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Temporal Heterogeneity of *Populus euphratica* Seed rain in Ejina Oasis, China

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Abstract

The seed rain of *Populus euphratica* in Ejina Oasis was continuously studied in the years of 2004, 2006, 2007, and 2008. The duration of *P. euphratica* seed rain in a community was usually 2 to 3 weeks, with a peak period of 7 to 14 days. Approximately 90% of the total number of seeds were dispersed in the peak period, and for a single day most seeds fell between the hours of 10:00 to 16:00. It was found that the seed rain of *P. euphratica* was determined by a combination of biological rhythms and weather conditions. Wind speed and atmospheric humidity were the two main meteorological factors influencing seed dispersal. More seeds fell when there was higher wind speed and lower RH. After we completed our comprehensive study of the *P. euphratica* seed rain, temporal heterogeneity was found not only in different populations but also in different individuals, and not only in different phases of the seed rain but also in different times of the day. *P. euphratica* extends its seed rain season by these different kinds of temporal heterogeneity to ensure some propagules survive and germinate when floods occur. Furthermore, marked inter-annual fluctuation in the seed rain exists in *P. euphratica* in the study area. Finally, in relation to the water supply for *P. euphratica* in Ejina in recent years, we concluded that there is no dislocation in time of water supply and the seed rain of *P. euphratica* in Ejina Oasis, and the reason for the failure of sexual reproduction of *P. euphratica* may lie in the human disturbances of channeling and the cement lining of the channels.

Key words: *Populus euphratica*, risk-sharing, seed rain, sexual reproduction, temporal heterogeneity

Introduction

Seeds are for the means by which plants produce offspring and broaden the dispersal area of their populations (Yang and Zhu 1991). As a sexual reproductive organ, the seed is the starting point and the endpoint of the life history for a plant population (Yu *et al.* 2007). In reproductive seasons the seeds leave their parent plants to settle in a new habitat. Seed dispersal from parent plants in a given time period is vividly described as a seed rain (Harper 1977). The seed rain stage is a key component in the regeneration of a plant population, and during this process seeds search for the most suitable conditions to germinate (Ban 1995, Clobert *et al.* 2001, Yu *et al.* 2007). Seed dispersal is the initial determinant of an array of individuals in a population (Thiede and Augspurger 1996, Wang *et al.* 2000). There is a large body of literature studying the seed shadow (Burrows 1973, Fei *et al.* 2005, Ford *et al.* 1983, Molau and Larson 2000, Wang *et al.* 2000, Long and Yu 2007), which mainly describes the spatial distribution of dispersed seeds (Janzen 1971, Yang 1990, Zhou and Xu 1998, Shen *et al.* 2007, Zhou *et al.* 2007), but little attention has been paid to the difference of temporal and spatial heterogeneity of seed dispersal of a population in different years.

Sixty-one percent of the world's *P. euphratica* forests are found in China, and most of them (about 80%) are concentrated in GanSu Province and the Inner Mongolia Autonomous Region (Wang *et al*. 1995). Among its distribution areas in China, Ejina Oasis of the Inner Mongolia Autonomous Region is of great importance in *P. euphratica* conservation because there are still well preserved forest forms (Photo. 1 and 2). However, the *P. euphratica* forests are in serious decline (Photo. 3). In the local area there have been almost no naturally seed-originated seedlings found in recent years. Therefore, *P. euphratica* is considered to be failing in sexual reproduction in Ejina Oasis. To help with sexual regeneration of *P. euphratica*, it is very important to understand characteristics of its seeds, including seed rain. Past research revealed that the dynamics of seed rain was interrelated with weather conditions, and could reflect the vitality of a population to some extent (Yang and Zhu1991). In this article, seed dispersal in *P. euphratica* in four years (2004, 2006, 2007, and 2008) was observed and recorded, as well as the relationship between seed rain and weather conditions. The objectives of this paper are 1) to understand the temporal dynamics of *P. euphratica* seed rain in different years; 2) to analyze the influence of weather conditions over seed dispersal of *P. euphratica*; 3) to explore the real reason for the failure of sexual reproduction of *P. euphratica*.

