

## Biomass, carbon sequestration, and physiological behaviours of *Paulownia* ‘Shan Tong’ plantation under a semi-arid bioclimate

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### Abstract

*Paulownia* is a forest species native to China and Korea, recently introduced to Tunisia for its valuable wood and forage potential. Few studies have been conducted on the response of this tree to water stress. In this context, a field experiment was carried out in the El Fahs delegation (Zaghouan governorate, Tunisia) to study the behaviour of *Paulownia* trees (‘Shan Tong’) subjected to three irrigation treatments (1/2, 1/7, and 1/21 days). The biomass allocation, carbon sequestration capacity, and physiological responses to water deficit were investigated. The results revealed that the majority of biomass (65%) was allocated to the stems, while the leaves and roots each accounted for approximately 36%, with roots contributing more than 34% of the total biomass, differing from previous reports. In terms of carbon sequestration, the species demonstrated a notable capacity, storing 42% in leaves, 38.57% in stems, and 38.86% in roots, highlighting its potential for reforestation and urban greening initiatives. Physiological analyses indicated significant decreases in water potential and relative water content under prolonged drought stress, with the most severe water deficit treatment (T1/21) showing water potential ( $\Psi_w$ ) values as low as -9.2 MPa. The leaf morphology also adapted to water scarcity, with increased specific leaf area in drought treatments, up by 40% from T1/2 to T1/21. Despite a decline in gas exchange efficiency and stomatal conductance under water stress, water use efficiency improved, suggesting an adaptive response. Chlorophyll content and stomatal density were optimized under drought conditions, reinforcing the species’ ability to withstand prolonged water deficits. These findings suggest that ‘Shan Tong’ exhibits physiological plasticity, making it a promising species for cultivation in semi-arid regions, though further studies on its long-term growth and biomass production under extreme drought conditions are warranted.

**Keywords:** biomass; carbon sequestration; hydraulic traits; net photosynthesis; *Paulownia* ‘Shan Tong’; water deficit

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## Introduction

Mediterranean ecosystems are characterized by challenging climatic conditions, such as scarce and irregular rainfall, along with long and dry summers. These factors, combined with increasing anthropogenic pressure, lead to the progressive degradation of vegetation cover and accelerated soil erosion (Peñuelas *et al.*, 2017; Vicente-Serrano *et al.*, 2020). In Tunisia, these challenges are further exacerbated by significant spatio-temporal climate variability, placing the country among the most vulnerable to climate change in the region (Dubois *et al.*, 2012). This difficult climatic context necessitates innovative solutions to maintain soil fertility, restore ecosystems, and improve the resilience of rural communities. One promising strategy is the introduction of plant species capable of tolerating water stress.

*Paulownia*, native to the temperate regions of China and Korea, is a fast-growing genus in the family Paulowniaceae. Several species exist, including *Paulownia tomentosa*, *Paulownia elongata*, and the hybrid *Paulownia* 'Shan Tong', which is increasingly used in reforestation and soil restoration projects due to its remarkable properties (Icka *et al.*, 2016). 'Shan Tong', a hybrid between *Paulownia fortunei* and *Paulownia tomentosa*, was developed for its rapid growth, disease resistance, and adaptability to harsh conditions (Jakubowski, 2022). In addition to being economically valuable for high-quality timber, it exhibits noteworthy ecological traits, including strong carbon sequestration capacity (Zhuang *et al.*, 2020), broad leaves, and deep roots that stabilize and enrich soils, and moderate drought tolerance (Da Silva Costa, 2024).

While its adaptability has been demonstrated in several Asian and European contexts (Baier *et al.*, 2021; Thevs *et al.*, 2021), its performance in North African Mediterranean climates remains largely undocumented. Although recent research has explored the chemical composition and nutritional value of 'Shan Tong' leaves in Tunisia (Ammar *et al.*, 2023), little is known about its physiological responses and water stress adaptation in semi-arid environments.

This study aims to fill this gap by assessing biomass production, carbon sequestration potential, and physiological performance of 'Shan Tong' under three irrigation regimes in the semi-arid region of Fahs (Zaghouan, Tunisia). Our findings offer insights into the species' adaptive mechanisms to water deficit and inform its suitability for afforestation and ecosystem restoration in the context of climate change.

