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Fractal analysis of the response of the Agriophyllum pungens root architecture to the habitat gradient in the oasis desert ecotone

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Abstract

In deserts, plant abundance is low, and the ecosystem is fragile. The study of the root architecture of desert plants combined with global fractal and multifractal analyses is helpful for revealing the survival strategies adopted by desert plants in response to harsh environmental conditions, which is important for understanding the phenotypic plasticity of desert plant roots and the protection of desert ecosystems. However, global fractal and multifractal analysis approaches have not been commonly combined in studies focused on the analysis of the root configurations of desert plants under the influence of habitat gradients. In this study, an interdunal depression area (Plot □), a gentle sand slope area (Plot □) and a slope crest area (Plot □) were selected in the oasis desert ecotone of Jinchuan District, Gansu Province. The responses of the root morphology and fractal characteristics of *Agriophyllum pungens* to heterogeneous habitat conditions were studied. The results revealed that the fractal abundance (FA) of *A. pungens* roots gradually increased, the multifractal singularity spectral width decreased, and the Rényi spectral width increased. In Plot □, the distribution of *A. pungens* roots was simple, with relatively high uniformity and symmetry, and the FA of roots decreased. In contrast, the root configuration was complex, with low uniformity and low symmetry. In Plot III, the FA of *A. pungens* roots increased, and a highly uniform and symmetrical root configuration was established. Under different habitat conditions, coevolution of the root geometry and fractal structure is realized on the basis of the balance in root–shoot biomass allocation, and the root architecture is adapted to the habitat. This reflects the high phenotypic plasticity of the roots of oasis desert plants and the ecological adaptation strategies adopted by these plants in response to harsh habitats.

Introduction

The root system is an important organ through which plants obtain underground resources, and its structure and function are closely related to the process by which plants absorb water and nutrients from soil (Pierret et al., 2016; Warren et al., 2015; Yu et al., 2016). The root architecture is defined as the physical form of roots, which regulates the distribution of roots in soil in time and space (Lynch et al., 2023), determines the ability of plants to absorb and transport water and nutrients (Wang et al., 2019), and serves as an important line of defence in plants against abiotic or biological stress (Bisht et al., 2019; Hu et al., 2018). The root architecture includes root geometric characteristics, branching characteristics, fractal characteristics and root spatial distribution characteristics (Lynch, 1995). Fractal analysis is a useful tool for studying changes in the root configuration geometry and spatial branching states in heterogeneous habitats. The fractal structure of the root system reflects the spatial branching status and complexity of the root system and the growth of roots in soil (Yang et al., 2015). The fractal dimension (FD) and the fractal abundance (FA) are important features of the root fractal structure. The FD of roots reflects the spatial distribution form, branching ability and degree of development of the root system (Walk et al., 2004) and directly affects its physiological function and soil resource utilization ability. Plant roots with high FD values usually encompass complex branches, relatively developed lateral roots, and a horizontal and diffuse root architecture (Cao, 2014). The FA of roots is closely related to the distribution density, expansion range and resource competitiveness of

roots in soil (Yang et al. 2009). The greater the FA value is, the greater the degree of taproot development and the larger the root distribution range are, i.e., the higher the support, transportation system and space occupancy capacity levels of plants are (Li et al. 2018; Ren et al. 2020). The root distribution is localized, and it exhibits multifractal characteristics. Traditional fractal analysis only facilitates the characterization of the overall root morphology, but it is difficult to distinguish roots with similar FD levels but different morphological characteristics (Ketipearachchi & Tatsumi, 2000; Izumi & Iijima, 2002). Multifractal analysis can be used to identify and characterize root systems with similar FD values but different forms and increase the ability to identify similar but slightly different roots. Moreover, multifractal analysis can be used to determine the complexity, uniformity and symmetry of the plant root distribution (Ketipearachchi & Tatsumi, 2000), which is helpful for understanding the functional differences and growth strategies of plant roots under heterogeneous environmental conditions. The combination of global fractal and multifractal analysis approaches can help increase the understanding of the root configuration strategies adopted by plants in response to heterogeneous environmental conditions and the differentiated root morphology and spatial distribution patterns caused by changes in local environmental conditions. At present, studies on the overall fractal characteristics of plant roots have focused mainly on *Melica przewalskyi* in alpine grasslands (Song et al., 2015), *Kobresia tibetica* in alpine meadows (Wang et al., 2023), *Elymus nutans* in wetlands (Li et al., 2018), *Agriophyllum pungens* in oasis desert ecotones (Ren et al., 2020) and *Saussurea salsa* in inland saltwater marshes (Li et al., 2022). However, few studies have been conducted to investigate the habitation-dependent mechanism controlling the plant root configuration on the basis of the combination of global fractal and multifractal analysis approaches.

Deserts are some of the most vulnerable ecosystems with harsh ecological environments and limited plant species (Scarrow, 2020; Zhao et al., 2023). The oasis desert ecotone is a habitat transition zone and a high-biodiversity area (Shan et al., 2004). The diversity of microenvironments, as manifested in varying site conditions including the soil water content, soil bulk density (SBD), soil compactness and soil porosity, in this region results in obvious differences in physical and chemical properties, which profoundly affect the structure of vegetation communities and intraspecies and species relationships, forcing plants to adjust the allocation of aboveground and subsurface resources (Hovenden et al., 2014). To increase habitat fitness (Li et al., 2011), the root system is commonly established according to the community environment and resource competition pattern (Huang et al., 2015). Therefore, studying the habitat-dependent mechanism controlling desert plant root configurations under different site conditions in the oasis desert ecotone is important for exploring the phenotypic plasticity of desert plant roots and ecosystem protection under heterogeneous habitat conditions.

Agriophyllum pungens is an annual shallow-rooted herbaceous plant that grows mainly on various types of sandy surfaces in arid and semiarid areas. It is an important wind- and sand-resistant plant. At present, relevant studies have focused mainly on the spatial distribution and allometry (Jia et al., 2015; Han et al., 2024), population dynamics (Ma et al., 2021), phenotypic plasticity (Yi et al., 2016), stoichiometric characteristics (Su et al., 2022), seed bank (Zhao et al., 2022; Liu et al., 2024), germination characteristics (Liu et al., 2024), and overall fractal characteristics of *A. pungens* (Ren et al., 2020).

However, from a fractal geometry perspective, few studies have been conducted to examine the habitation-dependent mechanism underlying the plant root architecture by combining global fractal and multifractal analysis approaches. In particular, the multifractal characteristics of *A. pungens* roots under the influence of microtopography remain unclear. Given these findings, the overall fractal and multisufficiency characteristics of the root system of *A. pungens* in three habitats, namely, an interdune lowland area, a gentle sand slope area and a slope top flat area, were studied. We hypothesized that the biomass distribution and the morphology and configuration of the roots of desert plant *A. pungens* would vary in the different habitats but that the global fractal characteristics would not change significantly, showing multiplicity. Therefore, this study aimed to solve this problem from a multifractal analysis perspective: (1) What are the changes in root biomass allocation and the root morphology of *A. pungens* in the different habitats? (2) How do the global fractal and multifractal characteristics of the root system vary among the different habitats? This study aimed to explain the response mechanism of the root system configuration to varying habitats from the perspective of the fractal characteristics of the root system.