Methods

Study site

This study was conducted in the National Natural Reserve of *Populus euphratica* in Ejina Oasis, Inner

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Photo. 1. Forests of *P. euphratica* in Ejina Oasis. Ejina Oasis is the only area where there are well-preserved *P. euphratica* forest forms.

Photo. 2. *P. euphratica* heterophylly. In an individual *P. euphratica* there are several types of leaves distributed at different heights. (Offered by Zhao Huijuan)

Photo. 3. Severe degeneration of *P. euphratica* forests in China.

Photo. 4. A mini weather station at plot 1. HOBO Weather Station (USA) was set up at plot 1 to monitor weather conditions synchronously during the seed rain season.

Mongolia Autonomous Region, China. The study area has an altitude of 900 - 1600 m, and an arid continental climate with an average annual temperature of 8.2 ˚C, average annual evaporation of 3700 mm, and a frost-free growing season of 145 d and an average of 3396 h of sunshine each year. The mean annual precipitation is only 38 mm with approximately 67% of the rain fall in June, July and August. The most common soil in the forest region of the study area is shrubby meadow soil. The dominant species of the arborous layer is *P. euphratica*, most of which are aged, and *Tamarix. ramosissima* dominates the shrub layer. The herb layer mainly consists of *Sophara alopecuroides*, *Nitraria sibrica* and *Achnatherum splendens*.

Experiment design

During the years of 2004, 2006, 2007, and 2008, four permanent sample plots were set in the study area, which were located at N41˚58'6"E101˚5'12", N42˚0'31"E101˚13'54", N42˚0'35"E101˚13'47", and N41˚58'8"E101˚5'13", and named plot 1, 2, 3, and 4, respectively (Table 1 and Fig. 1). The size of each plot was 100m long and 50m wide. In 2004, 2006 and 2007, seed collectors were deployed at plot 1 to retrieve *P. euphratica* seeds during the seed rain seasons. At the same time a mini weather station (HOBO Weather Station, USA.) was set to monitor and record weather conditions synchronously, including temperature, moisture, and wind speed and so on (Photo. 4). Seeds in the seed rain season at plot 4 were only retrieved by seed collectors and recorded daily in 2007. In 2008, seed dispersal of individual *P. euphratica* trees was investigated at plots 1, 2 and 3. The elementary, peak and decline periods of seed dispersal of every adult female individual in *P. euphratica* was recorded. According to the records for 2004, 2006 and 2007, more than 90% of total seeds in the seed rain were dispersed in the peak period, less than 5% percent in the elementary and decline periods. Hence the periods of seed rain were defined as follows:

Elementary period: 1% - 5% of all propagules on an individual dispersed;

Peak period: more than 5% of all propagules on an individual started dispersed;

Decline period: less than 5% of all propagules had not been dispersed.

Fig. 1. Location of study sites. Our study sites are located at the National Natural Reserve of *Populus euphratica* in Ejina Oasis, which lies in northwest China.

Table 1. Introduction to Plots.

Plot No.	Plot 1	Plot 2	Plot 3	Plot 4
Location	N41°58'6" E101°5'12"	N42°0'31" E101°13'54"	N42°0'35" E101°13'47"	N41°58'8" E101°5'13"
Tree layer	*P. euphratica*	*P. euphratica*	*P. euphratica*	*P. euphratica*
Mean height of *P. euphratica*	7.3 m	7.8 m	8.6 m	8.3 m
Mean DBH of *P. euphratica*	32.3 cm	27.0 cm	42.2 cm	58.4 cm
Shrub layer	*Tamarix spp.*	None	None	None
Herb layer	*Sophora alopecuroides Phragmites communis Elymus dahuricus*	*Sophora alopecuroides*	*Sophora alopecuroides*	None
Soil type	Desert saline soil	Shrubby meadow soil	Shrubby meadow soil	Sandy soil