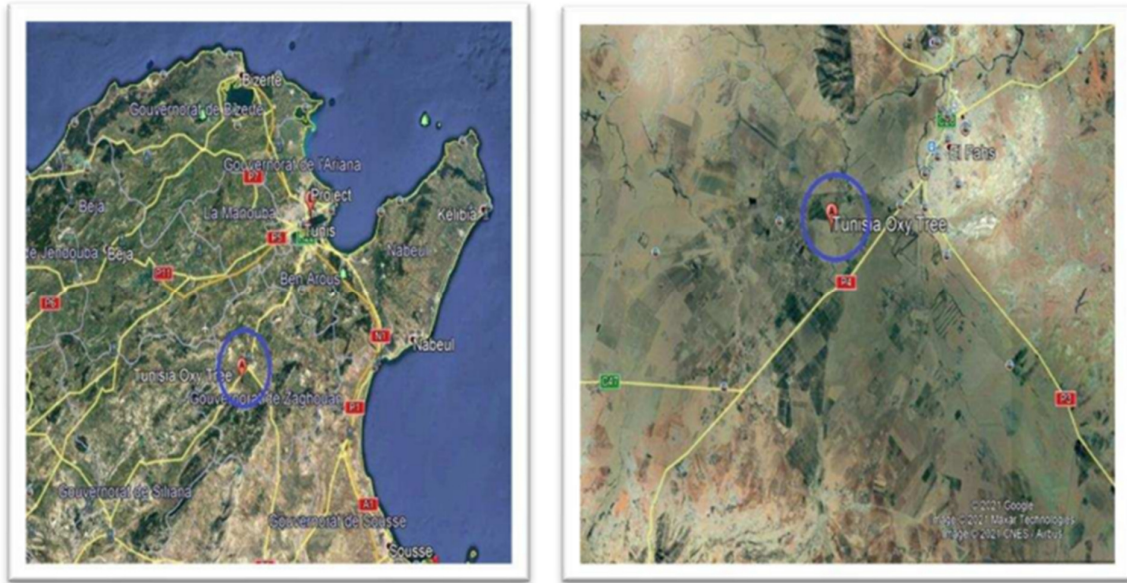
## Materials and Methods

### *Study area*

The study was carried out in an experimental plot of *Paulownia* 'Shan Tong' on the Fahs plain in the northern zone of the Zaghouan governorate (Longitude: 36°22'27" N, Latitude: 9°54'23"E) (Figure 1). The Fahs plain in northeastern Tunisia is classified as a medium semi-arid bioclimatic zone with mild winters. The climate is relatively dry, with an average rainfall of 415.1 mm/year. Rainfall is very irregular and often takes the form of heavy showers, the average temperature is 20 °C and the soil is fine-textured, clayey to silty-clayey and locally balanced.

### *Experimental trials*

The trees were 6 months old and were planted with a spacing of 4 × 3 m. Irrigation was carried out once a week (8L/tree), and two measurements were taken on each tree to monitor vegetative growth (height and diameter). Three trees per irrigation treatment (1 × 2 days, 1 × 7 days and 1 × 21 days) were monitored for this study.



**Figure 1.** Location of experimental trials

#### *Determination of biomass and carbon sequestration*

The biomass of the roots, stems, and leaves of three randomly selected uprooted trees per treatment was determined. After collection, the samples were dried in an oven at 80 °C for 48 hours to reach a constant weight, ensuring all moisture was removed. The dried biomass was then weighed using a high-precision electronic balance. The formula used to calculate the biomass is:

$$\text{Biomass (g)} = \text{FM (Fresh Mass)} / \text{DM (Dry Mass)}$$

For carbon sequestration, the Loss on Ignition (LOI) method was used, which directly measures the organic matter content in samples. This method involves of calcining the organic material in a muffle furnace, making it possible to deduce the quantity of carbon from the weight loss after incineration. The process began by drying the samples for 72 hours at 80 °C. Next, a 10 g portion of the dried and ground sample, sieved to 2 mm, was placed in pre-weighed crucibles. These crucibles were then placed in a muffle furnace at a temperature of 375 °C for 16 hours. After this incineration period, the samples were cooled and the weight loss was measured to determine the remaining organic matter. The difference in weight before and after incineration provided the amount of organic matter (OM), according to the following formula:

$$\% \text{ OM} = ((\text{Dry sample weight (g)} - \text{Incinerated sample weight (g)}) / \text{Dry sample weight (g)}) * 100$$

To determine carbon content, organic matter was assumed to contain around 50% carbon, in line with established guidelines for carbon estimation in biomass studies (Schlesinger, 1997; IPCC, 2006). Thus, the carbon content was calculated as follows:

$$C (\%) = \text{OM} (\%) / 2$$

#### *Determination of Specific Leaf Area (SLA)*

The Specific Leaf Area (SLA) is a key indicator for understanding plant responses to environmental conditions. It is defined as the ratio of leaf area (LA) to leaf dry mass (LDM) (Garnier *et al.*, 2001). SLA was expressed in cm<sup>2</sup>·g<sup>-1</sup>, where leaf area (LA) was measured in square centimetres (cm<sup>2</sup>) and leaf dry mass (LDM) was determined using a precision balance.

*Relative water content (RWC %)*

The experimental protocol involved taking a sample of four healthy adult leaves from each tree. The sample was weighed to determine its fresh weight (fw), and then soaked in distilled water for 24 hours until fully turgid. It was then removed from the water, wiped with filter paper and weighed (PSat). Finally, the leaves were placed in an oven at 80 °C for 72 hours and weighed to determine the dry weight (PS). The relative water content (RWC) was determined using the Clarke and McCaig (1982) equation:

$$TRE = (PF - PS) / (PSat - PS) \times 100$$

*Measurement of gas exchange data*

Gas exchange measurements were conducted on three seedlings per treatment using a LI-6400 gas exchange system (Li-Cor Inc., Lincoln, NE, USA) equipped with a 2 × 3 cm light source chamber (6400-02B LED, Li-Cor Inc.). The measured parameters included net CO<sub>2</sub> assimilation (A<sub>n</sub>, μmol m<sup>-2</sup> s<sup>-1</sup>), stomatal conductance (g<sub>s</sub>, mol m<sup>-2</sup> s<sup>-1</sup>), and transpiration rate (E, mmol m<sup>-2</sup> s<sup>-1</sup>). Following these measurements, the intrinsic water-use efficiency (WUE<sub>i</sub>, μmol mol<sup>-1</sup>) was calculated as the ratio A<sub>n</sub>/g<sub>s</sub>. During the measurements, leaf temperature was maintained at 25 °C, relative humidity of incoming air was kept between 50% and 60%, ambient CO<sub>2</sub> concentration was set at 380 ± 4 ppm, and a saturating photon flux density (PAR) of 1000 μmol m<sup>-2</sup> s<sup>-1</sup> was applied. The leaves of the *Paulownia* tree were placed in a small assimilation chamber swept by an air flow. The device measures the intercellular CO<sub>2</sub> flow in the palisade parenchyma of the leaf and the atmospheric CO<sub>2</sub>. The air passing around the sheet and leaving the chamber is depleted in CO<sub>2</sub> and enriched in water vapor. It is the measurements of the partial pressures of the gases at the inlet and at the outlet of the chamber that make it possible to estimate the leaf gas exchanges. This requires perfect control of the factors that influence them, namely temperature, light intensity, humidity and CO<sub>2</sub> concentration from which these measurements were taken under the conditions.

