


POPULATION STRUCTURE AND QUANTITATIVE CHARACTERISTICS OF *TETRACENTRON SINENSE* (TROCHODENDRACEAE) IN LEIGONG MOUNTAIN NATURE RESERVE, CHINA

ESTRUCTURA POBLACIONAL Y CARACTERÍSTICAS *TETRACENTRON SINENSE* CUANTITATIVAS DE (TROCHODENDRACEAE) EN LA RESERVA NATURAL DE LA MONTAÑA LEIGONG, CHINA

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Abstract

Background: Knowledge of plant population structure facilitates conservation, management, and utilization of endangered plants.

Research question: What is the current status of the natural populations of *Tetracentron sinense* in Leigong Mountain Nature Reserve (LMNR) and what future population development trends can be predicted?

Studied species: *Tetracentron sinense*.

Study site and period of research: *T. sinense* populations in LMNR in China in 2018.

Methods: The population structure and quantity dynamics of four typical patches were studied using static life tables, survival curves, survival analyses, and time series analyses.

Results: The age structures of the *T. sinense* populations were spindle-shaped, with few seedlings and saplings, and Deevey type II and III survival curves. The mortality rate (q_x) of each patch increased quickly, and then plateaued, finally increasing again. Survival rate (S_x) showed a contrary trend to q_x . Trends in cumulative mortality rate ($F_{(x)}$), killing power (K_x), mortality density ($f_{(x)}$), and hazard rate ($\lambda_{(x)}$) with increasing age class were similar: increasing at a younger age, gradually stabilizing in middle age, and then increasing slightly in older age. The number of individuals in these *T. sinense* populations was predicted to decrease sharply in future, with younger individuals being seriously deficient. The results showed that the natural populations of *T. sinense* in the LMNR were relatively stable but were in an early stage of decline.

Conclusions: The lack of younger individuals might reflect a bottleneck for regeneration of *T. sinense* populations, leading to a decline in population size.

Key words: Population structure, static life table, survival analysis, time series analysis.

Resumen

Antecedentes: El conocimiento de la estructura poblacional de una planta facilita su conservación, manejo y utilización.

Pregunta de investigación: ¿Cuál es el estado actual de las poblaciones naturales de *Tetracentron sinense* en la Reserva Natural de la Montaña Leigong (LMNR) y qué tendencias futuras de desarrollo de la población se pueden predecir?

Especies estudiadas: *Tetracentron sinense*.

Sitio y período de investigación: Poblaciones en LMNR, China, 2018.

Métodos: Se usaron tablas de vida estáticas, curvas de supervivencia, análisis de supervivencia y análisis de series de tiempo para el análisis de la estructura poblacional y dinámica de parches.

Resultados: Las estructuras de edad de las poblaciones de *T. sinense* mostraron forma de huso, con pocas plántulas y juveniles. Curvas de supervivencia Deevey tipo II y III. La tasa de mortalidad (q_x) de cada parche aumentó rápidamente, para estabilizarse y finalmente aumentar nuevamente. La tasa de supervivencia (S_x) mostró una tendencia contraria a q_x . Las tendencias en las tasas de mortalidad acumulada ($F_{(x)}$), mortalidad (K_x), densidad de mortalidad ($f_{(x)}$), y tasa de riesgo ($\lambda_{(x)}$) fueron similares con el aumento de la clase de edad. Las poblaciones naturales de *T. sinense* en el LMNR eran relativamente estables, aunque en etapa temprana de disminución. El número de individuos en poblaciones de *T. sinense* disminuirá drásticamente en el futuro, donde los más jóvenes mostrarán serias deficiencias.

Conclusiones: La ausencia de individuos más jóvenes podría reflejar un cuello de botella para la regeneración de las poblaciones de *T. sinense*, lo que lleva a una disminución en el tamaño de la población.

Palabras clave: Análisis de series de tiempo, análisis de supervivencia, estructura de población, tabla de vida estática.

Tetracentron sinense Oliver, the only species in the Trochodendraceae family (Fu & Bartholomew 2001), mainly distribute in southwestern and central China (Doweld 1998, Fu & Bartholomew 2001, Zhang *et al.* 2019). Its fossils appeared in the Eocene, indicating that this is a relict species, making it important for the study of ancient flora and phylogeny in angiosperms. Its importance in ornamental (Zhang *et al.* 2019), medicinal (Wang *et al.* 2006), and furniture products, has resulted in excessive deforestation of *T. sinense*. Thus, the populations are scattered in distribution, and their natural regeneration is very poor (Wang *et al.* 2006, Gan *et al.* 2013). As such, it is currently listed in CITES Appendix III (Convention on International Trade in Endangered Species of Wild Fauna and Flora, <https://cites.org/eng/node/41216>), and as a national second-grade protected plant in China (Fu 1992). To date, the conservation and management of the germplasm resources for *T. sinense* have attracted the most attention. Over the past 10 years, the community ecology (Tian *et al.* 2018), sporogenesis and gametophyte development (Gan *et al.* 2012), pollination ecology (Gan *et al.* 2013), seed and seedling ecology (Luo *et al.* 2010, Cao *et al.* 2012, Tang *et al.* 2013, Han *et al.* 2015, Li *et al.* 2015), and genetic diversity (Li *et al.* 2016, Han *et al.* 2017, Li *et al.* 2018) of *T. sinense* have been studied, with the aim of improving the conservation of its germplasm resources. Generally, the natural regeneration in plants is a complex process including some important links of life history, such as the production, diffusion and germination of seed, seedling settlement and sapling formation. Among them, the obstacles that occur in any link will lead to the failure of regeneration (Herrera 1991). To date, there are no relevant reports on the current situation of *T. sinense* natural population, and which link in its life history has the obstacle that causes it poor regeneration is unclear.

Plant population structure is the most basic characteristic of a population. It can reflect population dynamics and development trends, in addition to the correlation between a population and its environment, including its actual location within that environment (Chapman & Reiss 2001, Xie *et al.* 2014). Knowledge of plant population structure can illuminate the past and future trends of a population, and then elucidate the weak links in life history correlated to poor regeneration, which is of relevant for conservation, management, and utilization of endangered plants (Harper 1977). Life tables and survival curves are important tools for the evaluation of population dynamics as they show the actual numbers of surviving individuals, deaths, and survivorship trends for all age classes in the population. Life tables are also used to explain changes in population size (Smith & Keyfitz 1947, Skoglund & Verwijst 1989, Armesto *et al.* 1992). Survival curves can elucidate the trends in population changes directly and quickly (Zhang &

Zu 1999, Wu *et al.* 2000, Bi *et al.* 2001). The four survival functions (survival rate, cumulative mortality, mortality density, and hazard rate) can more accurately explain current population structure and the development parameters of a given population when combined with life tables (Harcombe 1987, Zhang *et al.* 2008). Time series analysis, an important method in population statistics, is usually used to forecast population dynamic trends in the future (Xie *et al.* 2014). Therefore, life tables and time series analyses based on the quantitative characteristics of an endangered plant population, are of practical importance for the effective conservation and management of endangered plants (Wu *et al.* 2000, Phama *et al.* 2014).

