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Long-term growth heterogeneity and survival strategy differentiation of *Haloxylon ammodendron* populations in extreme desert habitats

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Abstract

To reveal the long-term adaptive patterns of *Haloxylon ammodendron* in extreme arid deserts, this study focused on a natural population in the Badain Jaran Desert. Using three repeated monitoring datasets from 2015 to 2025, we analyzed temporal heterogeneity in plant height, crown diameter, and ground diameter, fitted allometric models, and constructed static life tables from two dimensions (bunch diameter, BDT, for survival; importance value, IVC, for competition) to determine survivorship curves. The results showed: (1) Significant temporal heterogeneity in growth indicators, with ground diameter as the core variable (coefficient of variation > 120%). Its mean exhibited a “sharp decline followed by slight recovery” pattern and was significantly inhibited by drought and intraspecific competition ($P < 0.01$); (2) Allometric models were highly significant ($P < 0.01$), but slopes and fit changed over time. ANCOVA confirmed a year-indicator interaction ($P < 0.01$), indicating time-regulated resource allocation with a ground diameter-oriented tendency; (3) Survival curves showed bidimensional differentiation: BDT-based curves followed a Deevey type III pattern ($R^2 = 0.92$), with a 96.5% survival drop from age classes 1-3, indicating a “juvenile bottleneck” effect. IVC-based curves approximated a Deevey type II pattern ($R^2 = 0.88$), where younger individuals gained advantage through rapid growth, reflecting community-level equilibrium competition. In conclusion, *H. ammodendron* employs a dual “individual survival vs. community competition” strategy: at the individual level, high juvenile screening ensures adult stability; at the community level, equilibrium competition maintains niche advantages. This study clarifies long-term adaptation to extreme drought and supports desert vegetation restoration.

Keywords: *Haloxylon ammodendron*; Desert habitat; Allometric growth; Static life table; Ecological adaptation strategy

1. Introduction

Drylands are a critical component of terrestrial ecosystems, covering approximately 41% of the Earth's land surface. Their structure and functioning are strongly constrained by water availability, making them particularly vulnerable to increasing aridity, land degradation, and other climatic and anthropogenic pressures (Právělie 2016; Berdugo et al. 2020). Dominant shrubs in arid and semi-arid regions can act as effective biological barriers against aeolian erosion by reducing near-surface wind speed and sediment transport, thereby contributing to sand fixation and soil conservation (Latif Bhutto et al. 2022). Species distributions, life-history and growth traits, and local adaptation strategies strongly influence ecosystem-service delivery and restoration planning in desert

ecosystems (Shryock et al. 2022). Field evidence from an Iranian desert ecosystem shows that the root and canopy development of *Haloxylon ammodendron* supports its establishment under water-limited conditions and contributes to wind-erosion control (Savartondrow et al. 2025). It serves as a core pioneer species in sand-fixing revegetation and sandy-land restoration across the desert regions of Northwest China (Fan et al. 2016). The persistence of its populations is therefore important for limiting desertification, sustaining carbon storage and soil protection, and maintaining the stability and resilience of desert ecosystems (Ma et al. 2021; Yin et al. 2022). Recent studies on *H. ammodendron* have commonly examined responses to environmental stress and the performance of specific afforestation or restoration techniques, often at individual sites or along spatial gradients (Qiang et al. 2025; Song et al. 2025). Despite several stand-age and chronosequence studies, true longitudinal investigations that repeatedly track population growth and ecological strategies over extended periods remain limited (Ahn et al. 2025). This gap constrains robust inference about the long-term adaptive and successional trajectories of *H. ammodendron* in extreme desert habitats (Dehghan Rahimabadi et al. 2024).

The Badain Jaran Desert, one of China's largest deserts, lies in the temperate hyper-arid interior of northwestern China and is characterized by low precipitation, high evaporative demand, strong aeolian activity, and pronounced spatial heterogeneity in soils and plant communities (Wang et al. 2021; Sun et al. 2023). These environmental characteristics make the desert a suitable natural system for investigating the ecological adaptation of desert shrub populations. Natural populations of *Haloxylon ammodendron* in and around this desert are exposed to chronic water limitation, frequent wind disturbance, and extremely sandy and nutrient-poor soils (Sun et al. 2023; Zhumabekova et al. 2020). Their growth, regeneration, and persistence are therefore expected to depend on coordinated responses involving germination timing, hydraulic regulation, functional-trait adjustment, and carbon allocation (Liu et al. 2023). Existing studies of natural *H. ammodendron* populations on the eastern margin of the Badain Jaran Desert have mainly examined cross-sectional population structure, spatial distribution, and static demographic patterns (Mao et al. 2023), whereas repeated observations capable of resolving temporal variation in growth indicators and long-term demographic strategies remain limited.

Allometric relationships provide a quantitative framework for examining how biomass and growth are coordinated among plant organs as individual size and environmental constraints change, thereby offering insight into resource-allocation and ecological adaptation strategies (Puglielli et al. 2021). At the population level, size-based static life tables and survivorship curves can summarize stage-specific survival, mortality, and recruitment patterns and thus contribute to the identification of demographic and life-history strategies (Enkhchimeg et al. 2020; Ohse et al. 2023). Combining these demographic analyses with measurements of population size structure, spatial pattern, competition, and regeneration can further connect individual persistence with community-level processes (Liu et al. 2022).

Because *H. ammodendron* forms successive cambia and its annual growth boundaries are difficult to distinguish reliably, chronological age generally cannot be determined using conventional tree-ring counts (Gunbilig et al. 2025). Previous demographic studies of *H. ammodendron* have therefore commonly used basal-diameter classes as proxies for age classes when constructing static life tables and survivorship curves (Chen et al. 2026). Building on this convention, the present study integrates basal diameter with multiple standardized growth indicators to construct a multidimensional size-stage classification framework, with the aim of reducing the bias associated with a single size proxy and resolving the survival patterns of natural *H. ammodendron* populations more robustly.

This study investigates the natural *Haloxylon ammodendron* population in Tamusu Sumu, Badain Jaran Desert, based on long-term monitoring data collected from 2015 to 2025. We systematically analyzed the temporal heterogeneity characteristics of three core growth indicators-plant height, crown width, and ground diameter. Allometric growth models among these indicators were fitted for different years, and their temporal regulation

effects were tested. Concurrently, static life tables were constructed and survival curve types were determined from two dimensions: basal diameter of the tuft (BDT), representing individual survival, and important value of the community (IVC), representing community competition. This study aims to elucidate the growth dynamics, resource allocation strategies, and differentiation characteristics of survival strategies of the *H. ammodendron* population in the Badain Jaran Desert, thereby revealing its ecological adaptation mechanisms to the extreme arid desert environment.