*Measurements of Photochemical Efficiency of PSII (Fv/Fm)*

Measurements of the maximum efficiency of PSII photochemistry (F<sub>v</sub>/F<sub>m</sub>) were carried out in situ on attached leaves using a portable pulse-modulated fluorometer, the PAM 2000 (Walz, Effeltrich, Germany). Leaves were dark-adapted with leaf clamps for 1 hour, which was deemed sufficient to allow complete relaxation of energy-dependent quenching. The F<sub>v</sub>/F<sub>m</sub> ratio was calculated as (F<sub>m</sub>-F<sub>o</sub>)/F<sub>m</sub>, where F<sub>m</sub> and F<sub>o</sub> are the maximum and baseline fluorescence yield, respectively, of dark-adapted leaves (Genty *et al.*, 1989).

*Measurement of stem xylem hydraulic conductivity*

The K<sub>h</sub> was calculated per unit cross-section of the xylem in summer and converted into specific hydraulic conductivity K<sub>s</sub> (Kg m<sup>-1</sup> MPa<sup>-1</sup> s<sup>-1</sup>). Sections of branches from three seedlings for each treatment were sampled during the four seasons of the year 2018/2019 (the same branches used for the gas exchange measurements) were cut in the field by placing both ends in a bath water at 95 °C. The hydraulic conductivity (K<sub>h</sub>) was measured according to the protocol of Sperry *et al.* (1988) with XYLEM. K<sub>h</sub> was measured at low pressure. All segments were perfused with pure, deionized, degassed and filtered water with 10 mM KCl (to minimize displacement of air bubbles in open vessels).

*Stomatal density*

The microscope slides were photographed and digitalized using a camera connected to the computer. The photos obtained are then analyzed by PIXEL PRO software in order to determine the number of stomata in a given area and measure the width and length of the stomata. For each trial, 9 observations are made to determine stomatal density. The size of the stomata was measured for 10 stomata.

*Determination of photosynthetic pigments*

The chlorophyll concentration of leaves from three irrigation trials of 'Shan Tong' was determined using a chlorophyll meter or SPAD.

*Statistical analysis*

An analysis of variance was performed to highlight the effect of the various factors and any interactions between them on the different physiological parameters. The results were statistically analyzed using SAS (9.0) statistical software. At the end of this analysis, a Newman and Keuls test was applied. Correlations were performed using SPSS.20.

**Results and Discussion***Biomass and carbon sequestration of Paulownia plants*

According to the data presented in Table 1, the analysis of biomass allocation in three distinct *Paulownia* plants revealed that the largest proportion of biomass was allocated to the stems, accounting for approximately 65% of the total biomass. In contrast, the leaves and roots exhibited similar proportions, around 36% each. For mature trees, many authors agreed that root biomass represents about 20% of the total tree biomass (Szabó *et al.*, 2022). In the present case, the biomass study showed that the root part represents more than 34% of the total biomass, which does not align with the results provided by Johnson and Curtis (2001).

**Table 1.** Distribution of dry biomass, organic matter, and carbon content in leaves, stem, and roots of *Paulownia* 'Shan Tong'

Parameter	Leaves	Stem	Roots
Dry biomass (%)	35.59 ± 0.87	65.30 ± 0.16	36.24 ± 0.16
Organic matter (%)	81.54 ± 3.10	73.02 ± 2.74	73.36 ± 2.91
Carbon content (%)	40.81 ± 1.49	36.55 ± 1.34	35.54 ± 1.46

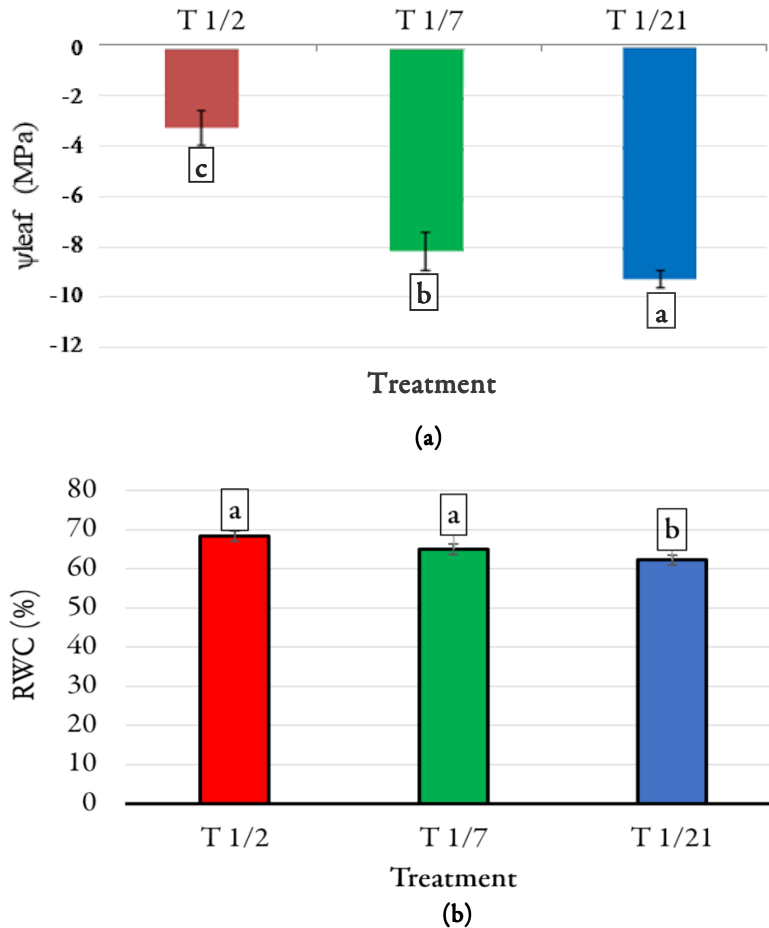
Values represent mean ± standard deviation. Dry biomass indicates the proportion of total plant biomass allocated to each organ (leaves, stem, roots). Organic matter and carbon content are expressed as percentages of dry weight (DW)

This species has demonstrated a significant carbon sequestration capacity, with 42% of organic matter stored in the leaves, 38.57% in the stems, and 38.86% in the roots. This makes the species highly appealing for reforestation purposes, both in urban environments to help mitigate air temperature, as emphasized by Gratani *et al.* (2015), and in natural forests.

