

Effects of soil drought stress on photosynthetic gas exchange traits and chlorophyll fluorescence in *Forsythia suspensa*

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Abstract To clarify the changes in plant photosynthesis and mechanisms underlying those responses to gradually increasing soil drought stress and reveal quantitative relationships between photosynthesis and soil moisture, soil water conditions were controlled in greenhouse pot experiments using 2-year-old seedlings of *Forsythia suspensa* (Thunb.) Vahl. Photosynthetic gas exchange and chlorophyll fluorescence variables were measured and analyzed under 13 gradients of soil water content. Net photosynthetic rate (P_N), stomatal conductance (g_s), and

water-use efficiency (W_{UE}) in the seedlings exhibited a clear threshold response to the relative soil water content (R_{SWC}). The highest P_N and W_{UE} occurred at R_{SWC} of 51.84 and 64.10%, respectively. Both P_N and W_{UE} were higher than the average levels at $39.79\% \leq R_{SWC} \leq 73.04\%$. When R_{SWC} decreased from 51.84 to 37.52%, P_N , g_s , and the intercellular CO_2 concentration (C_i) markedly decreased with increasing drought stress; the corresponding stomatal limitation (L_s) substantially increased, and nonphotochemical quenching (N_{PQ}) also tended to increase, indicating that within this range of soil water content, excessive excitation energy was dispersed from photosystem II (PSII) in the form of heat, and the reduction in P_N was primarily due to stomatal limitation. While R_{SWC} decreased below 37.52%, there were significant decreases in the maximal quantum yield of PSII photochemistry (F_v/F_m) and the effective quantum yield of PSII photochemistry (Φ_{PSII}), photochemical quenching (q_P), and N_{PQ} ; in contrast, minimal fluorescence yield of the dark-adapted state (F_0) increased markedly. Thus, the major limiting factor for the P_N reduction changed to a nonstomatal limitation due to PSII damage. Therefore, an R_{SWC} of 37.52% is the maximum allowable water deficit for the normal growth of seedlings of *F. suspensa*, and a water content lower than this level should be avoided in field soil water management. Water contents should be maintained in the range of $39.79\% \leq R_{SWC} \leq 73.04\%$ to ensure normal function of the photosynthetic apparatus and high levels of photosynthesis and efficiency in *F. suspensa*.

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Introduction

Photosynthesis is the foundation of plant growth and development and a decisive factor in productivity levels (Xu 2002). Because photosynthesis is highly sensitive to external environmental factors, plant growth and development and their relationship with various environmental factors can be evaluated by measuring the response of plant photosynthesis to environmental stresses (Anselmi et al. 2004). Soil drought is a common, major constraint of plant growth and development and is becoming increasingly severe and frequent in some areas as a result of climate change and thus seriously affecting photosynthesis (Ohashi et al. 2006; Smith et al. 2007; Li et al. 2011; Kebbas et al. 2015).

Numerous studies have investigated the mechanism by which drought stress affects plant photosynthesis (Lawson et al. 2003; Li et al. 2007; Lang and Wang 2015). In general, factors that limit plant photosynthesis under drought stress are either stomatal or nonstomatal, and can be evaluated as changes in the net photosynthetic rate (P_N), intercellular CO_2 concentration (C_i), and stomatal limitation (L_s) (Farquhar and Sharkey 1982; Xia et al. 2014). For example, a reduction of P_N is attributed to stomatal limitation if C_i decreases and L_s increases with a decrease in soil water contents within a certain range; in the contrary situation, a reduction of P_N is attributed to nonstomatal limitation (Wang et al. 2012; Xia et al. 2014; Lang and Wang 2015). Drought-induced P_N decreases have also been suggested to be the joint result of stomatal and nonstomatal factors (Zhang et al. 2010). Despite these differing opinions, the response process and mechanism of plants photosynthesis in drought stress are in association with the genotype and growth stage of the plant, the degree of drought stress, and the selection of measurement indicators (Bray 1993; Lang and Wang 2015). The mechanism limiting photosynthesis under drought stress is complex, especially when drought reaches a certain severity. A simple analysis of leaf gas exchange parameters cannot fully reflect the extent of damage to the photosynthetic apparatus in the blade. As a consequence, there has been a lack of in-depth research on the internal mechanism by which drought stress affects photosynthesis.

Chlorophyll fluorescence can be regarded as an inherent probe for studying the relationship between plant photosynthesis and the environment (Krause and Weis 1991; Lazar 1999) and has been extensively adopted in research addressing the mechanisms underlying the responses of different vegetation types to environmental stress (Masrahi et al. 2015; Yan et al. 2015; Ware et al. 2015). Therefore, it is necessary to study leaf gas exchange and chlorophyll fluorescence parameters simultaneously to obtain an in-

depth and systematic understanding of the mechanisms of how environmental stresses inhibits photosynthesis in different plants.

