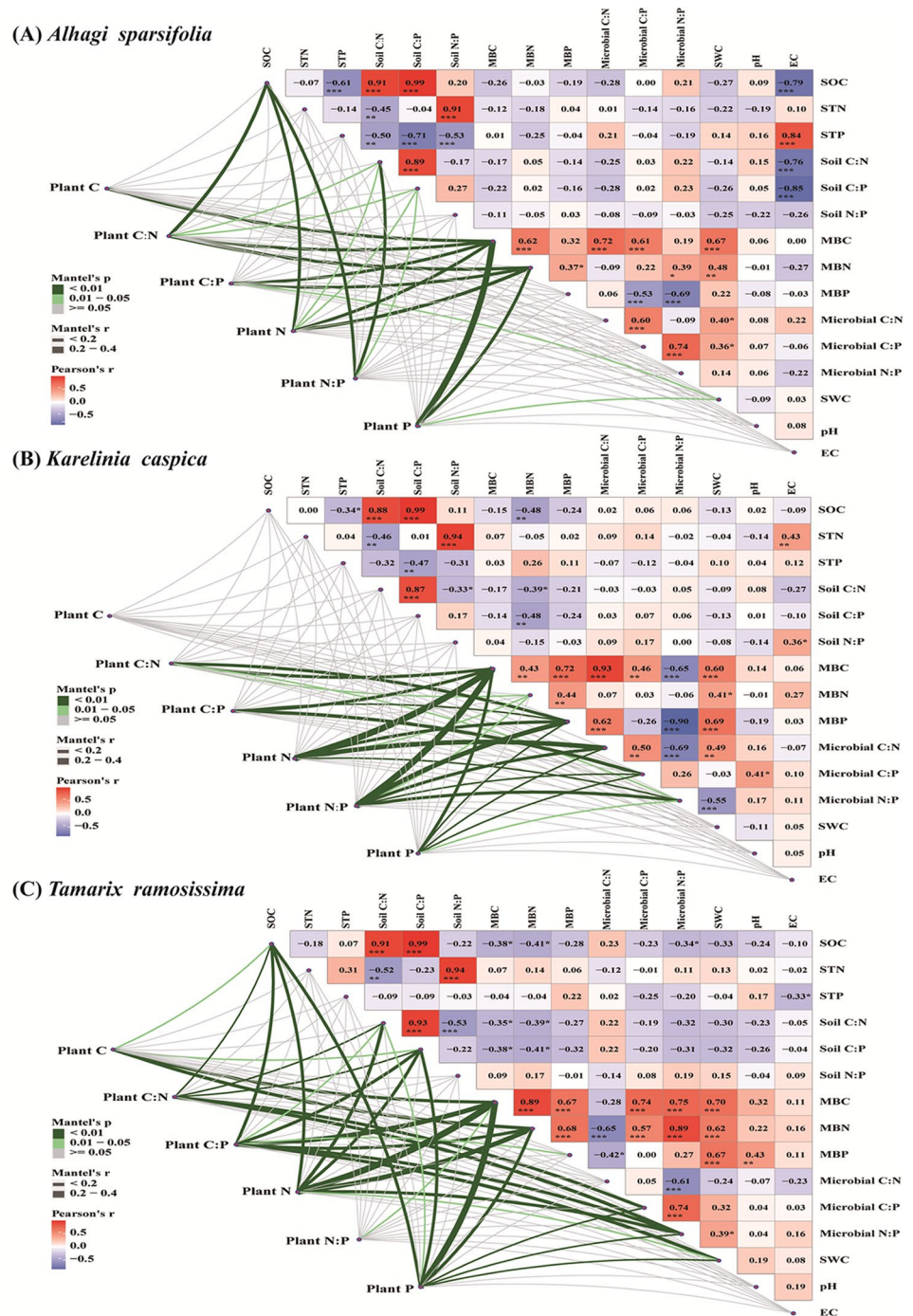
and MBN, SWC, soil C:N ratio, SOC, and soil C:P ratio significantly influenced the variation in nutrient concentrations and stoichiometry (Fig. 5B). In *Karelina caspica*, soil MBC, microbial C:N ratio, MBP, microbial N:P ratio, SWC, and MBN were the main factors that significantly influenced the variation in nutrient concentrations and stoichiometry (Fig. 5D). In *Tamarix ramosissima*, soil MBC, SWC, MBN, microbial C:P ratio, microbial N:P ratio, SOC, soil C:P ratio, MBP, and soil C:N ratio were the main factors that influenced the variation in nutrient concentrations and stoichiometry (Fig. 5F).

