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Correspondence and requests for materials should be addressed to M.Z.H. (hmzecology@lzb.ac.cn)

Leaf nitrogen and phosphorus of temperate desert plants in response to climate and soil nutrient availability

Mingzhu He[1], Feike A. Dijkstra[2], Ke Zhang[1], Xinrong Li[1,3], Huijuan Tan[1,3], Yanhong Gao[1] & Gang Li[1]

[1]Shapotou Desert Research and Experiment Station, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou, 730000, China, [2]Department of Environmental Sciences, Centre for Carbon, Water and Food, The University of Sydney, NSW, 2006, Australia, [3]Key Laboratory of Stress Physiology and Ecology in Cold and Arid Regions of Gansu Province, Lanzhou, 730000, China.

In desert ecosystems, plant growth and nutrient uptake are restricted by availability of soil nitrogen (N) and phosphorus (P). The effects of both climate and soil nutrient conditions on N and P concentrations among desert plant life forms (annual, perennial and shrub) remain unclear. We assessed leaf N and P levels of 54 desert plants and measured the corresponding soil N and P in shallow (0–10 cm), middle (10–40 cm) and deep soil layers (40–100 cm), at 52 sites in a temperate desert of northwest China. Leaf P and N : P ratios varied markedly among life forms. Leaf P was higher in annuals and perennials than in shrubs. Leaf N and P showed a negative relationship with mean annual temperature (MAT) and no relationship with mean annual precipitation (MAP), but a positive relationship with soil P. Leaf P of shrubs was positively related to soil P in the deep soil. Our study indicated that leaf N and P across the three life forms were influenced by soil P. Deep-rooted plants may enhance the availability of P in the surface soil facilitating growth of shallow-rooted life forms in this N and P limited system, but further research is warranted on this aspect.

Nitrogen (N) and phosphorus (P) availability affect community structure[1–2], species diversity[3–5], and other ecosystem functions[6], such as nutrient cycling and productivity[7–8], and the ratio of these two elements in leaf tissue may indicate if a system is limited by N, P or both[9]. Studies about ecological stoichiometry of N and P have been performed across local[10], regional[8,11] and global scales[12–14]. Plant N and P levels can be influenced by various biotic and abiotic factors, such as habitat[15], growth stages[16], and plant functional groups[3].

N- and P- limitation are typically determined by plant nutrient levels and/or soil nutrient availability[17]. In turn, plant adaptations to soil nutrient levels may exert control over critical N : P values. Studies from terrestrial plant species of China revealed that due to low soil P levels compared to the global average, overall leaf N : P ratios were markedly higher than that of global flora[8]. However, it was suggested that critical leaf N : P values could not effectively predict nutrient limitation of desert plants. Due to water and nutrient co-limitations and adaptation to low nutrient conditions, desert plants show little plasticity in N : P stoichiometry[17] and maintain low tissue nutrient uptake[18]. This unique pattern highlights the need of considering soil nutrient conditions for plant specific adaptation and plant-soil interactions in desert environments.

In desert ecosystems, low soil moisture coupled with high soil alkalinity acts to decrease both soil N and P availability[19]. Infrequent and low precipitation limits soil weathering, organic matter production, and mineralization[20], leading to slow P release from primary material, low soil organic matter content, and N bound in organic matter[17]. A study from 224 dryland sites indicated an increased decoupling of carbon (C), N and P with increased aridity resulting in greater P availability compared to N[18]. Plant N fixation rates in arid regions have long been considered to be low because of low soil moisture and high temperatures[21]. In contrast, ammonia volatilisation of dryland soils can be high, as volatilisation rates are positively related to soil pH, total salt content and $CaCO_3$, and negatively related to soil organic matter, cation-exchange capacity and clay content[22]. There is also good evidence that sometimes nutrients, with limited water, can limit plant growth[17], although relationships between plant growth and leaf N or P concentration are not always clear[16].