*Leaf water potential and relative water content*

Water potential ( $\Psi_w$ ) and relative water content (RWC) are key physiological indicators of plant water status under drought conditions. In this study, the water potential of the three treatments of 'Shan Tong' ranged from -3.13 MPa to -9.2 MPa (Figure 2A). The least negative value (indicating lower stress) was recorded for the T1/2 treatment (-3.13 MPa), while the most negative value (indicating higher stress) was observed for the T1/21 treatment (-9.2 MPa). These results suggest that as the duration of water deficit increases, leaf water potential reflecting enhanced water stress, indicating increased water stress. More negative  $\Psi_w$  values in the T1/21 treatment reflect greater tissue dehydration due to prolonged exposure to drought. These observations are consistent with those of Akter *et al.* (2023), who reported that water stress significantly reduces leaf water potential and RWC. Similarly, relative water content followed a decreasing trend across treatments. The highest RWC was observed in the T1/2 treatment (68.03%), while the lowest was recorded in the T1/21 treatment (62.23%) (Figure 2B). This decline in RWC with increasing drought duration indicates significant water loss, affecting cell hydration and metabolic activity. Sun *et al.* (2020) reported that water stress leads to a progressive reduction in RWC due to restricted water uptake and increased transpiration rates. A decrease in

RWC is widely observed in plants exposed to water stress, signalling tissue water deficit. Recent studies on *Paulownia* have shown similar trends. For example, Yan *et al.* (2019) studied the response of *Paulownia tomentosa* × *fortunei* to water stress and observed a decrease in water potential and RWC, accompanied by changes in microRNA expression affecting plant defense-related genes, transcriptional regulation, and hormone metabolism. Furthermore, Dong *et al.* (2014) reported that *Paulownia australis* activates several drought-tolerance-related genes, particularly those involved in osmotic adjustment and water transport regulation. Thus, these findings confirm that prolonged drought conditions significantly alter the water status of ‘Shan Tong’, leading to increased water stress, which may ultimately affect photosynthetic performance and growth (Cornic and Massacci, 1996).



**Figure 2.** Leaf water potential (a) and relative water content (b) of ‘Shan Tong’ (RWC) under three irrigations treatments (1/2; 1/7; 1/21)

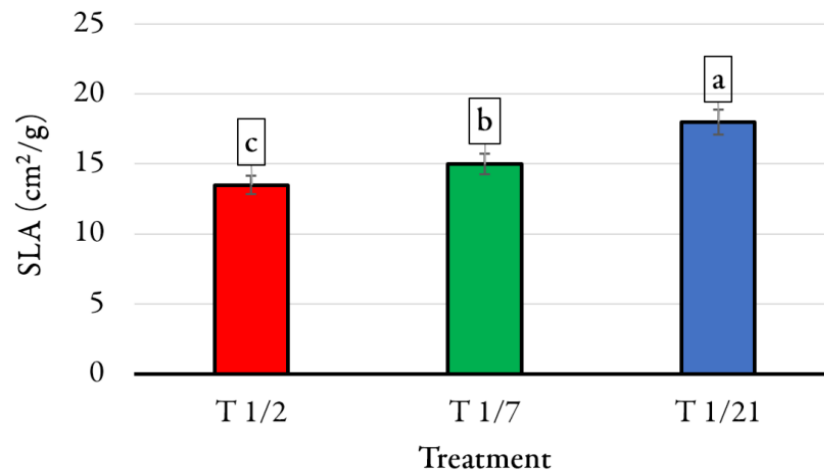
Different letters between treatments denote significant differences (SNK test,  $p < 0.05$ )

#### *Effect of water deficit on SLA of ‘Shan Tong’ plants*

Under increased water deficit, ‘Shan Tong’ plants showed a significant rise in specific leaf area (SLA), with individuals under the most severe stress (T1/21) developing thinner and larger leaves compared to those frequently irrigated (T1/2), which formed thicker and denser leaves (Figure 3). This morphological adjustment is consistent with drought-induced strategies observed in other woody species (Serrano and Peñuelas, 2005), aiming to optimize light interception per unit of biomass when carbon gain is limited by water availability. However, this increase in SLA under stress is not an isolated trait response, it is part of a coordinated suite of

physiological adjustments. Higher SLA often correlates with increased stomatal density and reduced leaf thickness, which together enhance initial photosynthetic potential but may compromise water-use efficiency (WUE) and desiccation resistance. In *Paulownia tomentosa* × *fortunei*, similar patterns were linked to down regulation of cuticle-related genes and upregulation of those involved in osmotic adjustment (Yan *et al.*, 2019). Likewise, *Paulownia australis* adjusts SLA in concert with the expression of aquaporins and dehydration-responsive elements (Dong *et al.*, 2014), underscoring the role of physiological plasticity in maintaining functional homeostasis under drought.

In ‘Shan Tong’, this plastic shift in SLA likely reflects a trade-off between maximizing carbon assimilation through greater leaf area and minimizing water loss through thinner tissues highlighting a strategic balance between growth and survival. These interactions suggest that SLA modulation in this hybrid is closely linked to changes in stomatal patterning and chlorophyll content, potentially influencing gas exchange dynamics and photosynthetic resilience under prolonged drought. This integrated response could be a key determinant of its adaptive capacity and should be further explored in relation to long-term performance and biomass allocation.



**Figure 3.** Specific leaf area of ‘Shan Tong’ plants under three irrigation regimes (1/2; 1/7; 1/21). Letters between treatments denote significant differences (SNK test,  $p < 0.05$ )

*Effect of water deficit on physiological parameters*

The results indicated that water deficit affected physiological parameters in ‘Shan Tong’ plants, with varying degrees of impact depending on the irrigation frequency (Table 2).