2 Materials and Methods

2.1 Study area

The field study was conducted at the “Tamusu Wild *Cistanche* and *Haloxylon* Seed Production Base” in Tamusu Sumu, Alxa Right Banner, in 2013. The geographical coordinates of the study area range from 103°25.162'E to 103°27.546'E and 40°33.059'N to 40°35.531'N. Administratively, it falls under Chahengzagan, Geltu Gacha, Tamusu Sumu. Based on measurements from 63 GPS points in 2013, the average elevation of the experimental area was determined to be 1260 m, with the highest point at 1264 m, the lowest point at 1256 m, and a total relief of 8 m.

The experimental site is located on an inland plateau and exhibits a typical temperate arid desert climate, characterized by low precipitation, high evaporation, and large diurnal temperature ranges. The mean annual precipitation ranges from 40 to 80 mm, the mean annual temperature ranges from 8 to 8.9°C, and the absolute maximum temperature reaches 37-43°C. The mean annual evaporation exceeds 3500 mm. The climate is extremely arid, with an aridity index of 7-12. The frost-free period lasts 150-165 days. The mean annual wind speed is 4 m·s⁻¹. Prevailing wind directions are northwest in winter and spring, northeast in August, and westerly during the remaining months (Chen et al., 2022; Zhang et al., 2022). Sandstorms frequently occur during high winds. The natural vegetation is sparse, poor in species, and characterized by low coverage, with the ground surface largely exposed. The flora is dominated by xerophytic and extremely xerophytic shrubs and semi-shrubs. The primary plant species is *Haloxylon ammodendron*, with main accompanying species including *Nitraria tangutorum* Bobr., *Reaumuria songarica* (Pall.) Maxim., *Sarcozygium xanthoxylon* Bunge, and *Salsola passerina* Bse. Herbaceous plants are relatively scarce, predominantly consisting of annual “summer rain” type species. Most plants in this area possess ecological and biological characteristics enabling them to tolerate drought, high temperatures, and wind-blown sand.

2.2 Sampling Design

The monitoring at the experimental site was conducted using the large-plot survey method. An area with relatively concentrated *Haloxylon ammodendron* distribution within the sampling range was selected as the large permanent plot (for long-term monitoring). The lower-right corner of the plot was designated as the absolute coordinate origin (0, 0), with the horizontal direction as the X-axis and the vertical direction as the Y-axis (Fig. 1A). Transect lines were established at 200 m intervals. Along these transect lines, each *H. ammodendron* individual was measured for height (cm), crown diameter (cm), and ground diameter (cm). The survey results are presented in Figure 1 (each “+” in Figure 1 represents an individual *H. ammodendron*; panels A, B, and C in the figure correspond to the monitoring results from 2015, 2020, and 2025, respectively). A total of 1,151, 1,151, and 1,364 individuals were monitored in 2015, 2020, and 2025, respectively.

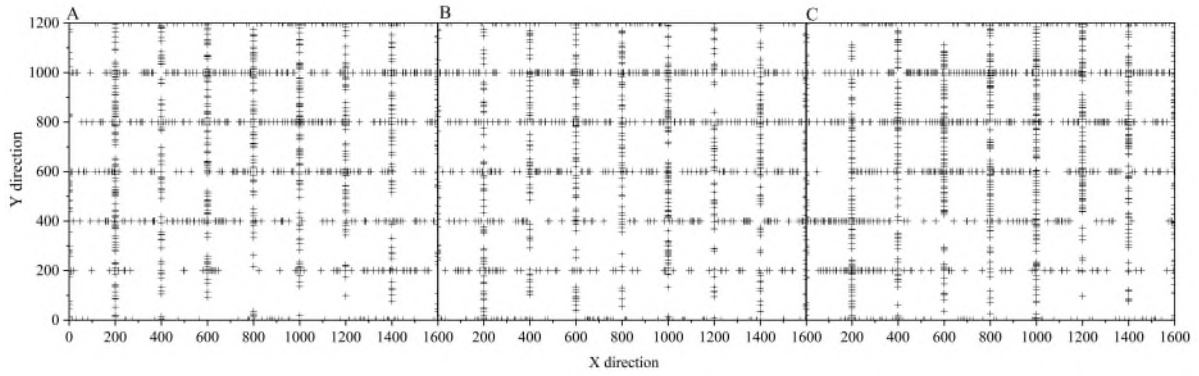


Fig. 1 Spatial distribution of *Haloxylon ammodendron* individuals surveyed in the experimental plot over a three-year period

Note: Panels A-C in the figure represent the locations of *Haloxylon ammodendron* individuals monitored in 2015, 2020, and 2025, respectively. The X direction and Y direction indicate west-to-east and south-to-north orientations, respectively. The tick numbers on the horizontal and vertical axes are in meters.

2.3 Data processing

2.3.1 Calculation of important value

For each individual *Haloxylon ammodendron* surveyed in 2015, 2020, and 2025, its height (cm), crown diameter (cm), and ground diameter (cm) were divided by the maximum value of the corresponding growth indicator (height, crown diameter, or ground diameter) for that respective year. The average of these three ratios was then calculated and multiplied by 100%. The calculation formula is as follows:

$$IVC = \left(\frac{H}{H_{\max}} + \frac{C}{C_{\max}} + \frac{D}{D_{\max}} \right) / 3 \times 100\%$$

In the formula, H , C and D represent the height (cm), crown diameter (cm), and ground diameter (cm) of *Haloxylon ammodendron*, respectively. The terms $H_{\max}$, $C_{\max}$, and $D_{\max}$ denote the maximum values of height (cm), crown diameter (cm), and ground diameter (cm) for *H. ammodendron* within each respective year (1151 individuals in 2015, 1151 in 2020, and 1364 in 2025) and across all years combined (3666 individuals in total).

2.3.2 Classification of age structure

Haloxylon ammodendron is a small arborescent plant that lacks distinct annual growth rings. Accurately determining its age based on ground diameter is challenging, as ground diameter can be affected by wind-blown sand, potentially leading to deformities such as plate-like or prostrate growth forms (Fig. 2). Crown diameter and height are even less reliable for directly estimating age. Nevertheless, ground diameter can still roughly reflect the growth period of *H. ammodendron* and can therefore be used as an indicator for age class grouping. Additionally, because the important value reflects the overall growth and development of *H. ammodendron*, it can also serve as a basis for age classification. Taking 2015 as an example, the maximum and minimum values of the important value and ground diameter for the 1,151 *H. ammodendron* individuals were determined. Subsequently, the 'seq()' function in R software was used to generate 10 equal intervals for each indicator. The number of *H. ammodendron* individuals within each interval was then counted, forming the basis for age group classification based on ground diameter and important value. The method used for classifying age classes for other years and for the overall dataset was identical to that used for 2015. The classification results are presented in Table 1.