In face of global climate change, the volatility in soil water levels in North China is becoming increasingly more severe and may significantly affect the photosynthesis and growth of plants in the region. *Forsythia suspensa* (Thunb.) Vahl. is a drought-resistant species used in afforestation and as a common medicinal and ornamental shrub in North China. Research on *F. suspensa* has mainly focused on its medicinal value (Piao et al. 2008; Hao et al. 2010; Xia et al. 2011; Sung et al. 2016). In contrast, little research has addressed the effect of environmental adversity, such as soil drought stress, on the photo-physiological characteristics of *F. suspensa*. Nor has research addressed changes in variables in leaf photosynthesis and chlorophyll fluorescence when plants are exposed to a multistage continuous gradient in the soil water level. As a consequence, many physiological problems, including the process and mechanism of photosynthesis reduction in *F. suspensa* plants under increasing soil drought stress, remain unclear, as do their quantitative relationships with soil water content. In the present study on greenhouse pot experiments using 2-year-old seedlings of *F. suspensa* under controlled water conditions, we measured changes in leaf photosynthesis variables and chlorophyll fluorescence variables as soil water was gradually decreased. We also investigated the quantitative relationship between plant photosynthesis and soil moisture. This study provides a reference for achieving an in-depth systematic understanding of the effect of drought stress on the photophysiological variables in *F. suspensa* and guidance for drought-resistant afforestation and rational water management when using *F. suspensa*.

Materials and methods

Plant and soil

The 2-year-old *F. suspensa* seedlings selected as plant materials had an average height of 0.45 m and average basal diameter of 0.8 cm. On March 25, 2012, we selected 15 plants from a nursery and planted them in 15 pots with a depth of 60 cm and a diameter of 40 cm. The pots were placed in a controlled greenhouse at the Shandong Key Laboratory of Eco-Environmental Science for the Yellow River Delta, Shandong Province, China (37°23'12"N, 117°59'12"E). In the greenhouse, the light transmittance of the glass exceeded 90%; the average relative air humidity was $45 \pm 6\%$; and the average atmospheric temperature was 25 ± 4 °C. The seedlings were grown under typical

conditions for 30 days. On April 25, 2012, three seedlings exhibiting healthy growth of uniform size (plant height and basal diameter) were selected from the 15 plants for measurements of leaf photosynthesis and chlorophyll fluorescence.

Brown soil was collected from Heban Mountain, in Zouping County, Shandong Province. The average soil bulk density (ρ) was 1.25 g cm^{-3} , and the average field water-holding capacity (F_C) was 30.95%.

Soil water measurement

A multistage continuous gradient of soil water content was achieved by artificially supplying adequate water, with subsequent natural consumption of water by plants. The plants were irrigated with sufficient water to reach F_C at 18:00 hours within the first 2 days (May 1, 2012) of the experiment. Beginning on the 3rd day (May 3, 2012), soil water was reduced through plant transpiration, and the volumetric soil water content (V_{SWC} , %) was measured daily. The soil surface was covered with a plastic film to prevent natural evaporation. A water gradient with adequate water content was achieved based on daily measurements. During each measurement, at 08:00 hours every day, a 6050X3K1B Mini Trase Kit (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) was used to measure V_{SWC} at the 0–60 cm depth. The measurements were continued until leaf wilting and $P_N = 0$. Three plants were measured at each soil water level; three sampling points were chosen for each plant; and three readings were recorded for each sampling point. The mean of the 27 V_{SWC} readings was used as the V_{SWC} of each treatment. The gravitational soil water content (G_{SWC} , %) was calculated as the ratio of V_{SWC} to ρ . The relative soil water content (R_{SWC} , %) was calculated as the ratio of G_{SWC} to F_C . A total of 13 soil water levels was obtained, at R_{SWC} of 92.97, 88.09, 73.04, 64.10, 58.96, 51.84, 42.55, 39.79, 37.52, 32.41, 30.44, 27.33, and 23.88%.