Materials and methods

Study sites

The study site is located in the oasis–desert transition zone of Jin Chang city, Jinchuan District, Gansu Province, China (102°27.15'~102°28.86' E, 38°38.50'~38°39.71'N; Fig. 1). It is located in the eastern section of the Hexi Corridor in Gansu Province, at the northern foot of the East Mountain branch of Longshou Mountain, at the southern edge of the Alashan platform and Badain Jaran Desert, and at the middle of Jinchuan District in Jinchang city, adjacent to the ancient channel of the Jinchuan River. The study area exhibits a continental temperate monsoon climate with typical characteristics of arid regions in Northwest China. The average altitude is 1478 m, with an annual average temperature of 9.4 °C, an annual average precipitation of 119.5 mm, an annual total evaporation of 2575.2 mm, abundant sunshine, little rainfall, and high evaporation. The main soil types are meadow soil, tidal soil, aeolian sand soil, swamp soil and peat soil. Primarily desert vegetation occurs in this area, and the main plants are *A. pungens, Nitraria tangutorum, Haloxylon ammodendron, Halogeton arachnoideus, Echinops gmelinii*, *Salsola collina* and *Grubovia dasyphylla*.

Experimental methods and design

From 15 to 27 August 2023, on the basis of field investigations, a research transect measuring 500 m in length and 200 m in width was arranged from east to west in an oasis desert ecotone in Jinchuan District, Jinchang city, Gansu Province, which exhibits limited human intervention and contains three distinct habitat types. Notably, the transect was divided into three plots according to the change in terrain morphology (Fig.1; Ren et al. (2020)). Plot I (an interdunal depression (ID) area) was less affected by wind and sand movement, belonged to the catchment area, and exhibited high vegetation coverage. The main plant species were *Haloxylon ammodendron*, *Nitraria tangutorum*, *Grubovia dasyphylla* and *A.*

pungens. Plot II, which occurs in an area with a gentle sand slope (GS) and a moderate vegetation coverage, largely contained *Halogeton arachnoideus*, *A. pungens*, *Haloxylon ammodendron* and *Nitraria tangutorum*. Plot III, which occurs at the slope crest (SC), was notably affected by wind and sand movement and contained sparse vegetation. The main plant species were *A. pungens*, *Salsola collina* and *Halogeton arachnoideus*, which are annual plants.

On the basis of the population gradient of *A. pungens* at the sample site, six 2 m × 2 m quadrats were established per plot, for a total of 18 quadrats. The community traits (height, coverage and aboveground biomass) were determined. A total of 6 well-growing *A. pungens* plants were selected from each quadrat. After the measurement of the plant height, the aboveground parts were removed and placed in numbered envelopes. The root system of each *A. pungens* plant was completely excavated after measuring the root depth and branch angle via the trench method and the whole-root excavation method, respectively (Böhm, 1979; Li et al., 2022). The roots were placed on a mesh screen (aperture = 0.25 mm), and water from an adjacent source was used to remove soil and debris attached to the roots. The soil was placed in a numbered self-sealing bag, and the roots were transported to the laboratory together with the aboveground parts to measure the biomass and other traits. Finally, the aboveground parts of all the plants from each plot were cut and transported to the laboratory. The aboveground biomass in each plot was obtained after drying the samples in an oven at a temperature of 80 °C for 48 h.

Measurement of the root morphological characteristics and organ biomass of A. pungens

Measurement of the fractal characteristics of A. pungens roots

(1) *Global fractal analysis of A. pungens roots*

The sampled roots of *A. pungens* were analysed with WIN-Rhizo (Pro 5.0) software (Regent Instrumentation, Canada), thereby employing squares with a side length of r, and the number of squares containing roots in the root distribution maps of each plot was counted. As the side length r of the squares decreased, Nr (i.e., the number of squares cut by the root system) gradually increased. After obtaining the Nr values at different levels of r, a graph was created with lgr and lgNr as the abscissa and ordinate, respectively. The equation of the regression line is lgNr = -FDlgr +lgK. In this equation, FD is the fractal dimension, and lgK is the FA (Ketipearachchi & Tatsumi, 2000). For r=1, the maximum FA value is obtained, namely, lgNr =lgK, with FD=0. In this case, there is no branching, which does not occur in practice.

(2) *Multifractal analysis of A. pungens roots*

Multifractal analysis of *A. pungens* roots was performed via the ImageJ-Fiji Fraclac plugin (Karperien, 2013), and the parameters f and Hausdorff dimension of the multifractal singularity spectrum and the Rényi spectrum were obtained. Moreover, α is the Holder index, Dq is the generalized FD, q is the quality index, D0 (q=0) is the capacity dimension (the box count dimension), D1 (q=1) is the entropy dimension

(the information dimension), and D2 (q=0) is the correlation dimension (Fig. 2). The width of the singularity spectrum represents the complexity and symmetry of the distribution of the study object, and the wider the singularity spectrum is, the more complex the root system of the plant and the lower the symmetry (Soto-Gómez et al., 2020).

The calculation equations are as follows:

$$D_q = \frac{1}{q-1} \lim_{\varepsilon \to 0} \frac{\log(\mu(q,\varepsilon))}{\log \varepsilon} \quad (7)$$

$$f(\alpha(q)) = q\,\alpha(q) - \tau(q) \quad (8)$$

$$\alpha(q) = \frac{d\tau(q)}{dq} \quad (9)$$

Notably, Dq, i.e., the generalized FD, usually conforms to the multifractal object and gradually decreases with increasing q (Lafond et al., 2012). In general, the Dq value increases with increasing root complexity (Ge et al., 2015). A positive q value indicates a denser region, whereas a negative q value indicates a sparser region. Moreover, τ(q) is the correlation index of order q, and α is the Holder index. For q=0, α0, f(α) reaches its maximum value.

Measurement of the soil moisture content, soil bulk density and soil compactness

During the community survey, the soil compactness in each plot was measured with an SC-900 soil compactness meter (Spectrum, America), and the measurements were repeated 3 times. Soil samples were randomly collected from the 1 m × 1 m × 0.5 m (length × width × depth) soil profile using a ring knife (200 cm^3). During the experiment, the roots of *A. pungens* were distributed mainly in the 0–30 cm soil layer, whereas no roots were observed below 30 cm. Five soil layers, at depth intervals of 10 cm, were sampled, with three replicate samples per layer. The replicate soil samples were mixed while fresh and then dried in an oven at a temperature of 105 °C for 12 h. The soil moisture content (SMC) and SBD were calculated for each soil layer. The SBD (ρb) can be obtained as Ms/Vs, where Ms is the weight of the soil sample after drying, and Vs is the ring knife volume.