Seed collectors

Seed collectors were plastic bowls, 10 cm in diameter (surface area of 0.00785m^2), and 7 cm in height, each of which was filled with water to prevent seeds from being blown away. Eighty-one seed collectors were deployed evenly at an interval of 5 meters in a 40×40 m^2 area at plot 1 before the seed rain seasons in 2004, 2006, and 2007. In seed rain seasons (in June, July and August) seeds of *P. euphratica* trapped in each seed collector were retrieved and calculated every two hours from 8:00 am to 20:00 pm every day. The same procedure was used for plot 4 in 2006.

Results

Temporal heterogeneity of seed rain in *P. euphratica*

It was found that there was marked temporal heterogeneity in the seed rain in *P. euphratica*. From the record of the seed rain in 2007 at plot 1 we can see a difference in seed rain density between day and night (Table 2), but also at different times of the day (Table 3).

Table 1 shows that approximately 90% of the seeds in the seed rain were dispersed during the day, while there were just a few (less than 10%) dispersed at night in the whole seed rain season, including in the elementary, peak and decline periods. Although the seed rain season lasted 21 days, more than 98% of the total seed rain occurred in the peak period of 15 days.

As shown in Table 3, there were seeds dispersed all day long, but more than 80% of the seeds were dispersed in the middle of the day, from 10:00 to 16:00. Hence, there was a peak period of seed rain in a day, as well as in the whole progression of the seed rain season.

Table 2. Comparison in seed rain density of daytime and night at plot 1 in 2007.

Phase	Date	SRD[a]			Daytime ratio (%)	Mean SRD[a] in each phase	Phase ratio (%)
		daytime	night	total			
Elementary period	1/8	278.4	28.3	306.7	90.77%	293.7	1.43%
	2/8	198.2	18.9	217.0	91.30%		
	3/8	324.0	7.9	331.8	97.63%		
	4/8	306.7	12.6	319.3	96.06%		
Peak period	5/8	668.4	136.8	805.2	83.01%	5381.9	98.21%
	6/8	2,599.7	18.9	2,618.5	99.28%		
	7/8	8,388.8	3.1	8,391.9	99.96%		
	8/8	2,654.7	407.3	3,062.0	86.70%		
	9/8	2,595.0	73.9	2,668.9	97.23%		
	10/8	4,032.4	39.3	4,071.7	99.03%		
	11/8	8,173.3	102.2	8,275.5	98.76%		
	12/8	6,470.1	83.4	6,553.4	98.73%		
	13/8	12,320.5	2,173.5	14,494.0	85.00%		
	14/8	15,637.3	605.5	16,242.8	96.27%		
	15/8	4,647.3	195.0	4,842.3	95.97%		
	16/8	5,995.1	561.5	6,556.6	91.44%		
	17/8	369.6	26.7	396.3	93.25%		
	18/8	618.1	25.2	643.2	96.09%		
	19/8	1,088.3	17.3	1,105.6	98.44%		
Decline period	20/8	191.9	1.6	193.4	99.19%	148.6	0.36%
	21/8	103.8	0.0	103.8	100%		
Mean	—	3,698.2	216.1	3,914.3	—	—	—
Total	—	77,661.4	4,538.8	82,200.2	94.48%	—	—

a. SRD stands for seed rain density (seeds/m^2)

Table 3. Record of seed rain density in different time in daylight in 2007 at plot 1.