In this paper, the population structure and derived metrics of four typical *T. sinense* patches in the Leigong Mountain Nature Reserve (LMNR) were studied. The aims of the study were: (1) analyze the current status of *T. sinense* populations in the LMNR, and to reveal the weak links in life history correlated to poor regeneration; (2) predict future development trends of natural *T. sinense* populations in the LMNR; (3) put forward some strategies for the conservation and management of these endangered plants.

Materials and methods

Study area. The LMNR, located in the central part of Qiandongnan, Guizhou Province, China, is made up of steep slopes, which lead into narrow valleys and small waterfalls. It spans the four counties of Leishan, Taijiang, Jianhe, and Rongjiang, and is a watershed between the Yangtze River and the Pearl River (26° 20' 25"-26° 25' 00" N, 108° 12' 00"-108° 20' 00" E, 2,178 m asl). LMNR is characterized by a typical subtropical humid climate, with abundant rainfall and less daylight time (Chen *et al.* 2012). The mean annual temperature is about 10 °C; July is the hottest month, with an average temperature of less than 25 °C. The soil is an acidic mountain yellow soil. The mountain forests are structurally and floristically heterogeneous (Tang *et al.* 2007, Tang & Ohsawa 2009), with a distinctive vertical distribution of vegetation. The flora is mainly divided into evergreen broad-leaved forests at lower elevations (below 1,350 m asl), evergreen and deciduous broad-leaved mixed forests at middle altitudes (1,350-2,100 m asl), and deciduous broad-leaved forests at higher altitudes (over 2,100 m asl). The *T. sinense* populations in the LMNR were mainly scattered throughout evergreen and deciduous broad-leaved mixed forests. We investigated the distribution of *T. sinense* throughout the China and found that the distributions of the population of *T. sinense* were patchy. In LMNR, we found that there were four patches which were the most typical, and they could well represent the distributions of the natural population of *T. sinense*. Therefore, the four representative patches were chosen as experimental plots rather than artificial plots

(population 1: 7 ha; population 2: 1.905 ha; population 3: 7.4 ha; population 4: 7.02 ha).

Age structure. In order to minimize the damage to *T. sinense*, 19 individuals with intact growth and different diameter grades were randomly selected in these four patches and their cores were taken to determine their ages. Then the relationship between the age and the DBH of the *T. sinense* were modeled to obtain the fitting curve (Wang *et al.* 1995, Harper 1977, Zhang *et al.* 2007). According to the fitting curve, the age of all individuals in the four populations were calculated (Hett *et al.* 1976). According to the life history characteristics of *T. sinense* and the methods of Brodie *et al.* (1995) and Guedje *et al.* (2003), these populations were grouped into 11 age classes. Pre-reproductive and juvenile trees were classified as seedlings and saplings (I, 0~20 ages), or juveniles (II, 20~40 ages; III, 40~60 ages; IV, 60~80 ages; V, 80~100 ages; VI, 100~120 ages; VII, 120~140 ages). Adult trees were grouped into four age classes (VIII, 140~160 ages; IX, 160~180 ages; X, 180~200 ages; XI, 200~220 ages). The number of *T. sinense* in each age class was counted, and then the age structure of the populations was analyzed.

Population dynamics analysis. The dynamic change in number of individuals between adjacent age classes (V_n) was analyzed according to the method of Chen (1998), using the following formula:

$$V_n = \frac{S_n - S_{n+1}}{\max(S_n, S_{n+1})} \times 100\% \quad (1)$$

where S_n and S_{n+1} are the number of individuals in the n^{th} age class and the next age class, respectively. $\max(\dots)$ represents the maximum value in parentheses; $V_n \in [-1, 1]$. When $V_n > 0$, this means the number of individuals is increasing in a dynamic relationship between adjacent age classes; when $V_n < 0$, this means there is a decline in the dynamic relationship; when $V_n = 0$, the dynamic relationship is stable.

The quantity dynamic index (V_{pi}) of the age structure of these populations was obtained by weighting the number of individuals (S_n) of each age class by V_n . Because there is no V_n for the maximum age class (K), the K value was excluded (Chen 1998):

$$V_{pi} = \frac{1}{\sum_{n=1}^{k-1} S_n} \sum_{n=1}^{k-1} (S_n \cdot V_n) \quad (2)$$

Because the external environmental effect on the population age structure is not considered in equation (2), the quantity dynamic index of population age structure (V_{pi}) should be corrected accordingly, that is:

$$V_{pi}' = \frac{\sum_{n=1}^{k-1} (S_n \cdot V_n)}{k \cdot \min(S_1, S_2, S_3, \dots, S_k) \cdot \sum_{n=1}^{k-1} S_n} \quad (3)$$

where $\min(\dots)$ means the minimum value of the sequence in parentheses, and K is the age class.

Establishment of a static life table. Given that *T. sinense* is, a long-life cycles tree species, a static life table was established. Static life tables capture discrete periods of the dynamic process of aging where multiple estimate the number of surviving individuals (x) (Jiang 1992, Zhou *et al.* 1992), based on the following formulas (Silvertown 1982, Jiang 1992). According to the assumptions underlying static life tables, the age combination is stable, and the proportion of each age class remains constant (Jiang 1992). Then the data of the four populations in LMNR were corrected by smoothing technique (Proctor 1980, Brodie *et al.* 1995, Molles 2002).

$$T = \sum_x^n a_x \quad (4)$$

$$\bar{a}_x = \frac{T}{n} \quad (5)$$

where T : the sum of all the individuals in each group; n : the number of age classes in each group; a_x : individuals of each groups in the x age class; \bar{a}_x : the means of each group, which were considered to be the mid-value. Based on the differences between the maximum and minimum values of number surviving in the two groups and the difference between the means of the two groups, the number of individuals in each age class was corrected by one unit of smoothing (Jiang 1992).

$$l_x = \frac{A_x}{A_1} \times 1000 \quad (6)$$

$$d_x = l_x - l_{x+1} \quad (7)$$

$$q_x = \frac{d_x}{l_x} \times 100\% \quad (8)$$

$$L_x = \frac{(l_x + l_{x+1})}{2} \quad (9)$$

$$T_x = \sum_x^\infty L_x \quad (10)$$

$$e_x = \frac{T_x}{l_x} \quad (11)$$

$$K_x = \ln^{l_x} - \ln^{l_{x+1}} + 1 \quad (12)$$

$$S_x = \frac{l_x + 1}{l_x} \quad (13)$$

where x : the age class; a_x : number of surviving individuals in age class x ; A_x : number of surviving individuals in age class x after smoothing; A_1 : number of surviving individuals in the I age class after smoothing; l_x : standardized number of surviving individuals at the beginning of age class x (generally converted to 1,000); d_x : standardized number of individuals dying between age classes x and $x+1$; q_x : mortality rate between age classes x and $x+1$; L_x : number of surviving individuals between age classes x and $x+1$; T_x : total number of individuals from age

class x ; e_x : life expectancy at age class x ; K_x : killing power; S_x : survival rate (Silvertown 1982, Jiang 1992).

Survival curve. Taking the \ln of the number of survivors as the vertical coordinate and each age class as the horizontal coordinate, the static life table was used as a basis for the survival curve, which was fitted using SPSS 23.0 software and was modeled by R language (R Core Team 1995). OriginPro 8.0 software was used to draw the mortality rate (q_x) and killing power (K_x) curves (Feng 1983).

