

POPULATION STRUCTURE AND DYNAMICS OF THE ENDANGERED TREE *TETRACENTRON SINENSE* OLIVER

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Abstract

Tetracentron sinense is an endangered tree in China in appendix III of CITES. The current status and dynamics of wild population of *T. sinense* are unknown, but are vital to its conservation. Diameter at breast height (or basal height for individuals <2.5 m) of all individuals of the *T. sinense* population in Meigu Dafengding Nature Reserve was investigated. Population size structure, time-specific life tables, survival analysis, and time series analysis were used to analyze the conservation status and dynamics of a natural population. The size structure of the population showed a spindle shape, with few younger individuals (including seedling and sapling) being present, and more middle-aged and aged individuals. The survival curve was a Deevey-type II. The mortality rate, killing power, mortality density, and hazard rate of the population all peaked in the 6th and 12th age-classes. In the first six age-classes, survival rate decreased monotonically, while the cumulative mortality rate rapidly increased, after which the change in trend became relatively gentle. The population size is expected to decrease rapidly in the future 6 and 12 age-classes. The result showed that the natural population was relatively stable, but was in the early stage of decline. The population size of *T. sinense* in Meigu Dafengding Reserve decreased during the early stage, stabilized in middle stage, and declined in the final stage. The lack of seedlings or saplings might reflect a bottleneck in the regeneration of *T. sinense* natural population.

Key words: Life table, Population structure, Survival analysis, *Tetracentron sinense* Oliver, Time series analysis.

Introduction

Studies of the structural characteristics and dynamics of plant populations are at the core of plant population ecology (Chapman & Reiss, 2001; Gurevitch *et al.*, 2002). Analysis of population age structure is an effective way to understand the demographic status and regeneration strategy of plant populations, as it reflects the relationship between the population and the environment (Díaz *et al.*, 2000). Life tables and survival curves are important tools to evaluate population dynamics as they show the actual numbers of surviving individuals, deaths, and the survivorship trend for all age groups in the population (Harcombe, 1987; Díaz *et al.*, 2000). Life table structure analysis is also used to explain the changes of population size (Smith & Keyfitz, 1947; Skoglund & Verwijst, 1989; Armesto *et al.*, 1992). For example, it can be used to assess the probability of survival and reproduction of the population under certain conditions, characterize the current state of the population, and analyze the structure and disturbance state of the past population, and the future population dynamics (Harper, 1977; Stewart, 1989; Stewart & Rose, 1990). Four functions (including survival rate, cumulative mortality, mortality density and hazard rate) of survival analysis contribute towards improving analyses of current situation of population structure and the development law of a given population (Harcombe, 1987; Zhang *et al.*, 2008). Time series analysis is an important field in population statistics that is used to forecast the population dynamic trend in the future (Xie *et al.*, 2014). Therefore, life tables and time series analysis that show the quantitative characteristics of an endangered plant population are of practical importance for implementing effective conservation and management (Wu *et al.*, 2000; Phama *et al.*, 2014).

Tetracentron sinense Oliver is the only species in the family of Tetracentraceae (Chen *et al.*, 2007). This species is mainly distributed in the mountains of central and southwest China. It is a homoxylous taxon, its fossils appeared in the Cenozoic Eocene, indicating its relict nature, making it important for the studying ancient flora and phylogenesis in angiosperms. Its importance in ornamental, medicinal, and furniture products, has resulted in *T. sinense* being excessively harvested. Consequently, its current distribution is scattered (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 it is listed as a national second-grade protected plant in China (Fu, 1992). The conservation of germplasm resources for *T. sinense* has attracted increasing attention. Previously, the systematic status (Chen *et al.*, 2007), sporogenesis and gametophyte development (Gan *et al.*, 2012), pollination ecology (Gan *et al.*, 2013), seed and seedling ecology (Zhou, 2007; 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) of *T. sinense* have been studied to improve the protection of its germplasm resources. However, to date, knowledge remains limited about the conservation status and trend of natural populations of *T. sinense*.