Date	Time 1	Time 2	Time 3	Time 4	Time 5	Time 6	Total
1/8	31.5	84.9	95.9	28.3	26.7	11.0	278.4
2/8	40.9	44.0	45.6	48.8	17.3	1.6	198.2
3/8	75.5	88.1	59.8	78.6	18.9	3.1	324.0
4/8	12.6	122.7	110.1	45.6	14.2	1.6	306.7
5/8	44.0	251.6	210.7	116.4	33.0	12.6	668.4
6/8	81.8	1,225.1	806.8	363.3	91.2	31.5	2,599.7
7/8	476.5	2,848.2	3,252.3	1,520.8	187.2	103.8	8,388.8
8/8	130.5	1,412.3	786.3	185.6	118.0	22.0	2,654.7
9/8	47.2	218.6	756.5	1,111.9	210.7	250.1	2,595.0
10/8	457.7	1,162.2	1,264.4	951.5	130.5	66.1	4,032.4
11/8	47.2	1,470.5	5,059.4	989.2	537.9	69.2	8,173.3
12/8	81.8	2,352.8	2,131.0	1,731.5	121.1	51.9	6,470.1
13/8	103.8	2,127.9	6,660.4	2,182.9	982.9	262.6	12,320.5
14/8	339.7	70.8	5,366.0	5,471.4	3,708.4	681.0	15,637.3
15/8	140.0	325.5	1,384.0	1,945.4	729.7	122.7	4,647.3
16/8	118.0	1,220.4	2,486.4	1,781.9	324.0	64.5	5,995.1
17/8	62.9	61.3	59.8	97.5	66.1	22.0	369.6
18/8	14.2	138.4	375.9	64.5	15.7	9.4	618.1
19/8	26.7	283.1	509.6	196.6	40.9	31.5	1,088.3
20/8	17.3	29.9	72.3	55.0	14.2	3.1	191.9
21/8	15.7	36.2	20.4	15.7	9.4	6.3	103.8
Total	236.0	15,574.0	31,514.0	18,983.0	7,398.0	1,828.0	77,661.4
Mean	112.6	741.6	1,500.7	903.9	352.3	87.0	3,698.2

a. SRD stands for seed rain density (seeds/m^2); Time 1to 6 stands for 8:00-10:00, 10:00-12:00, 12:00-14:00, 14:00-16:00, 16:00-18:00 and 18:00-20:00 respectively.

Some scholars (Zhang *et al.* 2005) have asserted that there is relationship between seed dispersal and atmospheric humidity. As atmospheric humidity declines more seeds are dispersed. At noon, when atmospheric humidity is at its lowest point, the most seeds are dispersed in the 10:00 to 16:00 time period.

Relationship between seed rain density and meteorological factors

In 2006 and 2007, weather conditions were recorded synchronously while seeds were retrieved and calculated. Correlation analyses between the amount of seeds dispersed and atmospheric humidity, temperature, and wind speed were performed by SPSS 13.0 (SPSS Inc.) (Tables 4, and 5; Fig.s 2, 3 and 4).

Tables 4 and 5 show that in the temporal scale of a day there was a close relationship between seed rain density and weather conditions, including atmospheric humidity and wind speed. And the regression equations show that wind was an important factor in seed dispersal. However, there was little interrelation between seed rain density and meteorological factors in the temporal scale of a whole seed rain season. This phenomenon is understandable for *P. euphratica* trees because they only disperse their seeds when fully ripe. As to a population, when there are more fully ripened seeds on a day, there is a higher SRD, so diurnal SRD of a population is determined by how many seeds are ripe on that day. We call this a "biological rhythm". A conclusion could be drawn on the basis of former analysis that seed rain of *P. euphratica* was determined by biological rhythm of the population and some meteorological factors, which meant that the date when seeds of *P. euphratica* left their parent trees was determined by biological rhythm, and on the basis that seeds are fully ripened, when there is good weather condition on this day (and this kind of "good weather" usually happens at midday), such as low atmospheric humidity and high wind speed, more seeds could be dispersed from their parent trees.

Table 4. Correlation coefficients between SRD and weather condition in the temporal scale of a day and stepwise regression equation.

Year	Temperature	RH	Wind speed	Stepwise regression equation
2006	0.292	-0.395*	0.572**	SRD=24.59+130.61·WS
2007	0.209*	-0.262**	0.349**	SRD=709.52+574.96·WS-9.82·RH

** Correlation is significant at the 0.01 level (2-tailed); * correlation is significant at the 0.05 level (2-tailed) SRD, seed rain density; WS Wind, speed; RH, atmospheric humidity.