According to Hett & Loucks (1976), three kinds of mathematical models (linear equation, exponential equation, and power function equation) can be used to test of the best fit of the survival curve on *T. sinense* data (Deevey 1947). These were:

$$\text{Deevey type I: } N_x = N_0 + bx \quad (14)$$

$$\text{Deevey type II: } N_x = N_0 e^{-bx} \quad (15)$$

$$\text{Deevey type III: } N_x = N_0 x^{-b} \quad (16)$$

where x is age class, N_x is the natural logarithm of the standardized number of surviving individuals in age class x , $N_x = \ln l_x$; N_0 and b were directly obtained by fitting the mathematical model.

Survival analysis. To better analyze the age structure of the *T. sinense* populations in each patch of LMNR and further clarify the survival rules for the populations, this study introduced four functions. The survival functions are functions relating to any age class, which are more intuitive than the survival curve, so survival analysis has a greater practical applied value in the analysis of population life tables compared to survival curves (Yang et al. 1991, Guo 2009). The four functions (population survival rate function $S_{(i)}$, cumulative mortality function $F_{(i)}$, mortality density function $f_{(i)}$, and hazard rate function $\lambda_{(i)}$) were calculated as follows:

$$S_{(i)} = S_1 \cdot S_2 \cdot S_3 \dots S_i \quad (17)$$

$$F_i = 1 - S_{(i)} \quad (18)$$

$$f_{(ti)} = \frac{S_i - 1 - S_i}{h_i} \quad (19)$$

$$\lambda_{(ti)} = \frac{2(1 - S_i)}{[h_i(1 + S_i)]} \quad (20)$$

where i is age class; S_i is the survival rate in age class i ; $S_i = S_x$ as in equation (2); and h_i is the width of the age class.

Time series analysis. Time series analysis is often used to predict dynamic changes in population size (Xiao et al. 2004, Zhang et al. 2017). In this paper, the moving average method was applied to the analysis:

$$M_t^{(1)} = \frac{1}{n} \sum_{k=t-n+1}^t X_k \quad (21)$$

where n is the time being predicted (age class period in the study); $M_t^{(1)}$ is the population size in age class t after n

age class periods in the future, and the population size of the current k age class of X_k . The population quantity dynamics in the next 2, 4, 6, 8, and 10 age class time periods were predicted.

Results

Age structure of *T. sinense* populations. The fitting results showed that the relationship between the ages and DBH was well fitted by the linear regression ($R^2 = 0.826$, $P < 0.01$). Therefore, in 95 % prediction range, the family had better fitting observation value. The ages of *T. sinense* in four populations were calculated by the formula ($y = 3.15 \times x + 21.68$) (Figure 1). Then the structures of age were analyzed according to the ages.

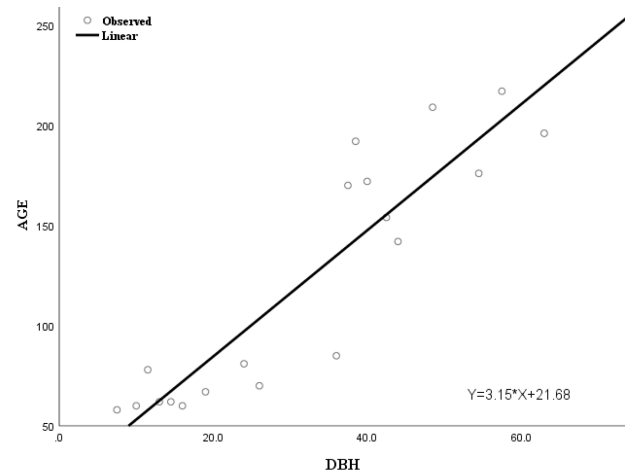


Figure 1. The relationship between DBH and Age

The age structures of the *T. sinense* populations in the LMNR were all close to the pyramid type, although their age structures were all incomplete. The maximum number of individuals in each population was observed in the II or III age class, there were relatively no seedlings and saplings existed in these populations except for Population 2 (Figure 2).

Quantitative dynamic analysis of the *T. sinense* populations. There were significant fluctuations among different age classes in these populations, with a decreasing trend between some age classes. The most obvious negative trends appeared between adjacent age classes. The dynamic indices of each population in I age class were the negative value. As the age class increased, the indexes fluctuated between positive, zero and negative (Table 1). The maximum V_{pi} appeared in Population 1, indicating the highest stability, but its value was only 50 %. Although the population dynamic indexes of the four populations were positive, the values were very small. Even though the

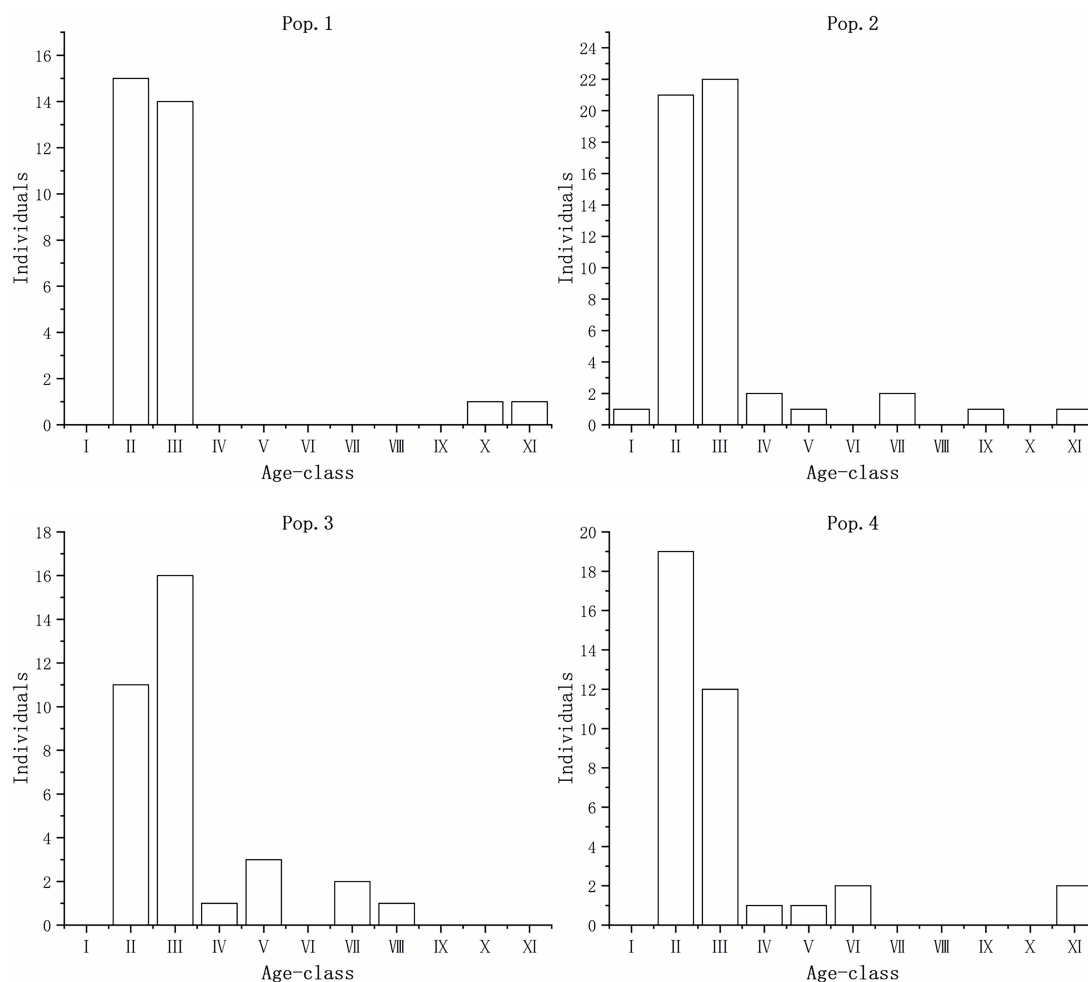


Figure 2. Age structure of *T. sinense* in the four populations

Table 1. Dynamic index (%) between adjacent age classes in the four populations of *T. sinense*

