

Tree Mortality and Regeneration in Euphrates Poplar Riparian Forests Along the Tarim River, Northwest China

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Tree mortality and regeneration in Euphrates poplar riparian forests along the Tarim River, Northwest China

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Abstract

Background: Tree mortality and seedling and sapling recruitment are essential components of forest dynamics in arid regions, especially those with serious eco-hydrological problems. In recent decades, the mortality of the Euphrates poplar (*Populus euphratica*) along the Tarim River in Northwest China has increased. However, few studies have quantified the causes of mortality and regeneration in this azonal riparian forest type.

Methods: The present paper describes the annual hydrological response of tree mortality and regeneration in forest gaps. A total of 60 canopy gaps were investigated in six replicate grid plots (50 m × 50 m) and the annual runoff and water consumption data during the period of 1955–2016 were collected from hydrological stations along the middle reaches of the Tarim River. In addition, we compared the regeneration density of seedlings and saplings within the canopy gap areas (CGAs), undercanopy areas (UCAs), and uncovered riverbank areas (RBAs) through detailed field investigation.

Results: Our study found that the mortality of young and middle aged gap makers has increased markedly over recent decades, particularly since 1996. The main results indicated that regional water scarcity was the primary limiting factor for long-term changes in tree mortality, as shown by a significant correlation between the diameter at breast height (DBH) of dead trees and the annual surface water. The average density (or regeneration rate) of seedlings and saplings was highest in the RBAs, intermediate in the CGAs, and lowest in the UCAs. Compared with the UCAs, the CGAs promote tree regeneration to some extent by providing favorable conditions for the survival and growth of seedlings and saplings, which would otherwise be suppressed in the understory. Furthermore, although the density of seedlings and saplings in the CGAs was not as high as in the RBAs, the survival rate was higher in the CGAs than in the RBAs.

Conclusion: This study shows that forest canopy gaps can play a decisive role in the long-term germination and regeneration of plant species. However, as a typical phreatophyte in this hyper-arid region, the ecosystem structure, functions and services of this fragile *P. euphratica*, floodplain forests are threatened by a continuous decrease of

water resources, due to excessive water use for monocultural cotton irrigation, which has resulted in a severe reduction in intact poplar forests. Furthermore, the survival of seedlings and saplings is influenced by light availability and soil water at the regional scale. Our findings suggest that policymakers may need to reconsider the restoration and regeneration measures implemented in riparian *P. euphratica* forests to improve flood water efficiency and create canopy gaps. Our results provide valuable reference information for the conservation and sustainable development of floodplain forest ecosystems.

Key words: Tree mortality; Regeneration strategy; Seedling and sapling recruitment; Gap makers; Riparian forest; Tarim River

Introduction

Riparian forests provide fundamental ecosystem services in arid regions, including maintenance of ecological stability and prevention of natural disasters such as sandstorms, heatwaves, and desertification (Song et al. 2000; Chen et al. 2013; Betz et al. 2015; Halik et al. 2019). The existence of trees, bushes, and grass vegetation on the banks of the Tarim River, which constitute the natural barriers of river oases, is absolutely dependent on the river (Halik et al. 2006). In recent decades, floodplain vegetation has been threatened by increased consumption of water resources, and large areas of riparian forests including seedlings and saplings, have withered (Gries et al. 2003; Aishan 2016). With China's rapid economic development and the implementation of the "Ecological Civilization" and "One Belt One Road" initiatives, the ecological restoration of the floodplain ecosystem along the Tarim River has been designated high priority by the Chinese government (Halik et al. 2006, 2019). Conservation of the remaining riparian forests and recovery of the degraded parts of the ecosystem are crucial for further sustainable development of the region (Rumbaur et al. 2015; Deng 2016; China Green Foundation 2018), especially if transport infrastructure, including railways, highways, and oil and gas pipelines between the Tarim Basin and inner China, is to be protected (Deng 2009, 2016; Aishan 2016; Keyimu et al. 2018; Halik et al. 2019). Thus, it is necessary to preserve the functions and services of these forests through adaptive management.

The riparian forest (so-called *Tugai* forests) at the Tarim River constitute a natural green belt at the northern edge of the Taklimakan Desert. The Euphrates poplar (*Populus euphratica* Oliv.) is a dominant tree species in the floodplain ecosystems. As a "Green Corridor" in the desert, *P. euphratica* forests have become increasingly important for preventing the unification of two neighboring sandy deserts, the Taklimakan and the Kuruktagh (Xu et al. 2006; Thevs et al. 2008; Betz et al. 2015). These forests have important ecological functions in addition to socio-economic and touristic value, such as protection of biodiversity, regulation of

the climate and hydrology of oases, fertilization of soils, and maintenance of regional ecosystem balance (Wang et al. 1995; Huang et al. 2010; Mamat et al. 2019). Nevertheless, the entire Tarim floodplain ecosystem, especially the riparian vegetation, has been seriously degraded, as the water conveyance in the main channel has rapidly decreased and many tributaries of the watershed have been disconnected from the main river (Chen et al. 2013).

Many studies have demonstrated that water shortages in the Tarim are mainly caused by climate change coupled with intensive anthropogenic activities, i.e., tree felling, overgrazing, excessive land reclamation and disorderly expansion of cotton monoculture. Therefore, restoring degraded floodplain ecosystems has become a major focus of applied forest research (Deng et al. 2009; Rumbaur et al. 2015; Thomas et al. 2017a, b). Among all processes of natural forest dynamics, the formation of forest canopy gaps was considered a vital regeneration strategy for maintaining floodplain forest structures. Gap disturbance is the main driving force of forest dynamics as it creates environmental heterogeneity (Albanesi et al. 2005; Zhu et al. 2003, 2007, 2018; Bottero et al. 2011). Forest gaps thus create important habitat for the regeneration of plant species, which may otherwise be suppressed by the undercanopy (Han et al. 2011; Sharma et al. 2018). They also play a vital role in forest regeneration and succession, especially in the establishment and development of plant species that differ in ecological recruitment (Runkle 1998; Han et al. 2013; Mountford et al. 2006; Zhu et al. 2014; Jankovska et al. 2015). It has been reported that canopy gaps close when the height of regenerations reached 20 m, consistent with the definition used by Nagel et al. (2008). In floodplain forests, canopy gaps may not be filled with regenerations within a short period because of high tree mortality. This leads to the continual expansion of canopy gaps (Keram et al. 2019). The majority of earlier studies have focused on the mortality of gap makers and the diversity of regeneration species in other climatic zones, such as tropical, subtropical, north temperate, and cold temperate regions (Runkle et al. 1987; Yamamoto, 2000; Dorotă et al. 2008; Petritan et al. 2013; Popa et al. 2017; Zhu et al. 2018; Kitao et al. 2018). Numerous studies have considerably improved our understanding of canopy gaps in temperate forests. However, almost no attention has been paid to forest regeneration in extremely arid regions. In particular, there is lack of research on tree mortality under various hydrological scenarios as well as seedling and sapling regeneration in different habitats, such as canopy gap areas (CGAs), undercanopy areas (UCAs), and riverbank areas (RBAs) of floodplain, the composition and structure of which are drastically different from those of other forest types.

Forest canopy gaps may provide opportunities for species regeneration and have therefore been widely exploited in forest recovery programs (Coates et al. 1997; Schliemann et al. 2011; Kern et al. 2013, 2017;

Nagel et al. 2016; Lu et al. 2018). Thus, it is necessary to conduct studies to better understand the mortality of gap makers under long-term hydrological processes and seedling and sapling establishment in CGAs, (UCAs, and RBAs, as well as to clarify the contribution of canopy gaps to plant regeneration in riparian forests. Such information may provide insights into the efficiency of gap usage and seedling planting in forest restoration activities along the Tarim River.

In the present study, we used comprehensive field investigation data to describe tree mortality as well as to compare the density of seedlings and saplings between the CGAs, UCAs, and RBAs to evaluate whether the CGAs are important for the regeneration of *P. euphratica* riparian forests along the Tarim River. We aimed to answer the following questions:

- 1) What are the characteristics of forest gaps or gap makers in desert riparian forests?
- 2) How does tree mortality respond to hydrological dynamics (such as stream flow) of Tarim River?
- 3) How do canopy gaps contribute to tree regeneration in riparian forests?
- 4) What is the difference in species diversity between gap makers and gap fillers in canopy gaps?