Table 5. Correlation coefficients between seed rain density and weather condition in peak period of the whole seed rain season in 2007.

	Temperature[1]	RH[2]	wind speed[3]
Correlation Coefficient	0.069	-0.324	0.010
Sig. (2-tailed)	0.814	0.259	0.972

1, average temperature of midday; 2, average atmospheric humidity of midday; 3, average wind speed of midday.

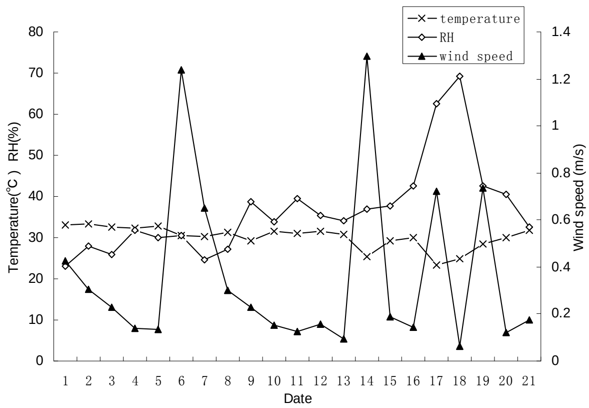

Fig. 2. Daily average temperature, RH and wind speed at plot 1 during seed rain season in 2007.

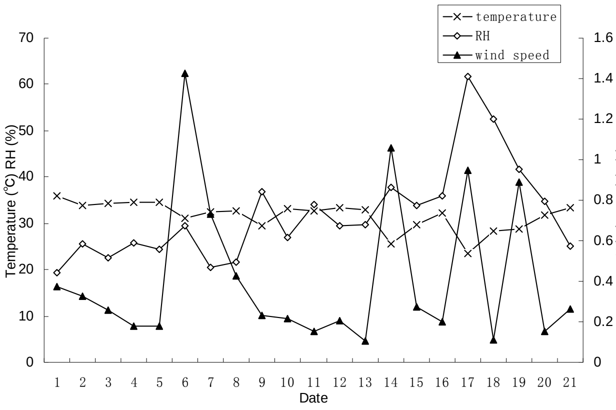

Fig. 3. Daily average temperature, RH and wind speed at midday (10:00 am to 16:00 pm) at plot 1 during seed rain season in 2007.

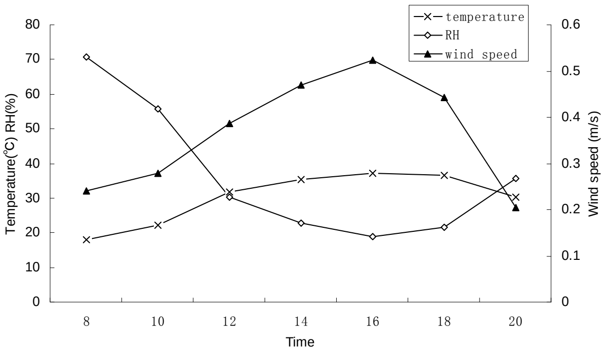

Fig. 4. Average temperature, RH and wind speed at different times of the day at plot 1 during seed rain season in 2007.

Table 6. Heterogeneity in seed rain in different communities of *P. euphratica*.

Plot No.	Plot 1	Plot 4
Start date of seed rain	12 Aug.	19 Jul.
Seed rain duration(d)	14	18
Duration of peak time(d)	10	11
Seed density per day(seed•m^{-2}•d^{-1})	2,968	3,627
Seed density in total(seed•m^{-2})	41,548	65,280

Table 7. Inter-annual fluctuation of seed rain at plot 1.

