International Journal of Bio-resource and Stress Management https://ojs.pphouse.org/index.php/IJBSM

Crossref

IJBSM November 2025, 16(11): 01-13

Article AR6471

Research Article

Stress Management

DOI: HTTPS://DOI.ORG/10.23910/1.2025.6471

Standardizing Phenotyping Technique for Drought Stress Assessment in Teak, Combining Morpho-physiology and Biochemical Indices

Ashwath M. N.[1], Santhoshkumar A. V.[2], Ankita[3], Shiran K.[4], Sourav Ranjan Mohapatra[5] and Binu N. K.[2]

[1]Dept. of Environmental Science and Agroforestry, College of Agriculture, Gangavathi, Koppala, Karnataka (583 227), India
[2]Dept. of Forest Biology and Tree Improvement, College of Forestry, Kerala Agricultural University, Thrissur, Kerala (680 656), India
[3]Dept. of Forestry, PGCA, Dr. Rajendra Prasad Central Agricultural University, Pusa, Bihar (848 125), India
[4]ICAR-Central Arid Zone Research Institute, RRS, Jaisalmer, Rajasthan (345 001), India
[5]College of Forestry, Bhubaneswar, Odisha University of Agriculture and Technology, Bhubaneswar, Odisha (751 003), India

Open Access

Corresponding ashufcp@gmail.com

0000-0002-4041-8343

ABSTRACT

The study was conducted in the month of August, 2023 at the College of Forestry, Kerala Agricultural University, Kerala, India to identify the peak drought stress period and optimize phenotyping techniques for drought tolerance screening in teak seedlings under tropical humid conditions. The experiment subjected eight-month-old vegetatively propagated teak seedlings to controlled drought conditions over 20 days. Morpho-physiological parameters such as number of leaves, relative water content (RWC), photosynthetic rate, stomatal conductance, transpiration rate, and chlorophyll fluorescence were monitored bi-daily. The results revealed that the 9th and 10th days after withholding irrigation marked the maximum drought stress period, with significant reductions in photosynthesis (0.372 mole CO_2 m^{-2} s^{-1}), stomatal conductance, and RWC (51.14%). Biochemical analysis showed increased levels of proline, glycine betaine, and total soluble sugars, confirming stress adaptation. Upon rewatering, partial recovery was observed in physiological traits, while biochemical markers indicated ongoing stress response adjustments. Correlation and regression analyses highlighted strong interrelations between photosynthesis and traits such as stomatal conductance, RWC, and chlorophyll fluorescence. The findings were revalidated through repeated trials, confirming the 10th day as the optimal time for drought phenotyping in teak seedlings in given condition. This study enhances our understanding of teak's drought response and offers critical insights for breeding programs and sustainable plantation management strategies.

KEYWORDS: Teak, phenotyping, photosynthesis, chlorophyll fluorescence, proline, regression, water-stress

Citation* (VANCOUVER)*: Ashwath et al., Standardizing Phenotyping Technique for Drought Stress Assessment in Teak, Combining Morpho-physiology and Biochemical Indices. *International Journal of Bio-resource and Stress Management,* 2025; 16(11), 01-13. HTTPS://DOI.ORG/10.23910/1.2025.6471.

Data Availability Statement: Legal restrictions are imposed on the public sharing of raw data. However, authors have full right to transfer or share the data in raw form upon request subject to either meeting the conditions of the original consents and the original research study. Further, access of data needs to meet whether the user complies with the ethical and legal obligations as data controllers to allow for secondary use of the data outside of the original study.

Conflict of interests: The authors have declared that no conflict of interest exists.

RECEIVED on 27th June 2025 RECEIVED in revised form on 19th October 2025 ACCEPTED in final form on 04th November 2025 PUBLISHED on 12th November 2025

1. INTRODUCTION

Plants being immobile, are constantly exposed to a wide range of environmental challenges throughout their life cycle from germination to maturity, adapting to disturbances by modifying their physiological and metabolic processes as well as their genetic structures. These challenges, both abiotic (such as drought, salinity, temperature extremes, and pollution) and biotic (like pests and pathogens), adversely affected their growth, development, and survival. In response to these challenges, plants have evolved a diverse array of strategies to cope with and adapt to their surroundings. These adaptations are evident not only in their physiology and metabolism but also in the alterations of their genetic makeup, enabling them to enhance their resilience and maintain productivity under stress (Hernandez et al., 2021). One of the promising approaches in modern plant science is the exploitation of these natural adaptive traits for improving stress tolerance through targeted breeding programs. Incorporating these physiological and molecular traits into crop improvement programs can bridge key research gaps and significantly improve agricultural productivity, especially under the increasing threat of climate change (Harfouche et al., 2014; Zhou et al., 2019).