Table 1 Results of age classification for *Haloxylon ammodendron*.

Class	Year and total	Age class										Sum
		Young age class			Middle age class				Old age class			
		1	2	3	4	5	6	7	8	9	10	

	2015	790	179	73	49	29	16	7	5	2	1	1151
Basal diameter	2020	996	138	7	4	2	2	0	1	0	1	1151
(BDT)	2025	1105	224	22	3	0	0	2	6	1	1	1364
	Total	3128	331	83	51	31	23	9	7	2	1	3666
	2015	140	300	340	206	84	46	21	7	6	1	1151
Important value	2020	237	332	307	158	58	40	17	0	1	1	1151
Index (IVC)	2025	135	281	297	278	176	95	55	33	9	5	1364
	Total	682	1144	1033	456	202	106	27	8	7	1	3666

Note: 1-10 represent age classes increasing at equal intervals based on ground diameter and important value.



Fig. 2 Ground diameter and spatial distribution of *Haloxylon ammodendron*

2.3.3 Descriptive statistics and statistical tests

First, boxplots of *Haloxylon ammodendron* height, crown diameter, and ground diameter were generated for the years 2015, 2020, and 2025. Subsequently, the mean, standard deviation (SD), median (Md), minimum (Min), maximum (Max), and coefficient of variation (CV) were calculated for each indicator. As the sample data did not meet the assumptions of normality (assessed using the Shapiro-Wilk test) or homogeneity of variance (assessed using Levene's test), the Kruskal-Wallis rank sum test was employed to examine differences in the same indicator across different years. Furthermore, Dunn's post-hoc test was used to compare differences in the same indicator between pairs of years. All relevant calculations, statistical tests, and graphical procedures were conducted in R, with the help of packages including “tidyverse”, “ggplot2”, “ggpubr”, “rstatix”, “car”, “emmeans”, “multcomp”, and “cowplot”.

2.2.4 Allometric growth model fitting and testing

Natural logarithms were applied to *Haloxylon ammodendron* height, crown diameter, and ground diameter, with the transformed variables designated as logH, logC, and logD, respectively. An analysis of covariance (ANCOVA) was then performed and tested using year as a covariate. Taking logH and logC as an example, the allometric growth model takes the form $\log H = b \cdot \log C + \log(a)$, where b and log(a) are the fitted coefficients. The ANCOVA model was specified as $\log H = \log C + \text{year} + \log C \cdot \text{year}$ to test the significance of the main effects of logC and year as well as their interaction. All relevant calculations and plotting were performed in R using the “dplyr”, “rlang”, “car”, “ggplot2”, and “cowplot” packages.

2.3.4 Construction and curve plotting of static life tables for *Haloxylon ammodendron*

Static life tables were constructed in order of age class, and the following parameters were calculated:

Number of individuals per age class: n_x

Standardized number of survivors: $l_x = n_x / \sum n_x \times 1000$

188 Number of deaths: $d_x = l_x - l_{x+1}$; Mortality rate: $q_x = d_x / l_x$; Disappearance rate: $k_x = \ln(l_x) - \ln(l_{x+1})$

189 Survival rate: $s_x = l_{x+1} / l_x$; Survival probability: $S_i = s_{x+1} s_x$; Cumulative mortality rate: $F_i = 1 - S_i$

190 Static life tables were generated based on age classes defined by basal diameter of the tuft (BDT) and
 191 important value (IVC) for the years 2015, 2020, 2025, and for the overall dataset. Survival curves (l_x), mortality
 192 rate curves (q_x), and disappearance rate curves (k_x) were plotted, along with S_i and F_i curves. The survival curves

193 $l_x = ae^{bx}$ were fitted to exponential (Deevey type I, convex), linear $l_x = a + bx$ (Deevey type II, line), and

194 power $l_x = ax^b$ (Deevey type III, concave) models. The Deevey type (Deevey, 1947) was determined based

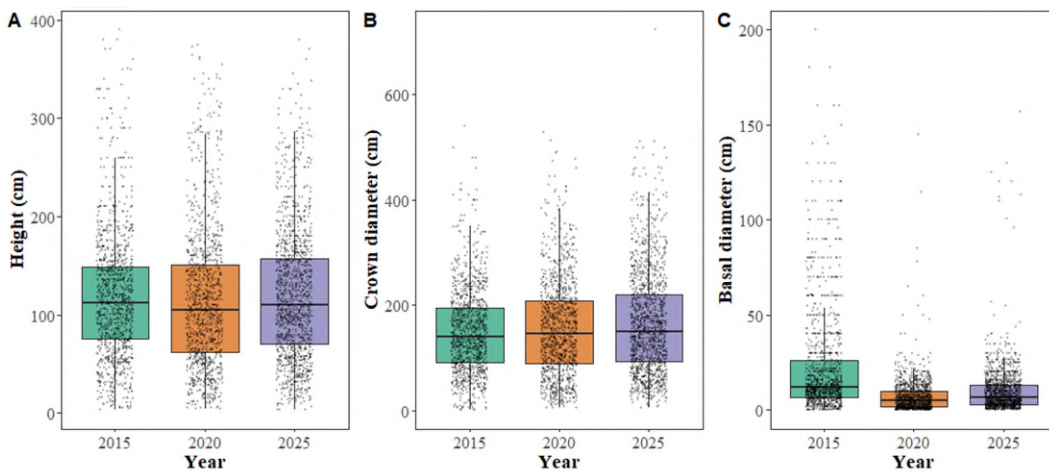
195 on the goodness of fit and the shape of the curves. All relevant calculations, model fitting, and plotting were
 196 completed in R software using packages including “ggplot2”, “gridExtra”, “readr”, “dplyr”, “grid”, and
 197 “cowplot”.