Year	2004	2006	2007
Start date of seed rain	8 Aug.	12 Aug.	1 Aug.
Seed rain duration(d)	15	14	21
Start date of peak time	14 Aug.	14 Aug.	6 Aug.
Duration of peak time(d)	7	9	14
Seed density per day(seed·m^{-2}·d^{-1})	1,522.2	2,967.7	3,914.3
Seed density in total(seed·m^{-2})	22,833.0	41,547.5	82,200.2

Heterogeneity in seed rain in different communities

Seeds in seed rain were investigated at plots 1 and 4 at the same time in 2006 (Table 6) and obvious temporal heterogeneity in seed rain in different communities was discovered.

There was a significant difference in seed rain condition between the different plots, such as starting date, seed rain density and duration of seed rain and peak period, and so on. Plot 4 performed much better than plot 1 in aspects of duration of seed rain and seed rain density. Obviously, there was heterogeneity in seed rain in different communities of *P. euphratica*.

Fluctuation in seed rain in different years

Not only heterogeneity in seed rain existed in different populations, but also there was significant inter-annual fluctuation in seed rain in the same population (Table 7 and Fig. 5). As shown in Table 7 when there was a higher seed density in total, there was a longer peak period. It seemed that if more seeds were produced, it would take more time to disperse them.

5. Seed dispersal of individuals

Seed dispersal of individual *P. euphratica* was investigated in three plots (plots 1, 2 and 3). Usually an individual *P. euphratica* had a mean duration of seed rain of about 13 days, and 3 to 7 days of mean duration of the peak period (Table 8, Photo. 5). This conformed to the seed rain of a community of *P. euphratica*.

Discussion

The study of seed fall of *P. euphratica* showed that there was a peak period of 14 to 21 days in each seed rain season, in which approximately 90% of all the seeds were dispersed. There was temporal heterogeneity in seed rain of *P. euphratica* populations, as well as individuals. The main reason for the differences in seed fall might lie in the difference of intensity of seed source, which included a difference in density and age of parent trees, as well as health of the individuals (Zhang *et al.* 2005). In fact, the temporal heterogeneity might be a kind of adaptation. By means of temporal heterogeneity of seed rain, *P. euphratica* populations and individuals shared the risk of failure in seed germination. For *P. euphratica* in arid areas water is available for a short time when flooding occurs between June and August. Considering *P. euphratica* seeds can survive less than 6 days in field conditions (Zhang *et al.* 2005) without water some communities of *P euphratica* disperses their seeds to make sure that some survive and germinate when floods come. The best way to achieve this is to disperse their seeds at different times according to the hydrologic regime.

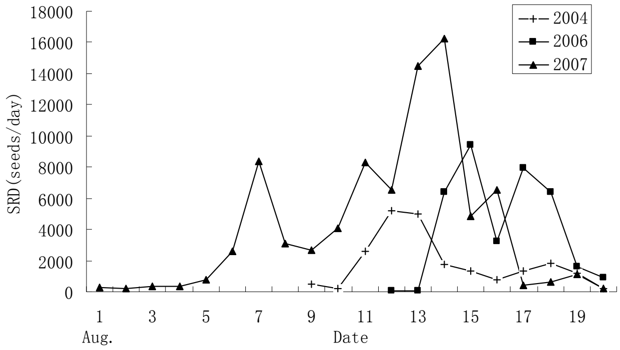

Fig. 5. Seed dispersal of *P. euphratica* at plot 1 in 2004, 2005 and 2006.

P. euphratica seeds, with a thousand-grain weight of just 0.0967g, are wind-dispersed (Wang *et al.* 1995). In addition, there is fuzz on the seeds, which makes them more suitable to be distributed long distances. As wind plays an important role in seed dispersal quality and distance there is a significant relationship between seed rain density and wind speed. In our analyses, atmospheric humidity was also a key factor influencing seed dispersal, which may also influence cracking and desquamation of *P. euphratica* seeds. They crack and desquamate, which is sometimes referred to as xerochasy (Burrows 1973, Van 1982), occurs more easily in a lower atmospheric humidity, like *Betula uber* seeds (Ford *et al.* 1983).