We intend to answer these questions by compiling data from six permanent monitoring plots located at undisturbed natural forest sites along the middle reaches of the Tarim River. We believe that addressing these questions will contribute to an improved understanding of the current state of the Tarim riparian ecosystem, where *P. euphratica* is now in urgent need of protection so that forests can recover. Additionally, it will provide an ecological framework for the design and implementation of close-to-nature restoration techniques to extend *P. euphratica* forests.

Methods

Study site

Field work was conducted in Yingbazha village (41.22°N, 84.31°E, ASL 1000m) in Tarim Huyanglin Nature Reserve (THNR) along the middle reaches of the Tarim River (Figure 1), which was established in 1984 and upgraded to a National Nature Reserve in 2006. The region is an extremely arid warm temperate zone, with an annual mean precipitation of 75 mm and an annual mean temperature of 11.05 °C. The annual potential evapotranspiration ranges from 2500 to 3500 mm (Rouzi et al. 2018). The forest structure and composition in the study area is relatively simple, and the local flora is mainly composed of *P. euphratica*, *Tamarix ramosissima* and *Phragmites australis* (Table 1). However, a few rare plant species are present, including *Populus pruinosa*, *Tamarix hispida*, *Tamarix leptostachys*, *Glycyrrhiza glabra*, *Inula salsoloides*, *Karelinia*

caspica, *Lycium ruthenicum*, *Alhagi sparsifolia*, *Apocynum venetum*, *Halimodendron halodendron*, *Poa cynosuroides*, *Cirsium segetum*, *Cynanchum auriculatum*, *Aeluropus pungens*, *Taraxacum mongolicum*, *Salsola collina*, *Calamagrostis pseudophragmites*, *Myricaria platyphylla*, *Halogeton glomeratus*, and *Elaeagnus oxycarpa* (Gries et al. 2003; Chen et al. 2004; Thevs et al. 2006, 2008; Huang et al. 2010; Lang et al. 2016; Halik et al. 2019).

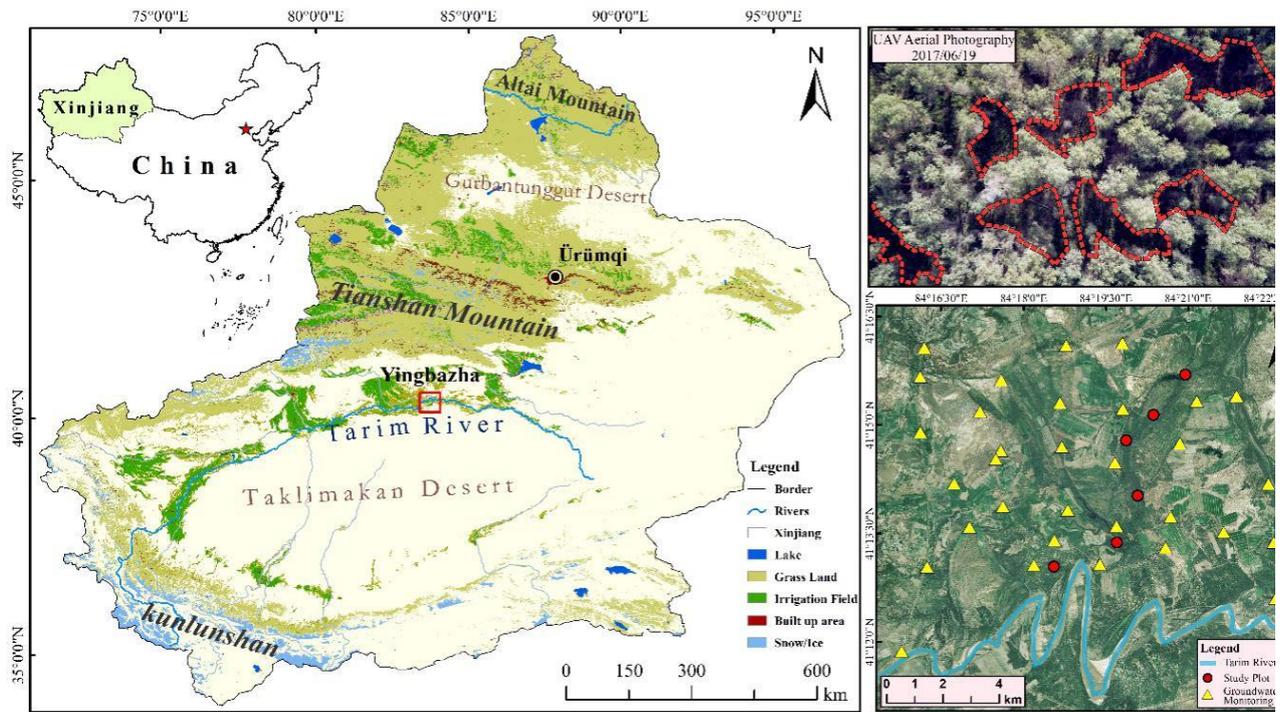


Figure 1 Sketch map of the study area

Field investigation

A complete field survey was carried out from May 15 to June 20, 2017. A total of 60 canopy gaps were investigated in six replicate grid plots (50 m × 50 m) (Table 1).

Table 1 Characteristics of six natural stands sampled for analysis of tree mortality

Plots	Area (m ²)	DRB (m)	GWL (m)	Lat. (N) (°)	Long. (E) (°)	Altitude (m)	<i>P. euphratica</i>		<i>T. ramosissima</i>		Gap openness (%)
							Ave. DBH (cm)	Ave. TH (m)	Ave. DBH (cm)	Ave. TH (m)	
1	50×50	100	2.00	41.175	84.240	929	35.4	9.8	1.6	3.2	43.10
2	50×50	150	2.68	41.229	84.333	920	21.6	12.1	4.2	2.6	66.16
3	50×50	300	3.41	41.176	84.241	920	15.5	9.1	2.3	1.6	50.54
4	50×50	600	4.55	41.174	84.237	916	23.5	11.0	3.2	2.4	41.38
5	50×50	1200	5.45	41.252	84.340	915	28.4	10.5	5.4	2.2	52.41
6	50×50	2400	7.50	41.228	84.334	916	21.1	12.1	2.6	1.7	52.12

*DRB: Distance from River Bank; GWL: Groundwater Level; DBH: Diameter at the Breast Height; TH: Tree Height

Canopy gaps were created by tree mortality (i.e., death) or by > 50 % loss of tree branches. The ratio of gap diameter to tree height on the border of the gap ($R_{D/H}$ value) ranged from 0.4 to 2.2 (Keram et al. 2019),

which is consistent with measurements reported by Zhu et al. (2015). For each canopy gap, all surrounding trees and gap makers were identified, and the species, diameter at breast height (DBH), and tree height (TH) or log length were recorded for each tree. Morphological characteristics were used to determine the degree of tree decomposition and the life expectancy of gap makers was estimated under the guidance of local experienced forest workers (Liu et al. 1991; Droessler et al. 2005; Thomas et al. 2006; Petritan et al. 2013; Wen 2016; Yang et al. 2017; Keram et al. 2019), and the relative ages of the gap makers were thus determined. In addition, we determined whether there were significant differences in the DBH distribution among living and dead trees. We regarded trees bordering canopy gaps as living trees and gap makers as dead trees. To investigate regeneration species, we selected five replicate plots in each habitat (CGAs, UCAs, and RBAs) and recorded the species and numbers of seedlings and saplings. We simultaneously compared the species diversity and density in these plots. We defined a CGA as an area where the canopy gap > 10 m². For the UCA, we chose plots around the canopy gaps in the study area; RBA plots were located near the riverbank, which was covered with excessive water. For each habitat, 15 repeated sampling plots (10×10 m²) were set, giving a total of 45 sampling plots. In each plot, we counted the number of species, for seedlings (≤10 cm tall) and saplings (10-100 cm tall) (Walker 2000).

Data processing

Classifying the DBH structure of gap makers

Over the entire area of canopy gaps, gap makers were classified into five categories according to their DBH and TH (Xu et al. 2016): Class I comprised juvenile trees (DBH < 5 cm, TH < 4 m), Class II comprised young trees (5 cm < DBH < 10 cm, TH ≥ 4 m), Class III comprised young/middle - aged trees (10 cm < DBH < 15 cm), Class IV comprised middle-aged trees (15 cm < DBH < 20 cm), and Class V comprised old trees (DBH > 20 cm).

