Effects of ecological water transport on photosynthesis and chlorophyll fluorescence of *Populus euphratica*

Chun Yan Zhao, Jian Hua Si, Qi Feng, Teng Fei Yu, Ravinesh C. Deo and Huan Luo

ABSTRACT

This study investigated the physiological response of *Populus euphratica* (*P. euphratica*) to ecological water transport. Results showed significant increases in net photosynthetic (32.71%), stomatal conductance (27.58%), and transpiration (25.18%) rates of *P. euphratica* prior to the ecological water transport treatment. Internal CO_2 concentrations (Ci) decreased significantly compared with the day preceding the treatment (23.69%; $P < 0.05$). During the treatment, the O, J, I, and P steps quickly increased, with the P step exhibiting the most significant change ($P < 0.05$). Moreover, Fv/Fm and Fv/Fo values were highest 7 d after the ecological water transport treatment. During the treatment, the initial fluorescence (F_0), the maximal fluorescence intensity (Fm), PI, and RC/CSo quickly increased, with an increasing percentage of 9.67%, 46.15%, 59.17%, and 48.54%. In contrast, V_j, ABS/RC, TRo/RC, and ETo/RC rapidly decreased, with a decreasing percentage of 30.43%, 43.54%, 37.50%, and 39.04%, respectively. After the treatment, the average chlorophyll content of a, b, and a + b increased by 26.36%, 8.89%, and 21.93%, respectively, compared with the day preceding the treatment. This study also found that the relationship between soil water content and the net photosynthetic rate, stomatal conductance, the transpiration rate, the internal CO_2 concentration, Fv/Fm, and Fv/Fo of *P. euphratica* were strongest during ecological water transport.

Key words | chlorophyll fluorescence, ecological water transport, photosynthesis, *Populus euphratica*

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INTRODUCTION

The Heihe River is the second longest inland river in China (Zhang *et al.* 2011). The ecological environment in the lower reaches of this river has evidently deteriorated, and this has resulted from a continuous decrease in discharge rates. Since 2000, an ecological water transport measure has been implemented to rehabilitate and protect ecosystems in this area. Ecological water transport is the groundwater recharge by river channel seepage to maintain growth of vegetation (Yu *et al.* 2012). Several scientifically significant and practical benefits related to this artificial water delivery program have already been substantiated, such as

an increase in groundwater levels (GWL) from −4.50 to −2.67 m and a reduction in groundwater mineralization from 2.00 to 1.44 g/L after the ecological water transport initiative was put into practice (Liu 2008). There has also been an obvious increase in vegetation cover area (Guo *et al.* 2009) and an increase in soil moisture at different depths (Yu *et al.* 2012). However, no study has been conducted on the effects of ecological water transport on the physiology of plants in this area, especially in relation to response processes and mechanisms in desert riparian zones.

Photosynthesis is an important physiological process that is affected by soil water content (SWC) (Qiu *et al.* 2013). Several studies, however, have indicated that photosynthesis is retarded by deficits in SWC (Long *et al.* 1994; Lee *et al.* 2016). When a rapid increase in SWC occurs after ecological water transport measures are implemented, negative photosynthetic effects could result in plants under long-term drought conditions in arid and desert zones due to excessive soil moisture (Li *et al.* 2009). Nevertheless, photosynthetic characteristics pertaining to different phases of ecological water transport have yet to be identified.

Chlorophyll fluorescence is a sensitive tool that is used to evaluate plant electron transport through light reactions as well as a means to examine plant response to water stress (Strasser & Strasser 1995; Dąbrowski *et al.* 2016; Lee *et al.* 2016). SWC changes considerably during ecological water transport processes, which could have a significant effect on the chlorophyll fluorescence of plants, including photosystem II (PSII) efficiency, which affects the fluorescence rise kinetics OJIP. On the one hand, negative effects of water stress on chlorophyll fluorescence processes have been investigated over a long period of time (Strauss *et al.* 2006; Padilla *et al.* 2016). On the other hand, relevant information on chlorophyll fluorescence during ecological water transport processes remains poorly understood.

Chlorophyll content is a reflection of the photosynthetic level (Gao *et al.* 2016). It is widely believed that leaf chlorophyll content often declines under severe stress (Anjum *et al.* 2011). However, some studies have shown no detectable reduction in chlorophyll *a* (Chla) or chlorophyll *b* (Chlb) content, even at maximum water stress levels (Sapeta *et al.* 2013). By contrast, an increase in the Chla/Chlb ratio during drought stress has been demonstrated in different species (Liu *et al.* 2011). Therefore, a clarification related to the response of chlorophyll content to water stress is still required, especially under conditions of progressive stress.