Trees, as long-lived organisms and key components of terrestrial ecosystems, provide a compelling model to study stress responses. Trees like teak (*Tectona grandis* L.f.) have evolved various strategies to endure extreme conditions such as prolonged drought, intense heat, cold temperatures, salinity, and air or soil pollution. During drought conditions, plants exhibit several physiological and biochemical responses. These include stomatal closure to reduce water loss through transpiration, reduction of leaf area to limit exposure, accumulation of compatible solutes like proline and glycine betaine, and modifications in cell wall elasticity to preserve structural integrity and water relations (Brunner et al., 2015; Zulfiqar et al., 2022; Preciado-Rangel et al., 2019; Coleman et al., 2021). The severity, duration, and frequency of stress are critical factors influencing how a plant responds. Chronic exposure to stress can stunt growth, reduce productivity, and impair reproductive development (Minocha et al., 2014; Galeano et al., 2019). Therefore, a thorough understanding of stress severity and duration is vital for screening plant genotypes for stress tolerance. Identifying tolerant genotypes can help develop superior varieties that are better equipped to withstand harsh environmental conditions, thereby enhancing sustainability in forestry and agriculture.

In this context, the current study is designed to investigate drought stress tolerance in teak, a tropical hardwood species widely prized for its high-quality timber (Moya et al., 2014). Despite its commercial importance, teak is vulnerable to environmental stresses, particularly heat and drought during its early developmental stages, such as in nursery and initial field establishment phases (Sinacore et al., 2019). These stresses not only affect its physiological health but also impact long-term productivity. To address this challenge, the study focuses on evaluating the drought tolerance of teak accessions by determining the maximum duration of stress they can endure. It emphasizes identifying optimal phenotyping methods to screen genotypes effectively. Physiological, morphological, and biochemical indicators such as leaf wilting, stomatal conductance, PSII photochemical efficiency, respiration rate, and water use efficiency were assessed to gain a comprehensive understanding of the plant's drought status. Additionally, intrinsic water relations and chlorophyll fluorescence were used to evaluate photosynthetic efficiency and membrane stability under stress. The insights from this study are expected to provide valuable guidance for teak breeding programs aimed at improving drought tolerance. By understanding the stress-response mechanisms at a deeper level, this research can contribute to more targeted selection strategies and support sustainable teak plantation management in the face of changing environmental conditions (Vishnu et al., 2022).

2. MATERIALS AND METHODS

2.1. Study location

The study was conducted at the College of Forestry, Kerala Agricultural University, Kerala, India (10°32'N, 76°26'E) from 6th August 2023 to 26th August 2023. The location experiences a warm, humid climate with an average annual rainfall of about 2100 to 2500 mm. The average temperature ranges from 24.4°C to 42.8°C with a relative humidity of 80% to 100%. The daily weather data during the study period was collected from the Weather Station, College of Agriculture, Vellanikkara, and is mentioned in Table 1. During the experiment, soil moisture content of soil from plant pots was determined gravimetrically to understand the field capacity at which drought symptoms began. The study aimed to develop and optimize phenotyping methods for drought screening in teak species within tropical humid regions by assessing photosynthetic activity. The peak sensitivity period was identified using morpho-physiological parameters, and biochemical analysis was employed to confirm the adaptation of teak seedlings, ensuring their survival through recovery.

2.2. Experimental setup

The eight-month-old plants were used for the drought screening. Plants were produced vegetatively and maintained in the forest nursery, College of Forestry, Vellanikkara, Thrissur (Ashwath et al., 2023). The experiment was

Table 1: Weather data of the study area during drought screening at two-day intervals

Sl. No.	Date	Temperature (°C)		Soil Temp. (°C)	RH (%)	Rainfall (mm)	Soil moisture (potting mixture) (%)
		Max.	Min.				
1.	06-08-2023	32.40	24.50	27.80	78.00	0.10	25.12
2.	08-08-2023	32.50	25.00	28.30	79.50	0.00	16.63
3.	10-08-2023	32.90	25.20	28.10	77.00	0.00	13.76
4.	12-08-2023	32.60	25.50	29.00	76.00	0.40	12.49
5.	14-08-2023	32.50	24.20	28.10	77.50	0.00	08.95
6.	16-08-2023	32.50	23.00	27.20	75.00	0.00	07.80
7.	18-08-2023	32.60	24.50	28.30	80.50	0.00	24.58
8.	20-08-2023	30.90	23.40	26.90	80.50	2.00	28.45
9.	22-08-2023	33.00	25.00	28.50	75.00	0.00	22.34
10.	24-08-2023	34.00	24.00	28.20	76.00	0.00	24.12

done with a completely randomised design having five replications. The plants were irrigated to the field level one day before the beginning of the experiment and plants were observed for the dynamics in all the observations mentioned. Based on the soil moisture content, the maximum stress level was defined by morpho-physiological parameters (Muthulakshmi et al., 2023).