What is the intrinsic relationship between soil nutrients and leaf nutrients of desert plants? Soil nutrients are the main driver for leaf nutrient concentrations. Plant available soil P, primarily derived from weathering of primary materials such as apatite, and from dissolution and diffusion of P within the soil solution, is considered lower than that of N[21]. Available forms of N and P mostly remain in the surface soil because the high temperature and low rainfall regimes characteristic of desert ecosystems prevent nutrients to be leached to deeper soil layers[23]. Desert plants play a vital role in vertically redistributing soil nutrients because nutrients intercepted by roots from soil at depth are recycled to the soil surface layer by throughfall and litterfall[24]. Jobbágy and Jackson[24] found that, as soil nutrients become scarce, that these limiting nutrients are transferred from deeper soil layers. Plant characteristics, such as tissue stoichiometry, above- and below-ground allocation of biomass, nutrient cycling rates, rooting depths and redistribution, may play a crucial role in shaping soil nutrient profiles[24–26]. However, to our knowledge, limited studies coupled the nutrient distribution in soil profiles to plant life forms and leaf nutrient stoichiometry, and explained the intrinsic relationships between them.

Here, we tested the response of leaf N and P stoichiometry to climate, soil N and P pools, for different life forms at 52 sites in the Alxa desert, northwest China. Our objectives were to understand the effects of potential drivers (climate, soil N and P) on leaf N and P stoichiometry of life forms in this temperate desert. We address the following questions: Under N- and P-limited conditions, how do leaf N and P concentrations and stoichiometry vary among different life forms (annuals, perennials, shrubs) of the temperate desert flora? How do leaf N and P vary with mean annual temperature (MAT) and mean annual precipitation (MAP) and with N and P levels in the soil? How are plant nutrient concentrations among life forms affected by the vertical distribution of soil nutrients?

Results

The concentrations of leaf N, P and N : P mass ratio of the desert plants varied markedly, ranging between 1.20 and 37.4 mg g^{-1} for N; 0.11 and 4.51 mg g^{-1} for P, and 2.55 and 36.9 for N : P. Leaf P was higher in annuals and perennials than in shrubs, while leaf N : P in shrubs was higher than in annuals and perennials (Table 1). Among these traits, greater variation was found in leaf N and P (overall mean CV of 0.62 and 0.67 respectively) than in leaf N : P (CV = 0.37). Among all species, leaf N was positively correlated to leaf P (Table 1).

Across all sites, total soil N and P were strongly correlated (Figure 1). Total soil N and P concentrations were highest at the surface and decreased with depth (Figure 2). On the other hand, total soil N : P did not show a clear pattern with soil depth and there were no significant differences among the three layers.

Life form effects on leaf N, P and N : P did not depend on MAT or MAP at the site (i.e., no significant interactions with MAT or MAP in the ANCOVA), but the covariate MAT had a significant effect on leaf N and P concentration (Table 2). Leaf N and P (averaged across species for each site) significantly decreased with increased MAT (Figure 3). Leaf N and P showed no relation with MAP.

Life form effects on leaf N, P and N : P did not depend on total soil N concentration at 0–10, 10–40, or 40–100 cm soil depth (no significant life form*soil N interactive effects in the ANCOVA). Leaf N, P and N : P were also not related to total soil N at any of the three soil depths (no significant covariate effect, data not shown). On the other hand, leaf N showed positive relationships with soil P at 0–10 and 10–40 cm soil depth (Table 3). Life form effects on leaf P depended on soil P at 0–10 and 10–40 cm soil depth (significant life form*soil P interactive effects in the ANCOVA) (Table 3). Leaf P was positively related to soil P in 0–10, 10–40 and 40–100 cm soil depth. Life form effects on leaf N : P did not depend on total soil P concentration at 0–10, 10–40, or 40–100 cm soil depth (no significant life form*soil P interactive effects in the ANCOVA) (Table 3). We conducted linear regressions between total soil P concentration at 0–10, 10–40 and 40–100 cm soil depth and leaf P for each life form separately to examine which life forms caused significant relationships with total soil P. Only regressions between total soil P and leaf P were significant, and only at specific soil depths for each life form (Figure 4). Specifically, leaf P of annuals was positively related to total soil P at 0–10 cm, but not at 10–40 and 40–100 cm soil depth (Figure 4a, b, c). Perennial leaf P was significantly related with total soil P at 0–10 and 10–40 cm soil depth (and together with annuals showing steeper slopes than shrubs at these shallower soil layers), but not at 40–100 cm soil depth (Figure 4d, e, f). Leaf P of shrubs showed a positive relationship with total soil P at all three depths (Figure 4g, h, i). In the deepest soil layer at 40–100 cm, total soil P explained the most of the variation in shrub P (greatest R^2), and showed a steeper slope than in shallower soil layers (0–10 and 10–40 cm).