Age-class	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Pop.1	-100	6.67	100	0	0	0	0	0	-100	100	-
Pop.2	-95.24	-4.55	90.91	50	100	-100	100	-100	100	-100	-
Pop.3	-100	-31.25	93.75	-66.67	100	-100	50	100	0	0	-
Pop.4	-100	36.84	91.67	0	-50	100	0	0	0	-100	-

numbers of medium and young age class individuals in the populations were greater than those of adult individuals, the number of seedlings and saplings was much less, and the fluctuations within populations were very large (Table 2). To some extent, the four populations are all at risk.

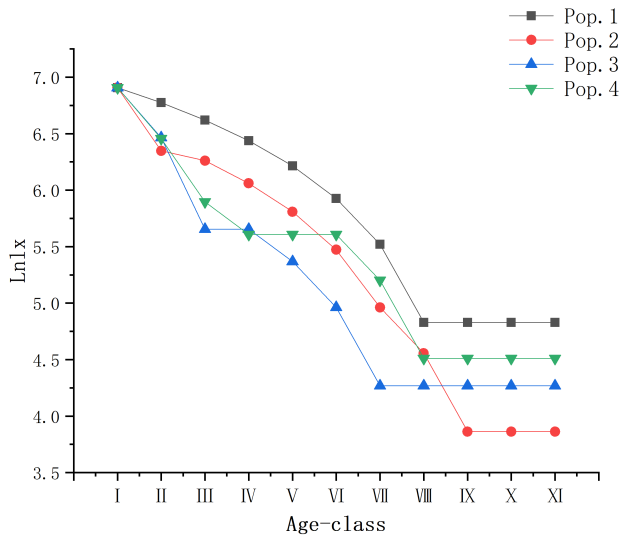
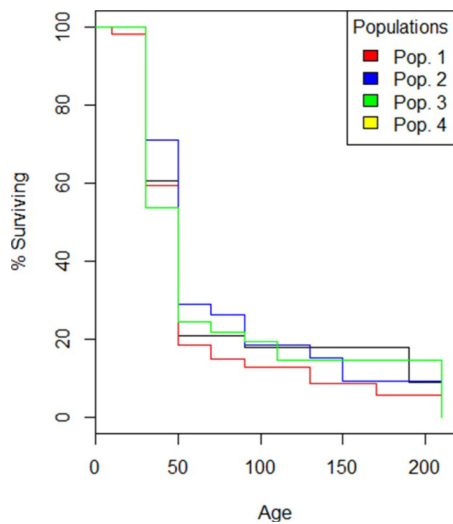
Static life tables and survival curves. As age class increased, l_x decreased, the trend of l_x in population 2 was more apparently. While a higher individual e_x was apparent in the I, II age classes. In the X and XI age classes, e_x became minimal. The d_x of populations were decreased

sharp in their younger age class, excepted population 1. Its d_x was more stable in I to VII ages classes (Table 3).

The l_x of *T. sinense* decreased rapidly in the I to VIII (Populations 1 and 2) or I to III (Populations 3 and 4) age classes, but more slowly in the IV or VII age classes, and then remained at a relatively low level thereafter (Figure 3). By modeling and comparing the survival curves of four populations, it was found that the fluctuating trend of the four populations was generally the same, and the P value = 0.6, which proved that there was no significant difference among the four populations (Figure 4).

Table 2. Dynamic index (%) of each population

Population	V_{pi}	V_{pi}'
Pop.1	50	4.55
Pop.2	46.18	4.20
Pop.3	46.75	4.25
Pop.4	25.92	2.36

**Figure 3.** Survival curve of the *T. sinense* populations**Figure 4.** Survival distributions of the *T. sinense* populations

Based on the change trend of the survival curve in the four populations, these survival curves all tended to the Deevey-II and Deevey-III types. The model simulation showed that the R^2 and F values from [equation \(13\)](#) were both greater than those from [equation \(14\)](#) did ([Table 4](#)), indicating that the survival curves of the *T. sinense*

populations 1, 2, 4 were a Deevey-II type, but population 3 were a Deevey-III typ.

Mortality rates and killing power curves. The variation patterns of q_x and K_x were similar ([Figure 5](#)). In Populations 1 and 2, there was a peak value in the VII age class; in Populations 3 and 4, the peak values appeared in the II and VI or II and VII age classes, respectively. When came to IX and X age classes, the values of two in all populations were stable. By the X and XI age classes, the q_x and K_x had dramatically increased.

Survival analysis. The survival function values were obtained according to the static life tables ([Table 5](#)). In the four populations, the $S_{(t)}$ declined monotonically with increasing age class, while the $F_{(t)}$ increased monotonically, showing a complementary trend. In the four Populations, the $S_{(t)}$ and the $F_{(t)}$ both changed noticeably during the I, II age classes, and then more gradually; while all the Populations in LMNR, a halcyon change trend appeared after the VII age class ([Figure 6](#)). The $S_{(t)}$ of the four populations generally continued to decline throughout the survival process until the individuals died.

In the four populations, the changing trend of $f_{(t)}$ was similar to that of $\lambda_{(t)}$, as both peaked in the II and IX age classes. The changing in population 4 was softer ([Figure 7](#)).

Time series analysis. The number of individuals in *T. sinense* populations in the LMNR is predicted to decline over time. When the 2-age class for new plants was reached, the numbers of surviving individuals in the younger age classes (III and IV age classes) in four Populations were predicted to decrease significantly; conversely, the number of individuals in the middle age classes all numbers of individuals remained relatively stable. When the 4-age class time for new plants was reached, the number of individuals showed a decreasing trend with increasing age class, which was similar to the change law of mortality curve. In the future, the number of individuals decreased sharply over time. When it was time for new plants to reach the 10-age class, the number of individuals predicted to survive in the four populations was no more than ten ([Table 6](#)).