P. euphratica is a typical tree species found in desert riparian forests in the lower reaches of the Heihe River in northwestern China. It is strongly drought-resistant and highly salt-tolerant (Zhao *et al.* 2017). Understanding the effects of ecological water transport on photosynthesis and chlorophyll fluorescence of *P. euphratica* is important in advancing scientific knowledge related to water use strategies and plant hydraulic functions for desert riparian species.

Therefore, the study was (1) to investigate the effects of ecological water transport on the net photosynthetic rate (*Pn*), intercellular CO_2 concentration (*Ci*), stomatal conductance (*Cs*), transpiration rate (*Tr*), chlorophyll fluorescence, and chlorophyll content of *Populus euphratica*; (2) to analyze the adaptive mechanisms of *P. euphratica* to ecological water transport; and (3) to determine the relationships between soil water and the photosynthetic and chlorophyll fluorescence performance of *P. euphratica* during different ecological water transport phases. Our main objective is to fill the gap to provide relevant information about plant management and ecological water transport initiative and to provide a theoretical basis for the conservation and restoration of desert riparian forest.

MATERIALS AND METHODS

Site description

The study area (42°01′ N, 100°21′ E) is located in the lower reaches of the Heihe River basin, northwest China, at an altitude of 883.54 m. The area is characteristic of a typical continental arid climate. The average annual precipitation is 38 mm, and approximately 75% of rainfall occurs between June and September. The average annual temperature is 8.2°C. The mean annual evaporation exceeds 3,390 mm, which is greater by a factor of 90 compared with precipitation. Average annual wind speed (*WS*) is approximately 3.4 to 4.0 m/s. The soil type derives from fluvial sediment (Si *et al.* 2008). In the study area, *P. euphratica* is the dominant plant species, followed by *Tamarix ramosissima*. The understorey is dominated by grasses and shrubs, including *Karelinia caspica*, *Achnatherum splendens*, and *Sophora alopecuroides* (Yu *et al.* 2013).

Materials

We conducted the experiment at a distance of 1,000 m from the Heihe River. The average tree height and average diameter at breast height (DBH) of *P. euphratica* were 3.04 ±

0.50 m and 4.77 ± 1.35 cm, respectively. The average projected canopy area was 4.09 ± 1.78 m^2. We selected ten representative sample trees for the experiment that we determined to be well grown, straight, and healthy (Table 1). Measurements were taken during five specified phases: before the ecological water transport treatment (BT) from July 1 to 9; during the ecological water transport treatment (DT) from July 10 to 17; 7 d after the ecological water transport treatment (AT-7) on July 24; 14 d after the ecological water transport treatment (AT-14) on July 31; and 21 d after the ecological water transport treatment (AT-21) on August 7. We took all measurements under uniform conditions on healthy leaves during cloudless, sunny days.

Measurements of photosynthetic parameters

We used a portable infrared gas analyzer (Li-6400, LI-COR Biosciences, Lincoln, NE, USA) to measure the net photosynthetic rate (Pn; μmol CO$_2$ m^{-2} s^{-1}), internal CO$_2$ concentration (Ci; μmol·mol^{-1}), the transpiration rate (Tr; mmol H$_2$O m^{-2} s^{-1}), and stomatal conductance (Cs; mol H$_2$O m^{-2} s^{-1}) of *P. euphratica* on the second or third fully expanded leaf during sunny days. The selected testing time was from 8:00 to 20:00 and the testing interval was 2 h.

Measurements of chlorophyll fluorescence parameters

We used a chlorophyll fluorometer (OS-30P+, Opti-Sciences, Inc., Hudson, NH, USA) to measure the chlorophyll fluorescence parameters of *P. euphratica*. Measured variables included minimal fluorescence (Fo), maximal fluorescence (Fm), maximal variable fluorescence (Fv), the optimal quantum yield of PSII (Fv/Fm), absorption energy flux (ABS), the performance index of intersystem electron acceptors (PI), electron transport (ETo), relative variable fluorescence at the J step (V_j), trapping (TRo), and fluorescence OJIP transients. After we adapted three fully expanded leaves to darkened conditions for 30 min, we calculated the chlorophyll fluorescence parameters on the adaxial surface of each sample tree at 10:00.