Photosynthesis measurements and analyses

Leaf photosynthesis was measured at the same time as the soil water measurements. Before the measurements, three healthy leaves were selected and marked for each plant, i.e., the 3rd to 4th leaves on the middle-upper branches. During each measurement, a LI-6400 portable photosynthetic system (LI-COR, Lincoln, NE, USA) was used to monitor the light response of photosynthesis in the marked leaves at 08:30–11:00 hours every day. The measurements were repeated three times for each leaf. The following variables were measured by the instrument automatically: P_N , transpiration rate (E), stomatal conductance (g_s), C_i , and atmospheric CO_2 concentration (C_a). Water-use

efficiency (W_{UE}) was calculated as $W_{\text{UE}} = P_N/E$, and L_s was calculated as $L_s = 1 - C_i/C_a$. For the measurement of the light response, the LED light of the photosynthesis system was used to set the photosynthetically active radiation (P_{AR}) to 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200, 150, 50, 20, and $0 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$. Each P_{AR} level was controlled for 120 s to obtain a stable value. A CO_2 controller was employed to set the CO_2 concentration to $375 \pm 6.0 \text{ } \mu\text{mol mol}^{-1}$.

The light saturation point (LSP) at each soil water level was calculated using the measured R_{SWC} and P_N data based on the modified rectangular hyperbola model (Ye 2007; Lang et al. 2013). We then obtained values for photosynthesis variables including P_N , W_{UE} , g_s , C_i , and L_s at the LSP for each soil water level. Data were analyzed using Excel 2007 (Microsoft, Redmond, WA, USA), SPSS 20.0 (IBM SPSS, Armonk, NY, USA), and Matlab 2010a (MathWorks, Natick, MA, USA). SPSS 20.0 was employed to evaluate the significance of differences between groups through a one-way analysis of variance. The polynomial fittings for P_N and W_{UE} at the LSP in response to R_{SWC} were performed using SPSS 20.0. P_N and W_{UE} were calculated using Matlab 2010a.

Chlorophyll fluorescence measurements and data analysis

Chlorophyll fluorescence was measured on the marked leaves when photosynthesis was measured. A pulse modulated fluorometer (FMS-2, Hansatech, Norfolk, UK) was applied at different soil water levels. The actual fluorescence (F_s) at a P_{AR} level of $1000 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ was measured after 40 min of activation under natural light. Then, fluorescence during the saturating pulse at a steady state (F_m') was measured following an intense flash of light ($5000 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$; pulse time, 0.7 s). Meanwhile, the leaf was covered, and the light source was turned off for 5 s, followed by dark adaptation for 3 s. Then, the minimal fluorescence yield of the light-adapted state after switching off the actinic light (F_0') was measured after the far-red light was turned on for 5 s. The minimal fluorescence yield of the dark-adapted state (F_0) was measured after 30 min of dark adaptation. Then, the maximal fluorescence yield of the dark-adapted state (F_m) was measured following an intense flash of light ($5000 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$; pulse time, 0.7 s). F_0 and F_m were measured in the early morning before dawn. During the measurements, the blade was evenly pressed in the leaf clamp, and the direction and angle of the probe were kept consistent to ensure that there was no shade and that the blade received light from the same direction. The following variables were calculated according to Roháček (2002): Maximal quantum yield of PSII photochemistry (F_v/F_m),

$$F_v/F_m = (F_m - F_0)/F_m \quad (1)$$

Effective quantum yield of PSII photochemistry (Φ_{PSII}),

$$\Phi_{\text{PSII}} = (F'_m - F_s)/F'_m \quad (2)$$

Nonphotochemical quenching (N_{PQ}),

$$N_{\text{PQ}} = (F_m - F'_m)/F'_m \quad (3)$$

Photochemical quenching (q_P),

$$q_P = (F'_m - F_s)/(F'_m - F'_0), \quad (4)$$

where F_0 and F'_0 are the minimal fluorescence yields of the dark-adapted and light-adapted states, respectively; F_m is the maximal fluorescence yield of the dark-adapted state; F'_m is the fluorescence during the saturating pulse in a steady state; F_s is the actual fluorescence; F_v/F_m denotes the maximal quantum yield of PSII photochemistry; N_{PQ} is the nonphotochemical quenching; q_P is the photochemical quenching; Φ_{PSII} is the effective quantum yield of PSII photochemistry.

Chlorophyll fluorescence variables at different soil water levels were analyzed using Excel 2007 and SPSS 20.0. The significance of the differences was evaluated through one-way analysis of variance using SPSS 20.0.