Dynamic index of gap maker structure

The dynamic structure of gap makers was quantitatively analyzed. The dynamic index of population structure (V_{pi}) can be represented by the change trend of gap makers in various structures. If $0 < V_{pi} \leq 1$, the quantity of gap makers increased with the V_{pi} value; If $-1 < V_{pi} \leq 0$, the quantity of gap makers decreased with the V_{pi} value. The dynamic index of gap maker individuals (V_n) without external disturbance is described by the following equation:

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

Where S_n is the number of individuals in n DBH class, S_{n+1} is the number of individuals in $n+1$ DBH class of gap makers, and $(\dots\dots\dots)_{\max}$ is the maximum value in the column. Below is the formula used to calculate the dynamic index of gap maker structure (V_{pi}):

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

Where S_n and V_n are the same as in Formula (1), K is the quantity of gap makers in different age classes, and the range of V_{pi} is consistent with V_n . We used the formula proposed by Chen (1998) to calculate the dynamic index value under completely random (V_{pi}') and non-random (V_{pi}'') disturbances.

We have calculated species diversity according to the Margalef richness index and Shannon Wiener index (Ma et al. 1994a, b). A fitting optimization t -test method was used to statistically analyze the change trend of gap makers that died in different years and to evaluate the distribution patterns of the DBH values of gap makers. We used a chi-square goodness-of-fit test to reveal the DBH distribution of dead trees versus living trees. Further, we comparatively analyzed plant regeneration density between the different habitats (CGAs, UCAs, and RBAs) using the Margalef and Shannon–Wiener indices. Values of $P < 0.05$ were considered to be statistically significant. The data were organized using Excel 2015 (Microsoft, Redmond, USA) and analyzed using OriginPro 2016 (OriginLab Corp. 2016).

Results

Tree mortality

Among the 245 gap makers identified, the mean DBH was 20.80 ± 9.03 cm (range 10.10 – 49.50 cm) and there were significant variations in different years. The chi-square goodness-of-fit test showed that the DBH structure of gap makers presented a common curve distribution (Figure 2). The DBH distribution of gap makers approximated a Gaussian fit ($R^2 = 0.762, 0.749, 0.829, 0.896, 0.918, \text{ and } 0.364$, respectively; $P < 0.05$). However, large young gap makers (DBH < 15 cm) were more common in the study area, especially in the 2007-2016 period (Gaussian fit, $R^2 = 0.364$, $P < 0.05$). During the investigation, we found that some young trees were injured or crushed by old trees.

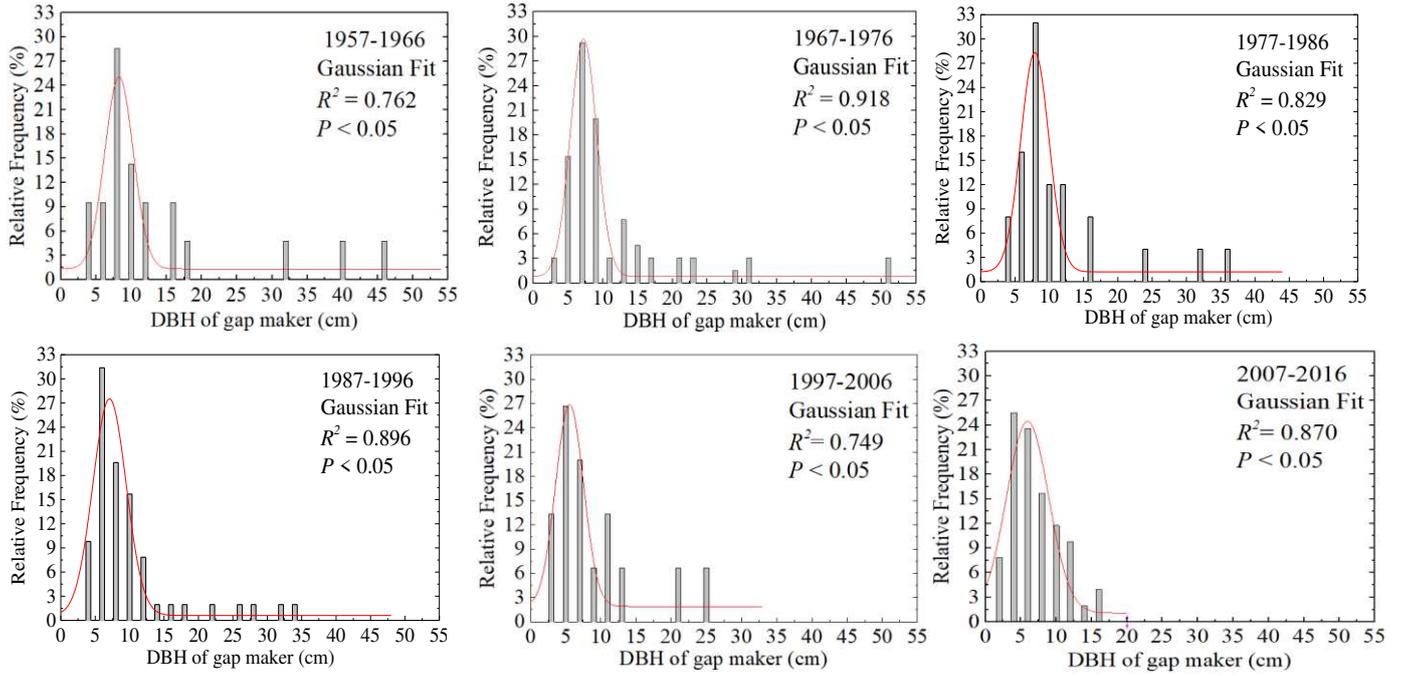


Figure 2 DBH class distribution of *P. euphratica* gap makers in the different years

Table 2 Analysis of population structure dynamics of gap makers under different volumes of runoff water

Years	Runoff/ 10^8m^3	V_1	V_2	V_3	V_4	V_{pi}	P	V_{pi}'	P'	V_{pi}''
1957-1966	33.34	-0.92	0.75	0.69	-0.67	-0.073	0.0095	-0.0040	0.2670	-0.0180
1967-1976	31.05	-0.77	0.55	0.25	0.00	-0.060	0.0040	-0.0019	0.1430	-0.0300
1977-1986	27.85	-0.84	0.78	0.71	-0.60	0.000	0.0080	0.0025	0.5000	0.0600
1987-1996	21.83	0.87	0.80	0.33	-0.33	0.040	0.0039	0.0071	0.6350	0.0970
1997-2006	22.84	0.00	0.40	1.00	-1.00	0.200	0.0133	0.0057	0.5600	0.0400
2007-2016	8.10	-0.57	0.57	0.13	0.33	0.460	0.0154	0.0084	0.6599	0.0554

V_1 : I - II Dynamic index value of I - II class sizes; V_2 : II - III Dynamic index value of II - III class sizes; V_3 : III - IV Dynamic index value of III - IV class sizes; V_4 : IV - V Dynamic index value of IV - V class sizes; V_{pi} : Dynamic index value under no external disturbance; V_{pi}' : Dynamic index value under completely random disturbance; V_{pi}'' : Dynamic index value of non-random disturbance; P : Maximum risk value under completely random disturbance; P' : Maximum risk value under non-random disturbance.