In this study, we analyzed the age structure and survival of a natural population of *Tetracentron sinense* in Meigu Dafengding Nature Reserve, southwest China, in addition to constructing a life table and carrying out a time series analysis. The aims of the study were to: (1) evaluate the conservation status of *T. sinense* natural population, (2) forecast the population dynamic trend in the future, (3) suggest effective strategies for the management and conservation of the natural populations of *T. sinense*.

Materials and Methods

Study area and field methods: This study was conducted in Dafengding Nature Reserve (28°30′–28°50′N, 102°52′–103°20′ E), located in northeast Meigu county, Sichuan Province, China. This reserve was established primarily for the conservation of rare and endangered wildlife and their habitats in 1979. The reserve is located in the subtropical monsoon climate zone, and covers a wide altitudinal range with elevations of 1356 to 3998 m. The annual average precipitation is about 1100 mm. The annual average relative humidity is about 80%, and annual average temperature is 11.4°C. Vegetation in the reserve shows a typical vertical band spectrum, with evergreen broadleaved forests (1356–2100 m), deciduous broad-leaved forests (2100–2500 m), mixed coniferous and deciduous broad-leaved forests (2500–2700 m), conifer forests (2700–3700 m), and shrub and meadows (≥3700 m). The study species *T. sinense* was mainly distributed at elevations ranging from 2000 to 2500 m, in association with *Acer franchetii*, *Padus brunnescens*, *Cercidiphyllum japonicum*, *Acer pictum* subsp. mono, and *Pterocarya stenoptera* populations.

In the reserve, the *T. sinense* population was scattered (Gan *et al.*, 2013; Tang *et al.*, 2013), with mean population density of just 0.45 individual/100 m². All individuals of *T. sinense* in the natural reserve were considered as one natural population. A census of all individuals (including seedlings and sapling) in the reserve was conducted in 2014 (Warren & Olsen, 1964), and the stem diameter at breast height (DBH) (or at the base for individuals ≤ 2.5 m in height) and tree height (H) of individuals were measured once a year.

Age structure: Due to the positive correlation between DBH and the age of *T. sinense* individuals (Tang *et al.*, 2013), DBH was used as a surrogate for age to protect

every individual of this endangered species. According to the life history characteristic of *T. sinense* and the methods of Brodie *et al.*, (1995) and Guedje *et al.*, (2003), the population was grouped into 13 age-classes based on plant size (Table 1). Pre-reproductive and juvenile trees were classified as seedlings and saplings (I: DBH <5cm) and juveniles (II: 5–10 cm DBH, and III: 10–20cm DBH). Adult trees were grouped into 10 age-classes (IV: 20–30 cm DBH; V: 30–40 cm DBH; VI: 40–50 cm DBH; VII: 50–60 cm DBH; VIII: 60–70 cm DBH; IX: 70–80 cm DBH; X: 80–90 cm DBH; XI: 90–100 cm DBH; XII: 100–110 cm DBH; XIII: 110–120 cm DBH).

Construction of static life table: Field investigation showed that multiple generations overlapped in the *T. sinense* population, and the number of surviving individuals (a_x) fluctuated very highly with different age-classes (Table 1); thus, the corrected value of survival number (a_x^*) was used to construct the static life table by use of additional smoothing techniques (Wratten, 1980; Brodie *et al.*, 1995; Molles, 2002). The following parameters were estimated:

$$l_x = a_x^*/a_0 \times 1000 \tag{1}$$

$$S_x = l_{x+1}/l_x \tag{2}$$

$$d_x = l_x - l_{x+1} \tag{3}$$

$$q_x = d_x/l_x \times 100\% \tag{4}$$

$$L_x = (l_x + l_{x+1})/2 \tag{5}$$

$$T_x = \sum_x^{\infty} L_x \tag{6}$$

$$e_x = T_x/L_x \tag{7}$$

$$K_x = \ln l_x - \ln l_{x+1} \tag{8}$$

Table 1. Static life table of *T. sinense* population.