Results

Response of P_N , g_s and W_{UE} in the leaves of *F. suspensa* to soil water

It is presented the threshold responses of P_N , g_s and W_{UE} in the leaves of *F. suspensa* to the R_{SWC} in Fig. 1. P_N , g_s , and W_{UE} gradually increased with a decreasing R_{SWC} within a certain range. After reaching a maximum, the three variables began to decrease with a further decrease of the R_{SWC} . Both P_N and g_s peaked at R_{SWC} of 51.84%, while the highest W_{UE} was obtained at R_{SWC} of 64.10% (Fig. 1a, b). P_N and W_{UE} showed relatively low values at $R_{\text{SWC}} \leq 37.52\%$. At R_{SWC} of 37.5%, P_N was reduced by 66.2% compared with its maximum value (at $R_{\text{SWC}} = 51.84\%$), while W_{UE} was reduced by 47.4% compared with its maximum (at $R_{\text{SWC}} = 64.10\%$). As P_N and W_{UE} are often used to characterize the photosynthetic productivity and efficiency, respectively, under different soil water conditions in trees (Zhang et al. 2012; Xia et al. 2013; Lang and Wang 2016), the response of P_N and W_{UE} to R_{SWC} indicated that an excessively high or low soil water content, especially drought stress at an $R_{\text{SWC}} \leq 37.52\%$, can reduce the productivity and efficiency in leaves of *F. suspensa*.

Figure 2a, b illustrate the polynomial fittings of P_N and W_{UE} in response to R_{SWC} . The response process of P_N to R_{SWC} is fitted well by the polynomial (5) ($R^2 = 0.927$):

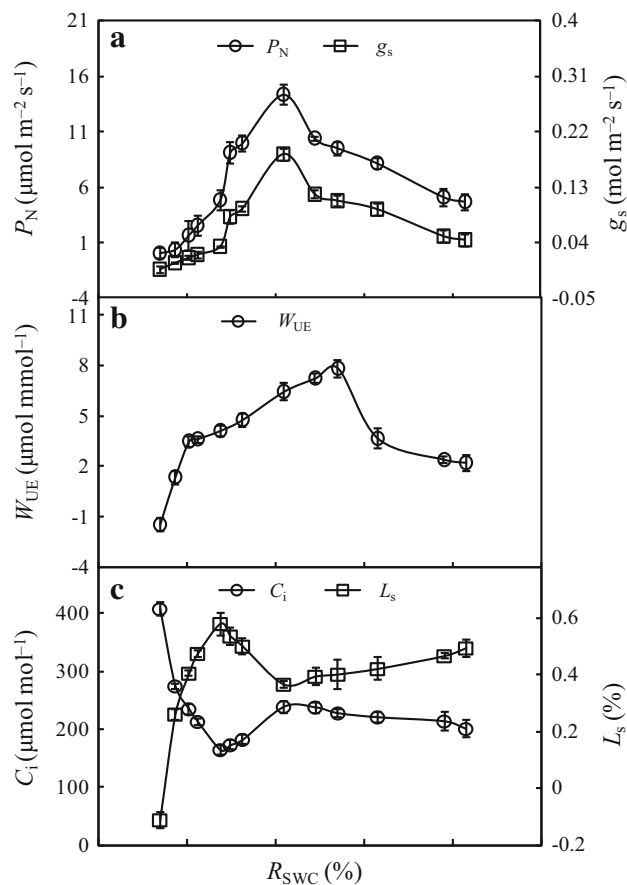


Fig. 1 Effect of different soil water conditions on photosynthetic variables in leaves of *F. suspensa* seedlings grown in pots in a greenhouse. Bars indicate \pm SE of the mean, $n = 27$. P_N is the net photosynthetic rate, g_s is the stomatal conductance, W_{UE} is the water-use efficiency, C_i is the intercellular CO_2 concentration, L_s is the stomatal limitation, R_{SWC} is the relative soil water content

$$P_N = 9E - 05R_{\text{SWC}}^3 - 0.024R_{\text{SWC}}^2 + 1.927R_{\text{SWC}} - 35.24 \quad (5)$$

where P_N is the net photosynthetic rate, and R_{SWC} is the relative soil water content. As a result, the average P_N (\bar{P}_N) within the range of $23.9\% \leq R_{\text{SWC}} \leq 93.0\%$ was 8.21 calculated by Eq. (6):

$$\begin{aligned} \bar{P}_N &= \frac{\int_{23.9\%}^{93.0\%} P_N dR_{\text{SWC}}}{93.0\% - 23.9\%} \\ &= \frac{\int_{23.9\%}^{93.0\%} (9E - 05R_{\text{SWC}}^3 - 0.024R_{\text{SWC}}^2 + 1.927R_{\text{SWC}} - 35.24) dR_{\text{SWC}}}{93.0\% - 23.9\%}, \end{aligned} \quad (6)$$

where P_N is the net photosynthetic rate, and R_{SWC} is the relative soil water content.