Water is the most important limiting factor in arid ecosystems and in the maintenance and growth of *P. euphratica*, which depend on ground water that lies within reach of their roots (Yu et al. 2019). In this study, we found that stream water was significantly negatively correlated with tree mortality rates over the last three decades. The dynamic index of population structure (V_{pi}) of gap makers can be represented by the change trend in gap maker quantity in various structures, i.e., growth, stability, or decline. V_{pi} , V_{pi}' , and V_{pi}'' were expressed by a dynamic index value without external, completely random and non-random disturbances, respectively (Xu et al. 2016). Based on the above data analysis, there was an ascending trend in the dynamic index of gap maker's population structure during the periods of 1977–1986, 1987–1996, 1997–2006, and 2007–2016, while in 1957–1966 and 1967–1976 there was a descending trend (Table 2). Furthermore, as clearly shown in Figure 3, there was a considerable negative interaction between the dynamic index value of gap maker population structure and annual runoff; the equation of the fitted model was $y = -0.0215x + 0.6146$ ($R^2 = 0.912$, $P < 0.01$) without external disturbances (V_{pi}), while the equation of the fitted model was $y =$

$-0.0005x + 0.0146$ ($R^2 = 0.8405$, $P < 0.01$) under completely random disturbances (V_{pi}') and $y = 0.0032x + 0.112$ ($R^2 = 0.356$, $P < 0.01$) under non-random disturbances (V_{pi}''). V_{pi} and V_{pi}' decreased markedly with increasing of stream runoff in the study area. The V_{pi}' value became positive and tended to increase when the runoff dropped to $25.86 \times 10^8 \text{ m}^3$ (Xu et al. 2016). Thus, water scarcity is the main reason for tree mortality in *P. euphratica* riparian forests.

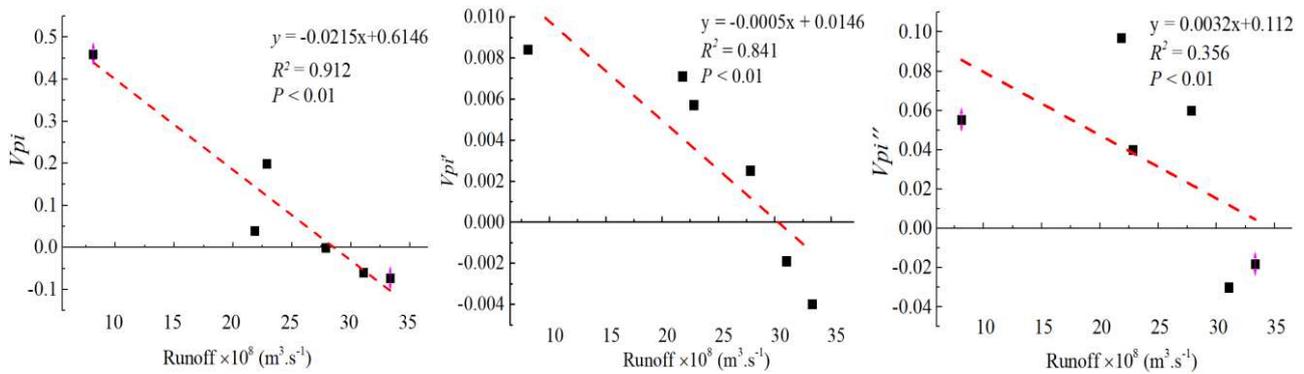


Figure 3 Relationship between population structure, dynamics of gap makers and annual runoff

Comparison of the DBH distribution of dead trees and living trees showed significant variation with a high proportion of young dead trees (Figure 4). As mentioned above, the trees surrounding CGAs and gap makers represented living trees and dead trees, respectively. Grid chart analysis showed that the median DBH of dead trees, especially those that died before 1996, was larger than that of living trees. However, by comparing DBH, we found that the trees that died in the 1997–2016 period were smaller than living trees.

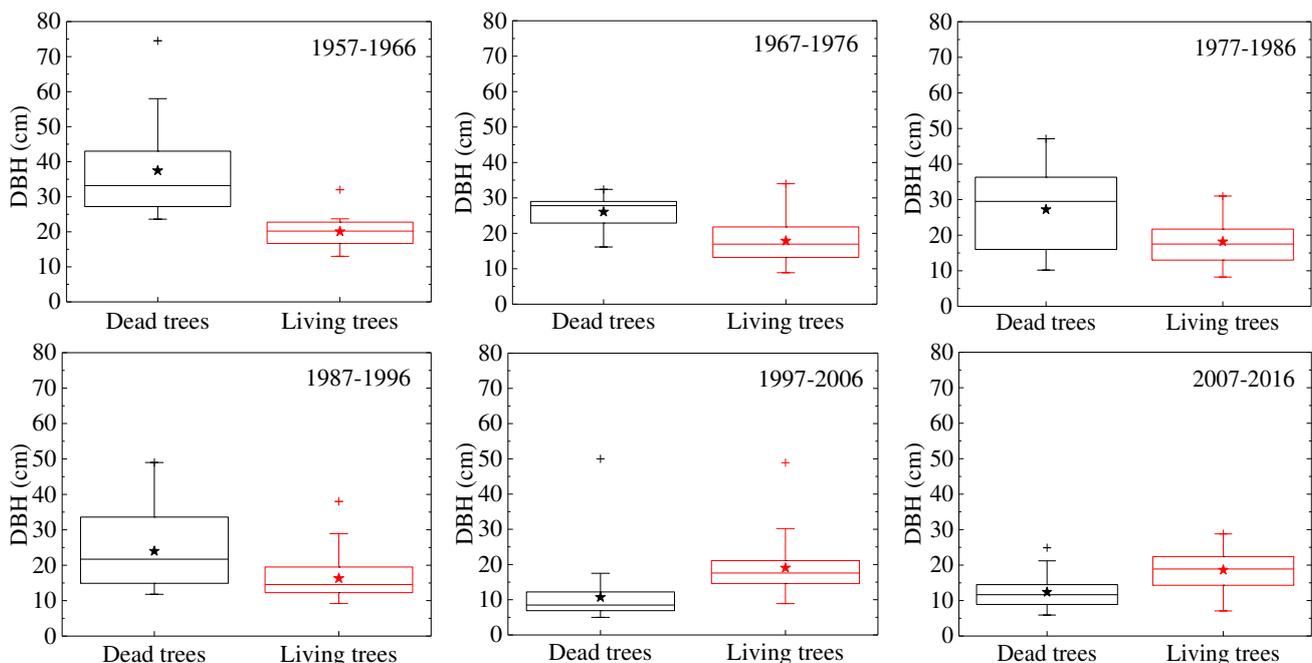


Figure 4 Boxplots of the DBH of dead trees and living trees on the grid charts in canopy gaps that were created at different times. The box encloses the middle 80 % of observations. Median and mean values are indicated by a vertical line (—) and a black star (★), respectively. The upper whisker indicates the largest DBH value, while the lower whisker shows the smallest. The plus sign (+) indicates the maximum DBH.

Forest regeneration

Riparian vegetation was distributed on both sides of the riverbank and was relatively simple and sparse in structure. In our field investigation, we counted 23 seedling and sapling species belonging to 12 families and 20 genera. In general, there were obvious differences in seedling and sapling regeneration among the habitats (CGAs, UCAs, and RBAs) (Table 3). Among the 14 plant species found in the CGAs, 7 were also found in the UCAs and 19 were also found in the RBAs; *P. euphratica*, *T. ramosissima*, *T. hispida*, *T. leptostachys*, *G. uralensis* and *E. oxycarpa* commonly appeared in all three habitats. *P. pruinosa*, *P. hendersonii*, *C. segetum*, *C. auriculatum*, *A. pungens*, *T. mongolicum*, *M. platyphylla* and *L. ruthenicum* were rare species, which only appeared in the RBAs. It was found that seedling appearance is closely related to flooding patterns. *P. australis*, *H. halodendron* and *A. sparsifolia* grew in the CGAs, but not in the UCAs or RBAs. Additionally, the RBAs contained a high number of *P. euphratica* species (30) compared to other habitats, and the number of *P. euphratica* and other species in the CGAs was higher than in the UCAs.

