Pak. J. Bot., 58(1): 127-132, January 2026.

ARTICLE | DOI: http://dx.doi.org/10.30848/PJB2026-1(21)

AGE STRUCTURE AND DEMOGRAPHIC DYNAMICS OF *AMMOPIPTANTHUS NANUS* AN ENDANGERED SPECIES ENDEMIC TO THE WESTERN TIANSHAN MOUNTAINS

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Abstract

Ammopiptanthus nanus is an endangered shrub that is endemic to the western Tianshan Mountains. The populations have continuously declined due to anthropogenic disturbances recent years. Incorporating static life table, reproductive life table, and Leslie matrix model, population age structure and demographic dynamics were estimated to reveal the population viability of *A. nanus*. The Deevey-II survival curve, low net reproductive rate (R_0 = 0.7831), low intrinsic rate of increase (r_m = -0.0281), and low finite rate of increase (λ = 0.9723), thus the age structure of the population exhibits a declining type. Leslie matrix model predicted the population size of *A. nanus* would decline by 35.8% over the next two decades. The small population size and rarity of seedlings and juveniles suggested difficulties in regeneration and a significant risk of extinction. With the aim of maintaining the viability of the species in the conservation plan, we suggest establishing a nature reserve to minimize human interference and setting up a germplasm resource nursery for the species' regeneration.

Key words: *Ammopiptanthus nanus*; Age structure; Survival curve; Leslie matrix; Demographic dynamics

Introduction

As a fundamental evolution unit, population serve as bridge connecting individuals, communities and ecosystems, and play an important role in maintaining the ecosystem stability (Li & Zhang, 2015). Population viabilities analysis (PVA), which incorporates static life tables, survival curves, reproductive life table and simulation models, could reflect current survival status of a species and its interactions with the environment, thereby enabling predictions about its development tendency (Zhang *et al*., 2020a). With sufficient data, PVA can effectively forecast the likelihood of population extinction within a given time frame, demonstrating reliable performance (Shaffer, 1990; Boyce, 1992; Brook *et al*., 2000). Due to this, it has been regarded as a valuable tool in developing conservation strategies for threatened species (Omelko *et al*., 2018; Carroll *et al*., 1996), and has been successfully applied in several threatened taxa (Chhetri *et al*., 2016; Akçakaya, 2000).

PVA compromises various kinds of models, such as birth-death process model, matrix model, single population stochastic model, and metapopulation stochastic model (Tian *et al*., 2011). Within these models, Leslie matrix model is a fundamental approach to model the life processes of species, with survival and reproduction rates as the critical parameters (Reed *et al*., 2002; Cushing & Zhou, 1994). It may help reveal the impact of biotic and abiotic factors on demographic dynamics, to model and predict population size changes across different age groups (Smith, 1974). This model has been widely used in threatened plants to provide useful conservation strategies, such as *Paeonia qiui* and *Disanthus cercidifolius* (Zhang *et al*., 2020b; Xiao *et al*., 2004).

Ammopiptanthus nanus (Popov) S.H. Cheng is an evergreen broad-leaved shrubs endemic to the deserts of Central Asia, and is a Tertiary relict originating from the coast of Tethys (Zhao & Zhu, 2003; Feng *et al*., 2019; Duan & Zhang, 2020). The genus comprises two species, *A. mongolicus* and *A. nanus* (Cui, 1998). Phylogenetic analyses also revealed two distinct *Ammopiptanthus* lineages corresponding to western Xinjiang and the Alxa Desert distributions, with divergence estimated at ~0.77 Mya. The extreme climatic conditions during this period likely drove the genus-level diversification (Su *et al*., 2016). *Ammopiptanthus mongolicus* grows in the Alxa-Ordos area in Inner Mongolia and extends into southern Mongolia, while *A. nanus* is distributed in the western Tianshan Mountains in the far west (Cui, 1998). *Ammopiptanthus nanus* is found only in valleys of Wuqia County, China, as well as in the valley regions of Naryn State, Kyrgyzstan (Cui, 1998). For the abundance in alkaloids and flavonoids, it can be used as a remedy for chilblains and chronic rheumatoid arthritis (Ji *et al*., 2013; Wei *et al*., 2007). Moreover, this species exhibits resilience to cold, drought and salinity, making it highly valuable for combating desertification. Additionally, its evergreen nature makes it a popular choice for ornamental gardening (Wei *et al*., 2007).