2.3. *Observations and data collection*

Morphological and photosynthetic observations were recorded every two days, starting from normal conditions to the maximum wilting stage and continuing until full recovery, while repeating the experiment for confirmation. The number of leaves was recorded throughout the study period. Irrigation was applied based on the maximum reduction in leaf foliage by considering maximum water stress. The physiological traits of plants, such as photosynthetic Rate (μmol $CO_2m^{-2}s^{-1}$), Stomatal Conductance (mmol $H_2Om^{-2}s^{-1}$), Relative water content (%), and Chlorophyll fluorescence (Fv/Fm), were recorded at a two-day interval to know the photosynthetic dynamics throughout the study period. The photosynthetic rate (Pn) and Stomatal Conductance (Gs) were measured for the third leaf from the tip using an IRGA (LI6400 portable photosynthetic system) between 9:00 AM to 11:00 AM, providing a photosynthetic photon flux density of 1000μmol m^{-2} s^{-1}. The leaf chamber air humidity was maintained at 60%, 370–380μmol mol^{-1} CO_2 concentration, 26–28°C air temperature, and 500μmol s^{-1} flow rate. The RWC was estimated using the Barrs method (1968). The RWC was then calculated using the formula;

$$\text{RWC (\%)} = \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \times 100$$

Chlorophyll fluorescence measurements were performed from 9:00 to 11:00 AM with the help of a portable Hansatech Plant Efficiency Analyser (Hansatech, King's Lynn, England). This Plant Efficiency Analyser (PEA) has a sensor head that helps illuminate leaves, detect resulting fluorescent signals, and measure them using a control box. The leaves of each accession were pre-darkened with leaf clips for 45 min before measurement. After this, the sensor head was gently placed over the clip, and the leaf was exposed for illumination by sliding the shutter plate, and fluorescence was recorded. Fluorescence was excited by red (actinic) radiation with 650nm peak wavelength obtained from light-emitting diodes. The irradiance used was 2000 μmol $m^{-2}s^{-1}$. The maximum quantum yield of PSII was estimated by the ratio Fv/Fm=(Fm–Fo)/Fm (Genty et al., 1989).

2.4. *Revalidation of maximum stress*

After knowing the days taken for maximum wilting and reduction in photosynthetic activity, the experiment was repeated to validate the maximum stress period for teak in the tropical humid conditions as discussed earlier. The plants underwent three different stages: Normal (before withholding water), Drought (after the 10th day of stopping irrigation), and Regain (after 5 days of reirrigation). All the physiological parameters and important biochemical traits were assessed for the current experiment. In all three water-stress conditions, healthy third or fourth-order leaves from the tip were collected and used for the assay. The important biochemical parameters related to osmoregulation and reactive oxygen species, namely, Proline (μg g^{-1}), Glycine betaine (μmol g^{-1}), Malondialdehyde (nmol g^{-1}), Total soluble sugar (μg g^{-1}), Total soluble protein content (μg g^{-1}), and total chlorophyll content (mg g 1), were probed to understand the response of teak seedlings to water-stress conditions. Proline was determined using the acid ninhydrin reagent (Bates et al., 1973). The glycine betaine was estimated using Grieve and Gratten's (1983) method. The anthrone method determined Total soluble sugar (Hedge and Hofreiter 1962). Protein content was assayed following Lowry's method (Lowry et al., 1951) with a standard curve prepared using bovine serum albumin. The total chlorophyll content was estimated with the help of Hiscox and Israelstam's (1979) method using DMSO (Dimethyl sulphoxide).

2.5. *Statistical analysis*

The series of data on morpho-physiological metrics collected during the experiment period were averaged, and the peak stress period was identified through a straightforward comparison. Correlation and regression analyses were conducted using R-Studio and KAU_GRAPES. The revalidation of the peak stress period was analyzed using one-way ANOVA principles in R Studio.

3. RESULTS AND DISCUSSION

3.1. *Assessment of maximum water-stress in teak seedlings*

The results revealed distinct variations in physiological adaptation in response to water-stress conditions. These results offer valuable insights into how plants respond to drought stress and subsequent recovery conditions, providing a foundation for understanding the underlying mechanisms and potential strategies for enhancing plant resilience in challenging environments. The data collected at two-day intervals following stress induction are presented in Figure 1. The sensitive range of the plants was determined based on the trends observed in various parameters, as illustrated in the graphs. It was found that after the 10th day of water-limited conditions at the polyhouse stage, the plants could not survive due to the disruption of their intrinsic activities.