Discussion

Leaf N and P stoichiometry of typical desert plants, across the Alxa desert of China, were analysed in this study. The average leaf N and P concentration of all 54 species was 10.9 and 1.13 mg g^{-1} respectively, lower than reported in other studies (Table 4). The average leaf N : P ratio of plants in the Alxa desert was 10.8, also lower than that reported elsewhere (Table 4). The leaf N : P mass ratio has been used to indicate plant N or P limitation conditions (i.e., N limitation when $N : P < 14$, P limitation when $N : P > 16$)[9]. The low N : P ratios in our study suggests that the desert flora in the Alxa desert were more N-limited than P-limited (Table 4). In general, desert ecosystems tend to have a high N-efficiency due to limited plant N fixation[27,28] and limited N losses as dissolved organic N[29] or as gaseous N[22,30]. Nevertheless, the extremely low plant N and P concentrations suggest that both nutrients were in low supply in this temperate desert.

Plant P concentrations are often positively related to soil P concentrations at the ecosystem scale[3,27,31]. Recent studies focusing on N and P stoichiometry of Chinese flora[8,10,11] and soil[32] have indicated that an underlying cause for the low leaf P concentrations of Chinese plants is the relatively low soil P content[32–33]. Soil P concentrations of Chinese soils are lower compared to global levels[33]; however average total soil P content of the Alxa desert (0.70 and 0.61 mg g^{-1} at 0–10 and 10–40 cm soil depth) was above the average of that in other parts of China[8]. A large fraction of the total soil P of the Alxa desert was in inorganic form that is mostly unavailable to plants (e.g., insoluble calcium phosphates)[34].

Some significant differences in leaf P and N : P were observed across plant life forms of the desert flora, but not in leaf N (Table 1). Leaf P concentrations were significantly higher (and leaf N : P lower) in annuals and perennials than in shrubs, consistent with other studies where higher P concentrations were observed in

Table 1 | Leaf N, P and N : P mass ratios averaged by life form of desert plants in Alxa desert

	N(mg g^{-1})			P (mg g^{-1})			N : P mass ratio			
Functional group	N	Mean	CV	N	Mean	CV	n	Mean	CV	r_s
Shrub	51	11.16^{a}	0.63	51	0.91^{b}	0.63	51	13.18^{a}	0.25	0.86*
Annual	32	10.39^{a}	0.62	32	1.26^{a}	0.61	32	9.33^{b}	0.39	0.85*
Perennial	31	10.88^{a}	0.64	31	1.37^{a}	0.67	31	8.57^{b}	0.41	0.83*
ANOVA P-value		0.93			0.02			<0.0001		

1) Different superscript letters (a, b) indicate significant differences (Tukey's HSD test, $P < 0.05$) in the mean value. N, sample size; CV, coefficient of variation.
2) Spearman's rank correlation coefficient (r_s) between species-specific leaf N and P was calculated for each life form. Correlations with *, $P < 0.001$.

