Competition, spatial pattern, and regeneration of Haloxylon ammodendron and Haloxylon persicum communities in the Gurbantunggut Desert, Northwest China Postprint

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Abstract

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Full Text

Preamble

Competition, Spatial Pattern, and Regeneration of *Haloxylon ammodendron* and *Haloxylon persicum* Communities in the Gurbantunggut Desert, Northwest China

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Abstract

Competition, spatial pattern, and regeneration are critical factors influencing community composition, structure, and dynamics. In this study, we surveyed 300 quadrats across three dune types (fixed dunes, semifixed dunes, and mobile dunes) in the Gurbantunggut Desert, Northwest China, from late May to early June 2021. Using the Hegyi competition index and point pattern analysis methods, we examined the intraspecific and interspecific competition, spatial patterns, and regeneration of *Haloxylon ammodendron* and *Haloxylon persicum*. The results revealed that the optimal competition distance for target trees in both communities was 6 m. The intraspecific and interspecific competition of *H. ammodendron* was greatest in fixed dunes, whereas the competition intensity of *H. persicum* was greater in semifixed and mobile dunes than in fixed dunes. Competition intensity across both species followed the order: seedlings > saplings > adults, decreasing gradually with increasing plant diameter. The spatial distribution patterns of all three life stages for both species were predominantly random, with no significant correlations between seedlings and saplings, adults and saplings, or seedlings and adults. The density of regenerated seedlings and saplings of *H. ammodendron* across the three dune types followed the order: fixed dunes > semifixed dunes > mobile dunes, while that of *H. persicum* followed the order: mobile dunes > semifixed dunes > fixed dunes. Therefore, when artificially planting these species for sand control, a spacing of 6 m is recommended, with seedlings planted adjacent to adults to minimize inter-plant competition and promote regeneration and ecosystem stabilization.

Keywords: competition; spatial pattern; regeneration; *Haloxylon ammodendron*; *Haloxylon persicum*; Gurbantunggut Desert

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1 Introduction

Competition occurs when two or more organisms vie for limited resources such as water, light, and nutrients to maximize individual growth and development at the expense of other species' resource availability (Craine and Dybzinski, 2013; Gao et al., 2017). In plant communities, populations experience both intraspecific competition from density pressure of conspecifics and interspecific competition from heterospecifics for environmental resources (Chen et al., 2018). These competitive interactions determine dynamic changes within plant populations, influencing individual growth, community structure, and succession processes. Competitive dominance often results in suppression of subordinate individuals, creating growth and developmental disparities (Xiang et al., 2015). When interspecific competition is weaker than intraspecific competition, each species more effectively limits its own population growth than that of its competitors (Adler et al., 2018).

In desert vegetation communities, shrub species exhibit clear advantages with relatively simple species composition (Ban et al., 2012; Niu et al., 2019). As a crucial community layer connecting tree and herb strata (He et al., 2011), studying competition dynamics in shrub communities helps elucidate vegetation stabilization mechanisms and self-organization processes. Previous research has shown that shrub-shrub competition interacts with soil characteristics to limit maximum shrub cover in the northern Chihuahuan Desert (Ji et al., 2019), while not necessarily limiting shrub proliferation during late-phase grassland-to-shrubland transitions (Pierce et al., 2019). Zhu et al. (2021) found intensified interspecific water competition after afforestation with *Robinia pseudoacacia* in native shrubland, recommending valley planting to avoid intense competition. Morcillo et al. (2022) observed no competitive effects between grasses and shrub seedlings on germination or survival.

Since the 1960s, scholars have employed various competition index models to study intraspecific and interspecific competition, including the Lotka-Volterra model (Sardar et al., 2016), improved Hegyi competition index (Long et al., 2020), and the Hegyi individual tree competition index (Chao et al., 2017). Among these, the Hegyi individual tree competition index effectively reflects resource demand and occupation by individual plants and is widely used. Studies have demonstrated its utility in controlling competition among trees in *Abies borisii-regis* forests (Alla and Pasho, 2015), revealing interspecific competition as the main source for endangered *Parrotia subaequalis* (Zhang et al., 2016), identifying competition as a driver of oak forest spatial distribution on the Loess Plateau (Kang et al., 2017), and showing interspecific competition dominance for *Acer catalpifolium* (Xu and Liu, 2018) and *Taxus chinensis* (Xu et al., 2020). These studies provide theoretical foundations for assessing community status and predicting population competition trends.