198

199 3 Result and analysis

200 3.1 Variation analysis of different indicators in the *Haloxylon ammodendron* population

201 The boxplots of three growth indicators-Height, Crown diameter, and Basal diameter-of the *Haloxylon*
 202 *ammodendron* population in the Badain Jaran Desert from 2015 to 2025 (Fig. 3) show that, relative to basal
 203 diameter, the medians for height and crown diameter exhibited a median-centered trend. This suggests that basal
 204 diameter exhibits substantial variation (as corroborated by the coefficient of variation in Table 2). The
 205 descriptive statistics (Table 2) indicate that their quantitative characteristics exhibited significant temporal
 206 heterogeneity. The mean height exhibited a trend of a slight initial decrease followed by recovery (119.0 cm in
 207 2015, 115.0 cm in 2020, and 119.0 cm in 2025), with the range of extreme values remaining stable between 3
 208 and 390 cm, indicating relatively small overall variation (Fig. 3). The mean crown diameter showed a
 209 continuously increasing trend (gradually rising from 150.0 cm in 2015 to 166.0 cm in 2025, with the maximum
 210 value increasing from 540 cm to 723 cm), reflecting an enhanced capacity for canopy spatial expansion of the
 211 *Haloxylon ammodendron* population over time; however, interannual variation in this indicator was minimal.
 212 In contrast, the mean ground diameter exhibited a pattern characterized by a sharp decline followed by a slight
 213 recovery (23.2 cm in 2015, 7.72 cm in 2020, and 10.2 cm in 2025). The mean ground diameter in 2015 was 3.0
 214 times that of 2020, and the range of extreme values narrowed from 0.1-200 cm to 0.2-157 cm, suggesting that
 215 ground diameter growth was significantly suppressed by the desert habitat conditions or intraspecific
 216 competition.



217

218

Fig. 3 Boxplots of quantitative characteristics of *Haloxylon ammodendron* at different monitoring times

The Kruskal-Wallis test results (Table 2) indicated that the overall differences among the study years for all three growth indicators reached statistically significant levels ($P < 0.05$). Among these, the difference in ground diameter was most pronounced ($\chi^2 = 463.259$, $d_f = 2$, $P < 0.01$), followed by crown diameter ($\chi^2 = 10.894$, $d_f = 2$, $P = 0.0043$), while the difference in height was relatively weaker ($\chi^2 = 7.484$, $d_f = 2$, $P = 0.024$). Duncan's post-hoc test further clarified the temporal characteristics of the variation in these indicators: significant differences in height were only observed between 2020 and 2015, and between 2020 and 2025 (adjusted P-values: P.adj < 0.358 and P.adj < 0.0379, respectively), while no statistically significant difference was found between 2015 and 2025 (adjusted P.adj = 0.8871 > 0.05). For crown diameter, significant differences were primarily concentrated between 2015 and 2025, and between 2020 and 2025 (adjusted P.adj = 0.0054 and P.adj = 0.0262, respectively, both < 0.05), whereas no significant difference was detected between 2015 and 2020 (adjusted P.adj = 0.4742 > 0.05). In contrast, ground diameter exhibited highly significant differences across all years (all adjusted P.adj values < 0.01), with coefficients of variation exceeding 100% in each year. Therefore, ground diameter is identified as the core indicator of growth variation in the *Haloxylon ammodendron* population during the study period.

Table 2 Descriptive statistics of quantitative characteristics of *Haloxylon ammodendron* at different monitoring times

Year	Descriptive statistical analysis						Kruskal-Wallis test			Dunn's post-hoc test				
	Indexes	Mean	SD	CV	Md	Min	Max	χ^2	DF	p value	Comparison	Z	P.unadj	P.adj
2015	Height	119	65.40	54.96	112	3	390				2015-2020	2.259	0.0239	0.0358
2020		115	71.20	61.91	105	4	375	7.484	2	0.0237	2015-2025	-0.142	0.8871	0.8871
2025		119	65.60	55.13	110	3	380				2020-2025	-2.494	0.0126	0.0379
2015	Crown diameter	150	80.00	53.33	140	1	540				2015-2020	-0.716	0.4742	0.4742
2020		156	91.10	58.40	145	5	528	10.894	2	0.0043	2015-2025	-3.124	0.0018	0.0054
2025		166	96.80	58.31	150	5	723				2020-2025	-2.377	0.0175	0.0262
2015	Basal diameter	23.20	28.00	120.69	12	0.1	200				2015-2020	20.951	<0.01	<0.01
2020		7.72	9.27	120.08	5	0.2	145	463.259	2	<0.01	2015-2025	15.116	<0.01	<0.01
2025		10.20	12.40	121.57	7	0.2	157				2020-2025	-6.711	<0.01	<0.01

Note: P.unadj and P.adj represent unadjusted and adjusted P-values, respectively.

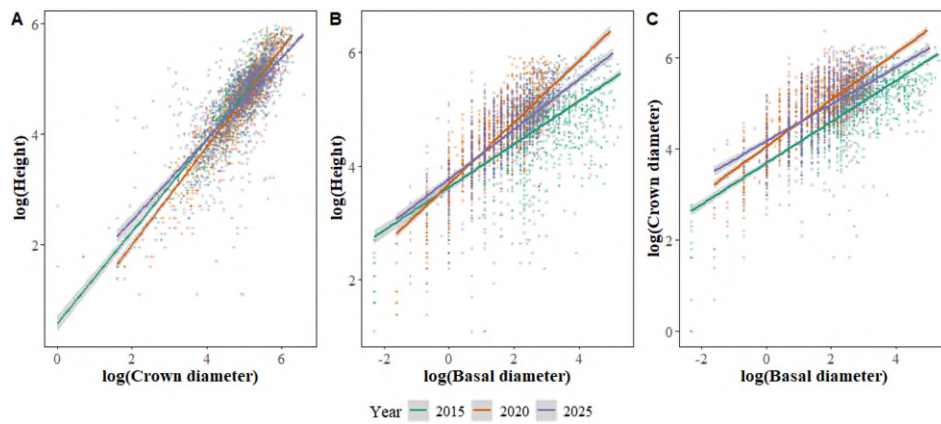
3.2 Analysis of allometric growth among different indicators of *Haloxylon ammodendron*

The allometric growth model fitting for *Haloxylon ammodendron* height vs. crown diameter (logH~logC), height vs. ground diameter (logH~logD), and crown diameter vs. ground diameter (logC~logD) from 2015 to 2025 all reached highly significant levels ($P < 0.01$). However, the goodness of fit, intercept, and slope characteristics of the models exhibited pronounced dynamic changes over the monitoring years (Table 3, Fig. 4), reflecting the temporal heterogeneity in the growth allocation strategies of *H. ammodendron*.