Statistical analysis

All the original experimental data were sorted in Microsoft Excel 2021, and the root–shoot ratio (RSR), stem mass ratio, leaf mass ratio and root mass ratio of *A. pungens* were calculated. The biological traits and soil properties of the plant communities in the three habitats were statistically analysed. One-way analysis of variance (ANOVA) was employed to compare the root morphological traits and fractal features, organ biomass values, and population traits of *A. pungens* among the different habitats (α = 0.05). Finally, a multifractal analysis of *A. pungens* roots was performed through the ImageJ-Fiji Fraclac plugin. All charts of the experimental data were created via Origin 2022 and R 4.0.2.

Results

Soil characteristics of each habitat

With the change in habitat from interdunal depression area I to slope crest area III, the SMC, soil compaction and SBD decreased by 59.15%, 50% and 25.40%, respectively (Fig. 3 and Supplementary Table 1)

Biological characteristics of the community in each habitat

With the change in habitat conditions from interdunal depression area I to slope crest area III, the average community height, coverage and density decreased by 47.81%, 34.24% and 55.58%, respectively. Moreover, the main species gradually changed from *Nitraria tangutorum, Haloxylon ammodendron,* and *A. pungens* to A. pungens and Salsola collina (Table 1).

Table 1 Biological characteristics of the communities in each habitat (mean ± standard error (*SE*))

Plot	AH /cm	Coverage/%	Density/strain.m^2	Main species
I	16.21 ± 0.24	24 ± 0.79	17 ± 0.76	*Nitraria tangutorum, Haloxylon ammodendron, A. pungens*
III	9.05 ± 0.17	21 ± 0.95	12 ± 0.70	*Haloxylon ammodendron, A. pungens, Halogeton arachnoideus*
III	8.46 ± 0.31	16 ± 0.56	7 ± 0.42	A. pungens, Salsola collina

The different lowercase letters in the same column indicate significant differences among the various plots ($p < 0.05$). I, interdunal depression area; II, gentle sand slope area; III, slope crest area. *AH*, average height.

Characteristics of the A. pungens *population*

With the change in habitat from interdunal depression area I to slope crest area III, the average height of the A. pungens population decreased by 52.22%. The root depth, RSR and root coverage first gradually increased and then increased 1.30, 0.79 and 0.40 times, respectively (Fig. 4 and Supplementary Table 2).

Comparisons of the stem biomass fraction, leaf biomass fraction and root biomass fraction in different habitats of A. pungens

Under the different habitat conditions, the organ biomass proportions of *A. pungens* significantly differed ($P < 0.05$, Fig. 5). With the change in habitat from interdunal depression area I to slope crest area III, the root biomass percentage (PRB) significantly increased ($P > 0.05$), namely, it increased from 21% in interdunal depression area I to 37% in slope crest area III and gentle sand slope area II; the stem biomass percentage (PSB) of *A. pungens* significantly decreased ($P < 0.05$), namely, the value decreased from 44% in interdunal depression area I to 27% in slope crest area III. Moreover, the leaf biomass percentage (PLB) first increased but then decreased.

Main morphological characteristics of A. pungens in each habitat

With the change in habitat from interdunal depression area I to slope crest area III, the root length, root surface area and specific root length all increased, namely, they increased 4.82, 4.36 and 0.48 times, respectively (Table 2). The root diameter exhibited a decreasing trend and decreased by 10%. The plasticity index values of the main morphological characteristics of *A. pungens* indicated the descending order of the root length, root surface area, specific root length and root diameter.

Table 2 Main morphological characteristics of *A. pungens* in each habitat (mean ± SE)

Plot	I	II	III	Plasticity index
Root length/cm	29.65±0.79c	126.52±1.40b	172.76±1.63a	0.83
Root surface area/cm^2	6.29±0.15c	27.19±0.45b	33.69±0.68a	0.81
Root diameter/mm	0.7±0.01a	0.66±0.01b	0.63±0.01c	0.1
Specific root length/$cm.g^{-1}$	281.83±7.03c	320.98±6.29b	417.39±10.31a	0.32

The different lowercase letters in the same column indicate significant differences among the various plots ($p < 0.05$). n=36. I, interdunal depression area; II, gentle sand slope area; III, slope crest area.

Characteristics of the fractal dimension and fractal abundance of A. pungens roots in each habitat

With the change in habitat from interdunal depression area I to slope crest area III, the one-way ANOVA results revealed significant differences in the FA values of *A. pungens* roots ($P < 0.05$, Fig. 6), but no significant differences in the overall FD values were observed ($P > 0.05$, Fig. 6). From interdunal depression area I to slope crest area III, the FA displayed increasing trends and ultimately increased 0.26 times. However, the FD increased by only 2.0%. Therefore, it is necessary to analyse the fractal characteristics of the root system through multifractal analysis.

Characteristics of the singularity spectra of A. pungens roots in each habitat

With the change in habitat from interdunal depression area I to slope crest area III, the multifractal characteristics of the singularity spectra of *A. pungens roots* significantly differed ($P < 0.05$; Fig. 7 and Supplementary Table 3). The average width of the singularity spectrum of *A. pungens* roots demonstrated the order of Plot III > Plot I > Plot II, indicating that the roots became increasingly complex and asymmetrical with the change in environmental conditions from interdune lowland area I to windward slope area III (Fig. 7 and Supplementary Table 3).

Characteristics of the Rényi spectra of A. pungens roots in each habitat

With the change in habitat from interdunal depression area I to slope crest area III, the multifractal characteristics of the Rényi spectra of *A. pungens roots* significantly differed ($P < 0.05$, Fig. 8 and

Supplementary Table 3). The D(Q) spectral width of the Rényi spectra of *A. pungens* roots decreased in the order of Plot II > Plot III > Plot I (Fig. 8, S Table 3), indicating that the uniformity of the distribution of *A. pungens* roots decreased with changes in environmental conditions.

Discussion

The root system architecture (RSA) describes the shape and spatial arrangement of roots in soil (Rogers and Benfey 2015) and governs the absorption and transportation of water and nutrients (Bisht et al., 2019). The RSA is very sensitive to the soil chemical and physical properties (Correa et al. 2019; Hodge 2004). Fractal characteristics are important characteristics of the root configuration and directly reflect the spatial expansion ability and resource utilization efficiency of plant roots. In this study, the FA of *A. pungens* roots gradually increased, the multifractal singularity spectral width decreased, and the Rényi spectral width increased with the change in habitat conditions from interdunal depression area (I) to slope crest area (III). The distribution of roots was simple, and the uniformity and symmetry of roots increased (Figs. 6–8).