Population spatial pattern refers to the spatial distribution characteristics of individuals within a population, resulting from combined effects of population ecological traits, interspecific relationships, and organism-environment interactions (Dang et al., 2014). Spatial pattern analysis reveals fundamental population characteristics and underlying ecological processes (Yang et al., 2022), encompassing both spatial distribution patterns and spatial associations (Li et al., 2022). Distribution patterns reflect horizontal spatial relationships among individuals, influenced by biological characteristics, interspecific relationships, habitat conditions, and their interactions (Dale, 1999; Xia et al., 2016). Spatial correlation forms the basis of community formation and evolution, reflecting functional relationships among individuals of different ages constrained by natural resources (Gao et al., 2014).

Point pattern analysis is commonly used for plant population spatial distribution studies, determining population distribution states and examining interspecific relationships across scales while overcoming limitations of traditional quadrat sampling (Wu et al., 2019). In desert ecosystems, shrubs play vital roles in spatial pattern evolution and community succession dynamics. Studying desert shrub spatial patterns and associations helps understand species distribution characteristics and ecological functions while providing scientific bases for vegetation protection and development measures. Tirado et al. (2015) found that *Whitania frutescens* and *Maytenus senegalensis* benefit from their spatial relationship in arid ecosystems. Zhang et al. (2021) observed random and regular distributions of relict *Helianthemum songaricum* at most scales in gravel habitats but clumped distributions in rocky habitats. Zhang et al. (2022) discovered that grazing disturbance caused positive interspecific relationships at small scales that shifted to negative relationships as competition intensified.

Plant spatial patterns depend on internal characteristics, interspecific relationships, intraspecific interactions, habitat conditions, and competitive dynamics (Wang, 2019). Analyzing competition indices and spatial patterns of dominant desert tree species helps understand species status, community condition, and future development trends, thereby informing conservation strategies.

Natural regeneration enables ecosystem self-reproduction and restoration, maintaining community dynamic stability and sustainable utilization. It represents gradual recovery of pre-disturbance ecosystem structure, function, and composition (Chazdon and Guariguata, 2016). Plant regeneration is influenced by soil factors (Wang et al., 2017), stand characteristics (Zhu, 2021), stand age (Zhang et al., 2015), and habitat conditions (Hu et al., 2015). Tree age determines reproductive individual numbers and long-term ecosystem development (Sharma et al., 2016), with adequate seedlings and saplings indicating good regeneration capacity (Ali et al., 2019). Seedling and sapling regeneration represents a critical, vulnerable life stage with high mortality, significantly impacting population stability and community succession (D'Amato et al., 2009).

The Gurbantunggut Desert, located in the central Junggar Basin of Xinjiang Uygur Autonomous Region, is China's second-largest temperate desert with rich plant diversity. Human activities and natural disturbances have destroyed habitats, degraded vegetation, reduced species diversity, and impaired ecosystem functions, causing significant environmental and economic losses. *Haloxylon ammodendron* and *H. persicum* are the main constructive species in this desert, belonging to Chenopodiaceae with scale-like leaves and strong drought and salinity resistance. Listed as nationally third-level endangered protected plants (Dai et al., 2013), they play crucial roles in maintaining regional ecological balance and sustainable development. While research has focused on photosynthesis (Hu et al., 2021), drought resistance (He et al., 2021), population structure (Song et al., 2021), plant diversity (Zeng et al., 2016), seed germination (Tobe et al., 2000), and biomass (Xu et al., 2017), little is known about their competition, spatial patterns, and regeneration.

2.1 Study Area

The study area (44°10′–46°19′N, 84°31′–90°00′E) covers approximately 5.11$×10^{4}$ km^2 in the Gurbantunggut Desert, Xinjiang Uygur Autonomous Region, China. Dune types include fixed dunes, semifixed dunes, and mobile dunes, with fixed and semifixed dunes comprising 87% of the total desert area. Dune orientation varies roughly from northwest to southeast, with heights of 15–20 m (Li et al., 2021). Natural vegetation is dominated by small trees (*H. ammodendron* and *H. persicum* as dominant species), low semi-shrubs (*Ephedra distachya*), and herbaceous plants (*Erodium oxyrrhynchum*, *Hyalea pulchella*, *Ceratocarpus arenarius*, and *Salsola ruthenica*) (Zhang et al., 2022).