As a morphological indicator, it was observed that on the 5th interval (10 days after stress induction), a significant number of leaves withered, and a sudden loss was recorded. Starting with 11.4 leaves, the water-limited conditions triggered an immediate drought escape mechanism, causing the plants to shed leaves. As the drought period progressed, there was a rapid foliage loss to reduce transpiration and minimize moisture loss. Based on this observation, it is concluded that the 9th and 10th days of withholding water represent the maximum stress period for teak seedlings in tropical humid conditions. Even after irrigating the plants on the 6th interval, foliage development and the production of new leaves took time to recover. Figure 1 illustrates that the plants undergo significant water-stress by the 5th interval, marked by the lowest relative water content. The recovery phase begins after the6th day interval of irrigation, indicating that the plants can regain water content over the subsequent days, particularly peaking at day 9. This data can help identify critical periods for water management in teak seedlings. The relative water content starts at 75.26%. There is a gradual decrease in relative water content until the 5th interval, where it reaches its lowest point at 51.14%. From 6th interval onward, the relative water content increases again as reirrigated, peaking at 76.98% on 9th interval. The

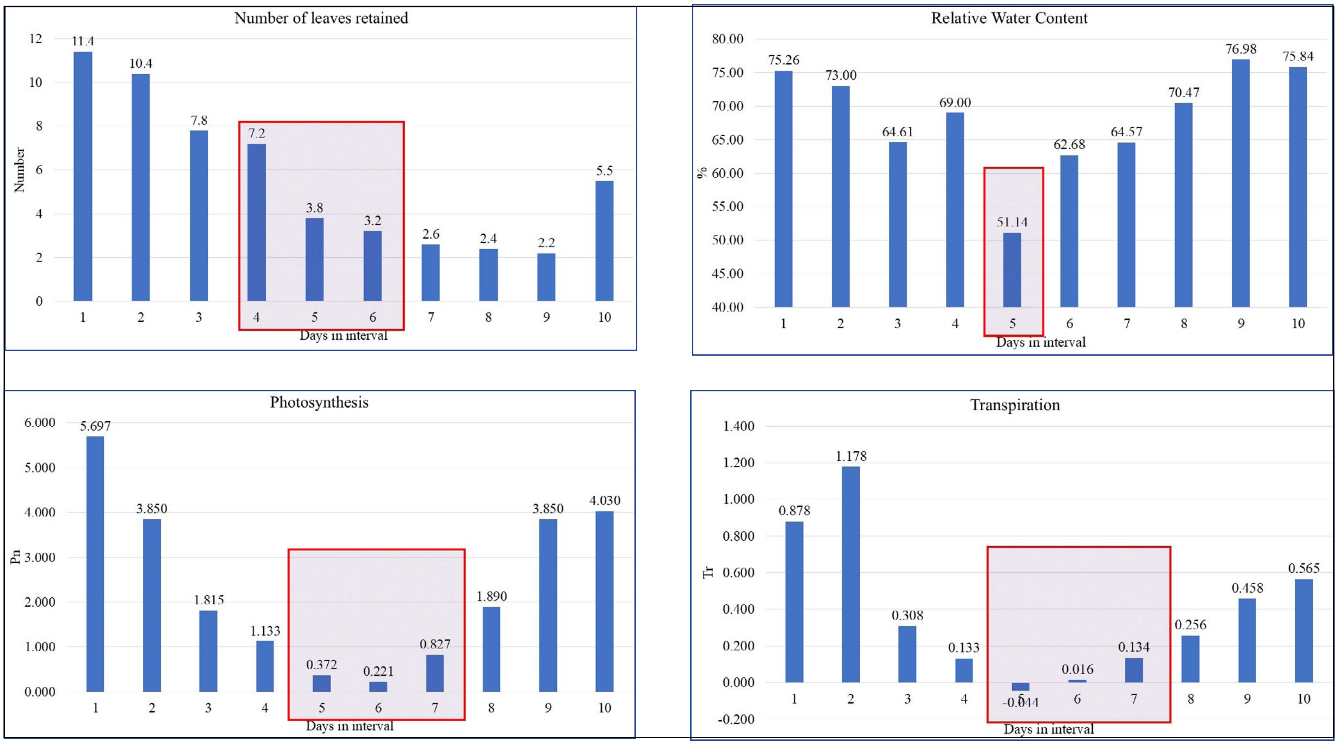

Figure 1: Continue...