Fractal analysis of the response of the A. pungens root architecture in the interdunal depression area

The root system configuration determines the ability of plants to absorb and transport water and nutrients (Rubio et al. 2001, Wang et al., 2019). Fractal analysis is an effective tool for studying the geometric feature changes and spatial branching state of the root structure in heterogeneous habitats and quantitatively represents a series of regularly changing root resource trade-off strategies, which is helpful for increasing the understanding of plant adaptation mechanisms to heterogeneous environments (Li et al., 2022). The study area belongs to the oasis desert ecotone, which is affected by wind and sand movement throughout the year and has developed desert plants such as *Nitraria tangutorum*, *Haloxylon ammodendron* and *A. pungens*. The height, coverage and density of the plant communities in the interdunal depression area (Plot I) were the highest, and the competition for resources within the community was intense (Table 2). The level of soil moisture was sufficient, and the maximum soil compactness and bulk density occurred (Fig. 2 and Supplementary Table 1). The population density of *A. pungens* was the lowest, while its height was the greatest (Fig. 3 and Supplementary Table 2). To avoid shading from neighbouring larger plants and to acquire more light resources, a greater amount of biomass was allocated to the growth of aboveground stems and leaves (Fig. 4). Under the condition of limited underground investment, a dense root system construction pattern characterized by minimal RSR and root depth values was established (Fig. 3 and Supplementary Tables 2 and 3), resulting in a complex and uneven distribution of roots with low symmetry (Figs. 5 and 6). The reasons are as follows: On the one hand, *A. pungens* exhibited limited vertical root expansion, and roots were concentrated in the surface soil layer (0–15 cm). In this habitat, the RSA, total root length (TRL), root surface area, and specific root length were the smallest (Table 3), and the FA of roots decreased (Fig. 5). This is conducive not only to narrowing the spatial distribution range of roots and reducing the resource inputs of root support and transport systems but also to decreasing the intensity of resource competition among roots and shortening the transport distance of root water, which helps to

optimize the relationship between root water and the nutrient absorption capacity and carbohydrate consumption levels (Ma, 2008). On the other hand, the level of soil moisture in this habitat was sufficient, and the RSR was minimal. In the case of a limited underground biomass, *A. pungens* uses more of its biomass to increase the number of lateral roots. The establishment of complex root configurations helps increase the soil porosity and maintain the effective transport of soil nutrients and gases between plant roots, thereby increasing population fitness (Chen et al., 2016). Compared with other desert plants such as *Nitraria tangutorum* and *Haloxylon ammodendron*, *A. pungens* not only enhances the soil adsorption capacity and resource extraction ability of its root system but also enhances the efficiency of nutrient absorption by the root system, ensuring high interspecific competition and normal plant growth (Forde & Lorenzo, 2001; Hodge, 2004). As an annual herbaceous plant, *A. pungens* is highly dependent on soil moisture, SBD, compaction and other soil physical properties. The field investigation results revealed that the interdune lowland area exhibited relatively high vegetation abundance and SBD levels, and soil was relatively compact (Fig. 2 and Supplementary Table 1). The soil moisture was mostly present in the soil surface layer. *A. pungens* allocated limited underground resources to the development of lateral roots for growth and reproduction, thereby increasing the number of fine roots and the FD, expanding the distribution of fine roots within a limited range, and increasing root overlap, thus establishing a complex root system with low symmetry and uniformity (Figs. 6 and 7). This could ensure that the normal demand of roots for nutrients is satisfied. Therefore, in the interdunal depression area, *A. pungens* exhibited the lowest RSR, the FA decreased, and a complex and compact root system with low symmetry uniformity was established, which are strategies aiming to increase population competitiveness and resource acquisition efficiency. This reflects the ecological adaptation mechanism of desert plants to form a root configuration system suitable for their habitat by adjusting root canopy biomass allocation.

Fractal analysis of the response of A. pungens root architecture in the slope crest area

Both leaves and roots regulate the uptake of essential above- and belowground resources by plants, and basic distributional trade-offs occur within plants (Weigelt et al. 2021; Ma et al. 2022). The root mass fraction is the relative investment of biomass in a specific subsurface portion and is a key feature in determining plant performance (Wilson, 1988; Poorter et al., 2012). Changes in the aboveground biomass also affect the root distribution and morphometric parameters (Tripolskaja et al., 2024). Owing to differences in the soil environment, the plant root distribution is often localized, i.e., it exhibits multifractal characteristics. The complexity, uniformity and symmetry of the plant root distribution can be effectively determined via multifractal analysis (Ketipearachchi & Tatsumi, 2000). Compared with the interdunal depression area, the slope crest area exhibited the smallest plant community height, coverage and density (Table 2) and the lowest interspecific competition. Moreover, the soil density, compactness and moisture in this habitat were the lowest (Fig. 2 and Supplementary Table 1), which does not facilitate the growth of desert shrubs such as *Nitraria sibirica* and *Haloxylon ammodendron*, and the interspecific competition of annual *A. pungens* was reduced. The height was the smallest, but the coverage was the highest (Fig. 2 and Supplementary Table 2). To increase the ability to obtain water resources, *A. pungens* increased the vertical resource input of roots and limited the resource input of the aboveground parts.

Driven by the foraging effect, a diffuse root construction model was established with the maximum RSR and root depth values (Fig. 3 and Supplementary Tables 2 and 3). Root systems are typically simple and evenly distributed, with increased symmetry (Figs. 6 and 7). The reasons are as follows. On the one hand, the slope crest area contains mainly aeolian sandy soil with low bulk density and compactness, poor soil quality and low water holding capacity. Affected by aeolian sand, surface soil water evaporates quickly, whereas deep soil water evaporates slowly. By increasing the FA of roots in the slope crest area, *A. pungens* aims to increase the distribution range of roots and the soil space occupied by unit roots, thereby enhancing the support and transport functions of *A. pungens* roots, increasing the absorption range of soil water and nutrients by roots, and alleviating soil water stress. On the other hand, in the case of limited resources, *A. pungens* reduces the biomass allocation to stems and leaves above ground and increases the biomass allocation to roots. The root mass fraction, TRL, RSA, and specific root length (SRL) of *A. pungens* were the greatest in the slope crest area (Fig. 4 and Table 4). When the underground biomass remains constant, an increase in the FA of the root system (Fig. 5) encourages *A. pungens* roots to move away from the soil surface layer, which contains a low water content, towards deep soil, thereby increasing the utilization space of water and nutrients (Li et al., 2022). In addition, the soil in this habitat was dominated by silty soil with minimal bulk density and compactness values (Fig. 2 and Supplementary Table 1), which is conducive to *A. pungens* forming a relatively simple, evenly distributed and highly symmetrical root system. Therefore, the increased FA of *A. pungens* in this habitat, the simple and uniform distribution of roots, and the increased symmetry are the results of the long-term adaptation of this annual plant in the oasis desert zone. This conclusion is consistent with the conclusions of relevant scholars that increasing the FA of roots can increase the space for root expansion and the ability of roots to absorb soil resources in arid areas (Wang et al., 2008; Shan et al., 2013).

Fractal analysis of the response of A. pungens root architecture in the gentle sand slope area

The pattern of resource allocation at the plant component level is the result of the long-term adaptation of plants to the habitat environment. The root system is an important organ through which plants obtain underground resources. Its structure and function are closely related to the process of controlling plant absorption of water and nutrients from the soil and the assimilation, distribution and release of carbon into the soil (Pierret et al., 2016; Yanget al., 2016; Warrenet al., 2015; Paungfoo-Lonhienne et al., 2013). Root system plasticity contributes to plant performance through the optimization of belowground resource foraging (Traboulsi et al., 2024). In gentle sand slope area II, the height, coverage and density of the plant communities occurred between those in interdunal depression area I and slope crest area III (Table 2), and the degree of interspecific competition was slightly reduced. The SMC, soil compactness and SBD were lower than those in Plot I (Fig. 2 and Supplementary Table 1). The height, density, RSR and root depth of the *A. pungens* population in this habitat were all between those of Plots II and III (Fig. 3 and Supplementary Table 2). To adapt to the existing living environment, *A. pungens*, by balancing the biomass allocation to aboveground stems and leaves and underground roots, achieved synergistic changes in root geometry and fractal structure and rationally invested the limited resources in root support, transport and absorption structure establishment. The FA of the root system was between

those of Plots I and III, with no significant change in the FD (Fig. 5), and a root system adapted to the habitat was produced. Therefore, the gentle sand slope area was an area where the FA of *A. pungens* roots gradually increased, and this habitat was a transition area from a complex uneven distribution of *A. pungens* roots with low symmetry to a simple uniform distribution with high symmetry. Its RSA belongs to the transition type from a compact to diffuse architecture.