Table 3 Seedling and sapling recruitment in different habitats in the study area

Species	CGAs	UCAs	RBAs
1. <i>P. euphratica</i>	6	3	30
2. <i>P. pruinosa</i>	/	/	5
3. <i>T. ramosissima</i>	10	5	11
4. <i>T. hispida</i>	3	2	4
5. <i>T. leptostachya</i>	2	1	3
6. <i>P. australis</i>	10	/	/
7. <i>H. halodendron</i>	2	/	/
8. <i>G. uralensis</i>	5	2	4
9. <i>A. sparsifolia</i>	2	/	/
10. <i>H. glomeratus</i>	/	/	2
11. <i>K. caspica</i>	3	/	4
12. <i>I. salsoloides</i>	1	/	2
13. <i>P. hendersonii</i>	/	/	1
14. <i>C. segetum</i>	/	/	2
15. <i>C. auriculatum</i>	/	/	3
16. <i>A. pungens</i>	/	/	2
17. <i>S. collina</i>	2	/	4
18. <i>C. pseudophragmites</i>	4	/	5
19. <i>T. mongolicum</i>	/	/	3
20. <i>M. platyphylla</i>	/	/	4
21. <i>L. ruthenicum</i>	/	/	2
22. <i>E. oxycarpa</i>	1	1	3
23. <i>A. venetum</i>	/	3	/

Table 4 Comparison of *P. euphratica* seedlings and saplings in different habitats in the middle reaches of the Tarim River

Plot	Occurrence frequency (%)	Seedling and sapling density (Plant number/m ²)	Plant height (cm)	Young tree density (Plant number/m ²)	Plant height (cm)
CGAs	45.63	0.12±0.06b	3.53±0.86b	8.31±1.64a	285.0±1.62a
UCAs	34.52	0.08±0.03b	3.12±0.45b	0.28±0.06b	167.0±1.55b
RBAs	100.00	17.56±3.12a	18.76±3.95a	0.34±0.04b	187.0±1.51b

*CGAs: Canopy gap areas; UCAs: Undercanopy areas; RBAs: Riverbank areas

The seedling and sapling density of *P. euphratica* was significantly higher in the RBAs than in the CGAs and UCAs. However, compared with the UCAs, the CGAs promote tree regeneration to some extent by providing favorable conditions for the survival and growth of seedling and saplings (Table 4). We also performed quantitative analysis of seedling and sapling regeneration, based on species diversity and richness (Figure 5). According to analysis of the Margalef and Shannon–Wiener indices, the species diversity of seedlings and saplings was remarkably higher in the RBAs than in the other two areas, and higher in the CGAs than in the UCAs ($P < 0.05$). Further, though the density and diversity of seedlings and saplings in the CGAs was not as high as in the RBAs, the survival rate of young trees was higher in the CGAs than in the RBAs (Table 4). Hence, forest canopy gaps can play a pivotal role in the long-term germination and regeneration of plant species.

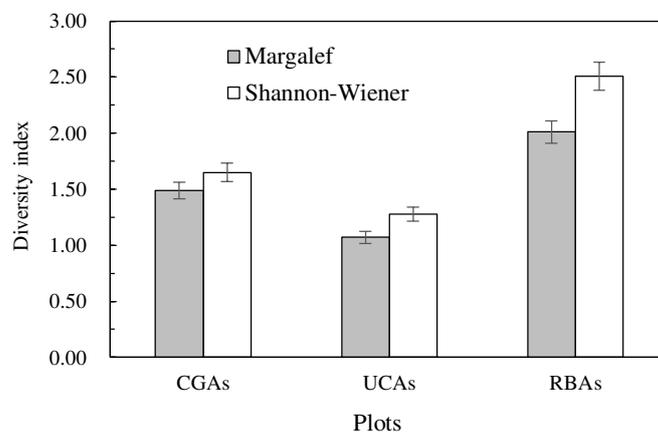


Figure 5 Species diversity of seedlings and saplings in different habitats

Comparison of gap makers and gap fillers

The statistical analysis showed that *P. euphratica* is the most common species of gap maker. However, it also existed as gap filler, along with *T. ramosissima* and *P. australis* (Figure 6). Other gap fillers include *P. pruinosa*, *A. venetum*, *H. halodendron*, *P. hendersonii*, *C. segetum*, *C. auriculatum*, *A. pungens*, *T. mongolicum*, *S. collina*, *C. pseudophragmites*, *M. platyphylla*, *H. glomeratu* and *E. oxycarpa*, as well as some herbs such as *G. glabra*, *I. salsoloides*, *K. caspica*, *L. ruthenicum*, and *A. sparsifolia*, although they were very rare.

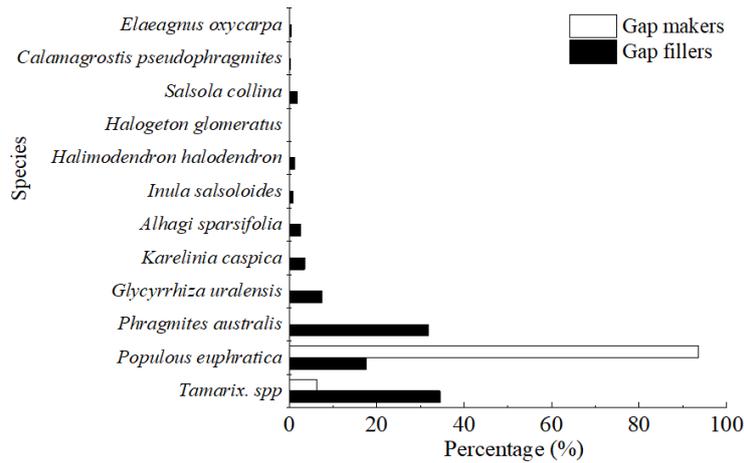


Figure 6 Comparison of gap maker and gap filler species in the middle reaches of the Tarim River

Discussion

One or more gap makers, i.e., dead trees, create canopy gaps in forests (Zang 1999). Keram et al. (2019) found that the mortality of gap makers did not substantially contribute to increased gap size in floodplain forests along the Tarim River. This could be explained by the small crown and DBH of gap makers. Tree mortality is caused by different agents, including drought or flooding, strong wind, diseases, and insect pests, and affects forest dynamics (Krasny et al. 1992; Battles et al. 2000). Host-specific disturbance was considered to be the most common agent of tree mortality in old-growth mixed beech forests in the Western Carpathians (Orman et al. 2017), while wind disturbance led to a disproportionate number of gap makers in old-growth red spruce–Fraser fir forests in North Carolina (White et al. 1985) and red spruce–balsam stands in New Hampshire (Foster et al. 1986; Worrall et al. 2005). However, the causes of tree mortality in riparian forests are different from those in other forest types, such as tropical and subtropical forests. The results of the present study showed that tree mortality in riparian forests along the Tarim River was mainly influenced by hydrological factors (surface water), although strong winds or insect pests may also play a role.

It is universally known that water is the factor with most influence on the survival, distribution, and development of vegetation in hyper-arid regions. In arid ecosystems, the vitality of *P. euphratica* forests strongly depend on the groundwater level (Halik et al. 2006, 2009; Wang et al. 2008; Ginau et al. 2013; Keyimu et al. 2018). Halik et al. (2019) reported that the vitality of *P. euphratica* diminished when the groundwater level was not sufficient for the development of tree stands. In addition, Xu et al. (2016) studied the correlation between groundwater and surface water using stable isotope technology. Their results indicated that the groundwater level is significantly affected by surface water. Chen et al. (2004) and Keilholz et al. (2015) also demonstrated that groundwater is often supplied by stream flow and infiltration from watercourses.

The groundwater depth in the Tarim Basin has dropped continuously as a result of the desiccation of streams and decreases in stream flow since an embankment was built in 2000. Thus, the physical characteristics of plant habitats have been changed. Consequently, the growth of *P. euphratica* cannot be sustained as before in this region, and forests have highly degraded or died. According to the present study, hydrological alterations may be the main cause of tree death in desert riparian forests along the Tarim River. DBH is one of the most common dendrometric variables and can reflect the population structure and growth status of tree stands (Condit et al. 2000; Di et al. 2014). Due to the unique climate and habitat conditions of desert floodplain areas, tree shape variables are obviously different from those in temperate or/and subtropical forests (Ling et al. 2015). In the present research, it was found that most young gap makers (DBH < 15 cm) died in the most recent two decades, i.e., 1997–2006 and 2007–2016. In the early 1970s, water resources were affected on a regional scale by climate change and anthropogenic activities (increased water use for irrigation), and then lag effects led to a progressive decrease in surface water from 1984 and caused a reduction in groundwater from 2004 (Keram et al. 2019). This resulted in habitat deterioration and a decline in the survival of young *P. euphratica* individuals. Based on quantitative correlation analysis, the present study revealed that gap maker mortality and DBH structure responded negatively to variations in surface water. This may be due to long-lasting exogenous disturbances, such as a scarcity of surface water or a decrease in groundwater level, having a notable influence on vegetation through drought stress. Thus, the water requirement of riparian vegetation was not satisfied. Therefore, gap makers of low DBH appeared frequently in *P. euphratica* forests, which experienced an increase in more resilient species. This may be because the vitality of *P. euphratica* in this arid area was directly affected by the hydrological conditions, and only a small proportion of young trees survived to reach canopy height. However, there were a large number of larger, mature trees among the living trees that have developed root systems and are therefore not significantly affected by the reduced groundwater level.