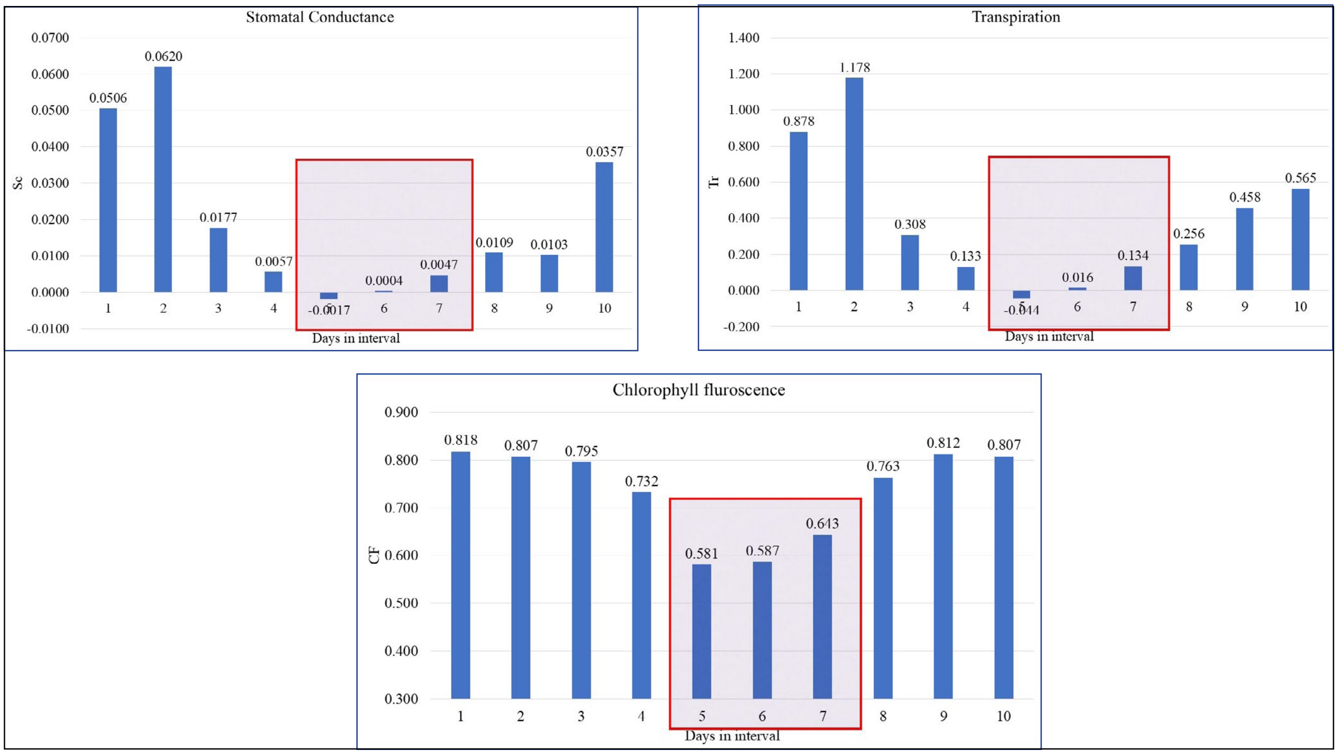

Figure 1: Graphs showing changes in morpho-physiological indices from normal to drought period and regain condition (Number of leaves, RWC, Photosynthesis, Transpiration, Stomatal conductance, Transpiration, Chlorophyll fluorescence). The boxed portion shows the maximum drought period and peak reduction in the studied characters

10th day is highlighted, indicating a critical period where the relative water content is at its lowest.

A useful tool for assessing the health of plants and the effectiveness of the photosynthetic machinery is chlorophyll fluorescence. Fluorescence patterns frequently alter in stressed plants. Because of this, chlorophyll fluorescence is a helpful non-invasive method for identifying stress in plants. Chlorophyll fluorescence levels were relatively high and stable during the initial days until plants underwent stress effects. On the 1st interval, the chlorophyll fluorescence was 0.818. The values slightly decrease to 0.807 on the 2nd and 0.795 on the 3rd interval. Further, the values decreased to 0.581 in the 5th interval indicating maximum damage and high stress level. On reirrigating the plants, starting from interval 8th, the chlorophyll fluorescence begins to recover, with values of 0.763 on 8th, 0.812 on 9th, and 0.807 on 10th interval.