Discussion

Variation in C, N, and P stoichiometry in plant organs of desert species

From an ecological and evolutionary perspective, nutrient distribution patterns among plant organs are tightly interrelated with corresponding functional characteristics (Delgado-Baquerizo et al. 2013). For example, as the main organ of photosynthesis, leaves are crucial to

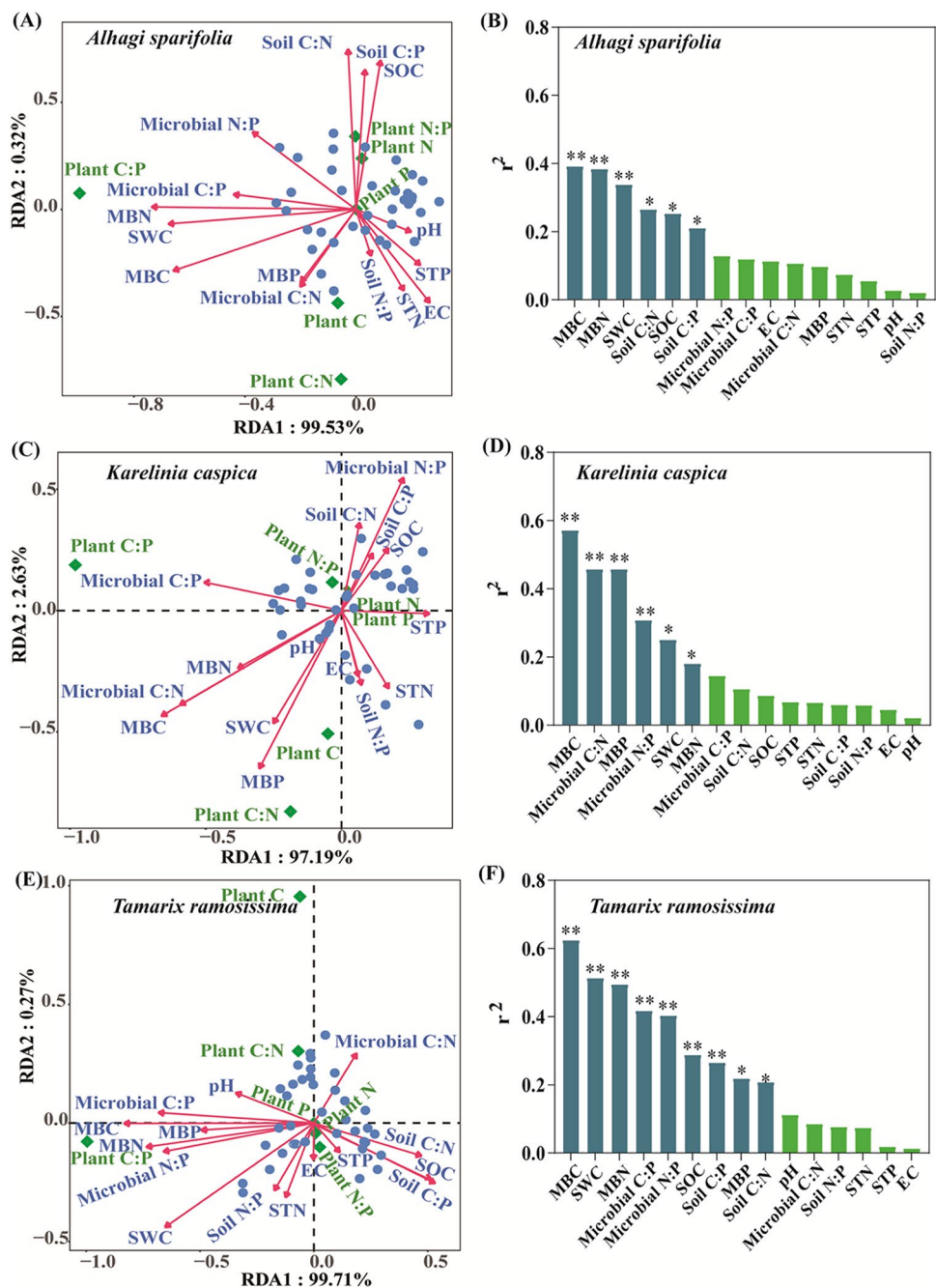
Fig. 4 Mantel tests between carbon (C), nitrogen (N), and phosphorus (P) concentrations and stoichiometry of plant–soil–microbial biomass. The different colors represent the type of relation between two factors, and the depth of color indicates the significance of the correlation coefficient. P represents plant. Asterisks indicate significant differences. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$