Discussion

The population dynamics and changes in population structure of *T. sinense* are the result of its biological characteristics and interaction with the environment ([Grubb 1977](#)). Population structure in plants can be divided into three types, *i.e.*, increasing, stable, and declining ([Guo 2009](#)). Relict and endangered plants with long lifespans tend to be of the declining type ([Zhang et al. 2004](#), [Zhang et al. 2008](#)). The reasons for population decline in endangered plants are mainly attributed to two factors: poor

Table 3. Life table of LMNR populations

Population	Age-class	Age	a_x	A_x	l_x	$\ln l_x$	d_x	q_x	L_x	T_x	e_x	K_x	S_x
Pop.1	I	0~20	0	8	1000	6.91	125	0.13	937.5	4375	4.38	0.13	0.88
	II	20~40	15	7	875	6.77	125	0.14	812.5	3437.50	3.93	0.15	0.86
	III	40~60	14	6	750	6.62	125	0.17	687.5	2625	3.50	0.18	0.83
	IV	60~80	0	5	625	6.44	125	0.20	562.5	1937.5	3.10	0.22	0.80
	V	80~100	0	4	500	6.21	125	0.25	437.5	1375	2.75	0.29	0.75
	VI	100~120	0	3	375	5.93	125	0.33	312.5	937.5	2.50	0.41	0.67
	VII	120~140	0	2	250	5.52	125	0.50	187.5	625	2.50	0.69	0.50
	VIII	140~160	0	1	125	4.83	0	0	125	437.50	3.50	0	1
	IX	160~180	0	1	125	4.83	0	0	125	312.50	2.50	0	1
	X	180~200	1	1	125	4.83	0	0	125	187.50	1.50	0	1
	XI	200~220	1	1	125	4.83	125	1	62.5	62.5	0.50	4.83	0
Pop.2	I	0~20	1	21	1000	6.91	428.57	0.43	785.71	2976.19	2.98	0.56	0.57
	II	20~40	21	12	571.43	6.35	47.62	0.08	547.62	2190.48	3.83	0.09	0.92
	III	40~60	22	11	523.81	6.26	95.24	0.18	476.19	1642.86	3.14	0.20	0.82
	IV	60~80	2	9	428.57	6.06	95.24	0.22	380.95	1166.67	2.72	0.25	0.78
	V	80~100	1	7	333.33	5.81	95.24	0.29	285.71	785.71	2.36	0.034	0.71
	VI	100~120	0	5	238.10	5.47	95.24	0.40	190.48	500	2.10	0.51	0.60
	VII	120~140	2	3	142.86	4.96	47.62	0.33	119.05	309.52	2.17	0.41	0.67
	VIII	140~160	0	2	95.24	4.56	47.62	0.50	71.43	190.48	2	0.69	0.50
	IX	160~180	1	1	47.62	3.86	0	0	47.62	119.05	2.50	0	1
	X	180~200	0	1	47.62	3.86	0	0	47.62	71.43	1.50	0	1
	XI	200~220	1	1	47.62	3.86	47.62	1	23.81	23.81	0.50	3.86	0
Pop.3	I	0~20	0	14	1000	6.91	357.14	0.36	821.43	2428.57	2.43	0.44	0.64
	II	20~40	11	9	642.86	6.47	357.14	0.56	464.29	1607.14	2.50	0.81	0.44
	III	40~60	16	4	285.71	5.65	0	0	285.71	1142.86	4	0	1
	IV	60~80	1	4	285.71	5.65	71.43	0.25	250	857.14	3	0.29	0.75
	V	80~100	3	3	241.29	5.37	71.43	0.33	178.57	607.14	2.83	0.41	0.67
	VI	100~120	0	2	142.86	4.96	71.43	0.50	107.14	428.57	3	0.69	0.50
	VII	120~140	2	1	71.43	4.27	0	0	71.43	321.43	4.50	0	1
	VIII	140~160	1	1	71.43	4.27	0	0	71.43	250	3.50	0	1
	IX	160~180	0	1	71.43	4.27	0	0	71.43	178.57	2.50	0	1
	X	180~200	0	1	71.43	4.27	0	0	71.43	107.14	1.50	0	1
	XI	200~220	0	1	71.43	4.27	71.43	1	35.71	35.71	0.50	4.27	0
Pop.4	I	0~20	0	11	1000	6.91	363.64	0.36	818.18	2863.64	2.86	0.45	0.64
	II	20~40	19	7	636.36	6.46	272.73	0.43	500	2045.45	3.21	0.56	0.57
	III	40~60	12	4	363.64	5.90	90.91	0.25	318.18	1545.45	4.25	0.29	0.75
	IV	60~80	1	3	272.73	5.61	0	0	272.73	1227.27	4.50	0	1
	V	80~100	1	3	272.73	5.61	0	0	272.73	954.54	3.50	0	1
	VI	100~120	2	3	272.73	5.61	90.91	0.33	227.27	618.82	2.27	0.41	0.67
	VII	120~140	0	2	181.82	5.20	90.91	0.50	136.36	454.54	2.20	0.69	0.50
	VIII	140~160	0	1	90.91	4.51	0	0	90.91	318.18	3.50	0	1
	IX	160~180	0	1	90.91	4.51	0	0	90.91	227.27	2.50	0	1
	X	180~200	0	1	90.91	4.51	0	1	90.91	136.36	1.50	0	1
	XI	200~220	2	1	90.91	4.51	90.91	1	45.45	45.45	0.50	4.51	0

DBH: diameter at breast height; a_x : individual number of age class x; A_x : the revised data of a_x ; l_x : the standardized number of surviving individuals of age class x; $\ln l_x$: the natural logarithm of l_x ; d_x : the standardized number of death individuals from age class x to age class x+1; q_x : mortality from age class x to age class x+1; L_x : the number of surviving individuals from age class x to age class x+1; T_x : the total individual number of age class x and age classes older than x; e_x : life expectancy of individuals in the age class x; K_x : killing power; S_x : survival rate.

regenerative ability and adaptation (including poor seed set and low germination), and anthropogenic factors (over-exploitation, over-grazing, forest floor denudation) (Gupta & Chadha 1995, Jasrai & Wala 2001). In our study, there was a significant positive correlation between age and DBH, the ages can be well fitted by the DBH in LMNR (Hett *et al.* 1976). The age structures of the *T. sinense* populations in the LMNR were all close to the pyramid type, with the survival curve approximating a Deevey-II type and Deevey-III type; in the four populations of LMNR, their survival was similar. The population dynamic indexes of these populations (V_{pi}) were all greater than zero. However, the dynamic index between adjacent age classes was negative, especially for the I age class. Furthermore, the seedling and sapling individuals were usually lacking that was consistent with those of *Davidia involucrata* (Liu *et al.* 2012). These results indicated that most of the *T. sinense* populations investigated in the LMNR were relatively stable, but some of them were in early recession (Deevey 1947).