The allometric growth slope for height vs. crown diameter exhibited an initial increase followed by a decrease (0.832 in 2015, 0.891 in 2020, and 0.738 in 2025). The coefficients of determination (R^2) for the model were 0.739, 0.774, and 0.544 in 2015, 2020, and 2025, respectively, indicating that the linear correlation between height and crown diameter was strongest in 2020, while their synergistic growth significantly decreased in 2025. For height vs. ground diameter, the allometric growth slope also showed a pattern of initial increase followed by a decrease (0.379 in 2015, 0.541 in 2020, and 0.439 in 2025), with R^2 declining from 0.622 in 2020 to 0.408 in 2025. This suggests that the explanatory power of ground diameter for height growth peaked in 2020 and then weakened substantially. The allometric growth slope for crown diameter vs. ground diameter followed a trajectory of 0.452 (2015) → 0.513 (2020) → 0.405 (2025), with R^2 continuously decreasing from 0.605 in 2015 to 0.348 in 2025, revealing a gradually diminishing regulatory effect of ground diameter on crown diameter

253 growth over time. Overall, the allometric relationship between height and crown diameter was relatively weak,
 254 whereas those between ground diameter and height, and between ground diameter and crown diameter, were
 255 stronger. Furthermore, the allometric relationships exhibited a tendency towards ground diameter (with slopes
 256 consistently less than 1).

257 The ANCOVA interaction test results (Table 3) revealed that the interactions between year and each growth
 258 indicator were all highly significant ($P < 0.01$). Specifically, the interaction effects for height~crown diameter
 259 $\times$ year ($F = 23.860$, $d_f = 2$, $P < 0.01$), height~ground diameter $\times$ year ($F = 40.593$, $d_f = 2$, $P < 0.01$), and crown
 260 diameter~ground diameter $\times$ year ($F = 16.116$, $d_f = 2$, $P < 0.01$) were all highly significant. This confirms that
 261 the allometric relationships among the growth indicators of the *Haloxylon ammodendron* population are not
 262 constant but are significantly regulated by the temporal scale, indicating fundamental differences in resource
 263 allocation strategies across different time periods. Furthermore, the significant main effects of crown diameter,
 264 ground diameter, and year ($P < 0.01$) also corroborate the strong intrinsic associations among these growth
 265 indicators.



266
267 **Fig. 4** Fitting results of the allometric growth models

268
269 Table 3 Tests for allometric growth models and interaction effects

Allometric model coefficients						ANCOVA interaction test (III type)				
model	year	intercept	slope	r^2	p value	model	Sum Sq	df	F value	Pr(>F)
logH~logC	2015	0.574	0.832	0.739	<0.01	(Intercept)	7.90	1	51.45	<0.01
logH~logC	2020	0.215	0.891	0.774	<0.01	logC	395.80	1	2576.13	<0.01
logH~logC	2025	0.966	0.738	0.544	<0.01	year	7.14	2	23.25	<0.01
						logC:year	7.33	2	23.86	<0.01
logH~logD	2015	3.63	0.379	0.453	<0.01	(Intercept)	2807.13	1	11477.00	<0.01
logH~logD	2020	3.69	0.541	0.622	<0.01	logD	242.56	1	991.70	<0.01
logH~logD	2025	3.77	0.439	0.408	<0.01	year	2.67	2	5.45	0.0043
						logD:year	19.86	2	40.59	<0.01
logC~logD	2015	3.68	0.452	0.605	<0.01	(Intercept)	2889.05	1	11910.59	<0.01
logC~logD	2020	4.04	0.513	0.575	<0.01	logD	346.09	1	1426.81	<0.01
logC~logD	2025	4.16	0.405	0.348	<0.01	year	29.60	2	61.01	<0.01
						logD:year	7.82	2	16.12	<0.01

270 **Note:** logH, logC, and logD represent the log-transformed values of height, crown diameter, and ground diameter, respectively. All
 271 models were fitted using linear regression. ANCOVA refers to analysis of covariance.

272 3.3 Changes in survival, mortality, and disappearance curves based on life tables

Based on the static life table constructed using basal diameter of the tuft (BDT) (Fig. 5), the survival, mortality, and disappearance curves of the *Haloxylon ammodendron* population exhibited pronounced stage-specific differentiation across age classes. The overall pattern conformed to a typical Deevey type III survival curve ($R^2 = 0.92$), reflecting the “juvenile bottleneck” survival strategy characteristic of desert plants (e.g., the standardized survival rate decreased by 96.5% from age classes 1 to 3, with mortality rates exceeding 80% in age class 1). The survival curve exhibited a three-stage pattern characterized by a sharp initial decline, followed by stabilization in the middle stages, and a gradual decline in later stages. The low age classes (1-3) represented the core phase of population mortality, with the standardized number of survivors plummeting from 788.6 to 27.8, a reduction of 96.5%. In the middle age classes (4-6), the survival rate stabilized between 8.5 and 15.3, indicating a relatively strong resistance of the population structure to disturbances. In the high age classes (7-9), the survival rate experienced a slight decline to 0.8, reflecting a modest increase in mortality pressure, though it remained considerably lower than that observed in the early stages. The mortality and disappearance curves were highly synchronized. In age classes 1-3, both the mortality rate (qx) and disappearance rate (kx) were significantly elevated, indicating that young individuals represent a critical limiting factor in population regeneration. In age classes 4-6, the rates of mortality and disappearance flattened considerably (mortality rate: 0.42-0.50; disappearance rate: 0.54-0.69), forming the core support for population stability. In age classes 7-9, the mortality and disappearance rates increased slightly, but no mass mortality occurred, suggesting that population decline exhibits a pronounced buffering capacity.

The static life table constructed based on the important value (IVC) exhibited a distinct stage-specific pattern characterized by an “initial increase - mid-stage gradual decline - later-stage stabilization”, approximating a Deevey type II survival curve ($R^2 = 0.88$). This reflects an equilibrium survival strategy at the competitive level, in stark contrast to the type III pattern revealed by BDT, which focuses on individual survival. The survival curve followed a “juvenile increase - middle-aged linear decline - old-aged stabilization” pattern. In the low age classes (1-3), the standardized number of survivors increased from 139.7 to 257.5, with a juvenile decline rate of -0.844. This does not signify an increase in the number of individuals but rather reflects that young individuals enhanced their competitive ability for resources through rapid growth, resulting in a relative increase in important value. In the middle age classes (4-6), the number of survivors decreased linearly from 175.1 to 49.4, indicating that competitive status entered a phase of dynamic equilibrium. In the high age classes (7-9), the number of survivors remained between 10.9 and 1.9, suggesting that although competitive advantage diminished, it was not abruptly lost. The mortality and disappearance curves also exhibited stage-specific equilibrium characteristics. The negative mortality and disappearance rates in the low age classes corroborated the enhancement of competitive advantage, where a “growth effect” obscured natural mortality losses. In the middle age classes, the mortality and disappearance rates turned positive and remained moderate, reflecting stable competitive status and forming the core support for population structure. In the high age classes, the mortality and disappearance rates increased slightly but remained at low-to-moderate levels, indicating that the decline in competitive advantage was a gradual process that did not profoundly impact population stability.