Chlorophyll extraction and quantification

We measured the content of chlorophyll *a* (Chla; mg/g) and chlorophyll *b* (Chlb; mg/g) of *P. euphratica* during the ecological water transport treatment. We soaked 0.25 g samples of fresh leaf material from three expanded leaves in 95% ethanol for 48 h under darkened conditions until leaf color became pellucid and was devoid of green. The solution was then centrifuged at 5,200 rpm for 10 min. We used a spectrophotometer (DU-70 Spectrophotometer, Beckman Instruments, USA) to measure the absorbance of the supernatant at 663.2 and 646.8 nm. Finally, we calculated chlorophyll content according to Lichtenthaler (1987), using the following equations:

$$\text{Chla (mg/g)} = 12.25 \times A_{663.2} - 2.79 \times A_{646.8} \tag{1}$$

$$\text{Chlb (mg/g)} = 21.5 \times A_{646.8} - 5.1 \times A_{663.2} \tag{2}$$

Measuring environmental factors

We measured environmental data using a standard automatic weather station (AWS) (Meteodata 3000, Geóniba Earth Sciences, Madrid, Spain) approximately 100 m from the experimental plots. Measured variables included air temperature (Ta; °C), relative humidity (RH; %), photosynthetically active radiation (PAR; mol·s^{-1} m^{-2}), wind speed (WS; m/s), and precipitation (P; mm). Dates were recorded using a Zeno 3200 data logger at intervals of 30 min. We measured soil moisture (θ; %) each day using time-domain reflectometry

Table 1 | Characteristics of *Populus euphratica* applied to experiments

Tree	Tree height (m)	Projected canopy area (m^2)	DBH (cm)
1	3.30	6.50	6.77
2	3.20	5.50	4.98
3	3.00	2.72	3.99
4	2.30	3.40	3.63
5	2.72	2.88	3.76
6	2.80	4.40	4.18
7	2.80	2.08	4.26
8	2.90	2.25	3.68
9	4.20	7.13	7.55
10	3.20	4.00	4.85

(LP TDR probes, Institute of Geophysics, Polish Academy of Sciences, Lublin, Poland) at four different depths (10, 30, 50, and 80 cm), which were recorded at intervals of 30 min, using a CR1000 data logger (Campbell Scientific, Inc., North Logan, Utah, USA). At the same time, we measured GWL using the electronic conductance method in a groundwater well imbedded into the *P. euphratica* sample site. We determined the vapor pressure deficit (*VPD*; kPa) using measured *Ta* and *RH*, following the empirical equation (Campbell & Norman 1998):

$$VPD = \left(1 - \frac{RH}{100}\right) \times 0.6108 \times EXP\left(\frac{17.27 \times Ta}{Ta + 237.3}\right) \quad (3)$$

Measuring leaf water content

We determined the leaf water content (LWC) of *P. euphratica* for 12 healthy detached leaves from each sample tree. We determined the fresh weight (*FW*) immediately after excision, while we measured the dry weight (*DW*) after leaves had been dried at 70°C for 48 h. We measured the turgid weight (*TW*) after rehydration of leaves (48 h). Finally, we calculated the LWC using the following equation:

$$LWC = \frac{FW - DW}{TW - DW} \quad (4)$$

where *LWC* is the leaf water content (%); *FW* is the fresh weight (g); *DW* is the dry weight (g); and *TW* is the turgid weight (g).

Data treatment and statistical analysis

All data obtained on photosynthesis (*Tr*, *Pn*, *Ci*, and *Cs*), chlorophyll fluorescence (*Fv*, *Fo*, *Fm*, *Fv/Fm*, *TRo*, *ETo*, *ABS*, *PI*, V_j, *ABS/RC*, *ETo/RC*, *RC/CSo*, and *TRo/RC*), and chlorophyll content (*Chla* and *Chlb*) measurements are represented as means ± standard deviation (M ± SD; $n = 10$). Statistical significance was set at $P < 0.05$ by ANOVA using SPSS 19.0. We fitted linear functions to the observed responses of *Tr*, *Pn*, *Ci*, *Cs*, *Fv/Fm*, and *Fv/Fo* of *P. euphratica* to SWC using Origin 8.0. Differences were evaluated at a significance level of 0.05, and data were plotted using Origin 8.0.
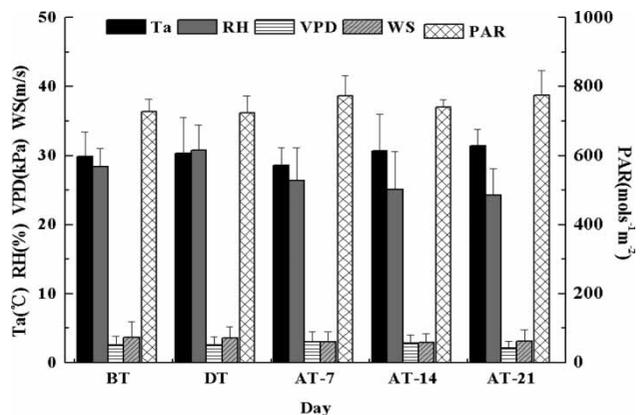
RESULTS