By creating environmental heterogeneity in terms of light availability, gap disturbances play a key role in forest regeneration as well as in the establishment and development of tree species with different ecological recruitment patterns (Runkle 1989; Peterken 1996; Mountford et al. 2006; Zhang et al. 2006; Li et al. 2013). Gap-based restoration provides a flexible system that emulates natural regeneration under different environments. Van et al. (2007) reported that seedling and sapling diversity and richness were promoted by light intensity. Zhu et al. (2014) stated in a review of published studies that compared to UCAs, the seedlings and saplings of shade-tolerant species have significantly higher density in CGAs. Overall, water, light

availability, and seedbed conditions potentially affect seedling emergence, germination, and establishment in floodplain riparian forests. To some extent, a higher density of seedlings and saplings is expected in gaps as they provide full light conditions. The results of the present observations showed that the seedling and sapling species diversity was higher in the CGAs than in the UCAs.

Oliver et al. (1996) stated that canopy gaps simultaneously result in mortality in some individuals and establishment and growth in others, and the ongoing process of death and replacement has a profound effect on forest structure and composition. Pham et al. (2004) showed that *Abies balsamea* is the most frequent successor in *Abies* forest stands and that *Picea mariana* is the most likely replacement species in *Picea* forest stands, regardless of the species of gap makers. In the present study, canopy gaps were filled with shrubs and herbs. When we examined the probability of replacement in floodplain forests, there seemed to be a reciprocal replacement of *P. euphratica* by *T. ramosissima*. and *P. australis* (Figure 6). However, the probability of *P. euphratica* replacement was lower when the mortality of young trees was particularly high.

Conclusion

As the largest riparian forest ecosystem in Northwest China, Euphrates poplar forests are facing considerable challenges (Halik et al. 2019). Monitoring of tree mortality in canopy gaps and plant regeneration in different habitats is considered the most effective way of ensuring the sustainable regeneration and ecological restoration of floodplain forests along the Tarim River. Based on evaluation of the correlation between tree mortality and water resources in the study area, hydrological conditions (runoff volume) are the main reason for the death of *P. euphratica* forests. At the beginning of the 1970s, hydrological conditions were affected on a regional scale by anthropogenic activities. Consequently, riparian forests were threatened under water scarcity, which resulted in high mortality among *Populus* species. Our observations of seedling and sapling density indicated that the frequency of plant species was different among the three studied habitats; it was highest in the RBAs, intermediate in the CGAs, and lowest in the UCAs. It may have been affected by light availability and hydrological conditions during seedling and sapling recruitment.

In conclusion, the protection and maintenance of the floodplain vegetation along the Tarim River are crucial to sustainable regional development in the Tarim Basin. There is a need for further applied experiment to establish test areas for flood water allocation and utilization strategies, which, if successful, should then be extended to the whole basin. We argue that, to some degree, canopy gaps can provide a favorable environment for seedlings to grow into saplings, thereby reaffirming the importance of gap creation for forest regeneration.

Abbreviations

DRB: Distance from River Bank; GWL: Groundwater Level; DBH: Diameter at the Breast Height; TH: Tree Height; CGAs: Canopy gap areas; UCAs: Undercanopy areas; RBAs: Riverbank areas; THNR: Tarim Huyanglin Nature Reserve.

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Author's contributions

Ayjamal Keram conceived, designed and performed the experiments, contributed the data collection, analyzed the data, prepared figures and/or tables, and authored or approved the final draft of the manuscript.

Ümüt Halik conceived and designed the experiments, contributed the data collection, reviewed the manuscript, and approved the final draft.

Tayierjiang Aisahan, Maierdang Keyimu and Kadeliya Jiapaer participated in field work, contributed the data collection and language proofreading.

Guolei Li read the manuscript with critical comments and reviewed the manuscript draft.

All authors checked and approved the final manuscript.

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Availability of data and materials

The data set generated for the study area is available from the corresponding author on reasonable request.

Ethics approval and consent to participate

The subject has no ethical risk.

Consent for publication

The subject matter has no ethical risk.

Competing interests

The authors declare that they have no competing interests.

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Figures

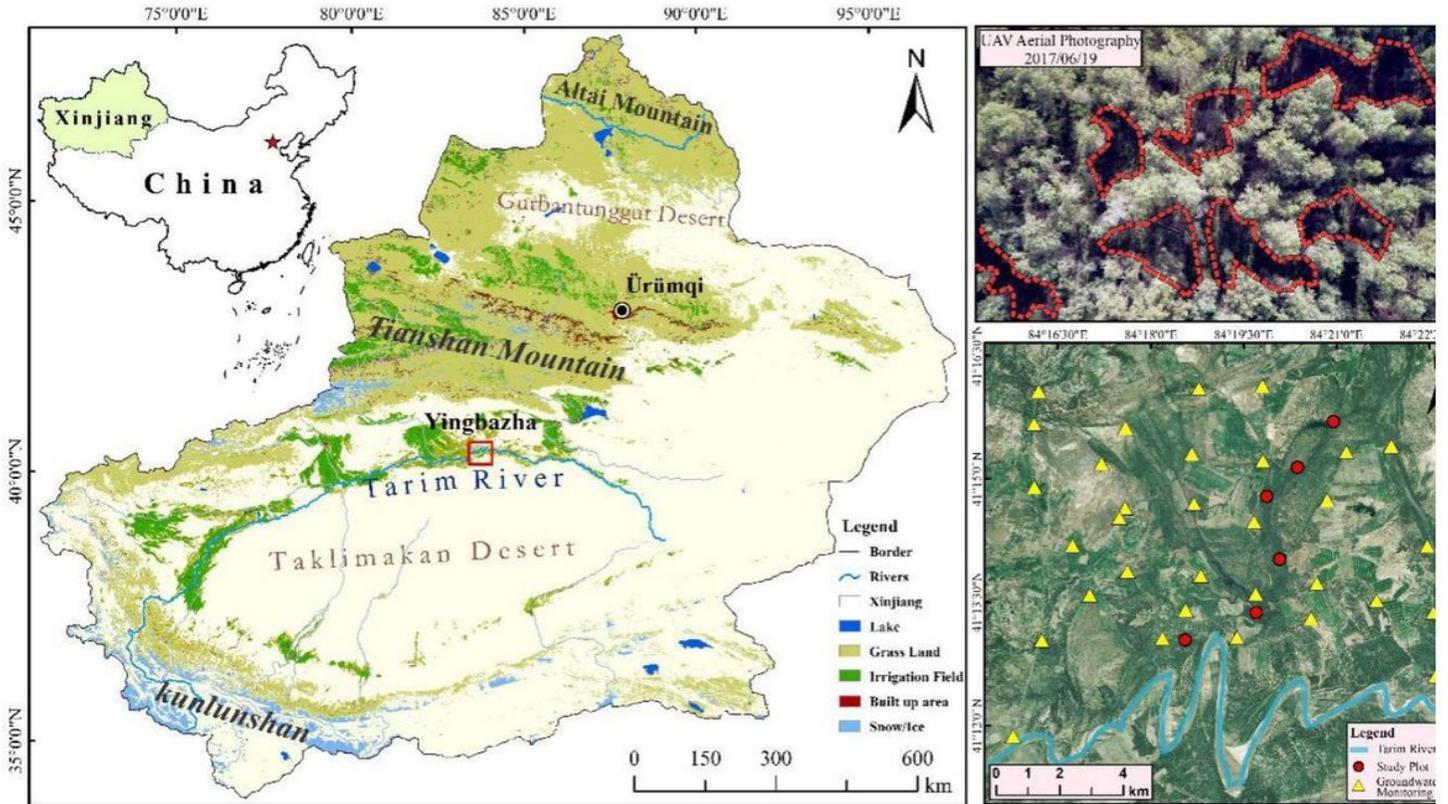


Figure 1

Sketch map of the study area. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