According to Eq. (5), within the experimental range of $23.9\% \leq R_{\text{SWC}} \leq 93.0\%$, when the average P_N was 8.21, the corresponding R_{SWC} was 39.5 and 80.0%. Similarly, the corresponding R_{SWC} of average W_{UE} was 35.47 and

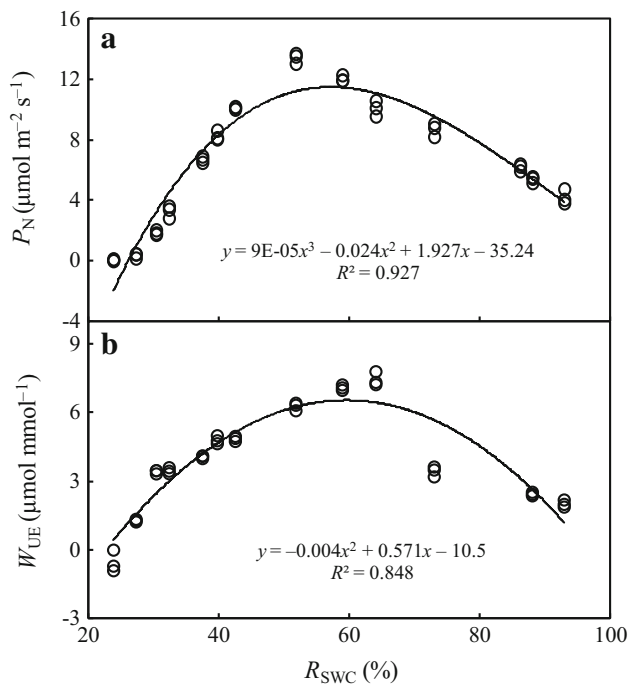


Fig. 2 Polynomial fittings of net photosynthetic rate (P_N) and water-use efficiency (W_{UE}) in response to relative soil water content (R_{SWC}) in leaves of *F. suspensa*

79.53%. Thus, for $39.5\% \leq R_{SWC} \leq 79.53\%$, *F. suspensa* plants had higher P_N and W_{UE} than the average levels within the experimental soil water range.

Response of C_i and L_s in the leaves of *F. suspensa* to soil water

Figure 1c shows the responses of C_i and L_s in the leaves of *F. suspensa* were opposite to the direction of R_{SWC} . At $R_{SWC} > 37.52\%$, C_i initially increased before decreasing with a decreasing R_{SWC} ; however, L_s showed the opposite pattern of variation and first decreased before increasing. At $R_{SWC} < 37.52\%$, C_i rapidly increased and L_s rapidly decreased with a further decrease in the R_{SWC} . These results indicated that within the range from a saturated soil water content to the level at $P_N = 0$ in *F. suspensa*, the leading factor in reducing photosynthetic productivity and efficiency in leaves of *F. suspensa* changed from stomatal to nonstomatal limitation with a decreasing water content; the turning point regarding the soil water content was 37.52%.

Response of F_0 , F_m , F_v/F_m , and Φ_{PSII} in leaves of *F. suspensa* to soil water

F_0 is the fluorescence yield at the full opening of the reaction center in photosystem II (PSII), and F_m is the fluorescence yield at full closure of the reaction center in photosystem II (PSII). These two variables can reflect

electron transport through PSII (Demmig and Björkman 1987; Demmig et al. 1987). In Fig. 3a, d, as R_{SWC} decreased, F_0 initially decreased and then increased; the opposite trend was observed for F_m . The lowest F_0 coincided with the highest F_m at $R_{SWC} = 51.84\%$. Variance analysis revealed no significant differences in F_0 or F_m with varying soil water levels in the range of $39.79\% \leq R_{SWC} \leq 73.04\%$ ($P > 0.05$). When R_{SWC} exceeded the above range ($R_{SWC} \geq 88.09\%$ or $R_{SWC} \leq 37.52\%$), F_0 was significantly higher, while F_m was significantly lower ($P < 0.05$) compared with values at $R_{SWC} = 51.84\%$. This result indicated damage to or reversible inactivation of PSII that inhibited photosynthetic electron transfer activity in its reaction center.

F_v/F_m can reflect the efficiency of the primary conversion of light energy in PSII; it is also an excellent indicator for measuring the degree of photoinhibition (Farquhar et al. 1989). Φ_{PSII} is often used to indicate the quantum yield of photosynthetic electron transfer in plants and can also be employed as a relative indicator of the photosynthetic electron transfer rate in plant leaves (Krause and Weis 1991). In Fig. 3b, c, F_v/F_m was approximately 0.8 in the range of $39.79\% \leq R_{SWC} \leq 73.04\%$, with no significant difference between varying soil water levels ($P > 0.05$). Both F_v/F_m and Φ_{PSII} were significantly reduced when R_{SWC} was below 37.52%. We inferred that within this range of soil water contents, the leaves of *F. suspensa* were damaged by light oxidation, and the proportion of opening of the reaction center of PSII was reduced, thus suppressing the electron transfer capability of PSII.