Age class	DBH class	Mean value	a_x	a_x^*	l_x	$\ln l_x$	d_x	q_x	L_x	T_x	e_x	K_x	S_x
1	0~5	5.5	5	64	1000.000	6.908	140.625	0.141	929.688	4062.500	4.063	0.152	0.859
2	5~10	7.5	16	55	859.375	6.756	140.625	0.164	789.063	3132.813	3.645	0.179	0.836
3	10~20	15	66	46	718.750	6.578	140.625	0.196	648.438	2343.750	3.261	0.218	0.804
4	20~30	25	42	37	578.125	6.360	140.625	0.243	507.813	1695.313	2.932	0.279	0.757
5	30~40	35	41	28	437.500	6.081	140.625	0.321	367.188	1187.500	2.714	0.388	0.679
6	40~50	45	31	19	296.875	5.693	140.625	0.474	226.563	820.313	2.763	0.642	0.526
7	50~60	55	12	10	156.250	5.051	31.250	0.200	140.625	593.750	3.800	0.223	0.800
8	60~70	65	8	8	125.000	4.828	15.625	0.125	117.188	453.125	3.625	0.134	0.875
9	70~80	75	9	7	109.375	4.695	15.625	0.143	101.563	335.938	3.071	0.154	0.857
10	80~90	85	2	6	93.750	4.541	15.625	0.167	85.938	234.375	2.500	0.182	0.833
11	90~100	95	2	5	78.125	4.358	15.625	0.200	70.313	148.438	1.900	0.223	0.800
12	100~110	105	3	4	62.500	4.135	15.625	0.250	54.688	78.125	1.250	0.288	0.750
13	110~120	115	2	3	46.875	3.847	-	-	23.438	23.438	0.500	3.847	-

x is the age class; a_x : the number of surviving individuals in age-class x ; a_x^* : corrected number of surviving individuals in age-class x after smoothing treatment; l_x : the standardized number of surviving individuals in age-class x , $l_x = a_x^*/a_0 \times 1000$; d_x : the standardized number of dead individuals from age-class x to $x+1$, $d_x = l_x - l_{x+1}$; q_x : the mortality rate from age-class x to $x+1$, $q_x = d_x/l_x \times 100\%$; L_x : the number of surviving individuals from age-class x to $x+1$, $L_x = (l_x + l_{x+1})/2$; T_x : the total number of surviving individuals from age x , $T_x = \sum_x^{\infty} L_x$; e_x : the life expectancy of the individuals in age-class x , $e_x = T_x/L_x$; $\ln l_x$: the natural logarithm of l_x ; k_x : the killing power; S_x : the survival rate.

Survivorship curve: The survivorship curve of the population was drawn according to the $\ln l_x$ in different age-classes in the static life table. Deevey (1947) divided the survivorship curve into three types: type I is a convex shape, which means that most individuals in the population can achieve their mean physiological life, and almost all individuals will die at the same time when reaching the mean physiological life; type II is a diagonal shape, which means that the same mortality rate appeared in each age-class; type III is a concave shape, which means that the mortality rate is higher in younger individuals, and then will become lower and stable. According to Hett & Loucks (1976), three kinds of mathematical models (linear equation, exponential equation and power function equation) were used to test whether the survivorship curve of the *T. sinense* matched a Deevey type I, II or III (Deevey, 1947). That is

$$\text{Deevey type I: } N_x = N_0 + bx \quad (9)$$

$$\text{Deevey type II: } N_x = N_0 e^{-bx} \quad (10)$$

$$\text{Deevey type III: } N_x = N_0 x^{-b} \quad (11)$$

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: The survival function is a function at any time, which is more intuitive than the survivorship curve, so the survival analysis has higher practical applied value in the analysis of population life table compared to survivorship curve (Yang *et al.*, 1991; Guo, 2009). To better analyze the population structure and dynamic changes of *T. sinense*, four functions of survival analysis were introduced: population survival rate function ($S_{(i)}$), cumulative mortality function ($F_{(i)}$), mortality density