plant metabolism and use of water and nutrients (Elser and Hamilton 2007; Finzi et al. 2011). Accordingly, leaves typically have the most advantageous N and P concentrations, especially in herbs of Fabaceae (He et al. 2015). Leaf N and P concentrations of the herb *Alhagi sparsifolia* (Fabaceae) were 20.5 and 1.1 g kg⁻¹, respectively, which were concentrations greater than those of the shrub *Tamarix ramosissima* (non-Fabaceae) but lower than those of the average values of global herbaceous species

(Castellanos et al. 2018). The results indicate that rapidly growing herbs require higher concentrations of N and P than those of shrubs with slower growth (Matzek and Vitousek 2009; Han et al. 2011). The possible explanations for the lower leaf N and P concentrations than those of global averages include low nutrient levels in the region and the hyper-arid climatic characteristics (Zeng et al. 2013; Gao et al. 2022a). In hyper-arid areas, serious water deficiency and high soil salinity weaken plant

Fig. 5 Redundancy analyses between carbon (C), nitrogen (N), and phosphorus (P) stoichiometry of plant–soil–microbial biomass. The green diamond represents plant nutrient concentrations and stoichiometry; the red line with an arrow represents soil and soil microbial biomass and soil water content (SWC), pH, and electrical conductivity (EC). P represents plant. Asterisks indicate significant differences. * $p < 0.05$; ** $p < 0.01$



ability to obtain soil available N and P and limit transport and metabolism of nutrients, ultimately restricting plant growth (He et al. 2016). Additionally, leaf N:P ratios indicated that *Alhagi sparsifolia* and *Tamarix ramosissima* were P-limited, whereas *Karelinia caspica* was N-limited. Some plants in the Fabaceae need more P than non-Fabaceae plants to maintain the N–P balance because of the increase in N from biological N fixation (Lambers et al. 2015). Consequently, the effect of P on Fabaceae in impoverished soils is more significant than that on non-Fabaceae, which was confirmed by this study. However,

the shrub *Tamarix ramosissima* was also limited by soil P, which might be related to the slow root turnover rate of *Tamarix ramosissima*. In addition, relatively low fine root production limits the ability of *Tamarix ramosissima* to obtain soil nutrients (Liu et al. 2016). Plants can also adapt to poor environments by increasing C investment in nutrient acquisition organs, such as roots (Peaucelle et al. 2012). In this study, C concentration of roots was greater than that of leaves, and concentration in the shrub *Tamarix ramosissima* was greater than that in the herbs *Alhagi sparsifolia* and *Karelinia caspica*. The differences were

most likely because of differences in root growth between shrubs and herbs, for example, compared with herbs, shrub roots are thicker and have slower growth (Liu et al. 2016). Furthermore, the higher C:N and C:P ratios of roots and stems of *Tamarix ramosissima* than those of the other species also indicated where C was invested in the N and P-limited environment.