Conclusion

The diversity of resources and environments required for plant survival results in changes in the plasticity of the plant root architecture. The differences in the overall fractal and partial morphological characteristics of plant roots reflect the survival strategies of plants in heterogeneous habitats. In this study, in the interdunal depression area, *A. pungens* reduced the FA of its roots, established a compact root architecture with high complexity, low uniformity and low symmetry and achieved high soil resource utilization efficiency. These are effective strategies for *A. pungens* to increase interspecific competitiveness. In the slope crest area, *A. pungens* increased the FA of its roots and developed a simple, homogeneous and symmetrical diffuse root architecture with high expansion ability, which is a survival strategy aimed at coping with the oasis desert habitat. This reflects the ecological adaptation strategy of oasis desert plants to maintain survival, growth and reproduction by effectively balancing the allocation of the plant root canopy biomass and realizing coevolution of the root geometry and fractal structure in harsh habitats. From the perspective of fractal characteristics, the responses of the root FD, FA and multifractal spectrum to the varying habitats were investigated by analysing the biomass distribution and geometric parameters of roots. The root topology and other root traits also play crucial roles in managing soil organic matter, texture and nutrient differences, which will be studied in the future.

Declarations

The manuscript has been approved by all authors. I would like to declare on behalf of my co-authors that the work described was original research that has not been published previously, and not under consideration for publication elsewhere, in whole or in part. All the authors listed have approved the manuscript that is enclosed.

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Declaration of Competing Interests

The authors declare that there are no conflicts of interest.

Availability of data and material

The data used in the present work have been listed in the Supporting information.

Author's contributions

Qun Li (QL), Ma Min (MM), Cheng Z Zhao (CZZ), Wen Jun (WJ), and Bo Li (BL) conceived and designed the experiments. QL performed the experiments, analyzed the data and drafted the manuscript. QL and CZZ support in the funding acquisition, resources and critical revision of the article. QL and MM undertook the investigation and contributed the methodology. All authors reviewed and approved the final manuscript.