Received: 06-02-2025 | Revised: 16-05-2025 | Accepted: 20-06-2025 | Online: 19-09-2025

Due to its small population size and distribution area, *A. nanus* has been list on list of wild plants under state protection in Xinjiang (http://www.forestry.gov.cn). Be that as it may, anthropogenic disturbances to *A. nanus* populations, such as grazing, logging, flooding, insect pests, and road-building, have never been stopped over the past two decades (Li *et al*., 2023). Given the continuous decline of *A. nanus* populations, what is the age structure like and what is the status of population viability? In this study, we used static life table analysis, survival curve assessment, reproductive life table analysis, and Leslie matrix model to address the following questions: (1) What is the population structure of *A. nanus*? (2) What is the demographic tendency over the next two decades? (3) What can be done to stop the tendency of the species to decline? This study is the first time to combine Leslie matrix with static life tables for analysis of population demographic dynamics of the species, making it distinct from our prior work (Zhu *et al*., 2025).

Materials and Methods

Study site: Wuqia County is located on the northern Pamir Plateau, the western Tarim Basin, and the confluence of the Tianshan and Kunlun Mountains. Here the annual range of temperature is 29.9℃~34.7℃, with an average temperature of 7.3℃. The mean annual precipitation is 172 mm, the average annual sunshine duration is 2797.2 hours, and the mean frost-free period spans 135 days (Yang, 2018).

In 2023, twelve 10 m×10 m quadrats were set in the valleys to study the population structure, and the geographical coordinates of the quadrats were also recorded (Figs. 1 and 2). The crown sizes were measured using a tape measure, and the basal diameters were measured with a vernier caliper. The plumpness rate of seeds of *A. nanus* were collected in August from the 12 quadrats, was calculated (Zhang *et al*., 2020b).

Fig. 1. Habitat of *A. nanus*.

Age structure: The size of the crowns in desert shrubs may reflect the age of the individual, and thus could be used to estimate the age of the shrub (Wei *et al*., 2005; Jin *et al*., 2010). A scale of 10 cm was used to classify the age of *A. mongolicus* (Wei *et al*., 2005). Having a close phylogenetic relationship between *A. mongolicus* and *A. nanus*, the same criteria were also used in *A. nanus*.

Static life table, survival curve and reproductive life table: Static life table was created for each population following the methods of Wu *et al*., (2012). In the static life table, X is the age class; a_x is the alive number at age x, l_x is the standardized alive number at age x, where $l_x = a_x/a_o \times 1000$; d_x is the death number from age x to x+1, where $d_x = l_x - l_{x+1}$; q_x is the mortality at age x, where $q_x = d_x/l_x$; L_x is the alive number from age x to x+1, where $L_x = (l_x/l_{x+1})/2$; T_x is the total alive number beyond age x, where $T_x = \int_x^\infty L_x$; e_x is the life expectation at age x, where $e_x = T_x/l_x$; K_x is the disappearance rate, where $K_x = \ln(l_x) - \ln(l_{x+1})$ (Wu *et al*., 2012).