A significant drop in the photosynthetic rate was observed during stress induction. On the 1st interval of the normal stage, the photosynthesis rate is at its highest, with a value of 5.697 µmol CO$_2$m^{-2} s^{-1}. The rate decreased to 3.850 µmol CO$_2$m^{-2} s^{-1} on 2nd day interval and continues to decline over the subsequent days. On days 5th, 6th, and 7th intervals, the photosynthesis rate is significantly low, with values of 0.372 µmol CO$_2$m^{-2} s^{-1}, 0.221 µmol CO$_2$m^{-2} s^{-1}, and 0.827 µmol CO$_2$m^{-2} s^{-1}, respectively. This period is highlighted, indicating a critical low phase. Starting from 8th day interval after the reirrigation, the photosynthesis rate begins to recover, with a value of 1.890 µmol CO$_2$m^{-2} s^{-1}. The rate further increases to 3.850 µmol CO$_2$m^{-2} s^{-1} on the 9th and reaches 4.030 µmol CO$_2$m^{-2} s^{-1} on the 10th interval, indicating recovery of plants at that particular region. Stomatal conductance was maximum on the normal stage of irrigation, indicating proper functioning of plants. The stomatal conductance rate was 0.0506 mmol H$_2$Om^{-2} s^{-1} at the 1st interval of the study, which increased to 0.0620 mmol H$_2$Om^{-2} s^{-1} on the 2nd interval, as increase in loss of water to keep the canopy cool. The conductance rate decreased over the next days, dropping to 0.0177 mmol H$_2$Om^{-2} s^{-1} on the 3rd and further to 0.0057 mmol H$_2$Om^{-2} s^{-1} on 4th. On the 5th and 6th intervals, the stomatal conductance is significantly low, marked by values of -0.0017 mmol H$_2$Om^{-2} s^{-1}, and 0.0004 mmol H^{2}Om^{-2} s^{-1}, respectively. This period is highlighted as indicating a critical low phase. Starting from the 8th interval, the stomatal conductance begins to recover, with values of 0.0109 mmol H$_2$Om^{-2} s^{-1} on the 8th interval and 0.0103 mmol H$_2$Om^{-2} s^{-1} on the 9th interval and further increased to 0.0357 mmol H$_2$Om^{-2} s^{-1}.

The transpiration rate during the drought stress decreased from normal to drought period. In the initial days of the study, the transpiration rate was 0.878 mmol H_2Om^{-2} s^{-1} and the rate increased to its peak at 1.178 mmol H_2Om^{-2} s^{-1} on 2nd interval. The rate decreases over the next days, dropping to 0.308mmol H_2Om^{-2} s^{-1} on 3rd interval and further to 0.133 mmol H_2Om^{-2} s^{-1} on 4th interval. On 5th, 6th, and 7th intervals, the transpiration rate is significantly low, marked by values of -0.044 mmol H_2Om^{-2} s^{-1}, 0.016 mmol H_2Om^{-2} s^{-1}, and 0.134 mmol H_2Om^{-2} s^{-1}, respectively. This period was a critical low phase. Starting from the 8th interval, the transpiration rate begins to recover, with values of 0.256 mmol H_2Om^{-2} s^{-1} on the 8th interval and 0.458 mmol H_2Om^{-2} s^{-1} on the 9th day. The rate further increased to 0.565 mmol H_2Om^{-2} s^{-1} on the 10th interval.

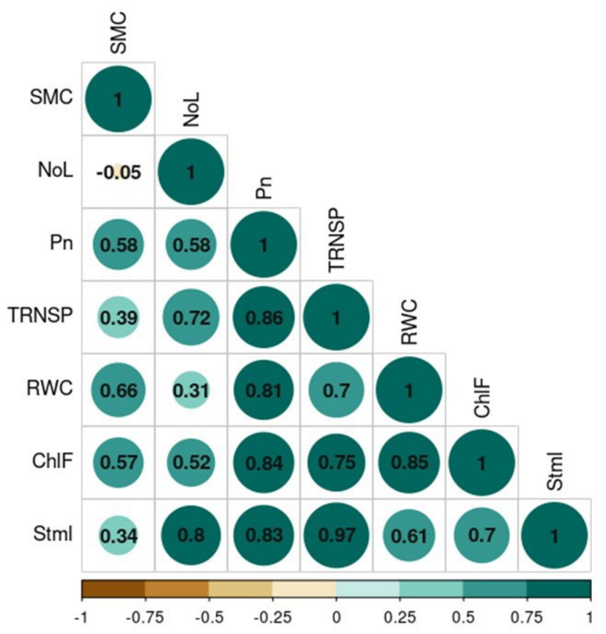

Figure 2: Correlogram showing the relationship between morpho-physiology traits of teak accessions during drought screening