Environmental factors and water status during the ecological water transport treatment

Environmental factors during the experimental period are provided in Figure 1. Air temperature (*Ta*) ranged from 29°C to 33°C. Daily average *RH* ranged from 28.40% to 30.79%. The *VPD* ranged from 2.53 to 3.07 kPa. Daily average *WS* and *PAR* ranged from 3.48 m/s to 747.13 mols^{-1} m^{-2}, respectively. Rainfall was 0 mm. Before the ecological water transport treatment, SWC was determined to be 15.32% ± 0.14% in the study site. During the ecological water transport treatment, SWC progressively increased to 53.96% ± 0.32% before continuously decreasing to 20.44% ± 0.05% on day AT-21. Before the ecological water transport treatment, LWC was 23.14% ± 1.31%. During the ecological water transport treatment, LWC reached 33.21% ± 0.43% before continuously decreasing to 22.09% ± 0.72% on day AT-21. Throughout the whole experimental period, the mean GWL of the study site was 1.82 ± 0.14 m (Figure 2). Results from these environmental variable values indicated that trees grew under similar environmental conditions but different soil water conditions.

Effects of ecological water transport on photosynthetic parameters of *Populus euphratica*

Figure 3 shows the diurnal variations in *Pn*, *Tr*, *Cs*, and *Ci* of *P. euphratica* during different phases of the


Figure 1 | Environmental variables during the experimental period (*VPD* = vapor pressure deficit, *Ta* = air temperature, *RH* = relative humidity, *PAR* = photosynthetically active radiation, *WS* = wind speed).
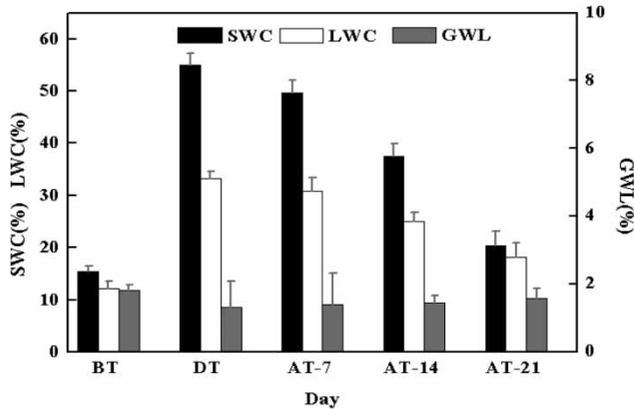
Figure 2 | Water status during the experimental period (LWC = leaf water content, SWC = soil water content, GWL = groundwater level).

transport treatment, *Pn* progressively decreased and reached an average of 7.12 μmol CO_2 m^{-2} s^{-1} on day AT-21. Stomatal conductance (*Cs*) of *P. euphratica* increased significantly compared with the day preceding the ecological water transport treatment ($P < 0.05$), with an increasing percentage of 27.58%. Twenty-one days after the ecological water transport treatment, *Cs* reached an average of 0.27 mol H_2O m^{-2} s^{-1}. The *Tr* of *P. euphratica* increased significantly during the ecological water transport treatment compared with the day preceding the treatment ($P < 0.05$), with an increasing percentage of 25.18%. For the day following the ecological water transport treatment, *Tr* progressively decreased and reached an average of 4.34 mmol H_2O m^{-2} s^{-1}. Changes in *P. euphratica Ci* following the ecological water transport treatment differed from *Pn*, *Cs*, and *Tr*, decreasing from 315.42 to 240.68 μmol·mol^{-1} compared with the day preceding the ecological water transport treatment, with a decreasing percentage of 23.69%.