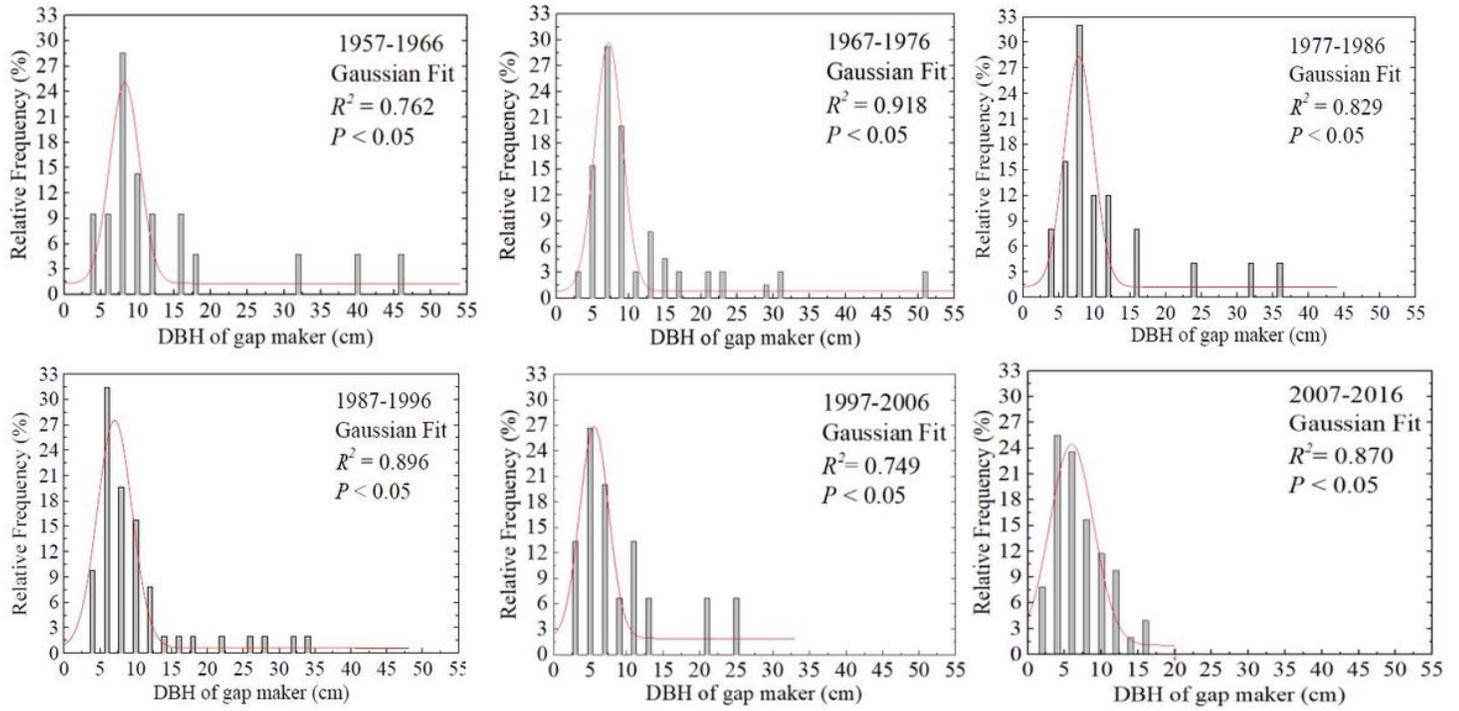


Figure 2

DBH class distribution of *P. euphratica* gap makers in the different years

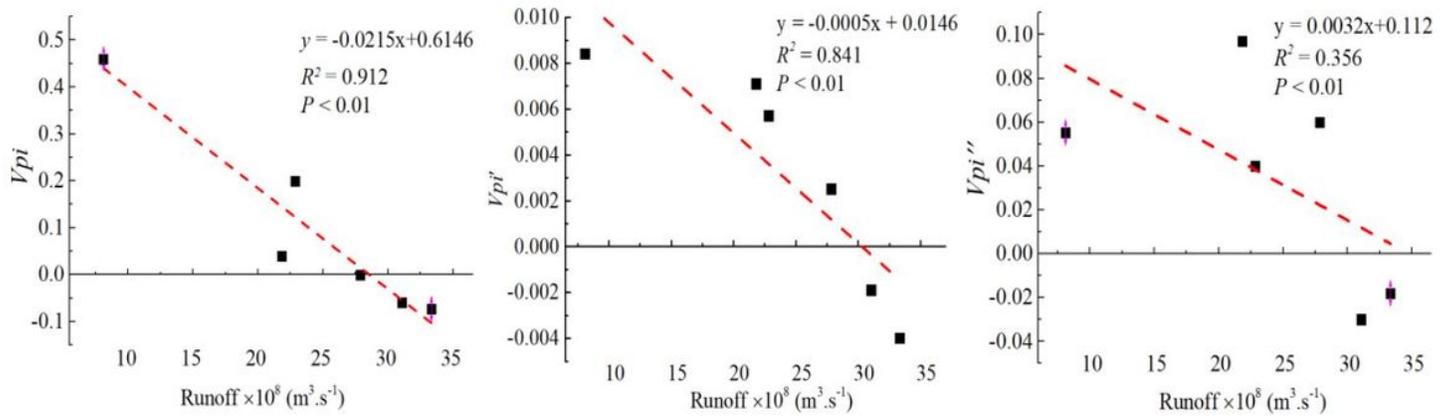


Figure 3

Relationship between population structure, dynamics of gap makers and annual runoff

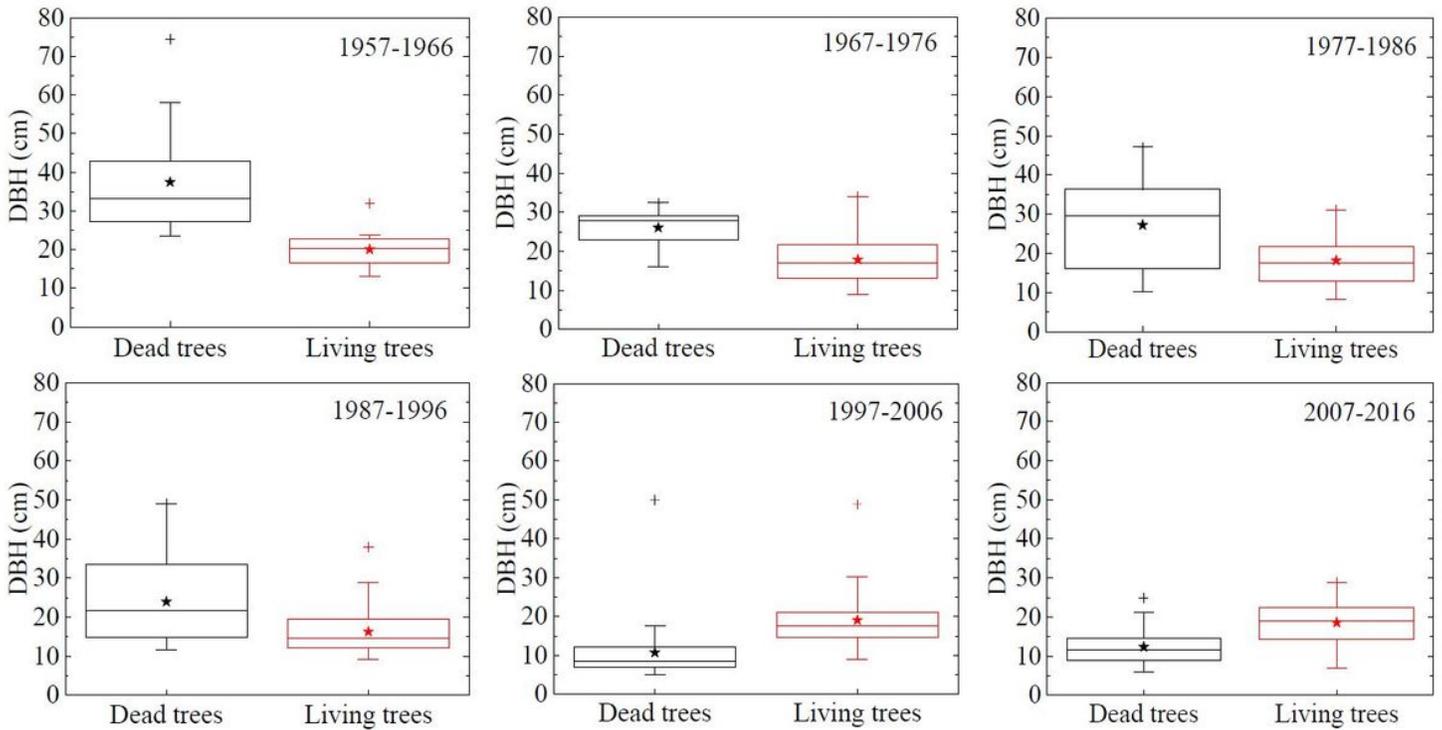


Figure 4

Boxplots of the DBH of dead trees and living trees on the grid charts in canopy gaps that were created at different times. The box encloses the middle 80 % of observations. Median and mean values are indicated by a vertical line (—) and a black star (⊠), respectively. The upper whisker indicates the largest DBH value, while the lower whisker shows the smallest. The plus sign (+) indicates the maximum DBH.