Response of q_P and N_{PQ} in leaves of *F. suspensa* to soil water

Fluorescence quenching, including q_P and N_{PQ} , is an important aspect regulating the quantum efficiency of photosynthesis in plants. q_P reflects the portion of light energy absorbed by antenna pigments in PSII that is used for photochemical transfer (Van and Snel 1990). N_{PQ} reflects the portion of light energy absorbed by antenna pigments in PSII that is dissipated in the form of heat but is not used for photosynthetic electron transfer (Gilmore and Yamamoto 1991). Figure 3e, f show the threshold response of q_P to the R_{SWC} . The highest q_P occurred at $R_{SWC} = 51.84\%$. Electron transfer activity was highest in the reaction center of PSII at this water level. There was a reduction in q_P when R_{SWC} surpassed 51.84%, and q_P was greatly reduced, showing low levels when $R_{SWC} \leq 37.52\%$. N_{PQ} exhibited a complex response to the R_{SWC} . Within the range of $39.79\% \leq R_{SWC} \leq 64.10\%$, the lowest N_{PQ} occurred at $R_{SWC} = 51.84\%$ and showed an upward trend with a change in R_{SWC} (increase or decrease). Conversely, N_{PQ} showed a downward trend with an excessively

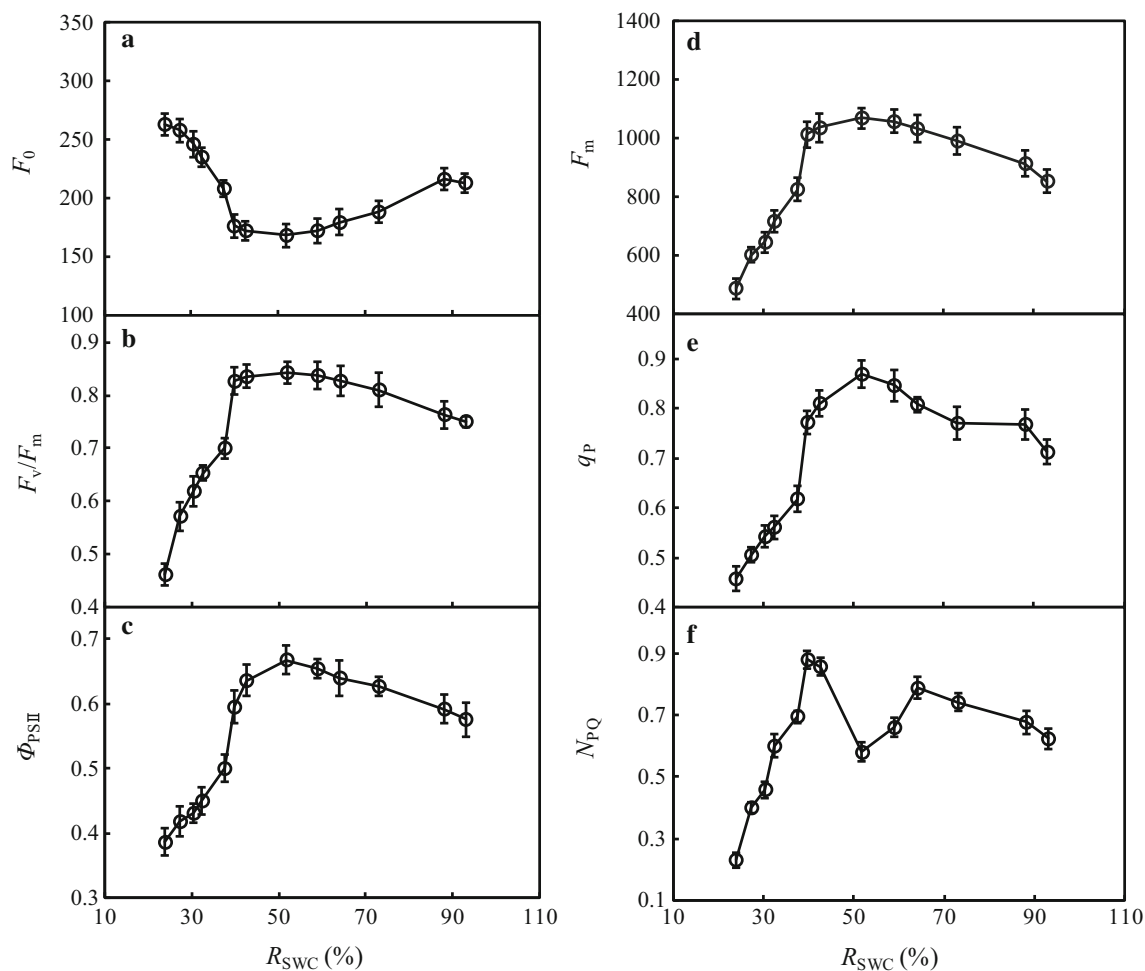


Fig. 3 Response of chlorophyll fluorescence variables to different soil water conditions in leaves of *F. suspensa* seedlings grown in pots in a greenhouse. Bars indicate \pm SE of the mean, $n = 27$. F_0 is the minimal fluorescence yield of the dark-adapted state, F_m is the maximal fluorescence yield of the dark-adapted state, F_v/F_m is the

maximal quantum yield of PSII photochemistry, Φ_{PSII} is the effective quantum yield of PSII photochemistry, q_P is the photochemical quenching, N_{PQ} is the nonphotochemical quenching, R_{SWC} is the relative soil water content

higher or lower R_{SWC} beyond the above range. The reduction in N_{PQ} was particularly significant when $R_{SWC} \leq 37.52\%$ ($P < 0.05$). These results showed that appropriate water stress can increase heat dissipation from the antenna pigments of PSII in the leaves of *F. suspensa* and, to some extent, alleviate the effect of water stress on photosynthesis. However, with increasing drought stress ($R_{SWC} \leq 37.52\%$), the heat dissipation capacity was reduced due to damage to PSII in the leaves.

Discussion

Soil water stress has multiple effects on the photosynthesis of plants. The factors leading to a reduction in P_N include stomatal and nonstomatal limitations (Wang et al. 2012; Xia et al. 2014; Lang and Wang 2015). Farquhar and

Sharkey (1982) suggested using C_i and L_s to determine whether stomatal or nonstomatal limitations are the cause of a reduction of P_N . For most plants, such as *Robinia pseudoacacia*, *Platycladusorientalis*, *Prunus sibirica* L. (Zhang et al. 2012; Lang et al. 2013), stomatal closure and the reduction of g_s in the early stage of drought stress can prevent CO_2 from entering the blade and thus reduce P_N via stomatal limitation; when the degree or duration of drought stress is increased, P_N is reduced via nonstomatal limitation, i.e., through structural and functional impairment of the leaf photosystem. A similar trend was found in the current study, as revealed through analysis of the response of photosynthetic variables in leaves of *F. suspensa* under different levels of drought stress. Within the range of $37.52\% < R_{SWC} \leq 51.84\%$, the reduction in P_N was associated with a decrease in C_i and increase in L_s . Additionally, within the same range of soil water content,