There is an evident fluctuation in seed rain in different years in many tree varieties (Salonen 1987, Yang and Zhu 1991, Armesto *et al.* 2001, Molau and Larsson 2000), and this was also the case with *P. euphratica*. There was numerical variance of seed fall, in addition to duration of seed rain. However, there also seemed to be a relative stable period of seed rain in the same plot in different years. As to the variance of seed fall, environmental factors might be a reason. For example, weather conditions in the growing season differ from year to year, with some years having more rain and flooding. These environmental factors lead to different reproductive abilities, thus inter-annual fluctuation in seed rain of *P. euphratica* occurs. Furthermore, there are many other factors that may influence seed production. For instance, biological factors such as heredity may also play an important role (Yu *et al.* 2007).

In this study, we noted an interesting phenomenon. Though a population might have almost a month long

Table 8. Seed dispersal of individuals.

Plot No.	Duration of seed rain (d)			earliest date	last date	Duration of peak time (d)			earliest date	last date
	Mean	Min	Max			Mean	Min	Max		
1	8.7	2	28	18 Jul.	14 Aug.	2.7	1	8	4 Aug.	13 Aug.
2	9.4	3	35	14 Jul.	25 Aug.	4.3	2	18	15 Jul.	25 Aug.
3	5.6	2	30	18 Jul.	28 Aug.	2.5	2	22	19 Jul.	27 Aug.

Table 9. Amount of water supply for *P. euphratica* in Ejina oasis passed Langxin Mountain Section of Heihe River in 2006 and 2007. * (10 thousand m^3)

	Nov.～Mar.	Apr.	May.	Jun.	Jul.	Aug.	Sep.	Oct.
2006	20,030	1,737	549	0	10,339	6,107	12,416	9,024
2007	18,650	2,851	2,241	0	10,678	1,082	15,033	10,626

* All data in this table was quoted from www.yellowriver.gov.cn

Photo. 5. Female individuals of *P. euphratica* in peak period of seed rain.

Photo. 6. A cemented channel in *P. euphratica* forests of Ejina Oasis.

seed fall, in some individuals it might be just a few days. Why didn't these individuals spend more time in dispersing their seeds so as to increase the probability that some propagules might settle in more beneficial environments? A hypothesis was raised to explain this phenomenon: the duration of seed rain rested with a gene, and an individual had duration of seed rain of just a few days, but the individuals distributed their seed fall in different period to extend the seed rain season for the whole population. It was also found that there were seeds dispersed from early July to late August. In 2008, the earliest date of seed dispersal for an individual was July 14th and the last was found on August 28th. In fact, there were individuals of *P. euphratica* dispersing their seeds every day during the period of July 14th to August 28th. Water was available for *P. euphratica* in Ejina Oasis during this period in recent years (Table 9), so we can say that there was no dislocation in time of water supply and seed dispersal of *P. euphratica*. In fact, failure of sexual reproduction of *P. euphratica* doesn't lie in the lack of water in the seed rain seasons.

In our opinion, the channeling has changed the natural hydrologic regimes and processes, and this has led to the failure of sexual regeneration of *P. euphratica*. There were several channels in local forests of *P. euphratica* (Photo. 6). These channels were cemented to prevent water from infiltrating into soil along the channels, so that water can be supplied to the lower reaches. However, this led to two problems: on one hand, *P. euphratica* trees regenerated along rivers by dispersing seeds to and germinated on the flooded delta along rivers in the past, so it's said that "*P. euphratica* goes with rivers". However, at present, water is regulated by the channels, so there was no longer natural flooding. Without natural flooding, *P. euphratica* can't regenerate successfully on flooded deltas; on the other hand, as the channels were cemented, of the *P. euphratica* along them were no longer able to obtain water smoothly even if there is plenty of water in the channels. In a word, the channels cemented harmed the *P. euphratica* trees along them by changing the natural hydrologic regimes and keeping them from water in the channels.

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