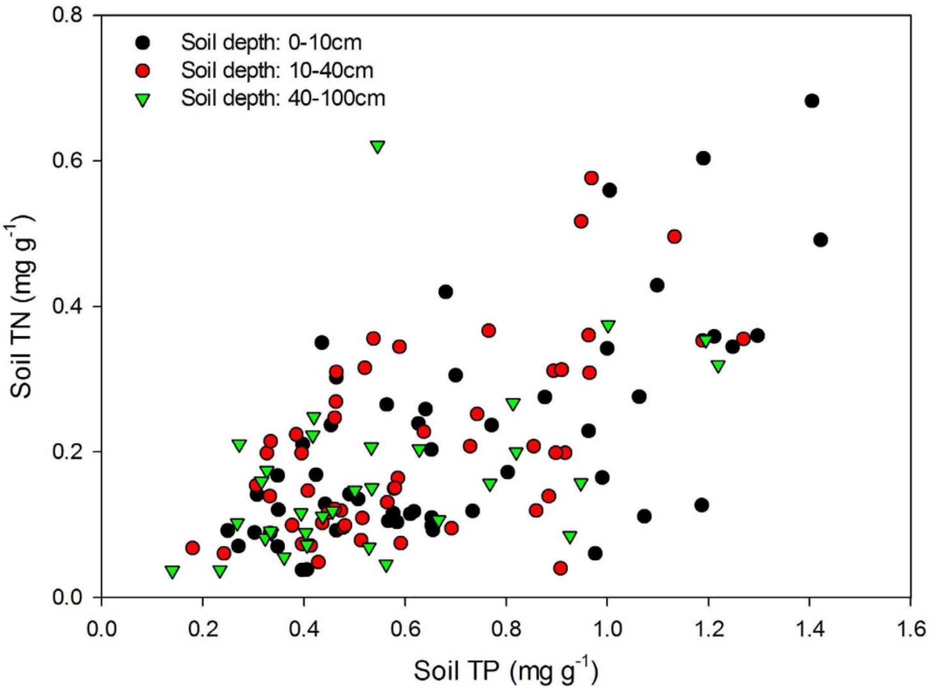

Figure 1 | Relationships between soil total nitrogen (TN) and total phosphorus (TP) concentrations at three soil layers. Spearman's correlation efficient between TN and TP were 0.548 at 0–10 cm ($P < 0.0001$), 0.513 at 10–40 cm ($P < 0.0001$) and 0.526 at 40–100 cm ($P < 0.0001$).

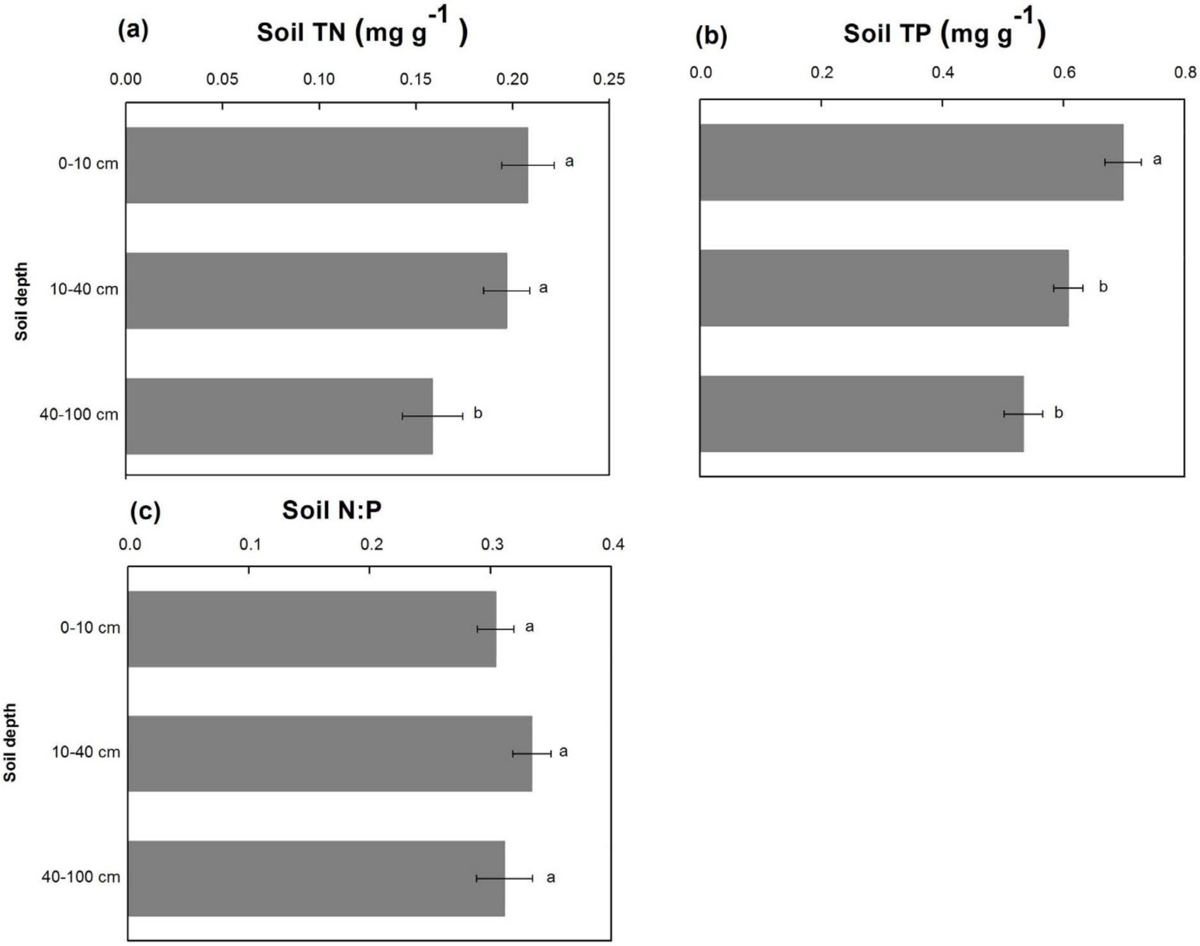

Figure 2 | Soil N, P and N : P with soil depth. The values of (a) total soil nitrogen (TN); (b) total soil phosphorus (TP) and (c) soil N : P ratio averaged by all sample sites ($n = 52$). Letters indicate significant differences of the mean ± SE at $P \leq 0.05$ using Tukey's HSD test.