The Deevey type II curve derived from IVC reveals the “equilibrium survival strategy” of the *H. ammodendron* population in competition. As a comprehensive indicator, the important value reflects the overall performance of the population in resource acquisition, spatial occupation, and interspecific competition. In contrast to the Deevey type III curve based on BDT, the IVC curve indicates that the competitive advantage of *H. ammodendron* at the population level does not differentiate significantly with age but remains relatively stable throughout the entire life cycle. This strategy helps the population maintain its long-term community position in harsh desert environments, ensuring population continuity through sustained resource competition rather than relying on juvenile bursts.

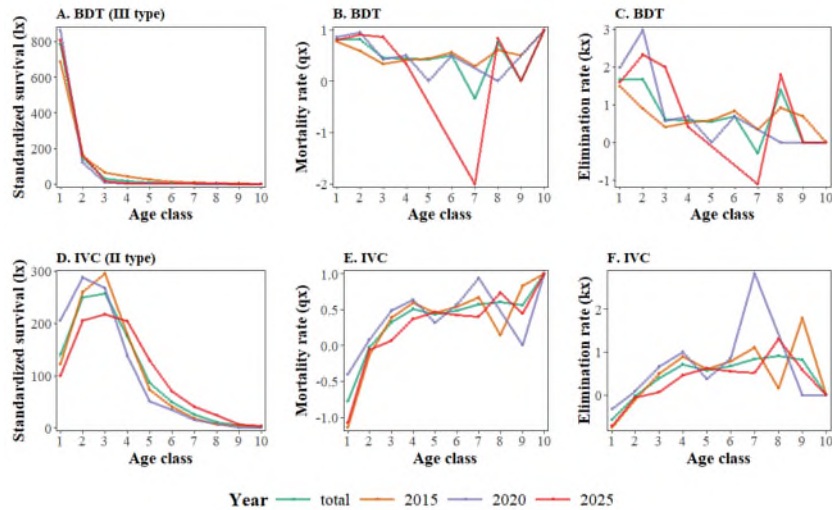


Fig. 5 Survival rate, mortality rate, and disappearance rate of the *Haloxylon ammodendron* population under different monitoring years

Note: The horizontal axis represents the age class of the *Haloxylon ammodendron* population (age classes 1-9), the left vertical axis represents the number of surviving individuals (BDT) and the number of dead individuals (IVC), and the right vertical axis represents the disappearance rate. The different curves represent the dynamics of survival, mortality, and disappearance, respectively. The age classes are classified according to a comprehensive grading standard based on plant height and ground diameter.

3.4 Cumulative survival and mortality curves based on life tables

Based on the cumulative survival and mortality curves constructed using BDT (Bunch Diameter) and IVC (Importance Value Index), the distinct survival strategies of the *Haloxylon ammodendron* population are clearly revealed across the dimensions of individual survival and population competition (Fig. 6). In the BDT dimension, the cumulative survival curve (S_i) exhibits a typical pattern of sharp decline: the cumulative survival rate for individuals in age class 1 is 100%, which drops rapidly to less than 10% by age class 2 and approaches zero after age class 3. Concurrently, the corresponding cumulative mortality curve (F_i) rises steeply between age classes 1 and 2, exceeding 90% by age class 2. This finding is highly consistent with the Deevey type III survival curve identified in the static life table, indicating a pronounced “seedling bottleneck” at the individual level for the *Haloxylon ammodendron* population. Specifically, young individuals (age classes 1-2) possess underdeveloped root systems, rendering them less adaptable to extreme environmental stresses such as drought and wind-blown sand. Furthermore, their high susceptibility to intraspecific competition and rodent herbivory results in extremely high early-stage mortality. In contrast, the cumulative survival and mortality curves for middle-aged and older individuals tend to flatten, suggesting that individuals surviving to age class 3 and beyond have developed stronger environmental adaptability, marking a relatively stable phase in the population structure.

In the IVC dimension, the cumulative survival and mortality curves exhibit distinct phased equilibrium characteristics: from age class 1 to 2, the cumulative survival rate is maintained at 100%, while the cumulative mortality rate remains nearly zero. After age class 2-3, the cumulative survival rate begins to decline linearly, accompanied by a synchronous increase in the cumulative mortality rate. By age class 7, the cumulative survival rate drops to approximately 10%, and the cumulative mortality rate rises to about 90%, stabilizing thereafter in the older age classes (7-9). This result aligns with the linear characteristics of the Deevey type II survivorship curve, reflecting the equilibrium survival strategy of *H. ammodendron* populations in terms of life history competition: for young individuals, rapid height growth allows them to preempt community space and enhance resource acquisition, where the “growth effect” on their dominance index masks the “loss effect” of natural mortality, thus preventing a significant decline in cumulative survival rate. For middle-aged individuals (age

classes 3-7), competitive advantage enters a dynamic equilibrium, with the rate of decline in their dominance index across age classes essentially matching the rate of loss due to natural mortality and interspecific competition, manifesting as a linearly decreasing cumulative survival curve. As for older individuals, although their absolute advantage within the population diminishes, they sustain a certain level of dominance index by occupying long-established niches, avoiding a sudden loss of competitive advantage and thereby maintaining the relative stability of the population.

Taken together, the cumulative survival/mortality curves serve as the cumulative representation of survival and mortality rates in a static life table. Their trends further validate the classification of the BDT dimension as Deevey type III and the IVC dimension as Deevey type II, essentially reflecting the differentiation of ecological strategies in *H. ammodendron* populations at two levels: “individual survival” and “population competition.”The type III curve in the BDT dimension focuses on survival pressure at the individual level, revealing high mortality risk during the early age stages. In contrast, the type II curve in the IVC dimension centers on competitive advantage at the population level, demonstrating a relatively balanced competitive capacity throughout the population's lifespan. This differentiated characterization not only illuminates the adaptive mechanisms of *H. ammodendron* populations to extreme desert environments but also provides a critical lens for understanding their population regeneration and maintenance.