3.2. Relation between morpho-physiological parameters

Correlation between soil moisture content and plant morpho-physiology is shown in the correlogram (Figure 2). The soil moisture had a weak positive correlation with the parameter, as it is a main component driving the plant health. Only under optimal soil moisture can plants survive and support growth and development. The strong positive correlation between photosynthesis and stomatal conductance, fluorescence, RWC, and transpiration is consistent with the plant's efforts to maintain photosynthetic activity and mitigate the effects of drought stress on cellular function. The exchange of gases (CO_2 and O_2) and water vapour through stomata is a common factor among photosynthetic rate, stomatal conductance, and transpiration rate (Hussain et al., 2018). The photosynthetic rate for CO_2 uptake depends on stomatal conductance (Niinemets, 2016). Plants lower their transpiration rate and stomatal conductance to preserve water under drought stress. Because of the restricted CO_2 uptake causes a drop in the photosynthetic rate. This modification minimizes water loss for the plant but at the expense of less photosynthesis (Wang et al., 2022). A decrease in transpiration rate aids in the plant's ability to retain its relative water content, avoiding excessive water loss and dehydration.

The number of leaves had a positive correlation with photosynthesis (0.58), fluorescence (0.52), stomatal conductance (0.80), and transpiration (0.72). Chlorophyll fluorescence had a positive correlation with all the parameters as it indicates the health status of plants, which is also related to photosynthetic activity. For photosynthesis, chlorophyll is necessary because it uses light energy to transform CO_2 into sugars. Chloroplast damage brought on by drought stress can result in a drop in chlorophyll content. This decrease in the plant's capacity to absorb light energy and perform photosynthesis effectively directly affects photosynthesis.

The number of leaves had a positive correlation with photosynthesis (0.58), fluorescence (0.52), stomatal conductance (0.80), and transpiration (0.72). Chlorophyll fluorescence had a positive correlation with all the parameters as it indicates the health status of plants, which is also related to photosynthetic activity. For photosynthesis, chlorophyll is necessary because it uses light energy to transform CO_2 into sugars. Chloroplast damage brought on by drought stress can result in a drop in chlorophyll content. This decrease in the plant's capacity to absorb light energy and perform photosynthesis effectively directly affects photosynthesis.

3.3. Multiple linear regression for photosynthesis and health traits

Photosynthesis being a prime important intrinsic activity, regression was done to determine the strength and direction of association. The regression between photosynthesis and transpiration suggests that as photosynthesis increases, transpiration tends to increase, and the regression model explains approximately 74.7% of the variation in photosynthesis. Similarly, chlorophyll fluorescence and photosynthesis had a positive association of 0.7042. Stomatal conductance and relative water content explain 68.66 and 66.12% of photosynthetic dynamics, respectively. On the other hand, the r^2 value of 0.3381 and 0.3338 indicates a weak to moderate linear relationship with the proportion of variance in photosynthesis that is predictable from soil moisture and the number of leaves, respectively. This indicates that the stomatal conductance, transpiration rate, relative water content, and chlorophyll fluorescence highly affect photosynthesis.

Table 2: Variation in morpho-physiological and biochemical traits during repeated confirmation drought periods

Parameters	Normal	Drought	Regain	*p*-value
Number of leaves	09.87^a	04.73^b	02.57^c	<0.0001
Photosynthetic Rate (µmol CO_2m^{-2} s^{-1})	04.33^a	02.08^c	03.47^b	<0.0002
Stomatal Conductance (mmol H_2Om^{-2} s^{-1})	00.08^a	00.01^c	00.04^b	<0.0003
Transpiration Rate (mmol H_2Om^{-2} s^{-1})	01.06^a	00.15^c	00.72^b	<0.0004
Relative water content (%)	74.13^a	57.96^b	76.42^a	0.0004
Chlorophyll fluorescence (Fv/Fm)	00.77^a	00.61^b	00.81^a	0.0003
Chlorophyll content (mg g^{-1})	03.24^b	02.86^b	04.83^a	<0.0001
Proline (µg g^{-1})	02.09^b	04.13^a	01.22^b	<0.0001
Glycine betaine (µmol g^{-1})	04.75^c	17.29^a	10.19^b	<0.0001
Malondialdehyde (nmol g^{-1})	12.63	14.90	12.88	NS
Total soluble sugar (µg g^{-1})	285.86^b	382.28^a	308.57^b	0.0130
Total soluble protein content (µg g^{-1})	378.20^b	1074.20^a	1018.40a	<0.0001

3.4. Re-validating the peak stress level

Based on these results, it was found that the maximum stress effect on teak plants occurred on the 10th and 11th days (5th interval) after irrigation was stopped. Therefore, teak plants in the nursery can be evaluated for water-stress on the 10th and 11th days after watering is stopped. To revalidate the maximum drought period, the experiment was repeated in three stages: normal conditions, maximum water-stress (on the tenth day after stopping irrigation), and the recovery period (on the tenth day after reirrigation began) (Table 2). After 10 days of withholding irrigation, most of the plants showed wilting symptoms. following this stage, the plants were reirrigated to bring them to normal condition.