function ($f_{(i)}$) and hazard rate function ($\lambda_{(i)}$). The calculation formula of the four functions are as follows:

$$S_{(i)} = S_1 \cdot S_2 \cdot S_3 \cdots S_i \quad (12)$$

$$F_{(i)} = 1 - S_{(i)} \quad (13)$$

$$f_{(i)} = (S_{i-1} - S_i) / h_i \quad (14)$$

$$\lambda_{(i)} = 2(1 - S_i) / [h_i(1 + S_i)] \quad (15)$$

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

Time series analysis: To forecast the dynamic trend of the *T. sinense* population, a moving average method was applied in time series analysis (Xiao *et al.*, 2004; Zhang *et al.*, 2017).

$$M_t^{(1)} = \frac{1}{n} \sum_{k=t-n+1}^t x_k \quad (16)$$

where, n is the time being predicted (age-class time in the study); (I) is a moving average; t is the t^{th} age-class; X_k is the number of surviving individuals in the k^{th} age-class; and $M_t^{(1)}$ is the population size in age-class t after n age-class times in the future. Based on the result from life table and survival analysis, the number of surviving individuals in each age-class of the *T. sinense* population was predicted after 2, 6 and 12 age-class times in the future.

Results

Age Structure: There were 239 individuals of *T. sinense* in the natural population, and the age structure presented a spindle shape (Fig. 1). Younger individuals (1st and 2nd age-classes) accounted for just 7.11% of total individuals, and no seedlings (Height <0.33m) or few saplings ($H \geq 0.33\text{m}$, and $\text{DBH} < 5\text{cm}$) were recorded.

Life-table and survivorship curve: The life-table analysis showed that the natural population structure of *T. sinense* fluctuated with different age-classes (Table 1). As age-class increased, l_x decreased, while a higher individuals e_x were apparent in the 1st and 7th age-classes, respectively, and then declined.

The l_x of *T. sinense* decreased slowly in the first six age-classes, but more rapidly in the 7th age-class, and then remained at a relatively low level thereafter (Fig. 2). The model simulation showed that the R^2 and F value from equation (10) were both larger than those from equation (9) and (11), indicating that the survivorship curve of the *T. sinense* population was a Deevey-II type (Table 2).

The q_x and K_x of the studied population showed a similar pattern, increasing and peaking in the 6th (q_x : 47.4%) and 12th (q_x : 25%) age-classes, respectively (Fig. 3).

Survival analysis: Survival rate declined monotonically with increasing age-class, while the cumulative mortality rate increased monotonically, showing a complementary trend. The survival rate and the cumulative mortality rate both changed noticeably in the first six age-classes, and then more gradually. By the 13th age-class, the survival rate of the population was less than 5%, and the mortality rate was higher than 95% (Fig. 4). Meanwhile, the changing trend in the mortality density was similar to that of the hazard rate, as both peaked in the 6th and 12th age-classes, respectively (Fig. 5).

Time series analysis: After the future 2 age-class times, the number of surviving individuals was predicted to decrease significantly in the younger age-classes (2nd and 3rd age-classes), and increase in the middle age-classes (from the 4th to 8th age-classes), and remained relatively stable after the 9th age-class. After the future 6 age-class times, the number of individuals was predicted to increase rapidly from the 6th to 8th age-classes, and then steadily increase. After the future 12 age-class times, the number of individuals in each age-class was predicted to decrease, and the total number of surviving individuals was predicted to decline from 239 to 48.2 (Table 3).