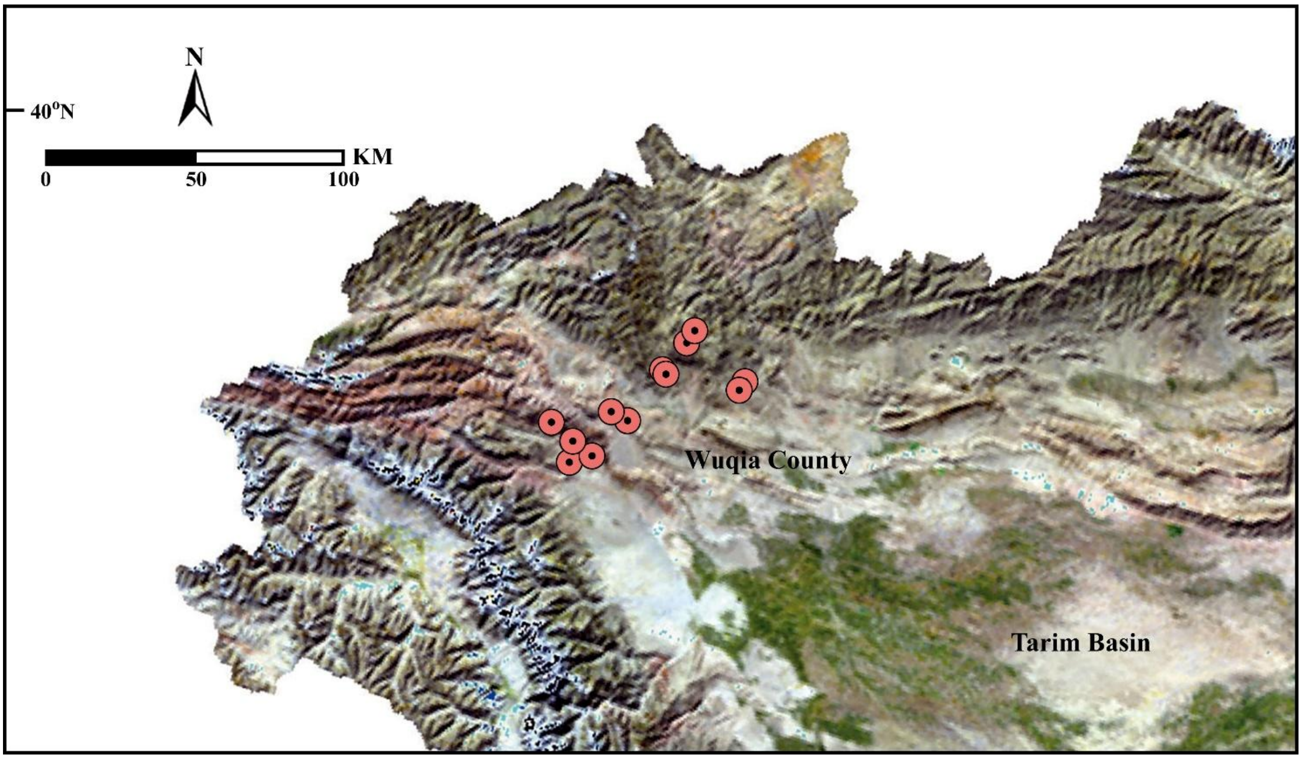

Fig. 2. Geographic locations of 12 quadrats of *A. nanus* in Wuqia County, Xinjiang.

The survival curve was plotted with the age class (x) and lnl_x (Zhang *et al*., 2020a). The Deevey type of the survival curve was determined by comparing R^2 values of two models: $N_x = N_0e^{-bx}$ and $N_x = N_0x^{-b}$. A higher R^2 value indicates a better fit of the model to the data (Zhang *et al*., 2020a). The corresponding Deevey type was then determined based on the model with the better fit, following the method of Hett & Loucks (1976). In the reproductive life table, X is the age class; l_x is the survival rate at the x age class; m_x is the mean number of progeny at age x. The population net reproduction rate (R_0), intrinsic growth rate (r_m), finite growth rate (λ), and mean generation time (T) were calculated as follows: $R_0 = \sum l_xm_x$, $r_m = \ln R_0/T$, $\lambda = N_{t+1}/N_t$, $T = (\sum Xl_xm_x)/(\sum l_xm_x)$ (Zhang *et al*., 2020a). The raw data were analyzed using SPSS v. 26.0, and diagrams were constructed with Origin v. 2022 and R v. 4.4.2.

Leslie matrix model: In the Leslie matrix, P_x (the sum of survival rates since age x) was estimated by the following equation: $P_x = (l_{x+1} + l_{x+2})/(l_x + l_{x+1})$, where l_x corresponds to the survival rate in static life table; f_x (the mean number of progeny survives to the next age at x age) was calculated by the following equation: $f_x = P_x * m_x$, where m_x corresponds to the mean number of progeny in the reproductive life table. The population size over next generation was estimated using the equation $N_{t+1} = M \cdot N_t = M_{t+1} \cdot N_0$, where N_t the population size in the t time interval, N_0 the population size at the time of this survey, and M the Leslie matrix, and M^{t+1} the matrix M at t+1 generation (Li *et al*., 2022; Wu *et al*., 2012).

Results

Age structure: A total of 18 age classes were recognized in this study, which were assigned further to 4 stages, that was seedling (0-10), juvenile (10-20), adult (20-60), and old (≥60). Of the total population examined, old individuals were accounted for 48.1%, adults for 29.9%, juveniles for 15.0%, and seedlings for 7.0%. *Ammopiptanthus nanus* exhibited a well-defined inverted pyramid shape in its age structure, indicating a declining trend (Fig. 3).

Static life table, survival curve and reproductive life table: The mortality rate (q_x) and disappearance rate (K_x) in *A. nanus* both increased with age, reaching a maximum of 0.67 and 1.10 in class XVII, respectively (Table 1). The mortality rate of seedlings was high, reaching at two death peaks at class III and XVII as showed by q_x and K_x. The e_x values fluctuated with the age, reaching a minimum of 1.0 at class XVIII (Table 1).