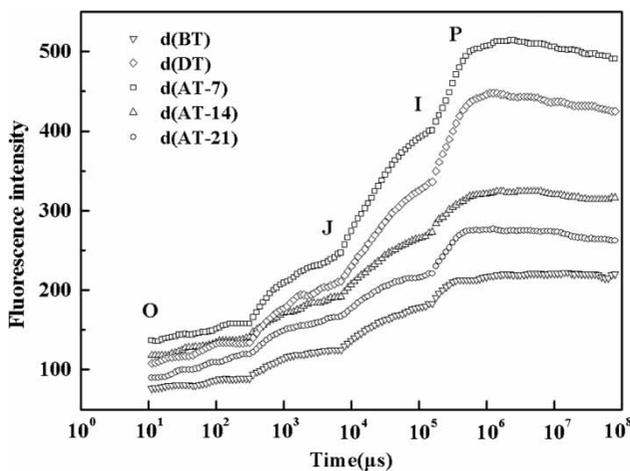ecological water transport treatment. It can be seen that *Pn* increased significantly during the ecological water transport treatment as compared with the day preceding the treatment ($P < 0.05$), with an increasing percentage of 32.71%. For the day following the ecological water
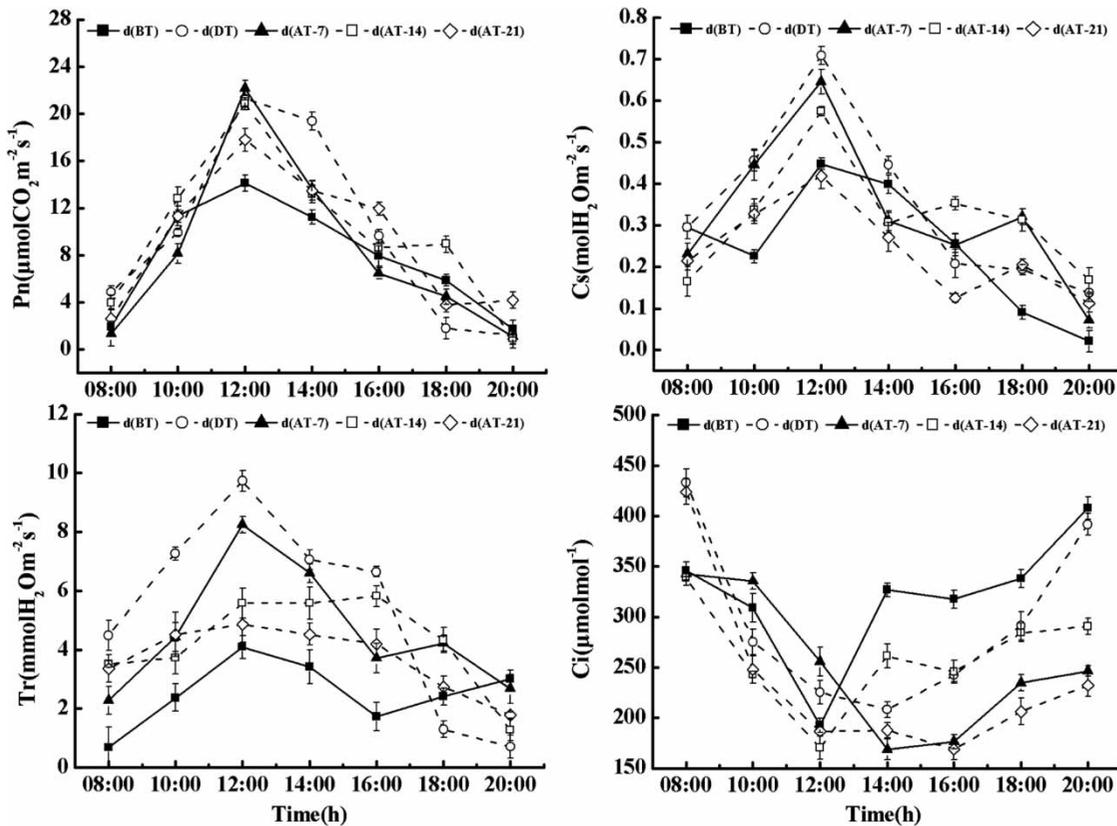
Figure 3 | Changes in the net photosynthetic rate (*Pn*), transpiration rate (*Tr*), stomata conductance (*Cs*), and intercellular CO_2 concentration (*Ci*) of *Populus euphratica* during different phases of the ecological water transport treatment.
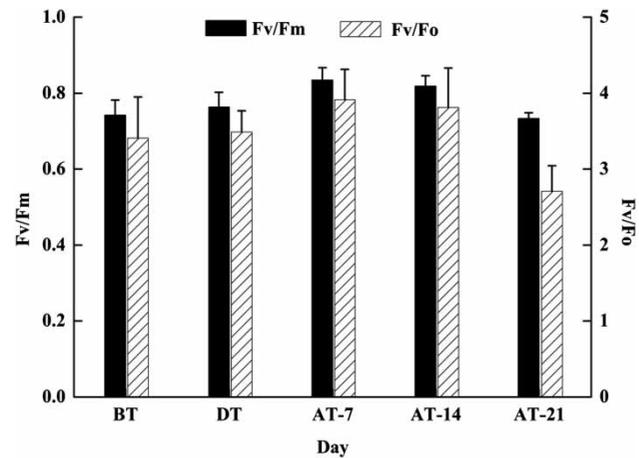
Effects of the ecological water transport treatment on chlorophyll fluorescence of *Populus euphratica*