F_0 was relatively low; both F_v/F_m and Φ_{PSII} were relatively high, showing no differences between different water levels; and N_{PQ} increased with a decrease of the R_{SWC} . These observations showed that *F. suspensa* plants protect the photosynthetic apparatus by enhancing thermal dissipation, and the reduction in P_N within the range of $37.52\% < R_{SWC} \leq 51.84\%$ was due to stomatal limitation. When drought stress was further increased ($R_{SWC} \leq 37.52\%$), P_N was further reduced. Additionally, there was a significant increase in C_i , in contrast to a substantial reduction in L_s . These results indicated that the primary cause of the reduction of P_N in the leaves of *F. suspensa* changed to nonstomatal limitation.

Nonstomatal limitation inducing a reduction of P_N under drought stress is associated with damage to the photosynthetic apparatus as well as photosynthetic electron transport activity and the efficiency of light energy conversion (Guo et al. 2009). It is possible to infer the condition of the reaction center based on the change in F_0 : nonphotochemical energy dissipation of antenna pigments in PSII often leads to a reduction in F_0 , while the destruction or irreversible inactivation of reaction centers in PSII often causes an increase in F_0 (Krause 1988). Under normal circumstances, the light energy absorbed by chlorophyll is mainly consumed through electron transfer, chlorophyll fluorescence, and heat dissipation; there is an inversely proportional relationship between the three pathways (Wu et al. 2003). Photosynthesis and heat dissipation can be analyzed by estimating q_P and N_{PQ} (Peterson et al. 1998). The greater the q_P value, the higher the electron transport activity in PSII (Guo et al. 2009). N_{PQ} reflects the portion of light energy adsorbed by antenna pigments that is dissipated in the form of heat. Excessive light energy in the reaction center of PSII will destroy the photosynthetic apparatus, if it is not dissipated in a timely manner (Gilmore and Yamamoto 1991). In the present study, we found a substantially higher F_0 and lower F_m , F_v/F_m , Φ_{PSII} , q_P , and N_{PQ} under drought stress when $R_{SWC} \leq 37.52\%$. This result indicated that PSII had been damaged and that the heat dissipation capacity was reduced in the leaves of *F. suspensa*. Excessive accumulation of light energy in the reaction center caused further damage to the photosynthetic apparatus. This mechanism inhibited photosynthetic electron transfer from the reaction center of PSII to the QA, QB and PQ pools, thus leading to a significant reduction in P_N . Therefore, $R_{SWC} = 37.52\%$ is the turning point of the soil water content for stomatal versus nonstomatal limitation of photosynthesis in leaves of *F. suspensa* and the maximum allowable water deficit for normal growth of *F. suspensa* (Zhang et al. 2012).