The exponential and power equation estimated for the survival curve were N_x=7.321$e^{-0.151x}$ (R^2 = 0.758, F = 50.159, p<0.001) and N_x = 7.559$x^{-0.844}$ (R^2 = 0.531, F = 18.094, p=0.001). The R^2 value of the exponential equation model was higher than that of the power equation model, thus we selected the exponential equation to create the survival curve. The approximately diagonal shape of the curve suggested a Deevey-II type (Fig. 4).

The values for net growth rate (R_0), intrinsic growth rate (r_m), and finite growth rate (λ) were 0.7831, -0.0281, and 0.9723, respectively, indicating the difficulty of self-renewal for *A. nanus*. The mean generation time was estimated to be 11.11a (Table 2).

Leslie matrix: The seed-setting rate for adult individuals of *A. nanus* was 1.3%, the seed plumpness rate was 67%, and natural germination rate was 17%. The effective seed yield rate of *A. nanus* was 0.15% (Xiao *et al*., 2004). For all tested generations (N_0-N_{20}), the Leslie matrix simulations demonstrated a consistent demographic trajectory: populations initially peaked in Age Class II, underwent a sharp decline by Age Class IV, displayed transient recovery at intermediate age classes, and progressively diminished to minimal levels by Age Class XVIII. The Leslie matrix model predicted that the number of individuals in each age class would decline over the next two decades (Table 3), with the total number of invested individuals falling from 187 in 2023 to 120 in 2043. The tendency to decline was consistent with the results of reproductive life table (Fig. 5).

Table 1. Static life table of *A. nanus* populations.

X	a_x	l_x	$\ln l_x$	d_x	L_x	T_x	q_x	e_x	K_x
I	13	464	6.14	-536	732	6393	-1.15	13.77	-0.77
II	28	1000	6.91	393	804	6071	0.39	6.07	0.50
III	17	607	6.41	357	429	5179	0.59	8.53	0.89
IV	7	250	5.52	-357	429	4607	-1.43	18.43	-0.89
V	17	607	6.41	71	571	4357	0.12	7.18	0.13
VI	15	536	6.28	107	482	3750	0.20	7.00	0.22
VII	12	429	6.06	0	429	3214	0.00	7.50	0.00
VIII	12	429	6.06	71	393	2786	0.17	6.50	0.18
IX	10	357	5.88	-107	411	2357	-0.30	6.60	-0.26
X	13	464	6.14	107	411	2000	0.23	4.31	0.26
XI	10	357	5.88	0	357	1536	0.00	4.30	0.00
XII	10	357	5.88	179	268	1179	0.50	3.30	0.69
XIII	5	179	5.18	-36	196	821	-0.20	4.60	-0.18
XIV	6	214	5.37	71	179	643	0.33	3.00	0.41
XV	4	143	4.96	0	143	429	0.00	3.00	0.00
XVI	4	143	4.96	36	125	286	0.25	2.00	0.29
XVII	3	107	4.67	71	71	143	0.66	1.33	1.10
XVIII	1	36	3.58	-	18	36	-	1.00	-

X: the age class; a_x: the alive number at age x; l_x: the standardized alive number at age x; d_x: the death number from age x to x+1; q_x: the mortality at age x; L_x: the alive number from age x to x+1; T_x: the total alive number beyond age x; e_x: the life expectation at age x; K_x: the disappearance rate

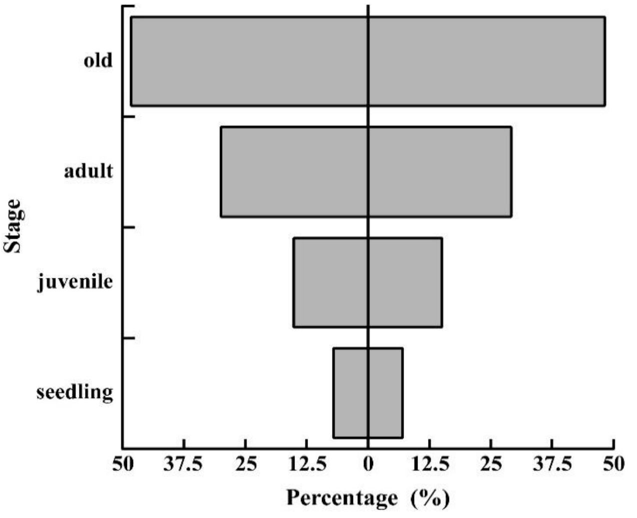

Fig. 3. Age structure of *A. nanus* populations.