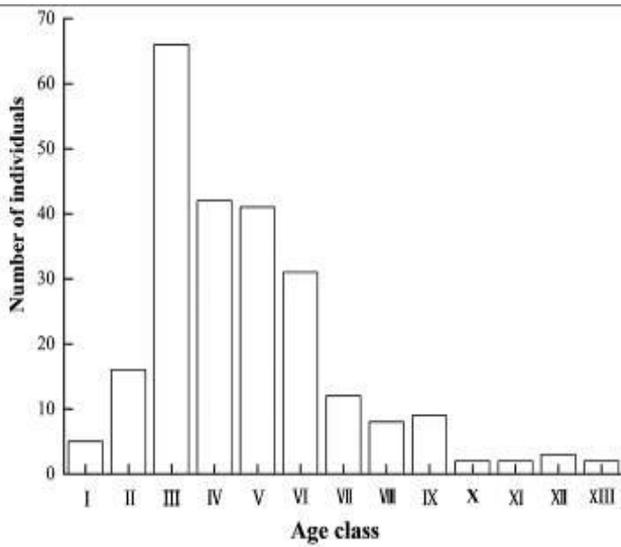


Fig. 1. Age structure of the *T. sinense* population.

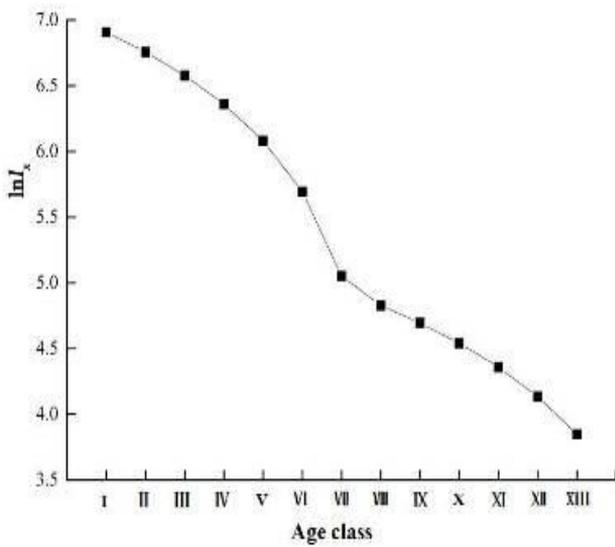


Fig. 2. Survival curve of the *T. sinense* population.

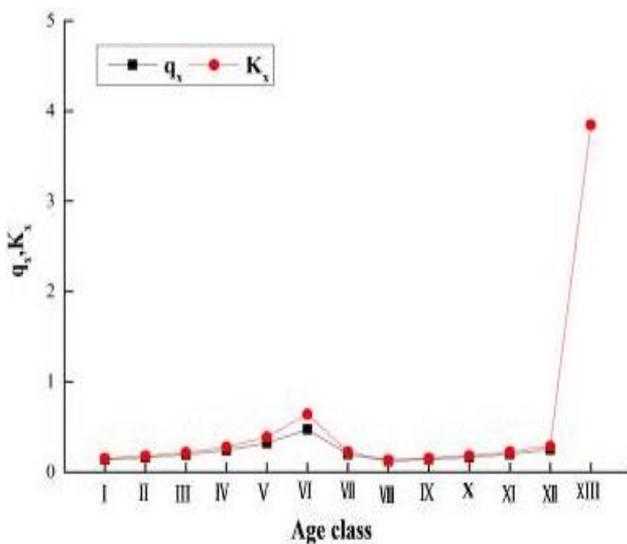


Fig. 3. Mortality (q_x) and killing power (K_x) curve of the *T. sinense* population.

Table 2. Test models fitted to the survival curve of the *T. sinense* population.

Equation	R ²	F	P	Type
$N_x = 7.723 - 0.272x$	0.977	476.812	0.000	Deevey- I
$N_x = 7.542e^{-0.051x}$	0.981	583.536	0.000	Deevey-II
$N_x = 8.01x^{-0.241}$	0.842	58.825	0.000	Deevey-III

Table 3. Time series analysis of age structure of *T. sinense* population in the future 2, 6 and 12 age-class times.