Variation in C, N, and P stoichiometry in soil and microbial biomass

The stoichiometry of soil elements is a critical factor affecting plant nutrient acquisition (Delgado-Baquerizo et al. 2013). The global average soil C:N:P ratio is 186:13:1 (Cleveland and Liptzin 2007), whereas in China, the ratio is approximately 60:5:1 (Tian et al. 2010). However, SOC and STN concentrations in the study area were significantly lower than those in the desert ecosystem of the Hexi Corridor (Zhang et al. 2019) and a grassland ecosystem (Zhang et al. 2020), whereas the concentration of STP was significantly higher. The heterogeneity in STN among different natural ecosystems may be attributed to differences in soil type, organic matter, and texture (Li et al. 2020). By contrast, STP is primarily influenced by soil weathering degree and parent material type (Helfenstein et al. 2018). In the study area, the soil type was associated with an alluvial fan with low weathering degree, low vegetation coverage, and low soil organic matter. Thus, the STP concentration is relatively high, whereas STN and SOC concentrations are relatively low (Gao et al. 2022a). By contrast, relatively high soil weathering, vegetation coverage, and soil organic matter and favorable soil moisture in the desert ecosystem of the Hexi Corridor and the grassland ecosystem indicate increases in soil C, N, and P cycling (Delgado-Baquerizo et al. 2013; Li et al. 2020). Additionally, SOC concentration decreased significantly with the increase in soil depth, with maximum concentrations at 0–30 cm, consistent with litter accumulation on the soil surface (Wang et al. 2014). The SOC at top layer under the shrub *Tamarix ramosissima* was significantly greater than that under the herbs *Alhagi sparsifolia* and *Karelinia caspica*. The differences were most likely due to the greater accumulation of plant litter under the relatively large canopy of the shrub *Tamarix ramosissima*. In a previous study, the “fertile islands” effect under the canopy of *Tamarix ramosissima* was stronger than that under the canopies of *Alhagi sparsifolia* and *Karelinia caspica* (Gao et al. 2022b). Moreover, the SOC concentration of 319 samples from temperate deserts in China is substantially higher than that in this study, which is likely due to the low SWC and sparse vegetation in the hyper-arid desert ecosystem of the study area (Tian et al. 2010). The results indicated that SOC and STN concentrations were relatively low and STP

concentrations were relatively high in the topsoil of the Cele oasis and desert junction zone.

Soil C:N:P ratios also regulate nutrient cycling and biological processes, and vice versa (Delgado-Baquerizzo et al. 2017). Analyses of SOC, STN, and STP in three soil layers under three desert plants indicated that soil C:N and C:P ratios under *Tamarix ramosissima* were significantly higher than those under *Karelinia caspica*. The difference might be primarily attributed to the greater SOC accumulation under the *Tamarix ramosissima* canopy than under the *Karelinia caspica* canopy (Gao et al. 2022b). In addition, soil available N in desert ecosystems is mostly from fixation by symbiotic microorganisms and the limited element stoichiometry in topsoil indicates that desert species can modify biochemical conditions to guarantee nutrient demands are met (Luo et al. 2021). Soil nutrient concentrations and stoichiometry can be regarded as the main driving factors for variation in soil microbial biomass (Yang et al. 2020). This study confirmed that conclusion because soil microbial biomass was closely related to most soil C:N:P ratios (Fig. 4). Specifically, there was a robust link between soil C:N:P ratios and microbial C:N:P ratios under *Karelinia caspica* and *Tamarix ramosissima*. The results of this study are also consistent with the conclusion that soil C:N ratio determines soil microbial biomass (Zhang et al. 2019). Furthermore, the relatively low soil C:P ratio under *Karelinia caspica* indicated an increase in extraordinary resource and energy availability for microbial growth (Elser and Hamilton 2007). In this study, soil MBC and MBP concentrations under *Karelinia caspica* were significantly greater than those under the herb *Alhagi sparsifolia* and the shrub *Tamarix ramosissima*. However, the greater soil microbial C:P and N:P ratios under *Alhagi sparsifolia* and *Tamarix ramosissima* than those under *Karelinia caspica* suggested that soil P was a limiting element for soil microbial growth under *Alhagi sparsifolia* and *Tamarix ramosissima*.

Factors that drive variation in the stoichiometry of plant C, N, and P

The stoichiometry of plant nutrients can characterize the stability of ecosystems (Delgado-Baquerizo et al. 2013). In the study area, extremely low-frequency rainfall events and little rainfall per event constrain leaching of soil nutrients, whereas high potential evaporation leads to salt crusts forming in high salinity habitats (Li et al. 2021; Gao et al. 2022b). In such a hyper-arid environment with severe salinity, the most severe limitations are imposed on plant acquisition and cycling of nutrients. The extreme conditions also affect desert plant–soil–microbial biomass nutrient cycling because of effects on stoichiometry of soil and microbial biomass elements (Gong et al. 2017).