Fig. 4. Survival curve of *A. nanus* populations.

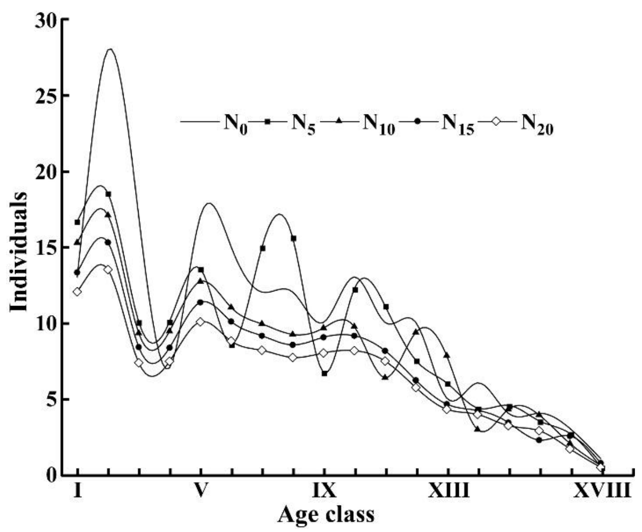

Fig. 5. Demographic dynamics of *A. nanus* in the next two decades. (N_0: number of existing individuals in each age group; N_5: number of individuals in each age class after the next five age classes; N_{10}: number of individuals in each age class after the next ten age classes; N_{15}: number of individuals in each age class after the next fifteen age classes; N_{20}: number of individuals in each age class after the next twenty age classes).

Table 2. Reproductive life table of *A. nanus* populations.

X	l_x	m_x	l_xm_x	Xl_xm_x	
I	0.4640	0	0	0	
II	1.0000	0	0	0	
III	0.6070	0.0345	0.0209	0.0628	
IV	0.2500	0.0465	0.0116	0.0465	
V	0.6070	0.0615	0.0373	0.1867	
VI	0.5360	0.0780	0.0418	0.2508	
VII	0.4290	0.0990	0.0425	0.2973	
VIII	0.4290	0.1230	0.0528	0.4221	R_0=0.7831
IX	0.3570	0.1485	0.0530	0.4771	T=11.1073
X	0.4640	0.1770	0.0821	0.8213	r_m=-0.0281
XI	0.3570	0.2100	0.0750	0.8247	λ=0.9723
XII	0.3570	0.2445	0.0873	1.0474	
XIII	0.1790	0.1770	0.0317	0.4119	
XIV	0.2140	0.3210	0.0687	0.9617	
XV	0.1430	0.3645	0.0521	0.7819	
XVI	0.1430	0.4110	0.0588	0.9404	
XVII	0.1070	0.4590	0.0491	0.8349	
XVIII	0.0360	0.5100	0.0184	0.3305	

X: the age class; l_x: the survival rate at the x age class; m_x: the mean number of progeny at age x

Discussion

Age structure: The inverted pyramid age structure, low net reproductive rate and low finite growth rate all pointed to a declining age structure of *A. nanus*. The rather low survival rate of seedlings has led to the rarity of seedlings (Table 1), that was speculated to be primarily responsible for the declining structure. Seedling rarity is common among endangered desert plants, generally resulting in difficulty in regeneration (Liu *et al*., 2023). For *A. nanus*, the low survival rate of seedlings could be attributed to multiple factors, both external and intrinsic. *Ammopiptanthus nanus* grows in areas with abundant groundwater, such as alluvial fans in front of mountains or seasonal runoff channels. The research conducted by Yang (2018) indicates that the average annual precipitation in Wuqia County during spring is only 1.81 mm, and germination of *A. nanus* seeds relies primarily on snowmelt in early spring (Yang, 2018). The snow melts during the day, but freezes at night (Zhu *et al*., 2022). Intermittent snowmelt typically leads to unstable water supplies in the soil, driving the seedlings to mass death. Unusually low temperatures in the local mountains, such as cold spells in late spring, occur frequently and also injure seedlings (Ding *et al*., 2006). In addition to environment factors, high rates of insect predation also contribute to the rarity of seedlings. Our field observations have found high seed predation rates up to 50% in some quadrats, and the usual pest of *A. nanus* has been reported as *Etiella zinckenella* (Pan *et al*., 2004; Fattah *et al*., 2023). Anthropogenic activities are the primary drivers behind the loss of a significant proportion of Earth's plant species diversity (Feng *et al*., 2017). They have been found to strongly correlate with species and population declines (Scharlemann *et al*., 2005; Linares *et al*., 2009). As well as, anthropogenic perturbation, such as frequent grazing, is another threat to the seedlings. As an intrinsic factor, the thick and hard coat of seeds hinders the seed germination of *A. nanus*. Laboratory experiments have shown that 10 to 30 minutes of immersion in concentrated sulfuric acid is required to remove the waxy layer on the surface of seed to break dormancy (Yang *et al*., 2004). In natural conditions, however, there is generally insufficient moisture penetration into the seed coat due to low precipitation, resulting in low germination rates. On the whole, the external environment conditions, insect predation, anthropogenic perturbations, self-limitation result in low survival rate of seeds and the demographic decline of *A. nanus*.