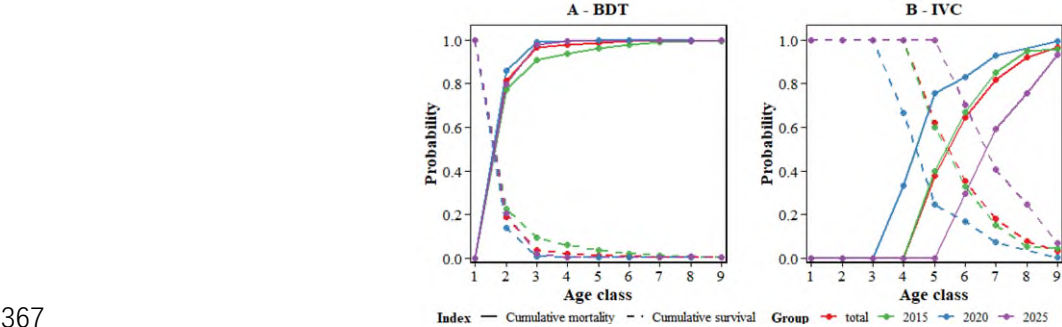


Fig. 6 The cumulative survival and death curves of *Haloxylon ammodendron* in different monitoring years

4 Discussion

4.1 Basal diameter as a key variable reflecting core variability and directional growth in *Haloxylon ammodendron*: an ecological perspective

A temporal heterogeneity analysis of growth indicators for *Haloxylon ammodendron* populations in the Badain Jaran Desert from 2015 to 2025 revealed that basal diameter was the most variable growth indicator, with its coefficient of variation consistently exceeding 120% and showing highly significant interannual differences. Allometric analyses further indicated a disproportionate investment in basal diameter relative to plant height and crown width, suggesting that radial structural development is an important component of the growth strategy of *H. ammodendron* under extreme arid conditions. Recent studies provide strong evidence that water availability plays a central role in regulating this growth pattern. Irrigation significantly promotes the growth of *H. ammodendron*, and increases in root collar diameter may exceed those in plant height, indicating preferential investment in radial growth under improved water conditions (Wu et al. 2024). Similarly, deep-root irrigation simultaneously increases root depth, root biomass, trunk diameter, and canopy diameter, demonstrating a close coordination between aboveground structural development and belowground water acquisition (Fan et al. 2024). Groundwater availability also strongly affects the morphological, physiological, and hydraulic performance of *H. ammodendron*, while stable-isotope evidence indicates that groundwater can represent an important water source for this species in arid environments (Qi et al. 2022). Therefore, the preferential increase in basal diameter observed in the present study is more appropriately interpreted as part of

a coordinated structural and water-acquisition strategy rather than as direct evidence that basal diameter itself determines rooting depth.

In this study, the basal diameter of *H. ammodendron* exhibited only a slight recovery after a pronounced decline from 2015 to 2020, suggesting that radial growth was strongly constrained by the harsh desert environment. This pattern may be associated with persistent water limitation and density-dependent competition. A recent meta-analysis based on 79 studies of *H. ammodendron* plantations showed that, within a broad range of planting densities, increasing stand density negatively affected survival, plant height, ground diameter, and canopy development; the same analysis also showed progressive depletion of shallow soil moisture with stand development (Huang et al. 2024). These findings support the interpretation that competition for limited soil water can constrain individual growth in relatively dense *H. ammodendron* populations. Moreover, experimental studies have demonstrated that groundwater drawdown substantially modifies plant morphology and biomass allocation (Feng et al. 2022) and reduces leaf water potential, photosynthetic capacity, and stomatal conductance (Liu et al. 2023). Thus, the relatively stable population density observed between 2015 and 2020 may have intensified competition for limited water resources and contributed to the suppression of basal diameter growth.

In contrast to basal diameter, crown width increased continuously during the study period, whereas plant height remained comparatively stable. This divergence suggests a shift in aboveground allocation toward horizontal canopy development rather than vertical extension. Such a pattern may represent an adaptive allocation strategy under water-limited conditions, although the present data do not directly demonstrate its underlying physiological mechanism. Experimental studies of *Haloxylon ammodendron* have shown that water availability significantly affects shoot height, root collar diameter, root development, and above- versus belowground biomass allocation, indicating that radial and vertical growth are closely coordinated with water availability during plant establishment (Enkhchimeg et al. 2022). More broadly, studies of dryland shrub communities demonstrate strong coordination between water-acquisition strategies and aboveground functional traits, supporting the view that morphological development and water use should be interpreted as components of an integrated whole-plant resource-use strategy (Illuminati et al. 2022). In addition, field studies in arid environments have shown that the capacity of individual woody plants to reduce wind speed and aeolian sediment transport is strongly related to plant architecture and its interaction with airflow (Miri and Davidson-Arnott 2021). Taken together, these findings suggest that the continuous crown expansion accompanied by comparatively limited height growth observed in the present study may represent a structural strategy that balances resource acquisition, water limitation, and exposure to wind–sand disturbance.

Allometric analysis showed that the slopes between basal diameter and both plant height and crown width were substantially lower than 1, with model fit declining over time. This indicates a gradual weakening of coordination between radial and aboveground growth. Such variation is ecologically plausible because stem–crown allometry can shift with climate and competition (Yambayamba et al. 2025). The higher slopes observed in 2020 suggest stronger coordination among growth traits, whereas their decline by 2025 may reflect increasing individual differentiation in resource acquisition and allocation. Competition and aridity are known to modify crown allometry and suppress crown development relative to stem size (Condés et al. 2020), while increasing neighbourhood density can reduce individual water uptake through intensified competition (Roberts and Hanan 2025). Moreover, woody plants exhibit multiple biomass-allocation strategies under drought rather than a uniform shift toward any single organ (Puglielli et al. 2021). Therefore, the reduced slopes and model fit in 2025 likely reflect increasingly heterogeneous growth strategies under changing competitive and environmental conditions.

The consistently high coefficient of variation in basal diameter indicates substantial phenotypic variability within the *H. ammodendron* population. However, a high CV alone cannot be regarded as direct evidence of phenotypic plasticity, because CV quantifies relative trait variation but does not distinguish its underlying sources (Pélabon et al. 2020). Phenotypic plasticity specifically refers to environmentally induced phenotypic changes and is more appropriately evaluated using trait responses across environmental conditions or reaction norms (Arnold et al. 2019). Moreover, pronounced environmental heterogeneity in drylands can substantially increase plant trait diversity, suggesting that spatial variation in resource availability may contribute to the observed differentiation among individuals (Gross et al. 2024).