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Figures

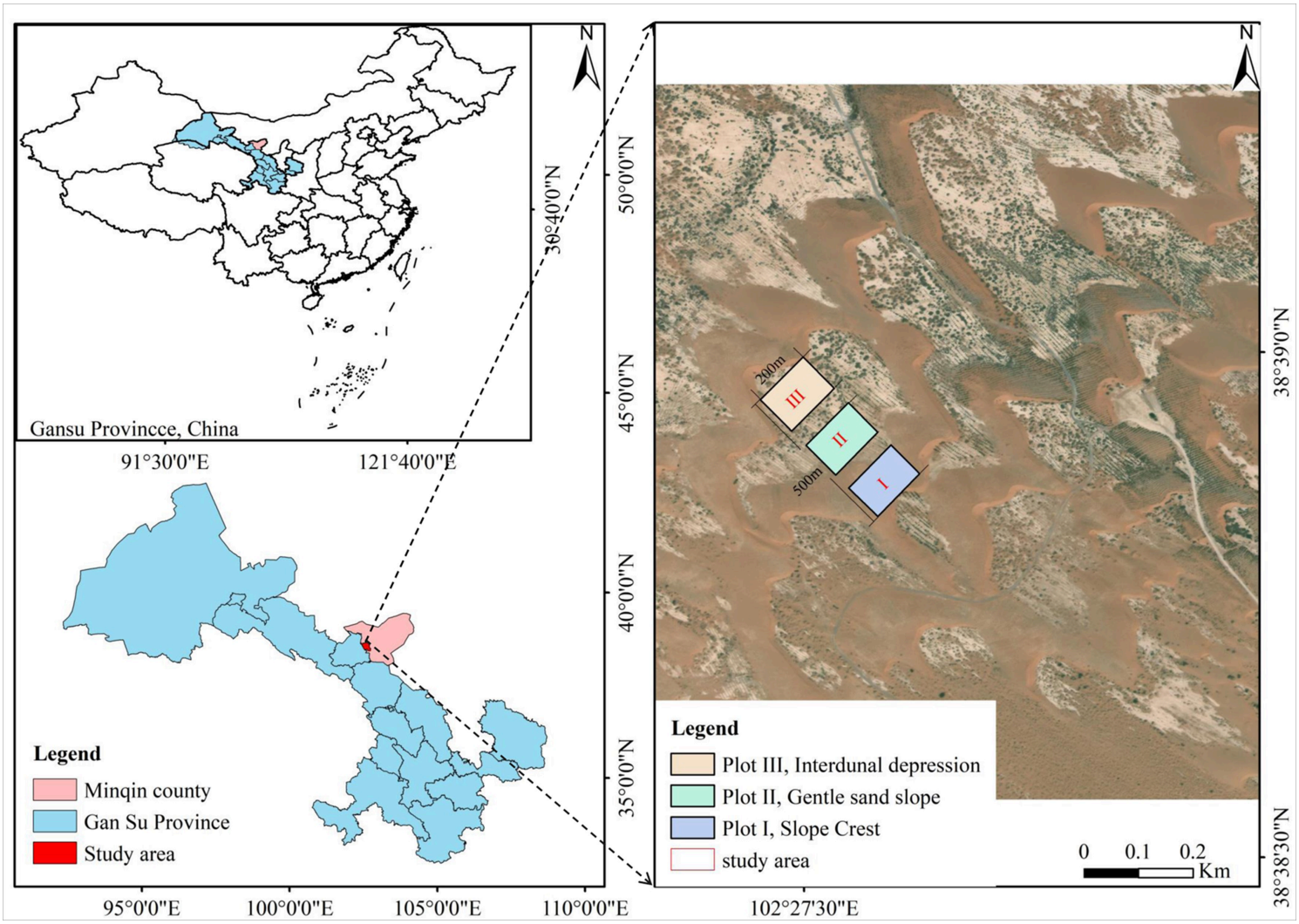


Figure 1

Study area and locations of the experimental plots

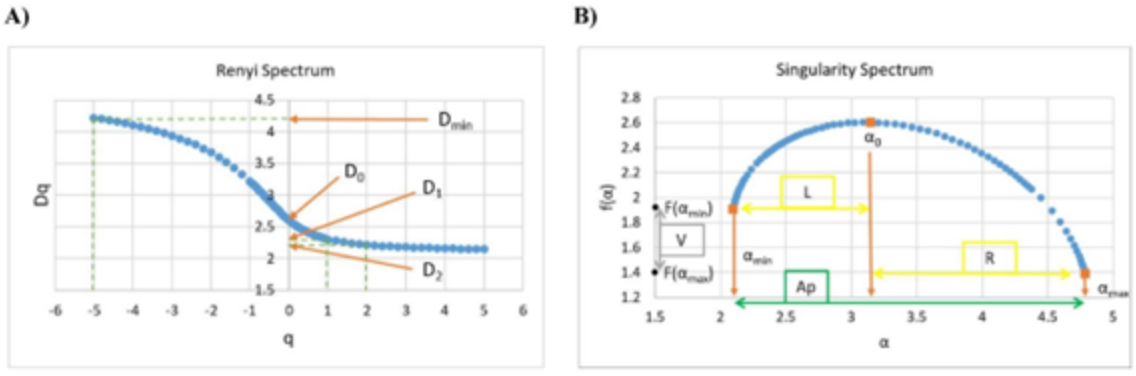


Figure 2

A) Example Rényi spectrum (q vs. D_q) and B) example singularity spectrum (α vs. f(α)).

Note: A) Example Rényi spectrum (q vs. Dq). The orange arrows indicate noteworthy values of the generalized dimensions: D_0 (D_q when q = 0), D_1 (D_q when q = 1), D_2 (D_q when q = 2), and D_{min} (D_q when q = -5). B) Example singularity spectrum (α vs. f(α)). The orange arrows indicate noteworthy values of α: α_0 (α when q = 0), α_{min} (α when q = +5), and α_{max} (α when q = -5). The green line denotes the total aperture of the spectrum (Ap), the yellow lines denote the apertures of the right (R) and left (L) branches, respectively, of the spectrum, and the grey line denotes the vertical symmetry of the spectrum (V). V is the difference between $f(\alpha_{min})$ (the value of f(α) when q = +5) and $f(\alpha_{max})$ (the value of f(α) when q = -5) (Soto-Gómez et al., 2020).

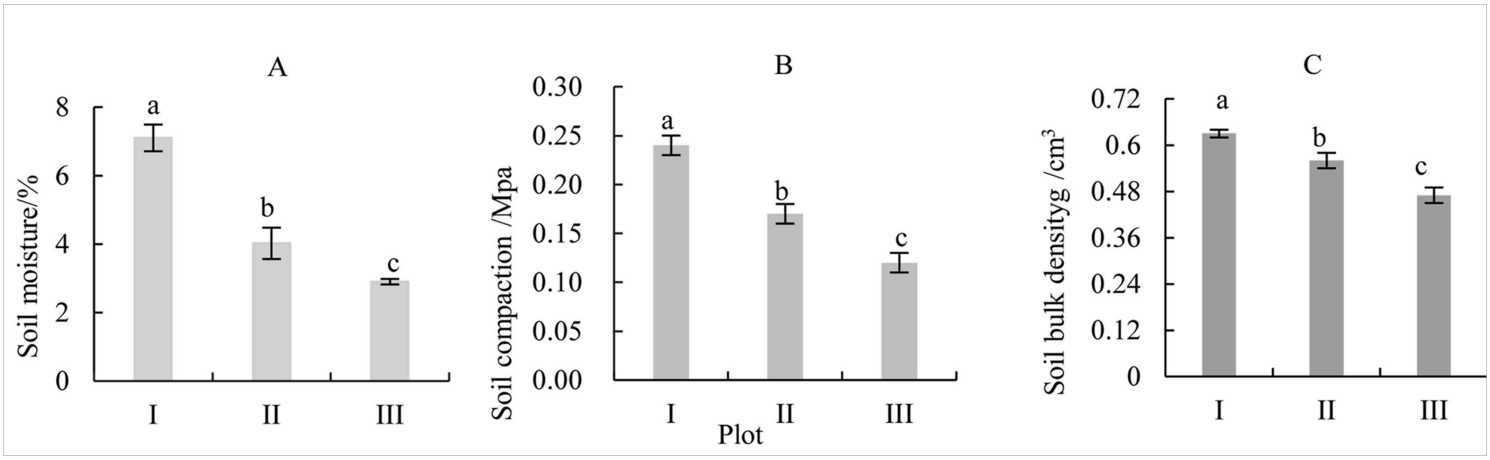


Figure 3

Soil characteristics of each habitat. I, interdunal depression area; II, gentle sand slope area; III, slope crest area. The different lowercase letters indicate significant differences among the various plots (P < 0.05).

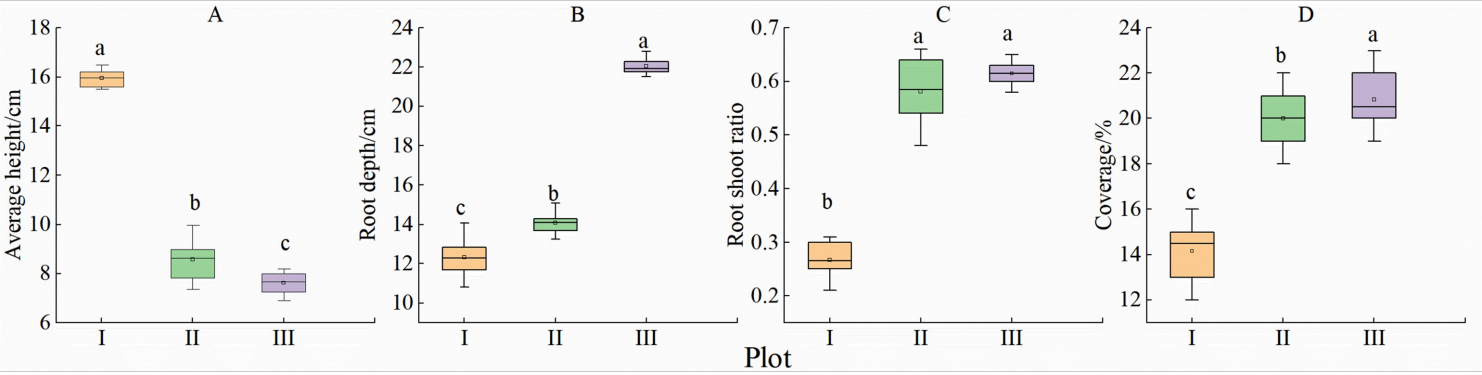


Figure 4

Characteristics of the *A. pungens*population in each plot. I, interdunal depression area; II, gentle sand slope area; III, slope crest area. The different lowercase letters indicate significant differences among the various plots (P < 0.05).