Age class	a_x	M ⁽¹⁾²	M ⁽¹⁾⁶	M ⁽¹⁾¹²
1	5			
2	16	10.5		
3	66	41		
4	42	54		
5	41	41.5		
6	31	36	33.5	
7	12	21.5	34.7	
8	8	10	33.3	
9	9	8.5	23.8	
10	2	5.5	17.2	
11	2	2	10.7	
12	3	2.5	6	19.75
13	2	2.5	4.3	19.5
Total	239	235.5	163.5	39.25

Discussion

The age structure and survivorship curve of a population can reflect the age distribution of individuals, the population dynamics and potential future trajectories (Wang *et al.*, 1995; Diaz *et al.*, 2000). The population structure of endangered plants is divided into three types: increasing, stable and declining (Guo, 2009); however, most long-lived, relict and endangered plants tend to be characterized as declining (Zhang *et al.*, 2004; Zhang *et al.*, 2008). The reasons for the declining population of endangered plants are mainly attributed to two factors: poor 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 the current study, the age structure of a natural population of *T. sinense* showed a spindle shape, with the survivorship curve approximating a Deevey-II type. These results indicated that the *T. sinense* population investigated here was relatively stable (Deevey, 1947). However, no seedlings or few saplings (the 1st age-class) were observed in the population. Previous studies showed that sufficient seedlings and saplings were 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). Thereafter, the deficiency of younger individuals reflects a bottleneck in the regeneration and recovery of this natural *T. sinense* population, which might eventually result in population decline. 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).

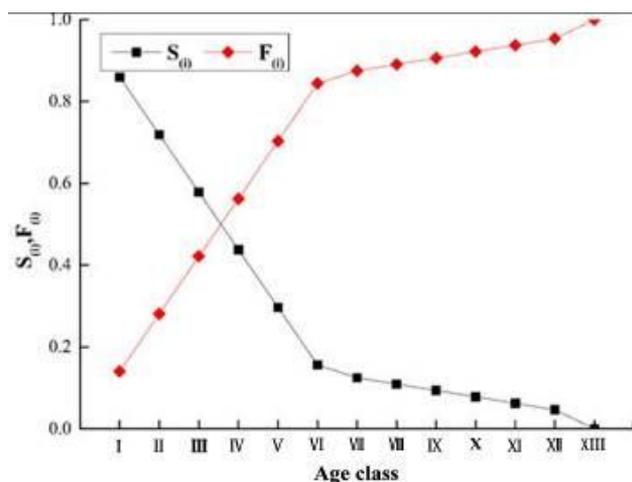


Fig. 4. Survival rate $S_{(i)}$ and cumulative mortality $F_{(i)}$ curve of the *T. sinense* population.

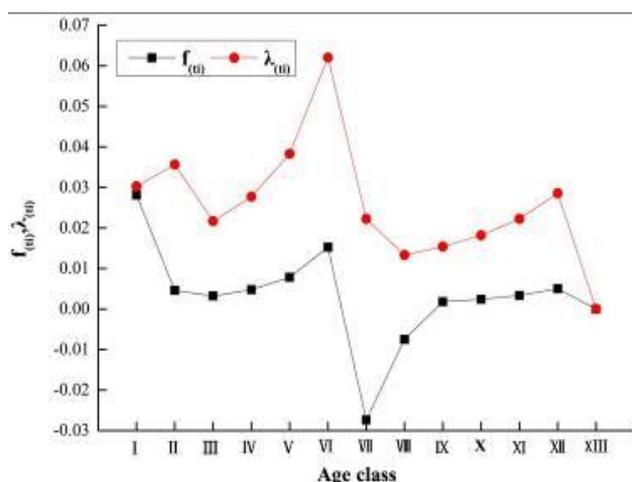


Fig. 5. Mortality density $f_{(i)}$ and hazard rate $\lambda_{(i)}$ curve of the *T. sinense* population.