All chlorophyll fluorescence *P. euphratica* samples exhibited a typical OJIP curve during the different phases of the ecological water transport treatment (Figure 4). During this treatment, the O, J, I, and P steps rapidly increased compared with the day preceding the ecological water transport treatment, and we determined the most significant difference to be at step P ($P < 0.05$) (Figure 4). However, 14 d after the ecological water transport treatment, the O, J, I, and P steps began to decrease compared with day AT-7, and we determined the most significant difference to be at step I ($P < 0.05$) (Figure 4).

The Fv/Fm and Fv/Fo ratios of *P. euphratica* changed significantly during the ecological water transport treatment ($P < 0.05$) (Figure 5). The values of Fv/Fm and Fv/Fo were highest on day AT-7. Seven days after the ecological water transport treatment, the values of Fv/Fm and Fv/Fo began to decrease, reaching 0.73 and 2.71, respectively, on day AT-21 (Figure 5). During the ecological water transport treatment, Fo, Fm, PI, and RC/CSo of *P. euphratica* rapidly increased compared with the day preceding the treatment, with increasing percentages of 9.67%, 46.15%, 59.17%, and 48.54%, respectively (Table 2). However, Fo, Fm, PI, and RC/CSo began to decrease following the ecological water transport treatment, and we determined that the most significant change was in Fm ($P < 0.05$). During the

Figure 5 │ Changes in Fv/Fm and Fv/Fo of *Populus euphratica* during the different phases of the ecological water transport treatment.

ecological water transport treatment, V_j, ABS/RC, TRo/RC, and ETo/RC of *P. euphratica* decreased compared with the day preceding the treatment, with decreasing percentages of 30.43%, 43.54%, 37.50%, and 39.04%, respectively (Table 2). However, V_j, ABS/RC, TRo/RC, and ETo/RC began to increase after the ecological water transport treatment, and we determined that the most significant change was in Fm ($P < 0.05$).

Effects of the ecological water transport treatment on *Populus euphratica* chlorophyll content

The chlorophyll content of *P. euphratica* changed significantly with SWC (Table 3; $P < 0.05$). During the ecological water transport treatment, the average chlorophyll content of a, b, and a + b of *P. euphratica* increased by 26.36%, 8.89%, and 21.93%, respectively, compared with the day preceding the treatment. However, the chlorophyll content of *P. euphratica* continuously decreased following the ecological water transport treatment, with decreasing values of 30.56%, 28.05%, and 29.88%, respectively, compared with the day of the treatment.

Relationships between SWC and photosynthetic and chlorophyll fluorescence performance of *Populus euphratica*

Relationships between SWC and photosynthetic and chlorophyll fluorescence performance of *P. euphratica* during

Figure 4 │ Changes in the fluorescence curve of *Populus euphratica* during different phases of the ecological water transport treatment.

Table 2 | Chlorophyll fluorescence parameters of *Populus euphratica* during different phases of the ecological water transport treatment

Time	Fo	Fm	V_j	PI	ABS/RC	TRo/RC	ETo/RC	RC/CSo
d(BT)	93	351	0.23	4.92	1.86	0.24	1.05	49.95
d(DT)	102	513	0.16	12.05	1.05	0.15	0.64	97.07
d(AT-7)	86	450	0.21	13.70	1.15	0.16	0.74	74.54
d(AT-14)	68	341	0.24	15.58	1.58	0.15	1.08	43.257
d(AT-21)	75	331	0.20	9.00	1.48	0.19	0.33	50.755

Table 3 | Chlorophyll content of *Populus euphratica* during different phases of the ecological water transport treatment

| Time	a(mg/g)	b(mg/g)	a + b(mg/g)	a/b
d(BT)	2.211	0.753	2.964	2.936
d(DT)	2.794	0.820	3.614	3.407
d(AT-7)	2.542	0.696	3.238	3.652
d(AT-14)	2.012	0.621	2.633	3.240
d(AT-21)	1.940	0.594	2.534	3.266

different phases of the ecological water transport treatment are provided in Figure 6. SWC had a significant effect on Pn, Tr, Ci, Cs, Fv/Fm, and Fv/Fo ($P < 0.05$). Relationships between SWC and Pn, Tr, Ci, Cs, Fv/Fm, and Fv/Fo of *P. euphratica* were stronger during the ecological water transport treatment compared with other phases. Moreover, Pn, Tr, Ci, Cs, Fv/Fm, and Fv/Fo were significantly affected by SWC when soil water dropped below 15% or rose above 50% ($P < 0.05$). The relationship between SWC and Cs was stronger during different phases of the ecological water transport treatment. We found a significant positive relationship between SWC and Pn, Tr, Cs, Fv/Fm, and Fv/Fo. However, we found a significant negative relationship between SWC and Ci during three phases of the ecological water transport treatment.