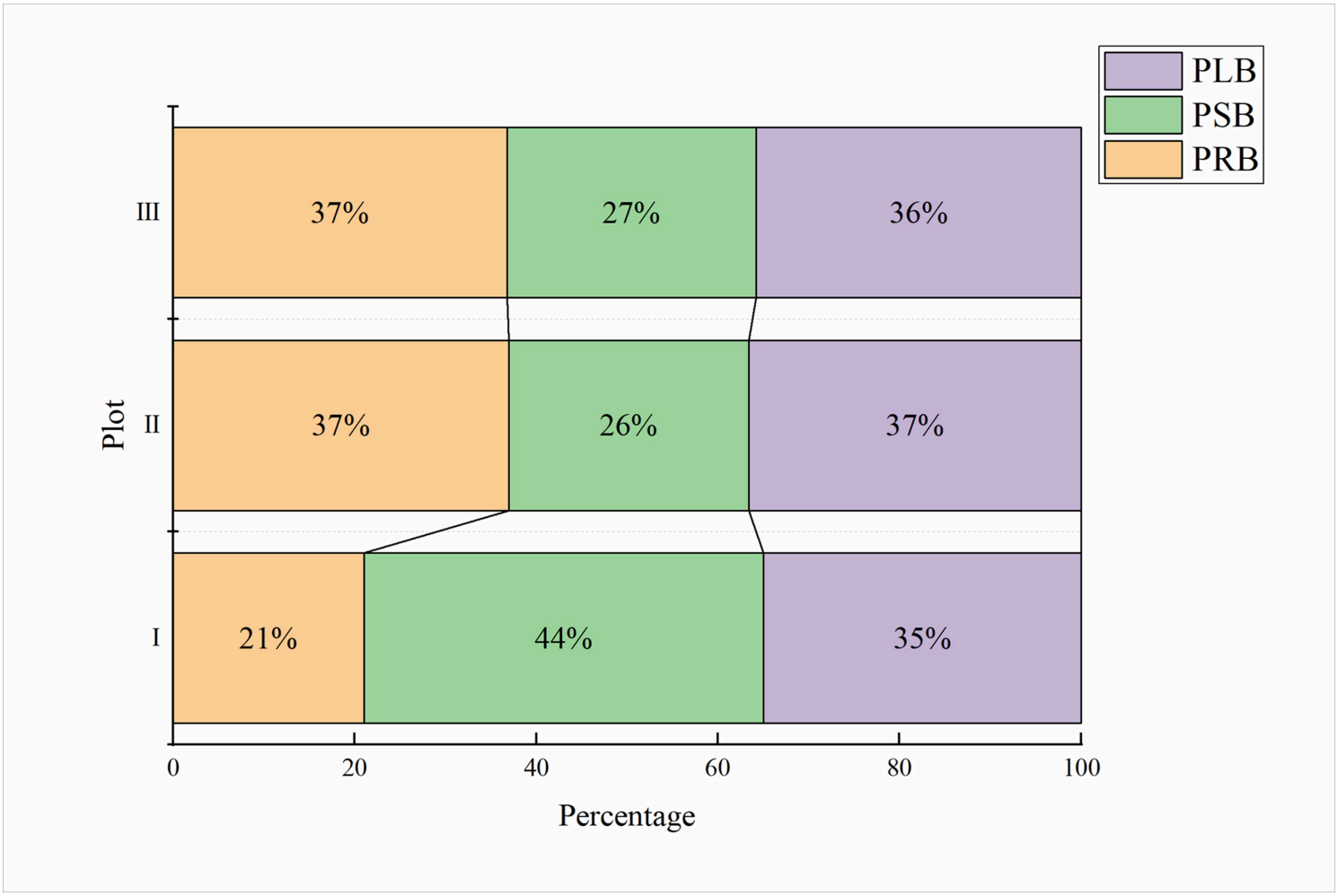


Figure 5

Comparisons of the shoot and root biomass fractions of *A. pungens* in the different habitats. I, interdunal depression area; II, gentle sand slope area; III, slope crest area. PSB, stem biomass percentage; PLB, leaf biomass percentage; PRB, root biomass percentage.

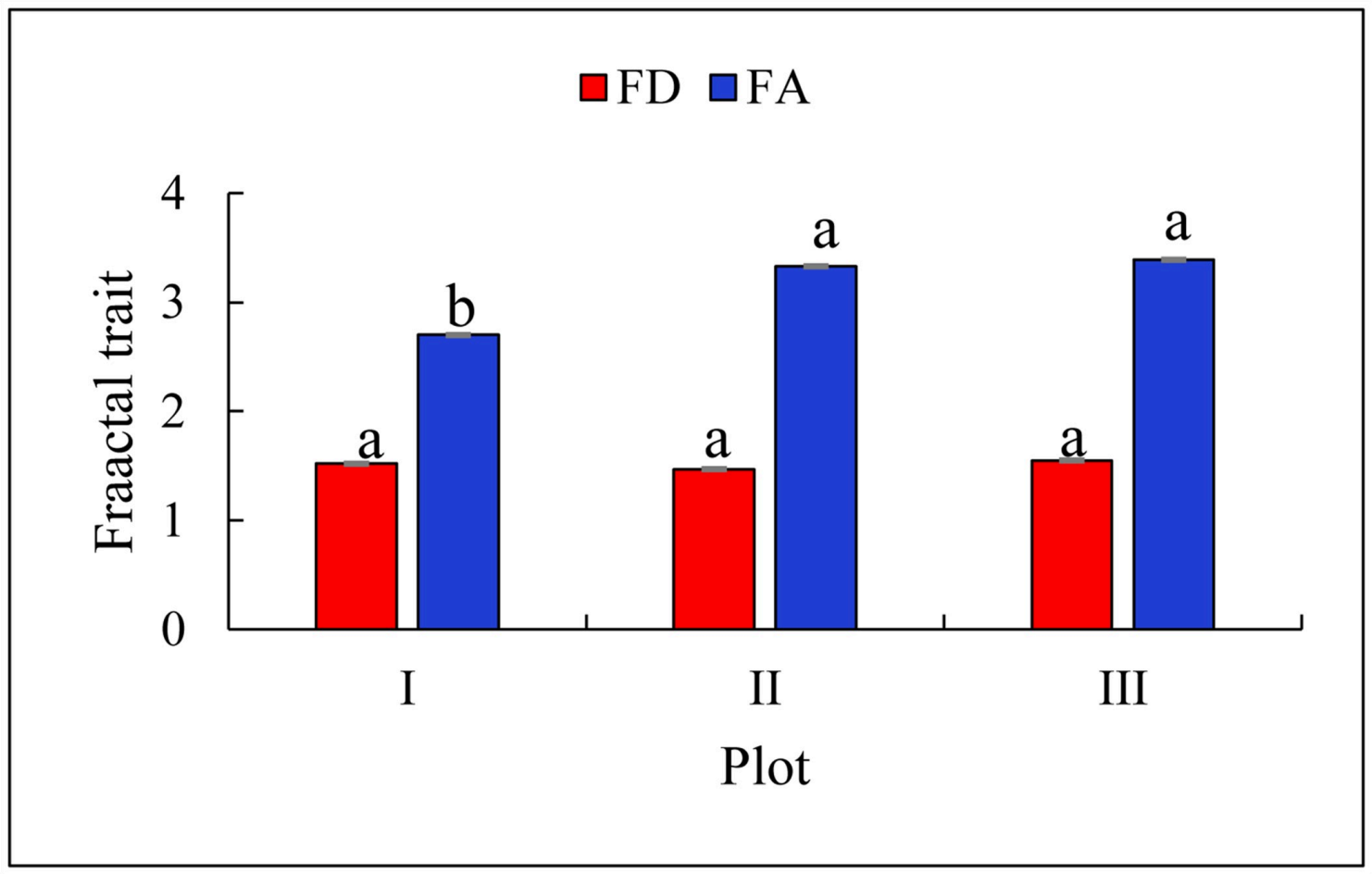


Figure 6

Fractal characteristics of the main plants in the different habitats. FD, fractal dimension; FA, fractal abundance. I, interdunal depression area; II, gentle sand slope area; III, slope crest area.