**Table 2.** Effects of water deficit on gas exchange parameters and chlorophyll content in ‘Shan Tong’ plants grown in Tunisia under three irrigation treatments (1/2; 1/7; 1/21)

Treatment	An ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	Gs ( $\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	Tr ( $\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	WUEi ( $\text{An/g s } \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{H}_2\text{O}$ )	Total chlorophyll (SPAD unit)
T1/2	$7.85^a \pm 0.38$	$0.0423^a \pm 0.00$	$0.738^a \pm 0.019$	$182.74^a \pm 19$	$40.37^a \pm 1.11$
T1/7	$7.57^a \pm 0.50$	$0.0415^a \pm 0.00$	$0.701^a \pm 0.014$	$185.44^a \pm 14$	$43.40^b \pm 2.27$
T1/21	$7.13^b \pm 0.31$	$0.0345^b \pm 0.00$	$0.674^b \pm 0.013$	$206.65^b \pm 20$	$46.37^c \pm 3.38$

Note: Different letters between treatments denote significant differences (SNK test,  $p < 0.05$ )

Gas exchanges patterns

The net photosynthetic rate (An) decreased progressively from T1/2 ( $7.85 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) to T1/21 ( $7.13 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ), suggesting that prolonged water deficit reduces photosynthetic efficiency. This decline was

associated with a decrease in stomatal conductance ( $G_s$ ), which dropped from  $0.0423 \text{ mol m}^{-2}\text{s}^{-1}$  in T1/2 to  $0.0345 \text{ mol m}^{-2}\text{s}^{-1}$  in T1/21. The decrease in  $G_s$  likely reflects stomatal closure as a protective response to water scarcity, limiting water loss but also restricting  $\text{CO}_2$  uptake (Cristiano *et al.*, 2020; Baier *et al.*, 2021)

Similarly, the transpiration rate ( $T_r$ ) declined as irrigation frequency decreased, from  $0.738 \text{ mol m}^{-2}\text{s}^{-1}$  in T1/2 to  $0.674 \text{ mol m}^{-2}\text{s}^{-1}$  in T1/21. However, intrinsic water use efficiency ( $\text{WUE}_i = A_n/G_s$ ) was improved under prolonged water deficit, reaching 206.65 in T1/21 compared to 185.74 in T1/2. This suggests that 'Shan Tong' adapts to drought by optimizing carbon assimilation relative to water loss, a key survival strategy in water-limited environments (Baier *et al.*, 2021; Lozano-Elena *et al.*, 2022).

The results demonstrated that 'Shan Tong' exhibited physiological plasticity in response to water deficit. The species showed a decline in gas exchange parameters under prolonged drought although  $\text{WUE}_i$  increased and maintained chlorophyll content. This suggests that it has potential for cultivation in semi-arid regions, though long-term drought effects on growth and biomass accumulation should be further investigated (Llano-Sotelo *et al.*, 2010).

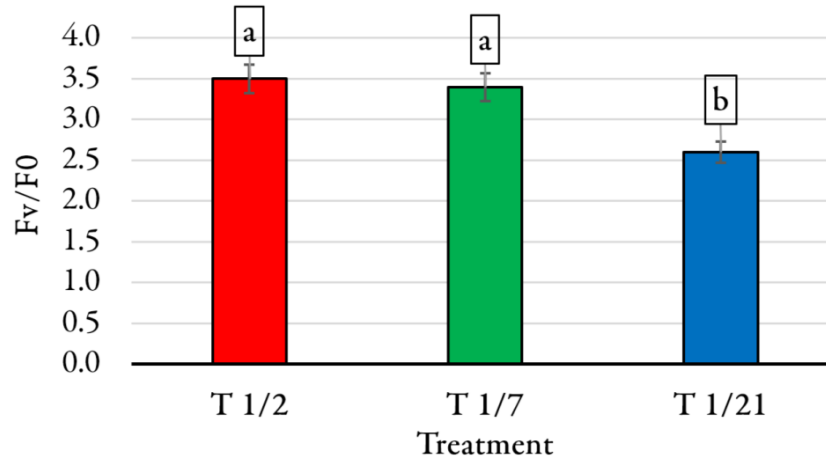
#### Total chlorophyll content

Total chlorophyll content, expressed in SPAD units, increased progressively with longer irrigation intervals, from 40.37 in T1/2 to 46.37 in T1/21, suggesting that 'Shan Tong' maintains or enhances chlorophyll accumulation under moderate to severe water stress. This physiological adjustment may serve as a compensatory mechanism to offset reductions in leaf area or specific leaf mass (SLA), thereby preserving the plant's light-harvesting efficiency despite structural limitations (Zhou *et al.*, 2013). Similar responses have been reported in drought-tolerant species where increased chlorophyll concentration is associated with sustained photosynthetic performance under stress (Qiao *et al.*, 2024). When considered together with increased SLA and higher stomatal density on the abaxial surface, the rise in chlorophyll content reveals a coordinated acclimation strategy. This strategy enhances the functional surface area for light capture, maximizes  $\text{CO}_2$  uptake efficiency, and maintains photosynthetic integrity, even under limited water availability. Such physiological plasticity illustrates a trade-off framework where structural and biochemical traits are modulated synergistically to achieve drought resilience. These combined responses underscore the potential of 'Shan Tong' to optimize resource use and maintain productivity under suboptimal conditions, highlighting its suitability for afforestation or agroforestry in water-limited environments.