DISCUSSION

Undoubtedly, water is critical for photosynthesis processes to take place, and extremely low or extremely high SWC could disrupt the function and structure of the photochemical apparatus; thus, such conditions are not conducive to photosynthesis (Hou *et al.* 2014). Our experimental results showed that Pn, Tr, and Cs of *P. euphratica* increased significantly after the ecological water transport treatment compared with the day preceding the treatment ($P < 0.05$). However, Pn, Tr, and Cs decreased with a decrease in SWC before the ecological water transport treatment. A possible reason for this decrease is that *P. euphratica* will restrict Pn and Tr via stomatal closure to maintain water and avoid harmful effects when SWC is too low (Yordanov *et al.* 2000). This is consistent with results from a previous study that reported that Pn, Tr, and Cs only increased under sustainable soil moisture levels (Tezara *et al.* 2002). For plants subjected to long-term drought conditions in arid and desert zones, we found that SWC increased rapidly during the ecological water transport treatment, but Pn, Tr, and Cs of *P. euphratica* did not continuously increase. It is plausible that under conditions of excessive SWC, photosynthetic processes will also be restricted. Moreover, Ci of *P. euphratica* decreased significantly after the ecological water transport treatment ($P < 0.05$), indicating that both stomatal and non-stomatal limitations are correlated to changes in Pn (Sicher & Bunce 2001).

The determination of chlorophyll fluorescence kinetics allows the quantification of effects on photosynthetic processes triggered by stress due to non-invasive, rapid measurement (Zhori *et al.* 2015). In our study, the fluorescence signal of *P. euphratica* at step P decreased significantly following the ecological water transport treatment ($P < 0.05$). This indicated that electron transport acceptors of *P. euphratica* around PSII were inhibited due to decreasing SWC (Kalaji *et al.* 2014). It is widely believed that if plants grow under favorable soil water conditions, Fv/Fm ratios will range from 0.78 to 0.83, but if plants grow under unfavorable soil water conditions, such ratios will be below 0.78 or above 0.83 (Demmig-Adams & Adams 2006; Murchie & Lawson 2013). Our results show Fv/Fm values greater than 0.78 were first observed 7 d after the ecological
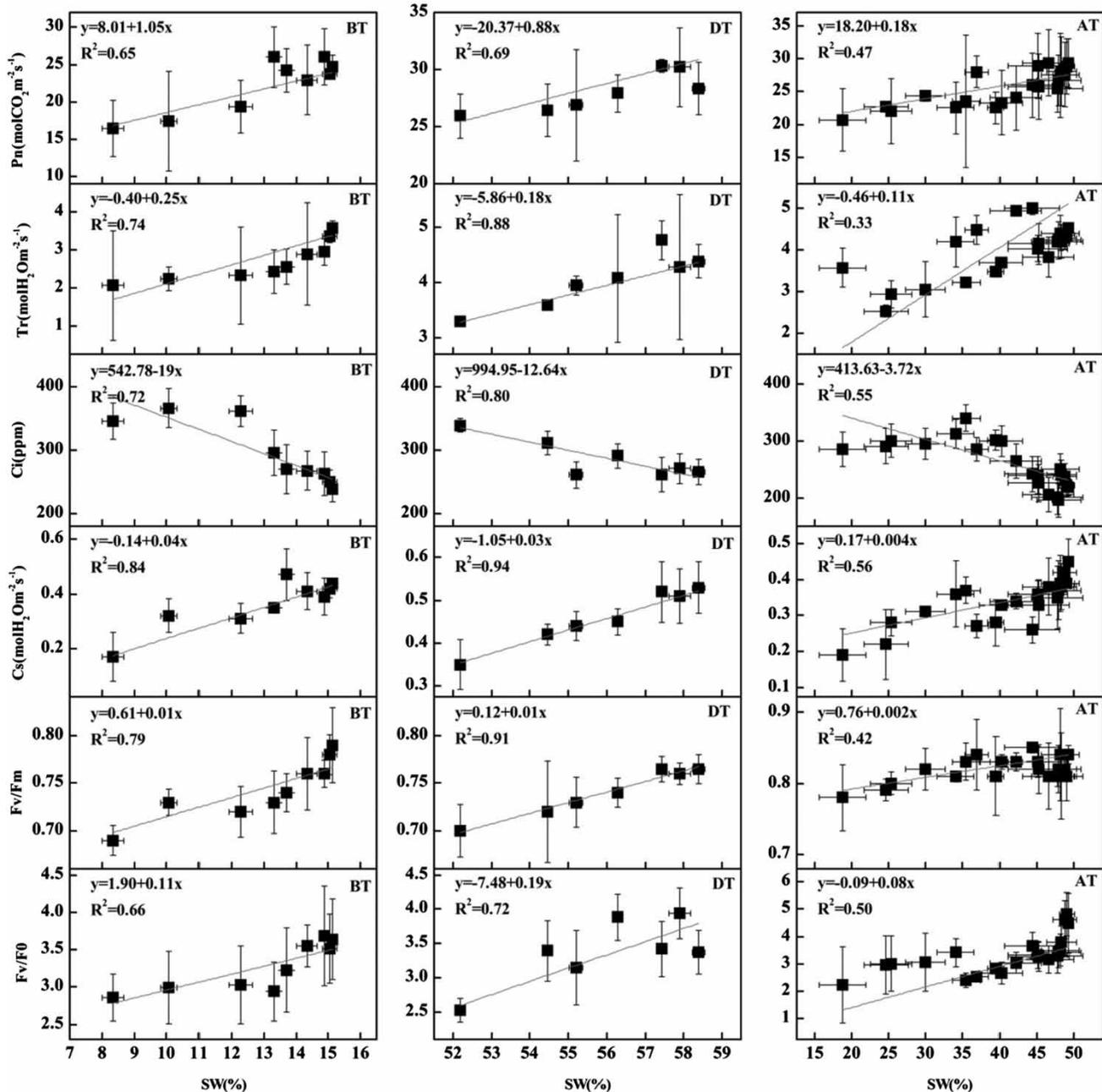
Figure 6 | Relationships between soil water content and photosynthetic and chlorophyll fluorescence performance of *Populus euphratica* during different phases of the ecological water transport treatment (*Pn* = net photosynthetic rate, *Tr* = transpiration rate, *Cs* = stomata conductance, *Ci* = intercellular CO_2 concentration, SWC = soil water content; $P < 0.05$).