Table 4. Test models fitted to the survival curve of the *T. sinense* population

Population	Equation	R^2	F	Type
Pop.1	$N_x = 7.44e^{-0.04x}$	0.931	120.609	Deevey-II
	$N_x = 7.63x^{-0.18}$	0.797	35.314	Deevey-III
Pop.2	$N_x = 7.59e^{-0.06x}$	0.952	178.981	Deevey-II
	$N_x = 7.83x^{-0.26}$	0.798	35.566	Deevey-III
Pop.3	$N_x = 6.89e^{-0.05x}$	0.895	76.858	Deevey-II
	$N_x = 7.32x^{-0.23}$	0.923	108.170	Deevey-III
Pop.4	$N_x = 6.97e^{-0.04x}$	0.926	117.879	Deevey-II
	$N_x = 7.27x^{-0.19}$	0.895	76.926	Deevey-III

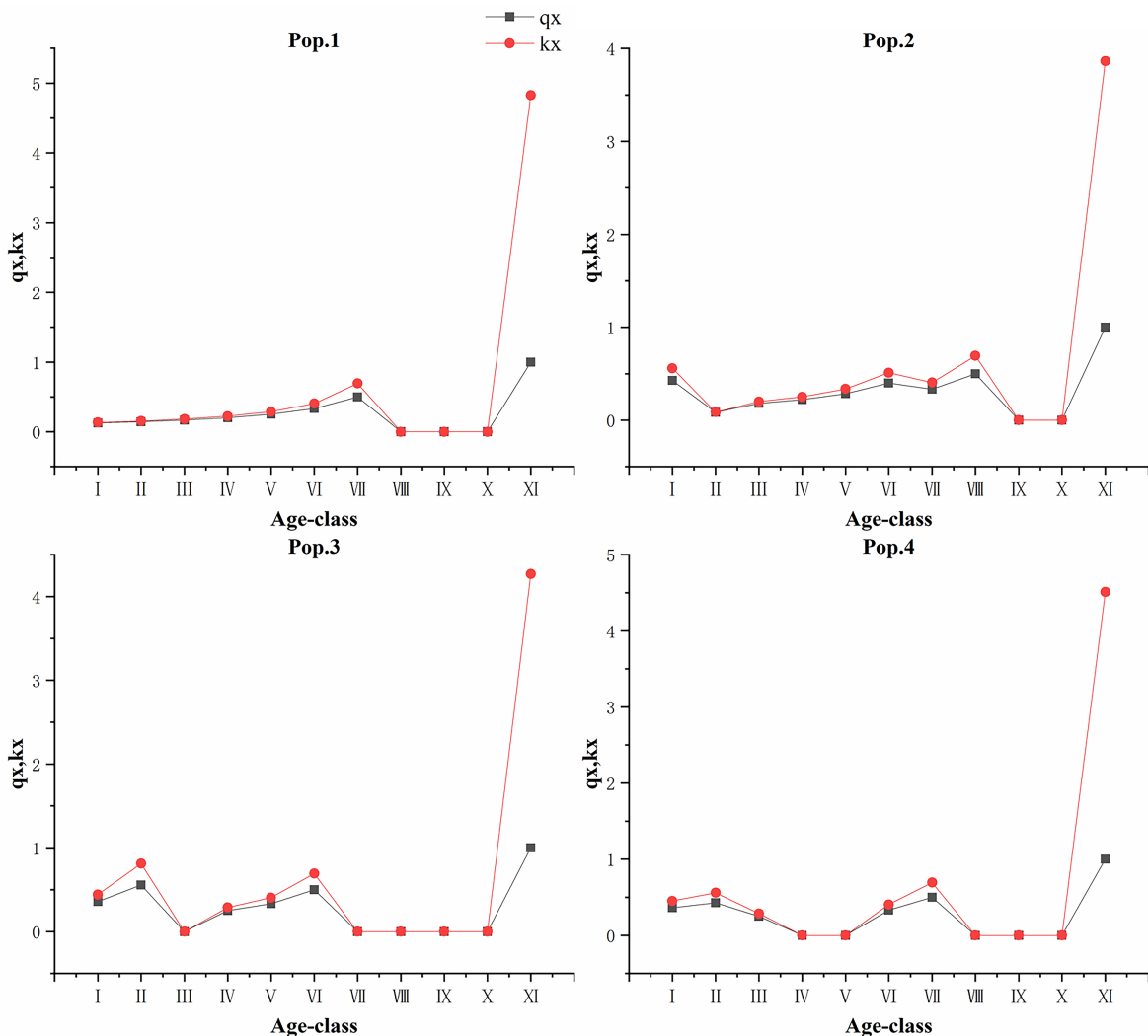


Figure 5. Mortality (q_x) and killing power (K_x) curve of the *T. sinense* populations

Table 5. Functional values of survival analysis of *T. sinense* population in LMNR

Population	Age-class	$S_{(t)}$	$F_{(t)}$	$f_{(t)}$	$\lambda_{(t)}$	Population	Age-class	$S_{(t)}$	$F_{(t)}$	$f_{(t)}$	$\lambda_{(t)}$
Pop.1	I	0.88	0.13	0.044	0.007	Pop.3	I	0.64	0.36	0.032	0.022
	II	0.75	0.25	0.006	0.014		II	0.29	0.72	0.018	0.056
	III	0.63	0.375	0.006	0.023		III	0.29	0.72	0	0.056
	IV	0.50	0.50	0.006	0.033		IV	0.21	0.79	0.004	0.065
	V	0.38	0.63	0.006	0.045		V	0.14	0.86	0.004	0.075
	VI	0.25	0.75	0.006	0.06		VI	0.07	0.93	0.004	0.087
	VII	0.13	0.88	0.006	0.078		VII	0.07	0.93	0	0.087
	VIII	0.13	0.88	0	0.078		VIII	0.07	0.93	0	0.087
	IX	0.13	0.88	0	0.078		IX	0.07	0.93	0	0.087
	X	0.13	0.88	0	0.078		X	0.07	0.93	0	0.087
	XI	0	1	0.006	0.1		XI	0	1	0.004	0.1
Pop.2	I	0.57	0.43	0.029	0.027	Pop.4	I	0.64	0.36	0.032	0.022
	II	0.52	0.48	0.002	0.031		II	0.36	0.64	0.014	0.047
	III	0.43	0.57	0.005	0.040		III	0.27	0.73	0.005	0.057
	IV	0.33	0.67	0.005	0.050		IV	0.27	0.73	0	0.057
	V	0.24	0.76	0.005	0.062		V	0.27	0.73	0	0.057
	VI	0.14	0.86	0.005	0.075		VI	0.181	0.82	0.005	0.069
	VII	0.01	0.91	0.002	0.083		VII	0.09	0.91	0	0.083
	VIII	0.05	0.95	0.002	0.091		VIII	0.09	0.91	0	0.083
	IX	0.05	0.95	0	0.091		IX	0.09	0.91	0	0.083
	X	0.05	0.95	0	0.091		X	0.09	0.91	0	0.083
	XI	0	1	0.002	0.10		XI	0	1	0.005	0.1

$S_{(t)}$: The population survival rate; $F_{(t)}$: Cumulative mortality rate; $f_{(t)}$: Mortality density rate; $\lambda_{(t)}$: Hazard rate.

The mortality rate and killing power curve can be seen to reflect the quantity dynamic change of *T. sinense* populations. The two curves for these populations showed that two peaks appeared in the II and IX age classes, or the VII age class. The peak in the II age class suggested that the juveniles in *T. sinense* populations were vulnerable to pests and diseases and adverse environments due to lower competitive ability (Han *et al.* 2015, Li *et al.* 2018); these harsh environmental conditions would result in the greater mortality rate of juveniles, this characteristic was common with *Abies fanjingshanensis*, the rare and endangered plant endemic to Guizhou (Li *et al.* 2011). In addition, the rapid growth of saplings into juveniles would gradually increase inter- and intra-species competition for limited environmental resources (such as light and mineral nutrition) in the *T. sinense* community (Tian *et al.* 2018).

This phenomenon might explain the higher mortality rate of juveniles.