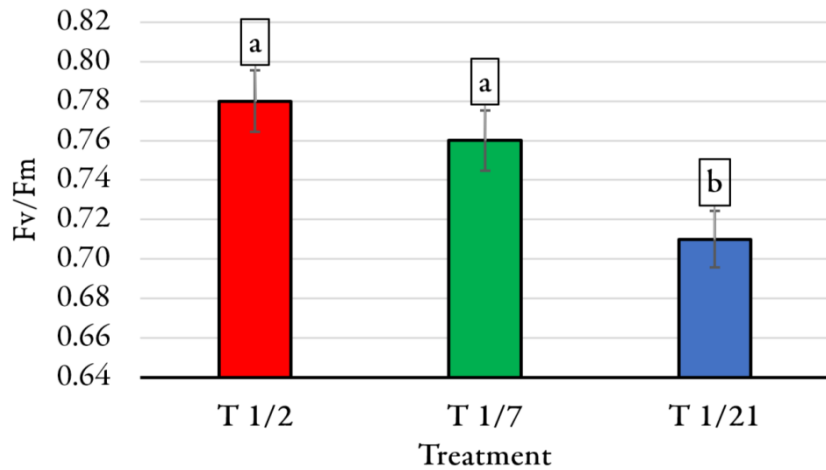
#### The chlorophyll fluorescence parameters $F_m/F_v$ and $F_v/F_0$

The chlorophyll fluorescence parameters of maximum primary yield of PSII photochemistry ( $F_v/F_0$ ) and maximum quantum efficiency of PSII ( $F_v/F_m$ ) are presented in Figures 4 and 5. The reduction in  $F_v/F_0$  and  $F_v/F_m$  under prolonged drought indicates a decrease in PSII efficiency, suggesting photoinhibition and stress-induced damage to the photosynthetic apparatus (Maxwell and Johnson, 2000; Zhuang *et al.*, 2020). A decline in these parameters is commonly associated with oxidative stress and reduced electron transport efficiency, which may affect long-term growth and biomass production (Baker, 2008).

Importantly, the decline in chlorophyll fluorescence coincided with changes in other traits, such as increased specific leaf area (SLA), altered stomatal density, and stabilized chlorophyll content. These concurrent adjustments suggest an integrated adaptive strategy: plants reduce photochemical efficiency under stress but maintain chlorophyll pigments while adjusting leaf morphology to optimize light capture and  $\text{CO}_2$  uptake. This trade-off reflects a form of physiological plasticity, where reduced PSII performance may be partially compensated by anatomical and biochemical modifications aimed at conserving water and maintaining carbon gain (Flexas *et al.*, 2004; Valladares *et al.*, 2007). Such coordination among traits illustrates how 'Shan Tong' balances competing functional demands under drought, sacrificing some photosynthetic efficiency to enhance water use efficiency and structural light capture capacity. Integrating chlorophyll fluorescence with leaf-level traits thus provides a clearer picture of drought adaptation mechanisms beyond isolated responses (Nicotra *et al.*, 2010).



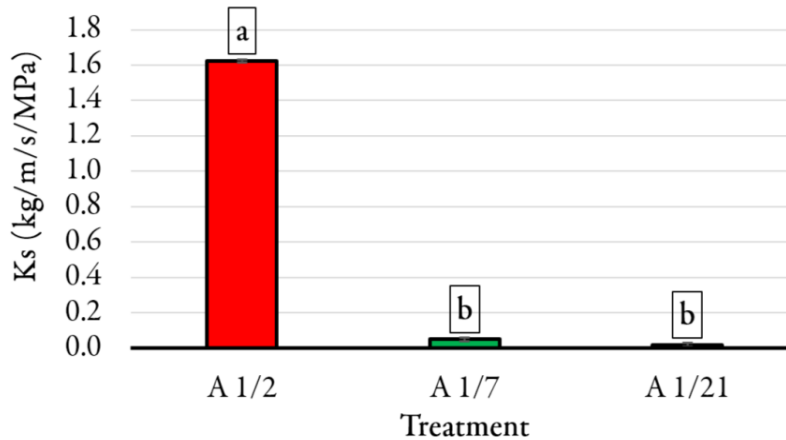
**Figure 4.** The maximum primary yield of PSII photochemistry (Fv/F0) under different irrigation treatments (1/2; 1/7; 1/21) in ‘Shan Tong’ plants  
Different letters between treatments denote significant differences (SNK test,  $p < 0.05$ )



**Figure 5.** The maximum/potential quantum efficiency of PSII (Fv/Fm) under different irrigation treatments (1/2; 1/7; 1/21) in ‘Shan Tong’ plants  
Different letters between treatments denote significant differences (SNK test,  $p < 0.05$ )

Xylem specific conductivity

Figure 6 shows a marked variation in xylem-specific conductivity (Ks) across irrigation treatments. The highest Ks value ( $1.623 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ ) was recorded under irrigation every 2 days (T1/2), reflecting enhanced water transport capacity in the xylem. In contrast, Ks dropped sharply to  $0.018 \text{ kg m}^{-1} \text{ sv}^{-1} \text{ MPa}^{-1}$  under the 21-day irrigation interval (T1/21), likely due to increased water stress from infrequent watering.



**Figure 6.** Xylem Specific Conductivity (Ks) under different irrigation treatments (1/2; 1/7; 1/21) in ‘Shan Tong’ plants

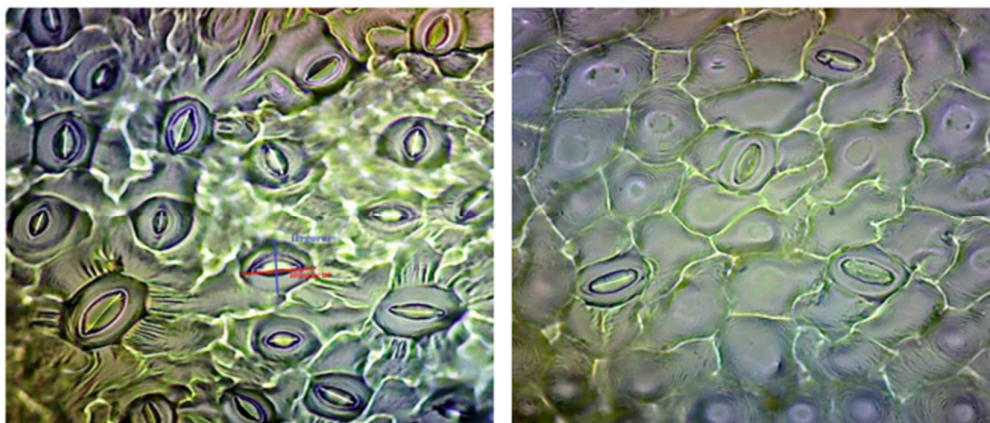
Different letters between treatments denote significant differences (SNK test,  $p < 0.05$ )