Plant nutrient stoichiometry can be affected by available soil nutrients as well as plant ability to adjust to nutrient limitations (Tian et al. 2019). In this study, the concentration range of nutrients in different plant organs was relatively narrow, which is consistent with the results of Zhao et al. (2016). Plant nutrient stoichiometry is affected by many factors, including available soil nutrients, soil microbial biomass, soil moisture, pH, and EC, as well as differences in plant life form (Sardans et al. 2017). Soil organic C and soil C:N and C:P ratios were the most important regulators of nutrient concentrations and stoichiometry of *Tamarix ramosissima* and also N and C:N and N:P ratios in *Alhagi sparsifolia*. Phosphorus may be the primary driver triggering multi-element stoichiometric changes in plants in P-poor environments (Yan et al. 2015). Nevertheless, in this study, although *Alhagi sparsifolia* and *Tamarix ramosissima* were constrained by P (leaf N:P > 16), the stoichiometry of plant nutrients was controlled by SOC rather than STP. A primary explanation for the result could be that STP is relatively stable because it is mostly influenced by soil weathering degree and parent material type (Helfenstein et al. 2018). However, the “micro-environment” formed by desert plant litterfall and sandy soil under plant canopies in desert ecosystems promotes litter decomposition, which provides additional C sources for soil microorganisms, ultimately accelerating soil nutrient cycles (Gao et al. 2022b). In this study, the importance of such micro-environments was demonstrated because soil MBC and MBN were the most important factors regulating C:N:P ratios in *Alhagi sparsifolia* and *Tamarix ramosissima*.

Notably, SWC was a regulator of plant P and C:P ratio in *Alhagi sparsifolia* and *Tamarix ramosissima*, which was most likely due to the strong correlations between SWC and soil N and P availability (Gong et al. 2017). Alternatively, soil moisture can increase litter decomposition by soil microorganisms, reduce the adsorption capacity of organic matter in the soil solid phase, promote the release of nutrients, and ultimately affect plant nutrient concentrations (Gao et al. 2019). Furthermore, nutrients in the shrub were more sensitive to variation in soil factors than nutrients in the herbs (Fig. 5). It is possible the relatively high biomass of branches makes shrubs more soil-dependent (Han et al. 2011; Luo et al. 2021).

Conclusions

The herb *Alhagi sparsifolia* and the shrub *Tamarix ramosissima* were P-limited in the Taklimakan Desert, whereas the herb *Karelinia caspica* was N-limited. A robust link was found between C, N, and P of three different life forms of desert plants and C, N, and P concentrations and stoichiometry of soil microbial biomass. Thus, soil microbial

biomass rather than soil nutrients was the primary driver of the variation in plant nutrient stoichiometries, suggesting that soil microbial biomass has a crucial role in the cycling of plant nutrients in nutrient-impooverished soils. In addition, SWC was also a crucial factor regulating nutrient concentrations and stoichiometries of *Alhagi sparsifolia* and *Tamarix ramosissima*. Most importantly, nutrient concentrations and stoichiometry in the shrub *Tamarix ramosissima* were more strongly affected by changes in soil factors than those in the herbs. Overall, the study demonstrated that soil microbial biomass and SWC are strong predictors of changes in C, N, and P of desert plant species. Future studies should consider the underlying mechanisms by which microbial nutrient balance determines plant nutrient balance and the coupling of plant–soil–microbial biomass in desert ecosystems.

Authors' contributions All authors contributed to the study conception and design. Yanju Gao performed field work, sample collection and data analysis. Yanju Gao wrote the first draft of the manuscript, Fanjiang Zeng revised and edited the manuscript and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability All data generated or analyzed during this study are included in this published article

Declarations

Ethics approval The study does not involve any human or animal subject study.

Consent to participate All authors reviewed and approved the final manuscript.

Consent for publication All authors agree to publish this manuscript in your journal.

Conflict of interest The authors declare no competing interests.

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