2.2.1 Data Collection

In 2021, we established three 100 m × 100 m sites (one each on fixed dunes, semifixed dunes, and mobile dunes) with good protection, growth, and large distribution areas of *H. ammodendron* and *H. persicum*. Site coordinates were 44°22′N, 87°52′E; 44°36′N, 88°14′E; and 44°56′N, 88°33′E, respectively. Each site included central dunes, lower dunes, upper dunes, and dune tops, and was divided into 100 quadrats (10 m × 10 m) using the adjacent grid method, totaling 300 quadrats. Vegetation surveys conducted from late May to early June recorded species name, number, density, height, crown width, basal diameter, and coordinates for each quadrat.

To characterize precipitation patterns, we analyzed meteorological data using forecast precipitation from the European Centre for Medium-Range Weather Forecasts at 0.125° latitude-longitude resolution for 2015 and 2019, calculating average annual precipitation and temperature. This method has demonstrated high accuracy (Liu et al., 2018). At each site, we randomly collected and mixed five soil samples (0–20 cm depth). Samples were air-dried, passed through a 2-mm sieve, and analyzed for electrical conductivity (5:1 water:soil leachate at 25°C), total salt (dry residue method), water content (aluminum box drying method), and organic matter (potassium dichromate external heating method) after filtering through a 0.25-mm sieve. Site locations were recorded using GPS for longitude, latitude, and elevation. In each quadrat, distances between all competing trees and target trees of *H. ammodendron* and *H. persicum* were measured, with spatial coordinate information shown in Figure 1 [Figure 1: see original paper].

2.2.2 Determination of Optimal Competition Range

We randomly selected 106 *H. ammodendron* and 101 *H. persicum* individuals with varying basal diameters as target trees across all dune types. For each target tree, we established sample circles and measured competition intensity from other trees within circles of 1–16 m radius (1 m increments). The average competition intensity was calculated for each radius, and piecewise regression plots were fitted. When both fitted equations reached significance with high R^2 values, the corresponding radius was identified as the competition range turning point.

2.2.3 Classification Criteria for Life Stages

Following Jia and Lu (2004), we classified *H. ammodendron* and *H. persicum* into three life stages: seedlings (basal diameter < 1.2 cm), saplings (1.2 cm $\leq$ basal diameter ≤ 6.5 cm), and adults (basal diameter > 6.5 cm). We used the Hegyi competition index, Ripley's K function ($K(r)$), and Ripley's g function ($g(r)$) to analyze competition, spatial patterns, and regeneration across life stages and dune types.

2.3.1 Competition Index Model

We used Hegyi's distance-dependent competition index model to calculate intraspecific and interspecific competition indices:

$$CI_i = \sum_{j=1}^{N} \frac{D_j}{D_i \cdot L_{ij}}$$

where i represents target trees, j represents competing trees, *CI_i* is the competition index of the ith target tree, *D_i* is the diameter at breast height of target tree i (cm), *D_j* is the diameter at breast height of competing tree j (cm), *L_{ij}* is the distance between target tree i and competing tree j (m), and N is the number of competing trees for target tree i. The overall competition index *CI* is the sum of individual *CI_i* values. Larger values indicate more intense competition and greater competitive pressure on target trees. Since *H. ammodendron* and *H. persicum* are shrub-like small trees, basal diameter was substituted for diameter at breast height (Li et al., 2016).

2.3.2 Relationship Between Competition Intensity and Basal Diameter

We performed regression analysis using competition intensity as the dependent variable and target tree basal diameter as the independent variable, fitting a power function:

$$CI = A \cdot D^{-B}$$

where D is target tree basal diameter (cm), and A and B are model parameters.