The results presented in Figure 6 revealed substantial variation in xylem-specific hydraulic conductivity (Ks) across irrigation treatments. The highest Ks value was recorded under the most frequent irrigation regime (T1/2), reaching  $1.623 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ , indicating enhanced efficiency in water transport through the xylem. In contrast, Ks declined sharply to  $0.018 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$  under the least frequent irrigation (T1/21), reflecting significant impairment in hydraulic function due to sustained water deficit. This marked reduction in Ks under drought is commonly associated with increased vulnerability to xylem embolism, a process in which air bubbles form and block water flow, leading to a breakdown in hydraulic conductivity (Tyree and Sperry, 1989). As plants close their stomata to limit water loss, xylem tension increases, exacerbating the risk of cavitation. This trade-off between maintaining water transport and avoiding hydraulic failure is a key feature of drought adaptation in many woody species (Brodribb and Holbrook, 2006; Gleason *et al.*, 2016).

In the case of ‘Shan Tong’, the observed plasticity in Ks suggests a responsive hydraulic architecture that adjusts to water availability. However, the extreme decline under T1/21 also indicates that prolonged drought can compromise the integrity of the vascular system. These results are in agreement with previous findings in *Paulownia* and other Mediterranean or semi-arid species, where water limitation led to reduced xylem conductivity and altered vessel structure (Miranda *et al.*, 2022). This decline in hydraulic efficiency may ultimately affect carbon assimilation, growth, and survival under long-term drought scenarios.

#### Stomatal density

Stomatal density in ‘Shan Tong’ exhibited significant variations both between leaf surfaces and across irrigation regimes (Figure 7), reflecting an adaptive response to water availability. Under severe water deficit (T1/21), the stomatal density on the abaxial (lower) surface reached its peak at  $599.41 \text{ stomata/mm}^2$  (Table 3), compared to lower values under frequent irrigation. This increase under drought conditions is consistent with previous findings (Wang *et al.*, 2024), which suggest that plants may elevate stomatal density on the lower surface to maintain sufficient  $\text{CO}_2$  uptake while minimizing transpirational water loss particularly when leaf thickness and mesophyll conductance are reduced.



**Figure 7.** Microscopic observation of the stomata density on the lower surface (a) and upper surface (b)

**Table 3.** Stomatal density of the lower and upper leaves surfaces of *Paulownia* for three irrigation regimes (1/2; 1/7; 1/21)

Lower or upper leaves surfaces	Treatments	Stomata density (stomata/mm <sup>2</sup> )
Inferior face	T1/2	526.31 <sup>a</sup> ± 13.22
	T1/7	561.40 <sup>a</sup> ± 14.21
	T1/21	599.41 <sup>c</sup> ± 15.35
Superior face	T1/2	61.4 <sup>a</sup> ± 2.23
	T1/7	64.32 <sup>b</sup> ± 1.32
	T1/21	70.17 <sup>c</sup> ± 2.34

Note: Different letters between treatments denote significant differences (SNK test,  $p < 0.05$ )

Interestingly, the adaxial (upper) surface consistently exhibited lower stomatal densities across all treatments (61.40 to 70.17 stomata/mm<sup>2</sup>), supporting the hypothesis that ‘Shan Tong’ employs an asymmetric stomatal distribution strategy to conserve water. This spatial regulation concentrating gas exchange structures on the shaded, cooler leaf side can be viewed as part of a broader water-saving strategy, a pattern also noted by Pirasteh-Anosheh *et al.* (2016) in drought-adapted species.

Moreover, when considered alongside increased SLA and changes in chlorophyll content, these stomatal adjustments illustrate a coordinated plastic response that balances photosynthetic performance and water-use efficiency. The increase in stomatal density may offset potential limitations from reduced stomatal aperture under drought, ensuring continued carbon assimilation despite adverse conditions. This suggests a functional trade-off, whereby ‘Shan Tong’ enhances its photosynthetic potential at the cost of increased anatomical complexity and metabolic investment in stomatal development. Such plasticity likely contributes to the hybrid’s resilience in fluctuating water environments.

#### *Correlation between different parameters*

The correlations observed in these two treatments revealed interesting relationships (Tables 4 and 5). For instance, in the well-watered treatment (T1/2), the strong positive correlations observed between transpiration ( $T_r$ ), stomatal conductance ( $g_s$ ), and leaf water potential ( $\Psi_h$ ) (e.g.,  $T_r-\Psi_h$ :  $r = 0.8198$ ,  $T_r-g_s$ :  $r = 0.8463$ ) confirm the tight coupling between stomatal regulation and plant water status, suggesting that under favorable water conditions, the species can optimize gas exchange and maintain efficient hydraulic conductance. The strong relationship between hydraulic conductivity ( $K_s$ ) and photosynthetic assimilation ( $A_n$ ) ( $r = 0.907$ ) further indicates that efficient water transport is a key driver of carbon gain, aligning with previous findings (Chaves *et al.*, 2003; Chavarria and dos Santos 2012).