water transport treatment rather than during the treatment itself. This indicated that both water stress or drought stress will result in a decrease in *Fv/Fm*. Furthermore, an increase in *Fo* is one of the most direct indicators of drought stress (Aro *et al.* 1993). In this study, the *Fo* of *P. euphratica* during the ecological water transport treatment increased

significantly compared with the day preceding the treatment. This indicated that excessive water conditions could also damage PSII acceptors and therefore result in a negative effect on plant growth (Kalaji *et al.* 2012). Additionally, Boisvert *et al.* (2006) believed that the O–J rise is related to the reduction of primary acceptors in photosystem II, but

several contradictory studies still exist. So a quantitative method must be used to detect more subtle differences in the induction trace of fluorescence.

The chlorophyll content of *P. euphratica* changed significantly with SWC ($P < 0.05$). During the ecological water transport treatment, the average chlorophyll content of a, b, and a + b of *P. euphratica* increased by 26.36%, 8.89%, and 21.93%, respectively, compared with the day preceding the treatment. However, the chlorophyll content of *P. euphratica* continuously decreased following the ecological water transport treatment, with a decreasing value of 30.56%, 28.05%, and 29.88%, respectively, compared with the day of the treatment. We suspected that the decrease in chlorophyll of *P. euphratica* could result from water-stress-related damage to chloroplast structures, which subsequently reduced chlorophyll content.

Furthermore, SWC had a significant effect on *Pn*, *Tr*, *Ci*, *Cs*, *Fv/Fm*, and *Fv/Fo* of *P. euphratica* ($P < 0.05$). Relationships between SWC and these six variables of *P. euphratica* were stronger during the ecological water transport treatment than during the other phases. Moreover, *Pn*, *Tr*, *Ci*, *Cs*, *Fv/Fm*, and *Fv/Fo* were significantly affected by SWC when soil water dropped below 15% or rose above 50% ($P < 0.05$). This indicated that SWC had a significant effect on plant physiology only when values were outside the threshold regime. Therefore, it is necessary to evaluate soil water efficiency and plant growth that is dependent upon water thresholds. Moreover, an excessive increase in SWC could result in a negative effect on plants under long-term drought conditions in arid and desert zones.

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