The l_x of *T. sinense* decreased steadily during the first six age-classes, and more rapidly in the 7th age-class, then remained stable at a low level. The cumulative mortality rate rapidly increased during the first six age classes, and then became more gradual. The mortality rate, killing power, the cumulative mortality rate, and the mortality density and hazard rate all peaked in the 6th and 12th age-classes. These findings suggested that the *T. sinense* population slumped during the early stage, and then remained stable in middle stage, followed by a decline in the last stage. This result was confirmed by the time series analysis; however, the dynamic trend detected for *T. sinense* differed to that obtained for *Pinus taiwanensis* (Bi *et al.*, 2002) and *Taxus yunnanensis* (Su *et al.*, 2005).

In the current study, no seedlings or few saplings were observed in the *T. sinense* population, which might be attributed to the environmental factors influencing seedling establishment and sapling survival. Biotic and abiotic factors, such as freezing injury, drought, and micro-habitat (including light level, air temperature and humidity) can affect the germination of seeds and seedling establishment (Korner *et al.*, 1998; Hoche *et al.*, 2002; Cheng *et al.*, 2005; Guo *et al.*, 2011). Our previous studies showed that there was no factor limiting seed

regeneration during sporogenesis and gametophyte development (Gan *et al.*, 2012), pollination and seed production (Gan *et al.*, 2013), or seed dispersal (Han *et al.*, 2015). After dispersal, the seeds of *T. sinense* remain in the litter and ground cover (shrub and herb layer), which changes the forest microhabitat, soil moisture and nutrient availability (Beckage *et al.*, 2000; Dupuy & Chazdon, 2008), and consequently affects the seed germination and seedling growth. Leaf litter was as a major barrier to the germination of small seeds and seedling establishment (Dupuy & Chazdon, 2008). For the small seeds of *T. sinense* (Luo *et al.*, 2010), litter and ground cover (shrub and herb layer) might have contributed to the lack of seedlings in the studied population. In addition, the rapid growth of seedlings into saplings and arborets would gradually increase inter- and intra-species competition for limited environmental resources (such as light and mineral nutrition) in the *T. sinense* community (Saito & Miki, 2010). This phenomenon might explain the higher mortality rate of saplings and arborets in the first six age-classes. To date, knowledge remains limited about how various factors (including litter and ground cover, and inter- and intra-specific competition) influence the establishment of *T. sinense* seedling and sapling survival. Further study is needed to determine why this species is endangered to develop an effective strategy to accelerate the natural regeneration of its populations.

Over time, saplings grow into arboret and arbor individuals, enhancing the ability of *T. sinense* individuals to adapt to environmental shifts (Zhang *et al.*, 2014), which, in turn, leads to a decline in mortality rates. As a result, the population size might remain relatively stable in the middle stage. By the time *T. sinense* enter the second peak (12th age-class), they are in the physiological senescence phase (Silvertown *et al.*, 2001; Xiao *et al.*, 2004; Zhang *et al.*, 2008), resulting in a higher mortality and disappearance rates. Thereafter, the population declines in last stage which might be attributed to the physiological senescence of *T. sinense* individuals.

According to our study results, we suggest possible management strategies for the conservation of *T. sinense*. First, the protection and management of the habitat of the *T. sinense* population and younger individuals (seedling and sapling) should be strengthened. Second, some competitive trees should be thinned to reduce interspecific competition and provide better habitat for the growth of adults of *T. sinense* trees, on the understanding that the habitat is not destroyed. In addition, some suitable conditions for the germination of *T. sinense* seeds and seedling establishment should be created to accelerate the natural regeneration of the population.

Conclusion

The size structure of the *T. sinense* population was spindle shaped, with fewer younger individuals (including seedling and saplings), indicating that the population was in the early stage of decline. The population size of *T. sinense* slumped during the early stage, and then remained relatively stable in middle stage, followed by a decline in final stage. The lack of seedlings or saplings in the population might reflect a bottleneck in the regeneration

of the *T. sinense* population. Based on our results, we suggest several strategies to conserve and manage the *T. sinense* population.

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