**Table 4.** Correlation matrix of the different parameters measured for the T1/2 treatment

Correlated traits	$\Psi_h$	Ks	An	gs	Tr	WUEi	RWC	Total chlorophyll
$\Psi_h$	1							
Ks	<b>0.7432</b>	1						
An	0.4442	<b>0.907</b>	1					
gs	<b>0.6982</b>	0.1953	0.0217	1				
Tr	<b>0.8198</b>	<b>0.9914</b>	<b>0.8463</b>	0.2738	1			
WUEi	0.142	0.6309	<b>0.8868</b>	0.0377	<b>0.5394</b>	1		
RWC	0.3267	0.0059	0.0532	<b>0.8619</b>	0.0286	0.2967	1	
Total chlorophyll	<b>0.9999</b>	0.7519	0.4542	<b>0.6889</b>	<b>0.8274</b>	1	0.3174	1

Note:  $\Psi_h$  Leaf water potential; Ks Specific conductivity; An Net photosynthesis; Tr Transpiration; WUEi Instantaneous water use efficiency; RWC Relative water content; Total chlorophyll. In bold, significant values (off the diagonal) at the alpha threshold (0.05)

**Table 5.** Correlation matrix of the different parameters measured for the T1/21 treatment

Correlated traits	$\Psi_h$	Ks	An	gs	Tr	WUEi	RWC	Total chlorophyll
$\Psi_h$	1							
Ks	0.4138	1						
An	<b>0.7078</b>	<b>0.9122</b>	1					
gs	<b>0.9576</b>	<b>0.6195</b>	<b>0.8734</b>	1				
Tr	0.0266	0.4231	0.157	0.0019	1			
WUEi	0.0812	<b>0.8412</b>	<b>0.5744</b>	0.2267	<b>0.8087</b>	1		
RWC	<b>0.9153</b>	0.7431	0.4193	<b>0.768</b>	0.1963	0.291	1	
Total chlorophyll	0.188	<b>0.9386</b>	<b>0.7257</b>	0.3718	<b>0.6698</b>	<b>0.9748</b>	0.0233	1

Note:  $\Psi_h$  Leaf water potential; Ks Specific conductivity; An Net photosynthesis; Tr Transpiration; WUEi Instantaneous water use efficiency; RWC Relative water content; Total chlorophyll. In bold, significant values (off the diagonal) at the alpha threshold (0.05)

Under severe drought (T1/21), however, the decoupling between transpiration and gs or An (e.g., Tr-gs:  $r = 0.0019$ ) and the weakening of certain relationships may reflect stomatal closure and reduced transpiration as drought intensifies, suggesting a protective strategy to minimize water loss. Nonetheless, the persistence of strong correlations such as gs- $\Psi_h$  ( $r = 0.9576$ ) and  $\Psi_h$ -RWC ( $r = 0.9153$ ) indicates that the species maintains coordinated control of water status and stomatal function even under stress, an adaptive trait that may support survival under episodic droughts.

Under increasing water stress, plants exhibited higher specific leaf area (SLA), reflecting the development of thinner and broader leaves that enhance light interception per unit biomass (Serrano and Peñuelas, 2005, Poorter *et al.*, 2009). Concurrently, an increase in stomatal density, particularly on the abaxial (lower) leaf surface, improves gas exchange efficiency while minimizing water loss through controlled transpiration (Pirasteh-Anosheh *et al.*, 2016; Wang *et al.*, 2024). In parallel, the total chlorophyll content increased with drought intensity, suggesting a compensatory mechanism to maintain photosynthetic capacity even as structural and stomatal traits are altered (Zhou *et al.*, 2013; Haghpanah *et al.*, 2024)

Moreover, the significant correlations involving total chlorophyll content and gas exchange traits (e.g., Total chlorophyll-An and Total chlorophyll-Tr) underline the importance of chlorophyll retention for sustaining photosynthetic activity under limited water availability, as also shown by Muhammad *et al.* (2024).

This could reflect an inherent resilience mechanism of the species, allowing it to maintain functional photosynthetic capacity despite stress.

Taken together, these findings suggest that 'Shan Tong' exhibits adaptive coordination between water transport, stomatal behavior, and carbon assimilation, which could contribute to its plasticity and potential viability under projected climate scenarios involving longer drought periods and irregular rainfall. The observed trait coordination suggests that 'Shan Tong' possesses functional plasticity in regulating water and carbon fluxes. This could enhance its drought resilience and support its use in afforestation or agroforestry programs in arid and semi-arid regions under climate change conditions.

## **Conclusions**

The findings of this study demonstrate that 'Shan Tong' exhibits notable physiological adaptability to water deficit conditions, highlighting its potential though not yet confirmed for cultivation in semi-arid environments. The species showed promising carbon sequestration capacity, with considerable organic matter stored in leaves, stems, and roots, which may support its use in future reforestation and agroforestry efforts aimed at carbon capture and mitigating urban heat. 'Shan Tong' responded to reduced irrigation frequency with increased instantaneous water use efficiency (WUEi) and maintained chlorophyll content under drought, both of which are critical for sustaining photosynthesis and biomass production under stress. Additionally, modifications in leaf traits such as increased specific leaf area and adjusted stomatal density indicate adaptive strategies to optimize water use and gas exchange under limiting conditions. These physiological adjustments reflect a degree of plasticity that could be advantageous in water-scarce environments. However, it is important to acknowledge that prolonged or severe drought led to declines in gas exchange parameters and xylem hydraulic conductivity, which could ultimately impair long-term growth and productivity. Therefore, while the short-term responses observed are encouraging, we caution against generalizing the suitability of 'Shan Tong' for large-scale afforestation without long-term, multi-site field trials that capture seasonal variability, climatic extremes, and soil differences.

## **Authors' Contributions**

SF, IO: Writing - original draft, Methodology, Investigation, Data curation. IO: Writing - review & editing, Funding acquisition, Formal analysis. M.TE: Resources, Formal analysis. S G: Writing - review & editing, Investigation, Funding acquisition. AD: Supervision, Formal analysis. ZN: Writing - review & editing, Re-sources, Formal analysis.

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## **Conflict of Interests**

The authors declare that there are no conflicts of interest related to this article.

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