Table 2 | Summary of ANCOVA results (*P* values) for the effects of MAT, MAP (covariates) and life form on leaf N and P stoichiometry

Effect	Log N	Log P	Log N : P
MAT	**0.04**	**0.01**	0.30
Life form	0.85	**0.01**	<**0.0001**
MAT × life form	0.78	0.70	0.73
MAP	0.54	0.91	0.25
Life form	0.88	**0.02**	<**0.0001**
MAP × life form	0.83	0.91	0.94

P –values are in bold when $P < 0.05$.

fast-growing, short-lived species than in slow growing, long-lived species[3,35]. Fast growing plants often require more P-rich RNA to support synthesis of proteins necessary for rapid growth[36]. Possibly, P uptake from deeper soil layers and redistribution to shallow soil layers by slow-growing shrubs may have contributed to meet the relatively high leaf P requirement in fast-growing annuals and perennials in this P-poor system.

Many studies focused on the broad biogeographic patterns with climatic indices (e.g., MAT or MAP). At the global scale, Reich and Oleksyn[14] identified that leaf P, and to a lesser degree leaf N, decreased as MAT increased and that leaf N : P increased as MAT increased[14]. These global patterns differed among taxonomic groups and were independent of changes in species composition[31] and were confirmed by studies in Chinese terrestrial flora and grasslands[8,37].

In contrast, leaf N, P and N : P of the desert flora in this study were unrelated to MAP, while relationships with MAT were weak (Figure 3). Possibly, the range in MAT (ranging from 5.8 to 8.8°C) and MAP (from 40 to 200 mm) in our area was too small to detect strong patterns with leaf N and P. Leaf N and P stoichiometry of different desert plants can fluctuate remarkably in time because of seasonal climate variation, obscuring spatial relationships between leaf N and P stoichiometry and mean annual climate parameters[10].

Leaf N and P were significantly related to total soil P (Table 3, Figure 4), but not to total soil N, suggesting that total soil P availability influences plant uptake of both N and P more than total soil N in this system. Total soil N in desert ecosystems may not be a good indicator of N availability to plants. In desert ecosystems, important N sources include ammonium (NH_4^+) and nitrate (NO_3^-) derived from rainfall, aeolian deposition with nitrate dust, and biological assimilation by N-fixing soil organisms[23]. Nitrogen uptake by plants is affected by temperature, soil water condition, microbial community and N-fixation. All these factors may result in total soil N being a poor indicator of N availability. However, P can be an equal or a more important limiting factor in many desert ecosystems compared to N, especially in calcareous soils with high pH[16,25]. Several studies from regional to global scales found that leaf P, for various plant groups and in different geographical regions, can be more variable and more strongly related to climate conditions and soil nutrients compared to leaf N or N : P[11,38–40]. Our results suggest that, leaf N and P are at least partially controlled by total soil P levels in the Alxa desert.

Because most N and P sources, derived from dust, rock weathering, and the decomposition of litter, often occur in the topsoil[26], higher N and P concentration are found in surface soils than that of deep soil in most environments. This phenomenon is pronounced in desert ecosystems because insufficient rainfall limits N and P leaching downward into soil[26], and is supported by decreasing soil N and P with depth in this study (Figure 2). This decrease in soil N and P with depth can be enhanced by the desert vegetation in this system. The relationship between leaf P and soil P at 40–100 cm suggests that shrubs may have taken up P (and N to a lesser degree) from deeper soil layers and returned these nutrients to the surface soil via litterfall. By enhancing P availability in the surface soil, deep-rooted shrubs could then relieve P limitation of shallow rooted and fast growing annuals and perennials with relatively high N and P requirements[41–43]. Indeed, leaf P of annuals and perennials were more responsive to soil P at shallower depths. This upwards movement of N and P could have important consequences for the vegetation structure in this N- and P-limited desert ecosystem, possibly facilitating co-existence of different plant life forms. We did not measure the rooting depths of the different life forms that could support this notion. However, a global analysis on rooting depths showed that shrubs had relatively more roots at greater soil depth than grasses[43]. Most studies in desert ecosystems have focused on horizontal nutrient patterns, including the development of "islands of fertility"[19]. However, desert plants may also play an important role in structuring vertical distributions of soil nutrients[24]. Soil nutrient distribution has been associated with plant characteristics including nutrient stoichiometry, allocation of above- and belowground biomass, biomass cycling rate and rooting depth[26], which could potentially have important consequences for plant community structure.