2.3.3 Analysis of Spatial Point Pattern

We analyzed spatial point patterns of *H. ammodendron* and *H. persicum* across life stages and dune types using spatial distribution maps (Fig. 1 [Figure 1: see original paper]) based on individual plant coordinates. Multiscale spatial distribution patterns and interspecific associations were examined using spatial point pattern analysis.

Ripley's K function was calculated as:

$$K(r) = \frac{S}{n^2} \sum_{i=1}^{n} \sum_{\substack{j=1 \\ j \neq i}}^{n} \frac{I_r(u_{ij})}{W_{ij}}$$

where S is study area (m^2), n is number of individuals, *u_{ij}* is distance between points i and j, *I_r(u_{ij})* is an indicator function (1 when *u_{ij}* $\leq r$, 0 otherwise), and *W_{ij}* is an edge correction weight.

The g function, derived from *K(r)*, overcomes cumulative effects and describes occurrence probability within a specified circular width:

$$g(r) = \frac{1}{2\pi r} \frac{dK(r)}{dr}$$

The univariate *g_{11}(r)* analyzes single-species distribution patterns: - *g_{11}(r)* = 1 indicates random distribution - *g_{11}(r)* > 1 indicates aggregated distribution - *g_{11}(r)* < 1 indicates uniform distribution

The bivariate *g_{12}(r)* analyzes spatial association between species, representing the probability of one species occurring within a specified distance of another (Zeng et al., 2019): - *g_{12}(r)* = 1 indicates no correlation - *g_{12}(r)* > 1 indicates positive correlation - *g_{12}(r)* < 1 indicates negative correlation

2.3.4 Population Renewal Analysis

Renewal density was calculated as: (number of seedlings + number of saplings) / circle area. Using adults as mother trees and seedlings/saplings as regeneration trees, we counted surviving and dead regeneration trees within 2, 4, and 6 m radius circles centered on individual mother trees.

2.4 Statistical Analysis

Data processing was conducted using Programita, with goodness-of-fit tests analyzing result significance. Spatial scale was 0–50 m, circular width 1 m, step length 10 m, and 199 Monte Carlo simulations were performed, selecting the fifth-highest and fifth-lowest values to construct 95% confidence intervals.

3.1 Overview of Target and Competitive Trees

A total of 207 target trees and 618 competing trees were sampled (Table 1). For *H. ammodendron*, there were 76 seedlings and saplings (71.70%) and 30 adults (28.30%). For *H. persicum*, there were 78 seedlings and saplings (77.23%) and 23 adults (22.77%). Both species showed high proportions of seedlings and saplings, indicating young population age structures.

3.2.1 Neighborhood Optimal Competition Range Determination

Regression analysis between sample circle radius and average competition index showed decreasing competition intensity with increasing radius, with a clear turning point at 6 m (Fig. 2 [Figure 2: see original paper]). Within 6 m, competition intensity decreased with radius, and fitted equations for both species reached significance with maximum R^2 values. Therefore, 6 m was identified as the optimal competition range for both species.

3.2.2 Intraspecific and Interspecific Competition Intensities in Different Dunes

Competition intensities varied with stand age and dune type. For both species, competition was strongest among seedlings, followed by saplings and adults (Table 2). Competition was predominantly intraspecific across all dune types. *H. ammodendron* experienced greater competition than *H. persicum* in fixed dunes, but less in semifixed and mobile dunes. Average intraspecific and interspecific competition intensities for *H. ammodendron* followed: fixed dunes > semifixed dunes > mobile dunes. For *H. persicum*, intraspecific competition was greater in mobile and semifixed dunes than fixed dunes, while interspecific competition followed: mobile dunes > semifixed dunes > fixed dunes.

Life-stage specific patterns showed *H. ammodendron* seedlings, saplings, and adults all followed: fixed dunes > semifixed dunes > mobile dunes. *H. per-*

sicum seedlings followed: mobile dunes > semifixed dunes > fixed dunes, while saplings and adults followed: semifixed dunes > mobile dunes > fixed dunes. Interspecific competition for all *H. persicum* life stages followed: mobile dunes > semifixed dunes > fixed dunes.