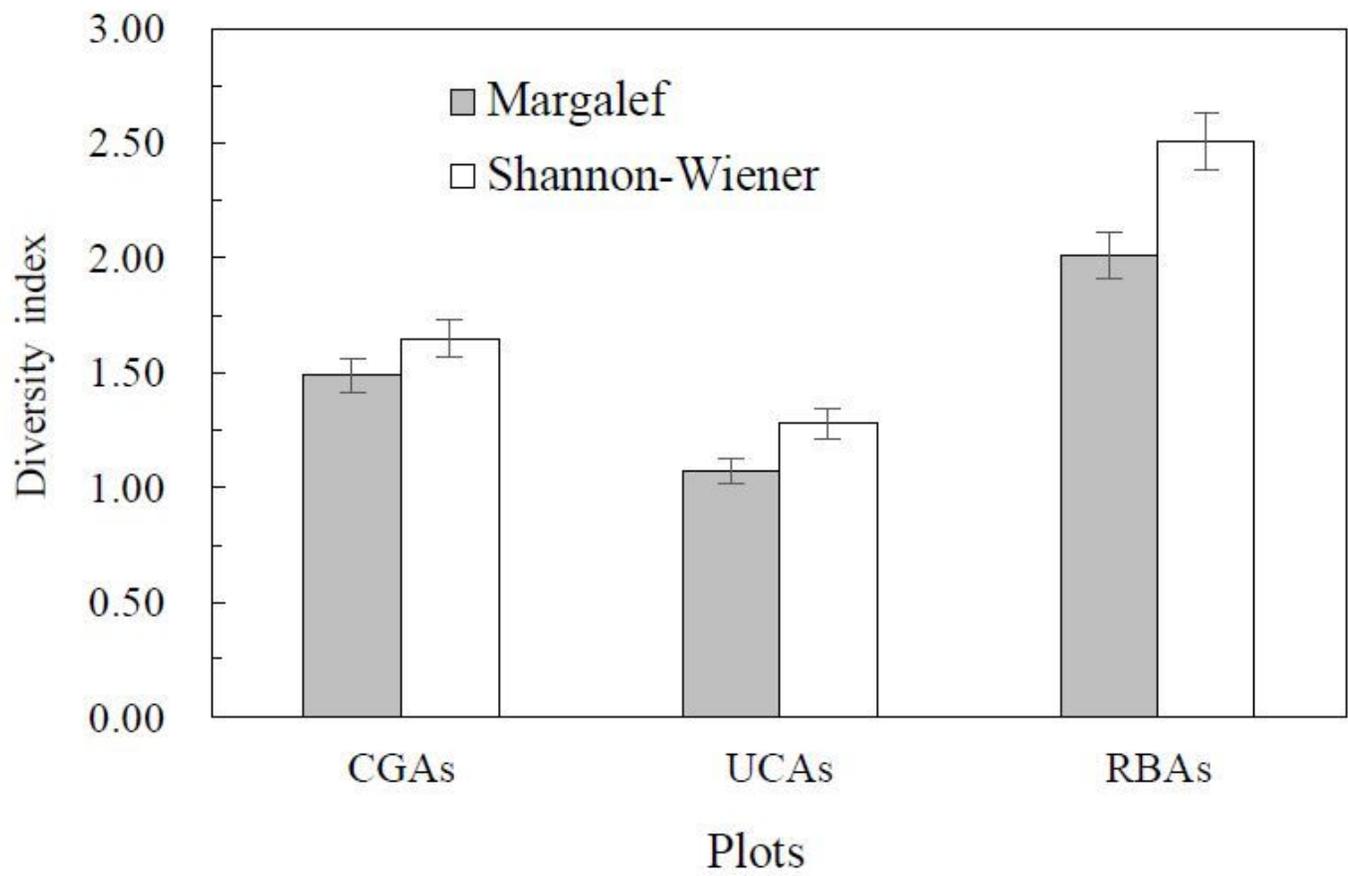


Figure 5

Species diversity of seedlings and saplings in different habitats

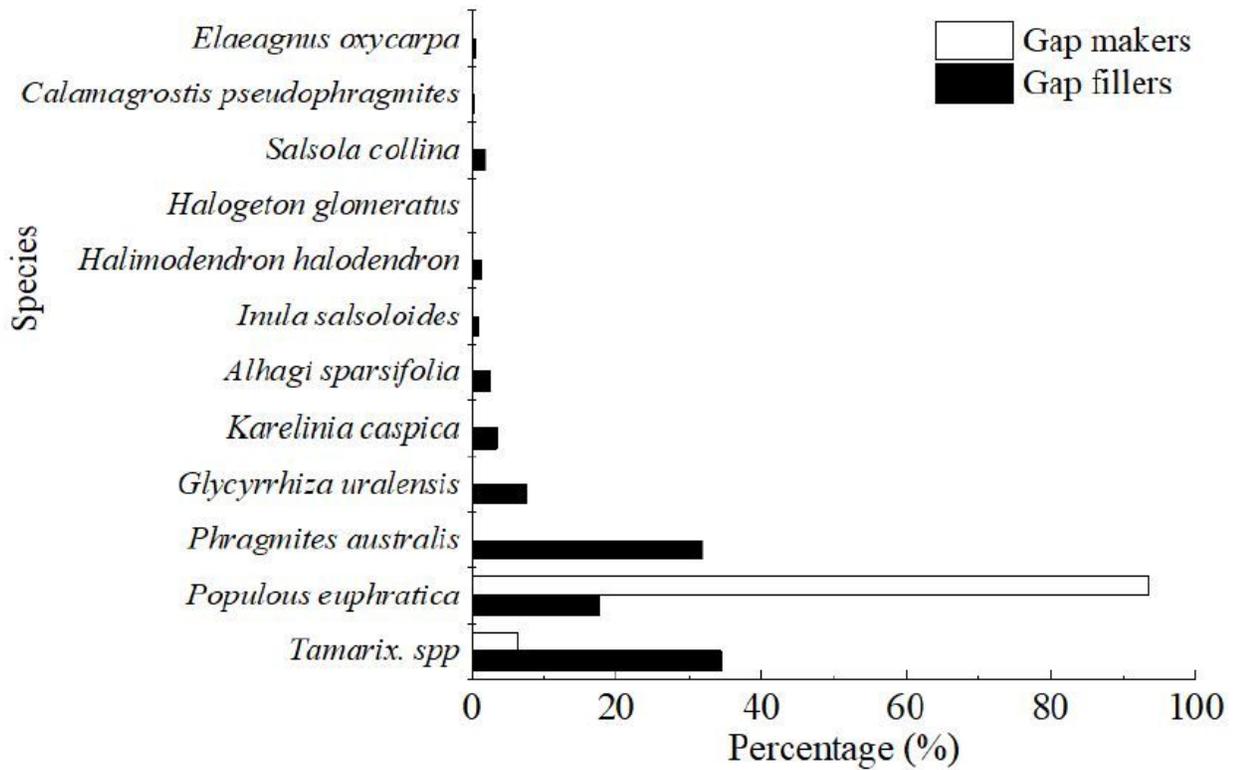


Figure 6

Comparison of gap maker and gap filler species in the middle reaches of the Tarim River

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