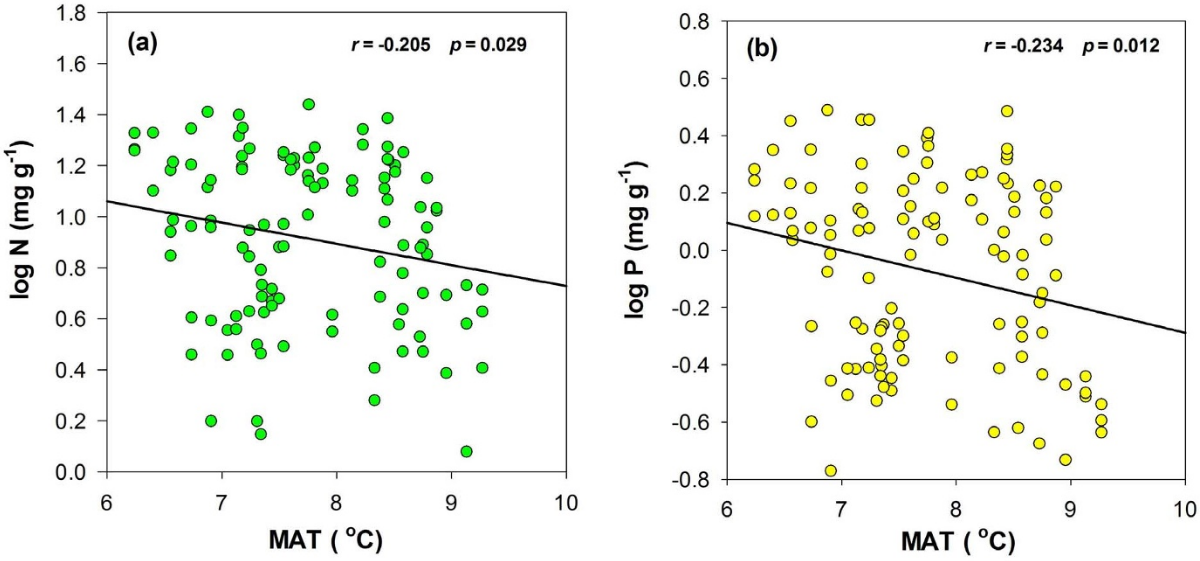

Figure 3 | **Relationships between leaf N, leaf P (log transformed) and mean annual temperature** (MAT). Species values were averaged at each site (n = 52).

Table 3 | Summary of ANCOVA results (*P*-values) for the effects of life form on plant N, P and N : P with soil P at 0–10, 10–40 and 40–100 cm soil depth as the covariate

Variable	Plant nutrient		
	N	P	N : P
Life form	0.23	<**0.0001**	<**0.0001**
Soil P (0–10)	**0.01**	**0.002**	0.49
Life form × soil P (0–10)	0.83	**0.008**	0.71
Life form	0.20	<**0.0001**	<**0.0001**
Soil P (10–40)	**0.01**	**0.001**	0.27
Life form × soil P (10–40)	0.99	**0.04**	0.51
Life form	0.49	**0.02**	<**0.0001**
Soil P (40–100)	0.24	**0.0003**	**0.03**
Life form × soil P (40–100)	0.85	0.9519	0.93

P –values are in bold when $P < 0.05$.

In conclusion, we document low concentrations of N and P in desert plants that have adapted to low nutrient conditions. There was no strong relationship between climate (MAT or MAP) and leaf nutrients, but soil P positively related to leaf N and P. In addition, we found that shrub N and P showed the strongest relationship with P in the deep soil (40–100 cm), while N and P in annuals and perennials were only significantly related to N and P in the shallow soil. Our results suggest that deep-rooted plants may enhance the availability of P in the surface soil facilitating growth of shallow-rooted life forms in this N and P limited system. This mechanism needs to be tested in more comprehensive arid/desert regions where plant cycling dominates the vertical distribution of soil nutrients.