Population dynamics: Predicted by the Leslie matrix model, demography of *A. nanus* would decline by 35.8% over the next two decades. The rarity of seedlings would arise chain reaction in the long-term survival of *A. nanus*. In the surveyed quadrats, juvenile and adult individuals are both rare, suggesting a difficulty in natural regeneration. Endangered plants with habitat fragmentation generally have less competitiveness in their environments (Frankham *et al*., 2002). *Ammopiptanthus nanus*, a relict Tertiary origin, is distributed across the valleys of the western Tianshan Mountains (Chen *et al*., 2009; Du *et al*., 2021). All the *A. nanus* populations are isolated from each other at a long geological distance, with a rather small population size. The present scenario would easily induce increased chance of random genetic drift and inbreeding, resulting in a reduction of genetic diversity. This has been verified in our population genetics study of *A. nanus*, which exhibits remarkably limited genetic diversity (mean He = 0.09) has been found within the species, as inferred from single nucleotide polymorphism (SNP) data generated via double-digest restriction site associated DNA (ddRAD) profiling (unpublished). Declining population size combined with the loss of genetic diversity in *A. nanus* may weaken population fitness and viability, pushing the species to an extinction vortice. The predicted declined trend of *A. nanus*, is consistent with some other endangered species, such as *Ammopiptanthus mongolicus* and *Paeonia qiui* (Wu *et al*., 2012; Zhang *et al*., 2020a).

Conservation implications: The inverted pyramidal age structure and declining demographic trend provide conservation implications for *A. nanus*. Habitats of *A. nanus* continue to shrink as a result of anthropogenic activities such as cage grazing, mining, and the construction of reservoirs. The remnant habitats and populations should be protected immediately. To minimize human disturbance, it is recommended to establish a nature reserve in Wuqia County to reduce human disturbance. Additionally, fencing should be installed around the existing populations to protect against livestock grazing. Also, artificial tending of the population, such as insecticides application, should be carried out to control infestations. A germplasm resource nursery should be set up for the regeneration of the species. Seeds of *A. nanus* should be collected across all the populations, and then seedlings should be cultivated by artificial propagation and transplanted into the existing populations to augment the population size. In the meantime, suitable habitats in the local area should be identified for the reconstruction of new *A. nanus* population.

Table 3. Leslie matrix of *A. nanus* populations.

0	0	0.0345	0.0620	0.0519	0.0694	0.0907	0.1285	0.1485	0.1539	0.1576	0.1793	0.1608	0.2572	0.3186	0.2351	0.1156	0
1.0977																	
	0.5333																
		1.0000															
			1.3337														
				0.8443													
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												0.9084					
													0.8011				
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Conclusions

The age structure of *A. nanus* is inverted pyramid, characterized by a high proportion of older individuals and a low proportion of seedlings. The declining age structure was also supported by a Deevey-II type of survival curve. Leslie matrix model predicted that the population size of *A. nanus* will continue to decrease over the next two decades. The small population size and rarity of seedlings imposed a significant risk of further extinction. There is an urgent need to protect the remnant populations and habitats, augment population sizes, and rebuild new populations. In future study, it is advisable to establish multiple long-term monitoring plots and continuously track the population of *A. nanus*, collecting detailed data on population size, age structure, and spatial distribution. These data can be utilized to construct more accurate population dynamics models, analyze the changing patterns of the population at different spatial and temporal scales, and predict the future development trends of the population.

Acknowledgements

This work was supported by Natural Science Foundation of Xinjiang Uygur Autonomous Region (2024D01E07), and Xinjiang Key Laboratory of Special Species Conservation and Regulatory Biology Bidding Project (XJDX1414-2022-01).

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