3.2.3 Relationship Between Competition Intensity and Target Tree Basal Diameter

Competition intensity decreased with increasing target tree basal diameter for both species across all dune types (Fig. 3 [Figure 3: see original paper]). When basal diameter exceeded 15 cm, competition intensity stabilized at low levels. Power function relationships were:

H. ammodendron:
- Fixed dunes: $CI = 4.847D^{-0}.^{726}$ ($R^2 = 0.338$, $P < 0.001$)
- Semifixed dunes: $CI = 4.369D^{-0}.^{731}$ ($R^2 = 0.711$, $P < 0.001$)
- Mobile dunes: $CI = 3.100D^{-0}.^{127}$ ($R^2 = 0.910$, $P < 0.001$)

H. persicum:
- Fixed dunes: $CI = 3.605D^{-0}.^{840}$ ($R^2 = 0.796$, $P < 0.001$)
- Semifixed dunes: $CI = 5.577D^{-1}.^{017}$ ($R^2 = 0.312$, $P < 0.001$)
- Mobile dunes: $CI = 4.374D^{-0}.^{870}$ ($R^2 = 0.463$, $P < 0.001$)

Overall relationships were: *H. ammodendron*: $CI = 4.515D^{-0}.^{776}$ ($R^2 = 0.359$, $P < 0.001$); *H. persicum*: $CI = 4.443D^{-0}.^{792}$ ($R^2 = 0.412$, $P < 0.001$); combined: $CI = 4.477D^{-0}.^{784}$ ($R^2 = 0.379$, $P < 0.001$).

3.3.1 Spatial Distribution Patterns Across Life Stages

H. ammodendron seedlings showed random distribution in fixed and mobile dunes, with primarily random but uniform distribution at 3, 7–9, 11–18, and 29–32 m scales and clustered distribution at 48 and 50 m scales in semifixed dunes (Fig. 4 [Figure 4: see original paper]). Saplings were randomly distributed in fixed dunes, primarily random with clustering at 18 and 40 m scales in semifixed dunes, and mainly random with clustering at 23 m scale in mobile dunes. Adults were predominantly random in fixed dunes (clustered at 1 m, uniform at 10 and 12–13 m), mainly random in semifixed dunes (clustered at 10 and 20 m, uniform at 28, 31, 36, and 48 m), and random in mobile dunes.

H. persicum seedlings were mainly random in fixed dunes (uniform at 50 m), primarily random in semifixed dunes (aggregated at 31 m), and random in mobile dunes (Fig. 5 [Figure 5: see original paper]). Saplings were mainly random in fixed dunes (clustered at 46 and 50 m), random in semifixed dunes, and primarily random in mobile dunes (clustered at 8 and 27 m, uniform at 47 m). Adults were mainly random in fixed dunes (uniform at 45 m), random in semifixed dunes, and predominantly random in mobile dunes (clustered at 31 m).

3.3.2 Spatial Association Analysis Across Life Stages

H. ammodendron seedlings and saplings showed no spatial correlation in fixed and mobile dunes. In semifixed dunes, they were primarily uncorrelated with significant negative correlation at 0–2 m scale and positive correlations at 9, 11, 13–18, and 30–32 m scales (Fig. 6 [Figure 6: see original paper]). Seedlings and adults showed no correlation in mobile dunes, primarily no correlation in fixed dunes (negative at 1 m), and mainly no correlation in semifixed dunes (positive at 11–15 and 43 m, negative at 0–5 m). Saplings and adults showed no correlation in fixed dunes, primarily no correlation in semifixed dunes (negative at 0–2 and 5 m, positive at 26, 28, 36–38, and 47–49 m), and mainly no correlation in mobile dunes (positive at 12 m).

H. persicum seedlings and saplings showed no correlation in fixed and mobile dunes, and primarily no correlation in semifixed dunes (positive at 42 m) (Fig. 7 [Figure 7: see original paper]). Seedlings and adults showed no correlation across all dune types. Saplings and adults were mainly uncorrelated, with significant negative correlation only at 3 m scale in fixed dunes, negative at 1 and 23 m and positive at 10–12, 30, and 35 m scales in semifixed dunes, and negative at 27 m and positive at 47–48 m scales in mobile dunes.