Methods

Site description. This study was conducted at 52 vegetated sites of the Alxa Desert in northwestern China (Supporting information, Table S1), which is situated in the arid zone of the East Asian continent and spans from 37′24″N, 97′10″E to 42′47″N, 106′53″E. The sampling sites experienced harsh climatic conditions, with MAT

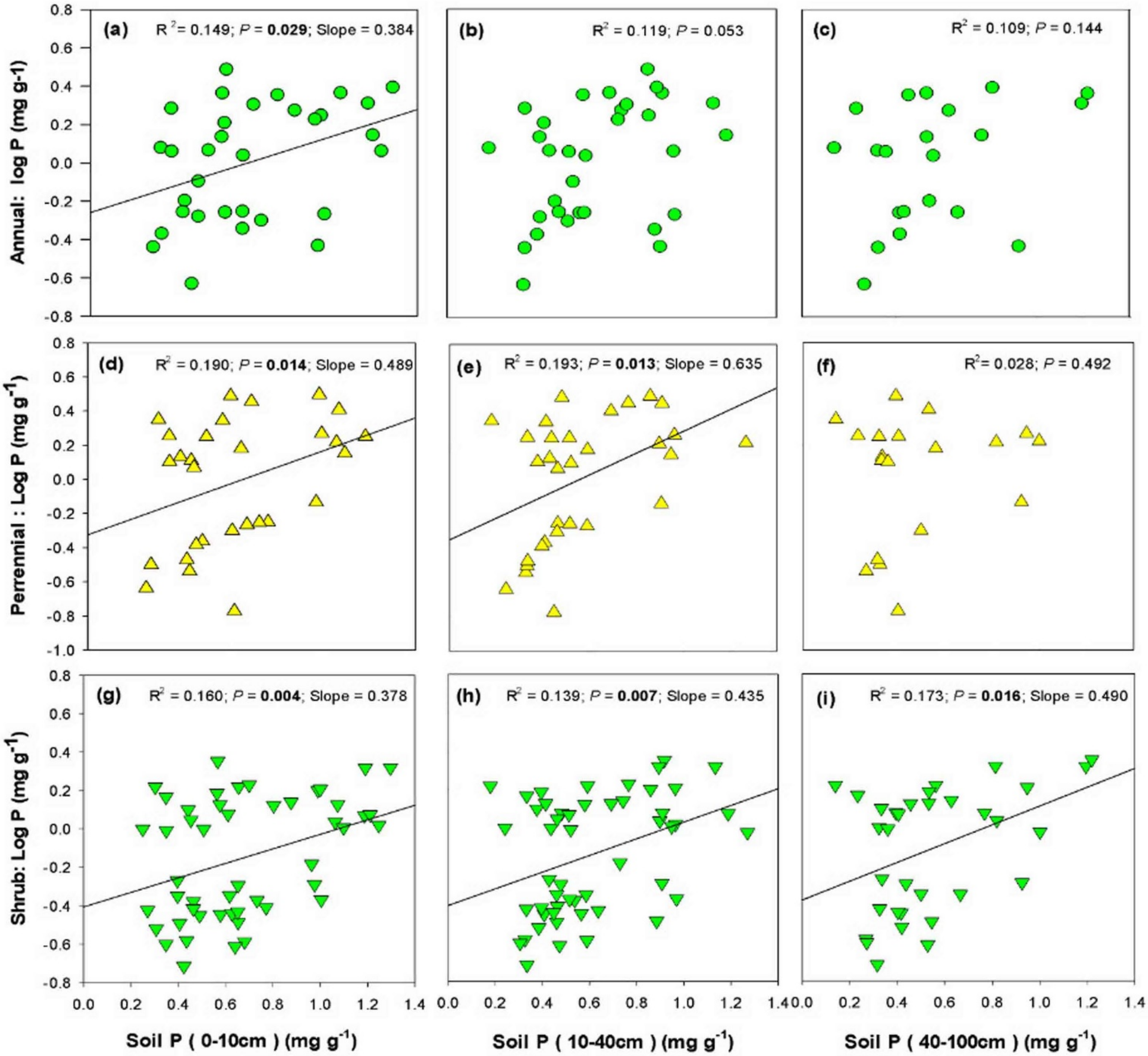

Figure 4 | Leaf P of three life forms in relation to total soil P at different depths. (a–c) Annual leaf P; (d–f) perennial leaf P; (g–i) shrub leaf P; (a,d,g) total soil P at 0–10 cm soil depth; (b,e,h) total soil P at 10–40 cm soil depth and (c,f,i) total soil P at 40–100 cm soil depth. Lines are shown when relationships were significant ($P < 0.05$).