Previous studies have showed that a sufficient number of younger individuals are a prerequisite for the successful regeneration of a tree population (Pala *et al.* 2012, Dutta & Devi 2013), especially for endangered species (Xie & Chen 1999, Guo 2009). Therefore, the deficiency of seedlings, saplings and the greater mortality rate of juveniles may cause a bottleneck in the regeneration and recovery of these natural *T. sinense* populations, which might eventually result in population decline (Cao *et al.* 2012). Therefore, the apparently relatively stable population of *T. sinense* might already be in the early stages of decline, similar to that reported for *Emmenopterys henryi* (Kang *et al.* 2007) and *Aloe peglerae* (Phama *et al.* 2014).

Population characteristics of *T. sinense*

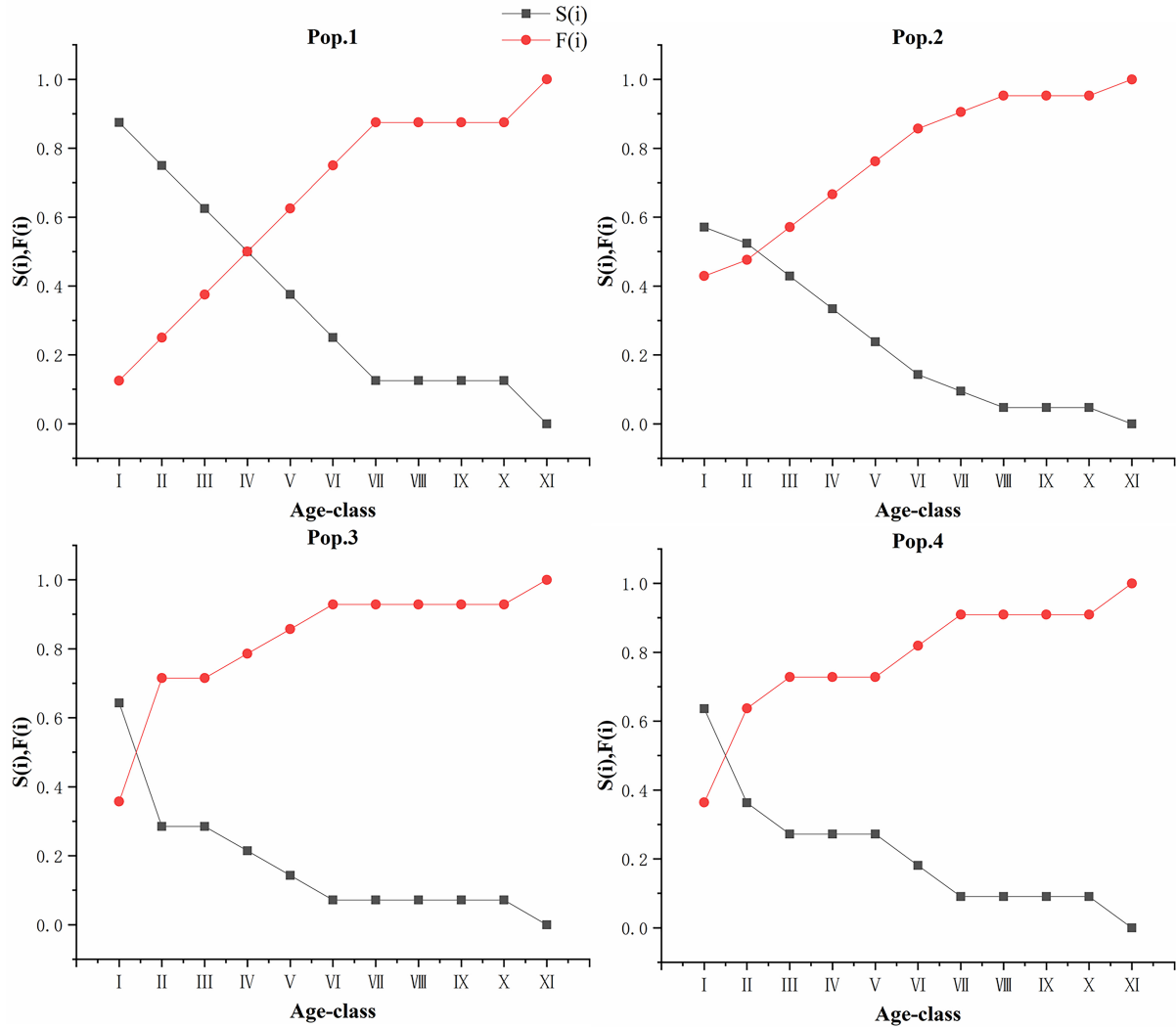


Figure 6. Survival rate $S_{(i)}$ and cumulative mortality $F_{(i)}$ curve of the *T. sinense* populations.

The survival curve showed that the l_x of *T. sinense* decreased rapidly in the I ~ VIII (Populations 1 and 2) or I ~ III (Populations 3 and 4) age classes, but more slowly in the IV or VII age classes, and then remained at a relatively low level. The $S_{(i)}$ and the $F_{(i)}$ both changed noticeably during the I, II age classes, and then more gradually. The changing trend of $f_{(ui)}$ was similar to that of $\lambda_{(ui)}$, as both peaked in the II and IX age classes. These findings suggested that the *T. sinense* population slumped during the early stage, and then remained stable during the middle stage, before a decline in the final stage. However, the dynamic trend detected for *T. sinense* differed from that obtained for *Pinus taiwanensis* (Bi *et al.* 2001) and *Taxus yunnanensis* (Su *et al.* 2005). The lower fitness of seeds and seedlings leads to a deficiency in the number of seedlings (Gan *et al.* 2013, Han *et al.* 2015, Li *et al.* 2018). The juvenile trees of *T. sinense* that survive this natural environmental screening process will have stron-

ger resistance and competitive ability, leading to a decline (Li *et al.* 2015, Cao *et al.* 2012). As a result, the population size might remain relatively stable in its middle stages. By the time *T. sinense* individuals enter the older ages, they are in a physiological senescence phase (Silvertown *et al.* 2001, Xiao *et al.* 2004, Zhang *et al.* 2008). Therefore, the population decline in its final stages might be attributed to the physiological senescence of *T. sinense* individuals (Han *et al.* 2015, Li *et al.* 2018).

Time series analysis showed that, over the next 10 age class times, the number of individuals in the *T. sinense* populations would decrease sharply, and the number of adult individuals would gradually increase, while the number of younger individuals was increasingly insufficient, seriously affecting the survival and development of the *T. sinense* populations. It can be inferred that as time goes by, there will be fewer and fewer individuals of the *T. sinense* population in LMNR (Li *et al.* 2015).