3.4 Regeneration of Seedlings and Saplings

Regenerated seedling and sapling densities were highest within 0–2 m of target trees, decreasing with increasing radius (Fig. 8 [Figure 8: see original paper]). For *H. ammodendron*, average regeneration densities followed: fixed dunes > semifixed dunes > mobile dunes within 0–6 m. For *H. persicum*, densities within 0–2 m followed: semifixed dunes > mobile dunes > fixed dunes, while at 2–4 m and 4–6 m they followed: mobile dunes > fixed dunes > semifixed dunes.

Correlation analysis (Table 3) revealed significant positive correlations between regeneration densities and competition index within 0–2 m for both species ($P < 0.01$). At 2–4 m, *H. ammodendron* showed positive correlations ($P < 0.05$) while *H. persicum* showed no relationship for total regeneration but significant correlations for surviving regeneration ($P < 0.01$). At 4–6 m, no significant relationships were found.

4 Discussion

4.1 Intraspecific and Interspecific Competition

Plant competition is determined by species density, individual size, and ecological habits. Our gradual expansion method identified 6 m as the optimal competition range for both species, likely because adjacent seedlings have strongly overlapping niches during early growth stages, creating intense intraspecific competition. As plants grow, increasing height and crown width enhance resource acquisition and space occupation, expanding the optimal competition range (Zheng et al., 2017).

Habitat significantly affected population numbers and competition intensities. *H. ammodendron* showed greatest abundance and competition in fixed dunes, while *H. persicum* dominated semifixed and mobile dunes. Although both belong to Chenopodiaceae, their suitable habitats differ markedly (Guo et al., 2005). *H. ammodendron* primarily occupies interdune lowlands, dry riverbeds, lake margins, piedmont plains, and gravel fields, whereas *H. persicum* mainly grows on mobile or semifixed dunes (Chang et al., 2006). Our findings align with this distribution pattern.

Higher soil water content in fixed dunes supports larger vegetation areas and alleviates competition, improving *H. ammodendron* survival (Wang, 2017). Increased soil organic matter and improved nutrient content with reduced alkalinity further benefit *H. ammodendron* growth. Species distribution differences relate to water utilization strategies. *H. persicum* has a well-developed root system in the 0–60 cm soil layer with abundant lateral roots, relying on rainfall and subsurface root synergy for precipitation utilization (Shi et al., 2016; Tian and Liu, 2020). In harsh, unshaded environments, *H. persicum* increases fine root specific surface area and length for efficient water absorption. Conversely, *H. ammodendron* has limited surface roots, primarily utilizing groundwater (Yang et al., 2011), making it less competitive in mobile dunes but more abundant in stable fixed dunes where intraspecific competition is intense but interspecific pressure from *H. persicum* is low.

Basal diameter is the main factor affecting competition intensity (Laungani and Knops, 2009). In the same habitat, competition intensity differed among size classes, following: seedlings > saplings > adults, decreasing with diameter class. Young plants experience vigorous growth with high resource demands, creating fierce competition. As age increases, canopy closure and self-thinning increase inter-plant distances, stabilizing growth and reducing competition for light, temperature, water, and nutrients.

We tested linear, hyperbolic, power, and logarithmic models, finding the power function provided the best correlation coefficient, making it suitable as a competition intensity prediction model. The model showed decreasing competitive pressure with increasing basal diameter, consistent with studies on other species (Zhang et al., 2016; Liu et al., 2020; Wang et al., 2021). When basal diameter exceeded 15 cm, competition intensity stabilized at low levels. Therefore, selective cutting and artificial tending should be implemented before trees reach 15 cm diameter to reduce competitive pressure on small- and medium-diameter trees.

4.2 Spatial Patterns of *H. ammodendron* and *H. persicum*

Under natural conditions, tree community spatial patterns are determined by biological characteristics, habitats, and interactions (Shen et al., 2016a). We found strong random distributions across all life stages for both species, with some aggregated or uniform patterns at specific scales. This differs from findings in the Ganjia Lake Haloxylon Forest Nature Reserve, where aggregated distributions occurred at small scales and random or uniform patterns at larger scales (Yan et al., 2021). This discrepancy likely reflects long-term species-environment adaptation and interactions.