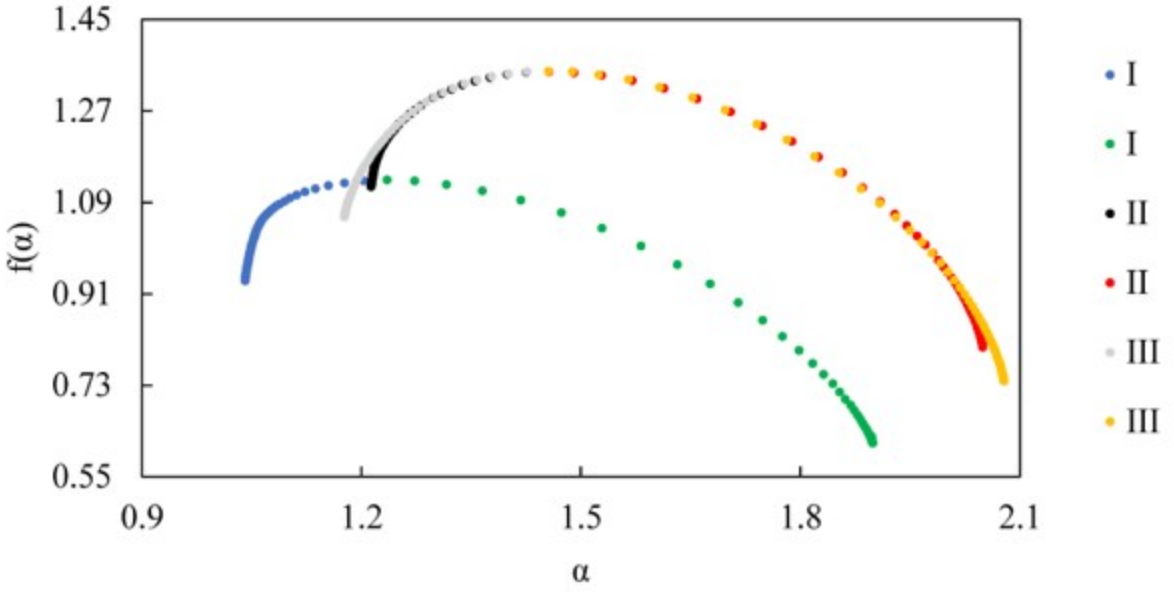


Figure 7

Characteristics of the singularity spectra of the main plants at different frequencies.

Note: f, Hausdorrf dimension; *a*, average singularity strength. I, interdunal depression area; II, gentle sand slope area; III, slope crest area.

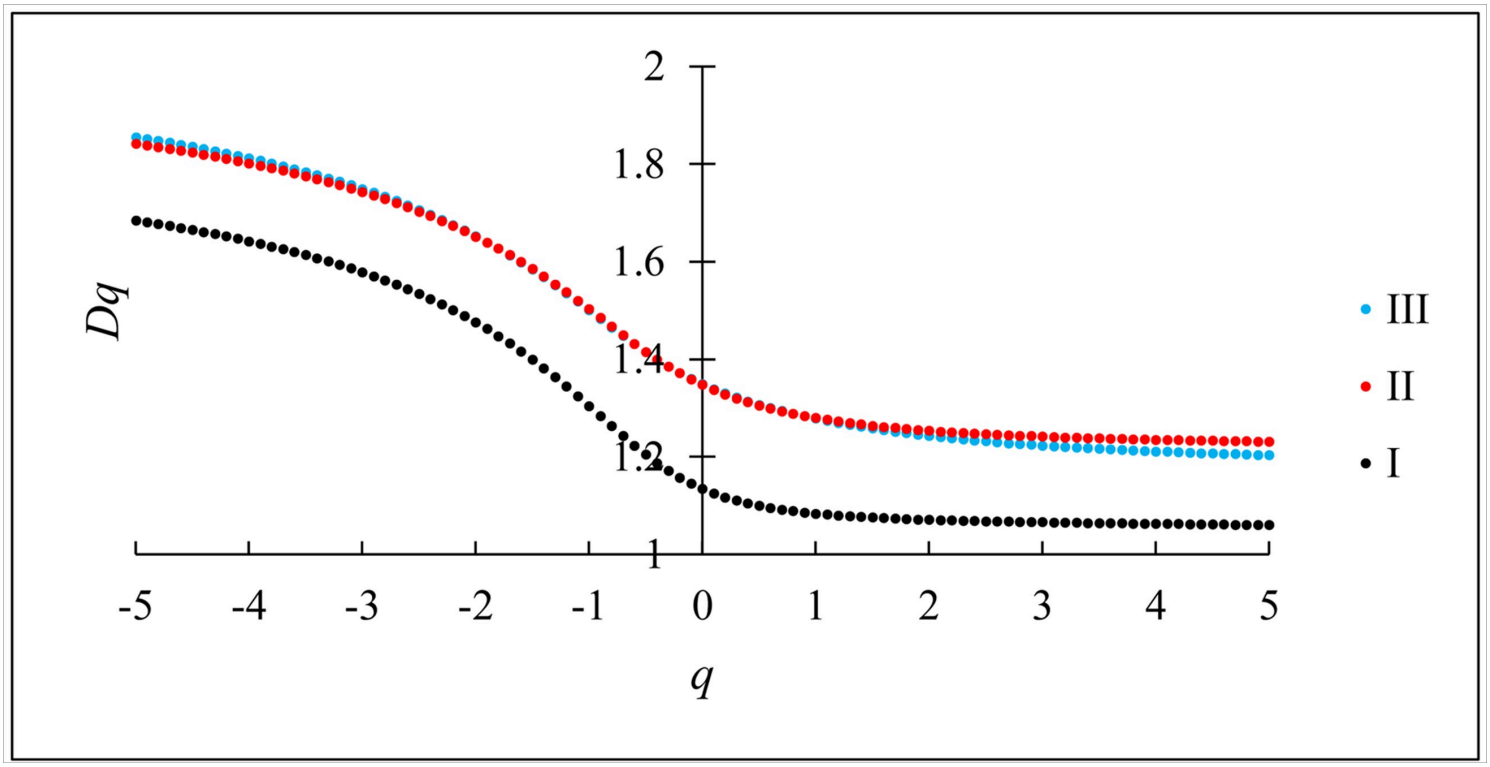


Figure 8

Characteristics of the Rényi spectra of the main plants in the different habitats.

Note: D(Q), generalized dimensions; Q, mass exponent. I, interdunal depression area; II, gentle sand slope area; III, slope crest area.

Supplementary Files

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