In recent years, much research has been done to investigate the quantitative relationship between soil moisture and photosynthesis of plants (Zhang et al. 2010, 2012; Xia

et al. 2013; Lang and Wang 2016). In most of these studies, P_N and W_{UE} are frequently used to characterize the productivity and efficiency of plant photosynthesis in relation to soil water levels, to evaluate the ranking of soil water productivity (Zhang et al. 2012; Xia et al. 2013; Lang and Wang 2016). However, because chlorophyll fluorescence is an inherent probe for studying the relationship between plant photosynthesis and the environment (Krause and Weis 1991; Lazar 1999), chlorophyll fluorescence should be evaluated at a soil water range appropriate for photosynthetic productivity in the plant. The current study showed that within the range from a saturated soil water content to the level at $P_N = 0$, P_N and W_{UE} in leaves of *F. suspensa* showed a clear threshold response to R_{SWC} . The highest P_N and W_{UE} were obtained at R_{SWC} of 51.84 and 64.10%, respectively. In the range of $39.5\% \leq R_{SWC} \leq 79.53\%$, both P_N and W_{UE} were higher than their average levels within the experimental range of soil water contents. The response of the fluorescence variables in leaves of *F. suspensa* to soil water levels showed that within the range of $39.79\% \leq R_{SWC} \leq 73.04\%$, F_0 was stable at low levels, while N_{PQ} was higher, and both F_v/F_m and Φ_{PSII} maintained high levels ($F_v/F_m > 0.8$, $\Phi_{PSII} \geq 0.6$). These results indicated that within this range of soil water content ($39.79\% \leq R_{SWC} \leq 73.04\%$), *F. suspensa* plants dissipate excessive excitation energy in the form of heat, effectively protecting the photosynthetic apparatus and contributing to efficient photosynthetic light reactions. Thus, *F. suspensa* can maintain the normal function of the photosynthetic apparatus and higher levels of photosynthetic productivity and efficiency (higher than average P_N and W_{UE}) at $39.79\% \leq R_{SWC} \leq 73.04\%$. Hence, this range of soil water content ($39.79\% \leq R_{SWC} \leq 73.04\%$) should be chosen to achieve high photosynthetic productivity of *F. suspensa*.

Conclusions

As the climate changes, soil droughts in some areas are increasingly severe and frequent, seriously affecting photosynthesis. However, there has been a lack of in-depth research regarding the internal mechanisms by which drought stress affects photosynthesis. Here we measured and analyzed changes in photosynthetic gas exchange and chlorophyll fluorescence variables under increasing soil drought in leaves of *F. suspensa*. Photosynthetic efficiency variables such as P_N , W_{UE} , F_v/F_m and Φ_{PSII} , exhibited a clear threshold response to soil moisture. When soil water contents were in the range of $39.79\% \leq R_{SWC} \leq 73.04\%$, both P_N and W_{UE} were higher than the average levels, and the photosynthetic apparatus of *F. suspensa* maintained normal function.

Soil drought stress ($R_{\text{SWC}} < 51.84\%$) reduced photosynthesis in *F. suspensa* in association with soil water levels; within the range of $37.52\% < R_{\text{SWC}} < 51.84\%$, P_{N} was reduced mainly because of the decrease in leaf stomatal conductance and subsequent blocking of the CO_2 supply. With increasing drought stress ($R_{\text{SWC}} \leq 37.52\%$), P_{N} was reduced mainly because of nonstomatal limitation, as reflected by the damage to PSII. As a result, R_{SWC} of 37.52% is the maximum allowable water deficit for the normal growth of *F. suspensa*.

In our analysis of the complex process and mechanism of photosynthesis in response to different soil drought conditions, we revealed the appropriate and lowest threshold of soil water conditions of *F. suspensa*. These results can guide practices for drought-resistant afforestation and field soil water management of trees in water deficit areas and aid the development of a system of drought-adaptive measures in the background of climate change.

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