In this desert environment, water limitation restricts plant survival and growth, creating intense competition among mature plants. To ensure growth, development, and reproduction, populations exhibit random distribution due to resource and space competition (Sun et al., 2020). Both species are wind-pollinated with effective reproduction and pollination (Wei et al., 2005). Strong winds and harsh desert conditions affect flowering and pollination, dispersing seeds farther and preventing strong aggregations under parent trees due to their light-demanding nature (Chi et al., 2020). As basal diameter increases, intraspecific and interspecific competition intensifies, causing self- and other-thinning that inhibits surrounding individuals and reduces aggregation. Aggregated or uniform patterns at some scales likely reflect environmental heterogeneity, where local microenvironments with better conditions support higher densities of small- or large-diameter individuals (Lv et al., 2012).

Spatial correlations among diameter classes describe distributions and functional relationships within populations at specific times (Shields et al., 2014; Wang et al., 2016), reflecting population status and internal relationships (Wang et al., 2010). Our results showed no correlation among seedlings, saplings, and adults, with only localized negative and positive correlations at small scales. The lack of significant correlation among life stages across dunes suggests low intraspecific competition and niche overlap, possibly due to large growth spaces and strong light requirements. Seedlings and saplings cannot obtain sufficient light under adult canopies, reducing interdependence and favoring community development and population stability (Zhang et al., 2010; Shen et al., 2016b).

Negative correlations at small scales in semifixed dunes indicate strong inhibitory effects of saplings and adults on seedling regeneration, with fierce intraspecific competition. As saplings develop stress resistance and increased resource demands, competition among age classes intensifies (Song et al., 2010). Positive correlations at mesoscales suggest resource abundance or subtle habitat changes create micro-niche differences allowing coexistence (Qi, 2011). However, groundwater scarcity can shift these positive relationships to non-correlation due to water competition (Feng, 2017). Large-scale non-correlation may indicate that one growth stage creates conditions for another, showing complementary habitat requirements (Cui, 2015).

4.3 Natural Regeneration of *H. ammodendron* and *H. persicum* Communities

Natural regeneration is a crucial ecological process for forest restoration and the fundamental way to restore forest stands (Li et al., 2021). Good natural regeneration optimizes ecosystem structure and function, forming high-quality, stable natural forests (Zhang et al., 2014). We found highest seedling and sapling regeneration densities within 0–2 m, decreasing with radius, consistent with competition intensity patterns. As competition index increased, regeneration density increased, indicating that higher competition indices correspond to smaller basal diameters, weaker individual competitiveness, and lower competitive pressure on surrounding regeneration, causing young trees to cluster around high-competition-index individuals (Pan et al., 2019). Additionally, mother trees with more individuals produce more seeds, providing adequate provenance (Li et al., 2009), and strong seed germination ability (Zhang et al., 2010) increases regeneration density at smaller scales.

H. ammodendron regeneration densities were higher in fixed dunes than semifixed and mobile dunes, while *H. persicum* densities were lower in fixed dunes than in semifixed and mobile dunes. This relates to dune stability—*H. ammodendron* is more suitable for stable dunes with higher regeneration density, whereas *H. persicum*'s developed root system and strong adaptability to harsh environments enable better growth and survival in semifixed and mobile dunes, leading to high sapling regeneration density.

The significant positive correlation between regeneration density and competition index within 0–2 m, which disappeared at larger radii, may reflect the highest regeneration density and better understory environment near mother trees with stronger competitiveness. As radius increased, changing light conditions and increased water and nutrient competition negatively impacted seedling germination and growth, reducing regeneration density (Hu, 2022).

5 Conclusions

Using Hegyi competition index and point pattern analysis, we revealed competition, spatial pattern, and regeneration characteristics of *H. ammodendron* and *H. persicum* across dune types and life stages. *H. ammodendron* dominated stable fixed dunes with significantly greater competition intensity than *H. persicum*, which dominated semifixed and mobile dunes with more intense competition. Competition intensity was greatest for seedlings of both species across all dunes. Both species showed strong random distributions across life stages, with mainly uncorrelated spatial associations among seedlings, saplings, and adults. Regeneration density was highest within 0–2 m. These findings improve predictions of plant community development in the Gurbantunggut Desert and inform sand control planting strategies.

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