Table 4 | Comparison of leaf N and P stoichiometry between Alxa desert and other regions

Data source	N (mg g^{-1})	P (mg g^{-1})	N : P (mg g^{-1})	References
Alxa desert	10.87 ± 7.91 (n = 54)	1.13 ± 0.81 (n = 54)	10.84 ± 5.06 (n = 54)	This study
China	20.20 ± 8.41 (n = 554)	1.46 ± 0.99 (n = 745)	16.30 ± 9.32 (n = 547)	8
Grassland of China	27.60 ± 8.60 (n = 213)	1.90 ± 0.84 (n = 525)	15.30 ± 5.20 (n = 525)	11
Global flora	20.10 ± 8.71 (n = 1251)	1.77 ± 1.12 (n = 923)	13.8 ± 9.47 (n = 894)	14
Global flora	20.60 ± 12.23 (n = 398)	1.99 ± 1.49 (n = 406)	12.7 ± 6.82 (n = 325)	13

ranging between 5.8 and 8.8°C, MAP rangeing between 40 and 200 mm. There are four main vegetation subtypes, namely, psammophytic vegetation, typical desert vegetation, desert steppe vegetation and steppified desert vegetation[44].

Sampling and measurement. Collection and measurement of samples were conducted in late August of 2012. The distribution and locations of dominant plant communities have been initially identified based on the Vegetation Map of Inner Mongolia[45]. During the field surveys and plant samplings, the research sites were located away from grazing activity and anthropogenic disturbances. Quantitative surveys of the vegetation was carried out at each site and fully expanded sun-exposed and newly matured leaves from five to ten individuals were collected for each dominant plant of three life forms (i.e., annual, perennial and shrub). In total, we collected 276 plant samples, belonging to 12 families, 41 genera and 54 dominant species (See Table S2) from 52 research sites. The leaf samples were rinsed with deionized water at least two times to reduce the influences of dust or soil. After oven-drying at 60°C for 72 h, plant samples were ground and then measured for N and P concentrations. Leaf N was measured with a CHNS/O Elemental Analyzer (Pekin-Elmer, USA). Leaf P was measured colorimetrically after H_2SO_4-H_2O_2-HF digestion using the molybdate/stannous chloride method[46].

At each sampling site, soil samples were randomly collected at three soil depths with three replicates: shallow layer (0–10 cm), middle layer (10–40 cm), and deep layer (40–100 cm). Soil samples in each soil layer were mixed evenly. Air-dried and ground soil samples were sieved using a 100-mesh sieve. Soil total nitrogen (TN) was analysed with a Kjeltec System 2300 Analyzer Unit (Tecator, Höganäs, Sweden). Soil total phosphorus (TP) content was determined with the molybdate/ascorbic acid blue method[47] after digestion with $HClO_4$ and H_2SO_4 acid. The MAP and MAT used in this study were obtained through linear interpolation models based on variables of latitude, longitude, and altitude, using the climate database from the Inner Mongolia Weather Bureau.

Data analysis. We classified species into three life forms: annual, perennial and shrub. We used ANOVA to test effects of life form on leaf N, P and N : P across all sites. We also used ANOVA to assess how soil N, P, and N : P varied with soil depth across all sites. Sampling site was included in the ANOVAs as a random factor with life form (plant analyses) or soil depth (soil analyses) nested within site. When life form or soil depth effects were significant ($P < 0.05$), we used Tukey's HSD posthoc tests to compare means of the three life forms and soil depths. To assess how life form effects on leaf N and P traits depended on MAT and MAP, we included MAT or MAP as a covariate and its interaction with life form in the ANCOVA. We also used soil N and P at different depths as a covariate and the interaction with life form in the ANCOVA. For these latter analyses we averaged the species leaf N and P by life form for each site so that for each site there was one soil value and one plant value for each life form in the analyses. All data were log-transformed to normalize distribution of leaf N, P and N : P. We used linear regression analyses to examine the effects of MAT, MAP, soil N and soil P on leaf N and leaf P averaged across all species, and within each life form at each site. All analyses were conducted using JMP (v.10.0.0; SAS Institute, Cary, NC, USA).

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Author contributions

M.Z.H. conceived and designed the experiment. M.Z.H. and F.A.D. analysed the data and wrote the paper. M.Z.H., K.Z., X.R.L., H.J.T., Y.H.G. and G.L. carried out the field investigation and sample analyses, and contributed to the draft manuscript.

Additional information

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