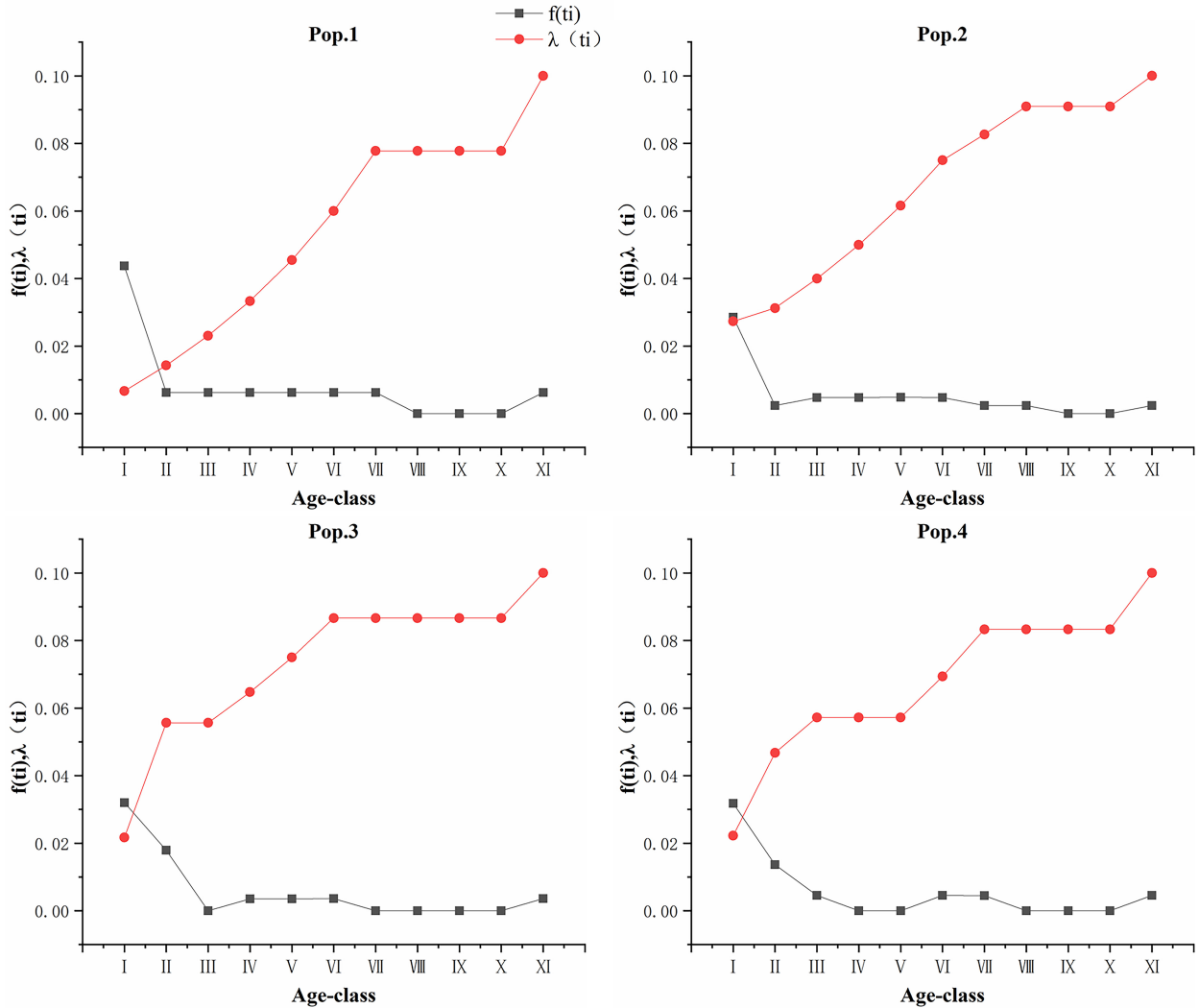


Figure 7. Mortality density $f_{(t_i)}$ and hazard rate $\lambda_{(t_i)}$ curve of the *T. sinense* population

Table 6. Time series analysis of age structure of *T. sinense*

Population	Age-class	a_x	M_2	M_4	M_6	M_8	M_{10}	Population	Age-class	a_x	M_2	M_4	M_6	M_8	M_{10}
Pop.1	I	0						Pop.3	I	0					
	II	15	7.5						II	11	5.5				
	III	14	14.5						III	16	13.5				
	IV	0	7	7.25					IV	1	8.5	7			
	V	0	0	7.25					V	3	2	7.75			
	VI	0	0	3.5	4.83				VI	0	1.5	5	5.17		
	VII	0	0	0	4.83				VII	2	1	1.5	5.5		
	VIII	0	0	0	2.33	3.625			VIII	1	1.5	1.5	3.83	12.25	
	IX	0	0	0	0	3.625			IX	0	0.5	0.75	1.17	4.25	
	X	1	0.5	0.25	0.167	1.875	3		X	0	0	0.75	1	2.875	3.4
	XI	1	1	0.5	0.33	0.25	3.1		XI	0	0	0.25	0.5	0.875	3.4
total		31	30.5	18.75	12.487	9.375	6.1	total		34	34	24.5	17.17	20.25	6.8

Population characteristics of *T. sinense*

Population	Age-class	a _x	M ₂	M ₄	M ₆	M ₈	M ₁₀	Population	Age-class	a _x	M ₂	M ₄	M ₆	M ₈	M ₁₀
Pop.2	I	1						Pop.4	I	0					
	II	21	11						II	19	9.5				
	III	22	21.5						III	12	15.5				
	IV	2	12	11.5					IV	1	6.5	8			
	V	1	1.5	11.5					V	1	1	8.25			
	VI	0	0.5	6.25	7.83				VI	2	1.5	4	5.83		
	VII	0	1	1.25	8				VII	0	1	1	5.83		
	VIII	1	1	0.75	4.67	6.125			VIII	0	0	0.75	2.67	4.375	
	IX	0	0.5	0.75	1	6.125			IX	0	0	0.5	0.67	4.375	
	X	0	0.5	0.75	0.667	3.5	5		X	0	0	0	0.5	2	3.5
	XI	1	0.5	0.25	0.667	0.875	5		XI	2	1	0.5	0.67	0.75	3.7
	total	51	50	33	22.834	16.625	10		total	37	36	23	16.17	11.5	7.2

In general, in order to adapt to the abominable environment (the flowering period coincides with the rain period), most of them were inbred, which led to the low germination rate of seeds in the field. The survival rate of seedlings was affected by the environment in which they lived (including the associated species and the litter thickness) (Cao *et al.* 2012, Tian *et al.* 2018). In the natural population of *T. sinense*, the niche of associated species was larger, the natural regeneration of *T. sinense* population was poor, and there was a danger that it would be replaced by its associated tree species (such as *Cercidiphyllum japonicum*, *Acer pictum subsp. mono*) (Li 2015, Tian *et al.* 2018). Therefore, the populations of *T. sinense* in LMNR will gradually decline if the current problem is not resolved.

In order to effectively protect the endangered plants *T. sinense*, some management strategies should be carried out. First, some of the more competitive tree species should be thinned to reduce interspecific competition and provide a better habitat for the growth of juveniles of *T. sinense*. In addition, improved conditions for the germination of *T. sinense* seeds and seedling establishment should be created to accelerate the natural regeneration of the population.

Conclusion

The age structure of *T. sinense* populations in the LMNR were all close to the pyramid type, with few seedlings and saplings, indicating that the population was in the early stages of decline. The population size of *T. sinense* slumped during the early age classes, and then remained relatively stable in the middle, followed by a decline in the final stages. The lack of seedlings or saplings in the populations might reflect a bottleneck in the regeneration of the *T. sinense* populations that were studied here. Through the investigation of *T. sinense* population in the LMNR, we

have confirmed that it is in a dangerous situation. Based on our study, we have suggested several strategies to conserve and manage the *T. sinense* population.

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