From an ecosystem perspective, variation in basal diameter and canopy development may influence the windbreak and sand-stabilization functions of *H. ammodendron* stands. Rather than being determined by basal diameter alone, aeolian protection depends on integrated vegetation structure, including plant size, canopy cover, and spatial configuration. Vegetation height, cover, and gap structure strongly regulate aeolian sediment transport by modifying surface aerodynamic sheltering (Shumack et al. 2022). In semi-arid shrublands, increased foliar cover enhances drag partitioning and substantially reduces soil-surface shear velocity (Ziegler et al. 2023), while field evidence further shows that changes in vegetation cover and structure can produce order-of-magnitude shifts in aeolian sediment transport (Webb et al. 2025). Therefore, basal-diameter dynamics should be interpreted as one component of overall plant structural development that may contribute to the windbreak and sand-stabilization capacity of *H. ammodendron* populations.

The ecological relationship between *Haloxylon ammodendron* and the root holoparasite *Cistanche deserticola* should be interpreted within the broader framework of Orobanchaceae host–parasite interactions. Root parasitic plants establish haustorial connections through which they acquire water, minerals, and carbon from their hosts, making parasite performance inherently dependent on host resource status (Mutuku et al. 2021). However, host–parasite outcomes are regulated by complex processes involving host recognition, haustorium formation, resource transfer, and host defence rather than by a single morphological trait such as basal diameter (Clarke et al. 2019). Parasitic plants can also affect host growth and broader ecosystem processes, including nutrient cycling and community interactions (Těšitel et al. 2021). Therefore, variation in basal diameter may reflect differences in host structural development and resource status, but its direct role in determining *C. deserticola* establishment or growth requires experimental verification.

4.2 The impact of high juvenile mortality and sustained population competitiveness on the stability of *Haloxylon ammodendron* populations

Static life-table analyses based on basal diameter (BDT) and importance value (IVC) revealed high juvenile mortality but sustained population dominance in *Haloxylon ammodendron*. The BDT-based Deevey type III curve showed a 96.5% decline in standardized survival from age classes 1 to 3, indicating a pronounced recruitment bottleneck. Such early-stage mortality is common in drylands, where water availability strongly constrains seedling establishment (Duncan et al. 2019). Long-term studies further show that juvenile survival is closely related to precipitation and water-use traits (Ehleringer and Driscoll 2022). Rather than representing an active “sacrifice” of juveniles, this pattern is better interpreted as environmental filtering, whereby individuals with traits better suited to drought are more likely to persist (Balazs et al. 2022). This filtering may contribute to the subsequent stability of the *H. ammodendron* population.

Although juvenile *H. ammodendron* individuals experience high mortality, surviving individuals may rapidly increase in size and ecological importance, partly compensating for losses during early establishment. High juvenile mortality is common in desert shrubs, where most newly recruited individuals may die before reaching maturity and survival is strongly size dependent (Bitter and Ehleringer 2021). The IVC-based survivorship curve

observed here approximated the Deevey type II pattern, suggesting that the population maintained a relatively balanced demographic structure despite substantial early-stage losses. Such persistence is consistent with evidence that desert shrubs exhibit strong growth–survival trade-offs across water-limited environments (Custer et al. 2022).

The coordinated increases in crown width and basal diameter of surviving juveniles may enhance aboveground resource capture and overall structural development, thereby improving their ability to persist under stressful desert conditions. However, juvenile recruitment remains highly sensitive to precipitation and other biotic constraints, which can strongly regulate first-year survival in drylands (Weber-Grullon et al. 2022). As individuals develop, competitive effects may also change markedly; experimental evidence from arid shrub systems shows that competition can strongly suppress shrubs during early establishment but becomes less important once woody individuals are well established (Pierce et al. 2019). Accordingly, the relatively stable survival and high importance values of middle-aged *H. ammodendron* individuals in the present study likely reflect successful passage through the most vulnerable recruitment stage and increasingly stable resource acquisition, thereby contributing to overall population persistence.

The gradual decline in the competitive advantage of older *H. ammodendron* individuals suggests that adult persistence may buffer population stability under desert stress. Long-term experiments in drylands show that dominant shrubs can remain comparatively resistant to prolonged drought, partly through access to deeper water sources (Winkler et al. 2019). In contrast, recruitment is generally more vulnerable, and seedling establishment represents a major constraint on dryland restoration (Shackelford et al. 2021). Seed germination within *Haloxylon* is also strongly inhibited by osmotic stress, emphasizing the sensitivity of early life stages to water limitation (Rasheed et al. 2019). Therefore, restoration of *H. ammodendron* should prioritize improvement of juvenile establishment conditions while maintaining a structurally balanced population. Water availability is a major determinant of revegetation success in arid environments, and measures that improve early-stage moisture conditions can enhance restoration outcomes (Stapleton et al. 2024).

5. Conclusion

(1) From 2015–2025, *Haloxylon ammodendron* growth in the Badain Jaran Desert showed significant temporal heterogeneity. Basal diameter was the primary variability indicator (CV: 120.08%–121.57%), exhibiting a sharp decline followed by a slight increase, significantly inhibited by drought and intraspecific competition (Kruskal-Wallis: $\chi^2=463.259$, $df=2$, $P<0.01$).

(2) Allometric models for *H. ammodendron* traits were significant ($P<0.01$). Trait correlation peaked in 2020 (R^2 0.622–0.774) then dropped by 2025 (R^2 0.348–0.544), showing resource allocation is temporally regulated (ANCOVA interaction: $P<0.01$).

(3) The survival curve of *H. ammodendron* reveals dual-dimension differentiation: BDT-based is Deevey type III ($R^2=0.92$), with 96.5% survival drop in age classes 1–3, indicating a “recruitment bottleneck”. IVC-based approximates Deevey type II ($R^2=0.88$), where rapid juvenile growth masks mortality, enabling balanced competition.

(4) *H. ammodendron* adapts to desert stress via dual strategies: “high juvenile screening & adult stability” for population continuity, and “life-cycle equilibrium competition” for community dominance. This underpins desert restoration theory.

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Authors' contributions

Conceptualization: H.S. and C.W.; methodology: H.S., S.L. and B.Z.; formal analysis: H.S.; data curation: H.S., S.L. and B.Z.; validation and investigation: B.Z.; software and supervision: S.L.; resources: C.W. and B.Z.; visualization: B.Z.; funding acquisition and project administration: C.W.; writing—original draft preparation: H.S. and B.Z.; writing—review and editing: C.W. and B.Z..

Data availability

The data that supports the findings of this study are available in the supplementary material of this article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

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