The number of leaves varied among the conditions. The number of leaves significantly decreased from 9.87 in normal conditions to 4.73 under drought, suggesting a possible resource allocation strategy. Concurrently, the photosynthetic rate (4.33 to 2.08 µmol CO_2m^{-2} s^{-1}), stomatal conductance (0.08 to 0.01 mmol H_2Om^{-2} s^{-1}), and transpiration rate (1.058 to 0.154 mmol H_2Om^{-2} s^{-1}) showed significant reductions. The regain phase showed improvements in photosynthetic rate (3.466 µmol CO_2m^{-2} s^{-1}), stomatal conductance (0.037 mmol H_2Om^{-2} s^{-1}), and transpiration rate (0.719 mmol H_2Om^{-2} s^{-1}), but does not fully recover to normal levels. Relative water content decreased significantly during drought (57.96%), indicating lowered plant water potential. The regain phase shows a full recovery (76.42%), comparable to normal (74.13%). Chlorophyll fluorescence (Fv/Fm) decreased significantly during drought (0.609) but showed improvement in the regain phase (0.806), suggesting a recovery of photosynthetic efficiency.

Chlorophyll content decreased during drought (2.857 mg g^{-1}) but exhibited a full recovery in the regain phase (4.834 mg g^{-1}), which was higher compared to normal conditions (3.242 mg g^{-1}). Biochemical traits indicated significant changes in response to water stress. Proline levels increased during drought (4.132 µg g^{-1}) compared to normal (2.091 µg g^{-1}), indicating osmotic adjustment, with a partial decrease in the regain phase (1.221 µg g^{-1}). Glycine betaine also exhibited a similar trend; it increased to 17.285 µmol g^{-1} under drought conditions compared to normal (4.750 µmol g^{-1}) and regained (10.185 µmol g^{-1}). There were no significant differences in malondialdehyde levels and superoxide dismutase activity. Total soluble sugar content increased significantly during drought (382.283 µg g^{-1}), whereas the regain phase showed a decrease (308.570 µg g^{-1}) but remained higher than normal (285.867 µg g^{-1}). Drought conditions lead to an increase in the soluble protein levels (1074.20 µg g^{-1}), followed by regain (1018.40 µg g^{-1}) and normal conditions (378.20 µg g^{-1}).

These results collectively suggest that drought conditions negatively impact various physiological parameters of the plants, including photosynthesis, stomatal conductance, and PSII. Regain conditions show intermediate values, indicating partial recovery compared to drought but not reaching the levels observed under normal conditions.

The results reveal distinct variations in physiological adaptation in response to water-stress conditions in teak seedlings. These findings provide valuable insights into how plants respond to drought stress and subsequent recovery, laying the groundwork for understanding the underlying mechanisms and potential strategies for enhancing plant resilience in challenging environments. Research has shown that teak plants respond to water-stress by reducing their evaporative surfaces, limiting CO_2 availability, and decreasing stomatal conductance, which leads to a lower rate of carbon fixation (Husen 2010; Borah et al., 2019; Hassan et al., 2021).

As a morphological indicator, the water-limited conditions triggered an immediate drought escape mechanism, causing the plants to shed leaves (Plate). Plants undergo leaf rolling, drop-off of the leaf, reduce leaf area, change leaf orientation, etc., to cope with stress conditions (Seleiman et al., 2021). As the drought progressed, there was a rapid foliage loss to reduce transpiration and minimize moisture loss. Leaf retention is a primary indicator of how well a plant maintains its leaf cover under stress conditions and continues to remain or maintain normal cellular activity (Xiao et al., 2009; Zoghi et al., 2019; Husen 2010). Sneha et al., (2012) revealed that water-limiting conditions for long-term periods have reduced foliage with maximum biomass allocation towards roots. Further, the functional balance of the plant was affected by altering the shoot and root growth and its ratio. The relative water content determines the water condition of plant cells. It indicates the turgor pressure and degree of hydration of the plant. The relative water content falls as water is lost during drought stress (Anjum et al., 2011). A decrease in RWC can result in wilting and decreased cell turgor. It is an early indicator of drought stress. Under normal circumstances, plants retain a high relative water content signalling that they are hydrated (Guo et al., 2010). When a plant is under drought stress, its relative water

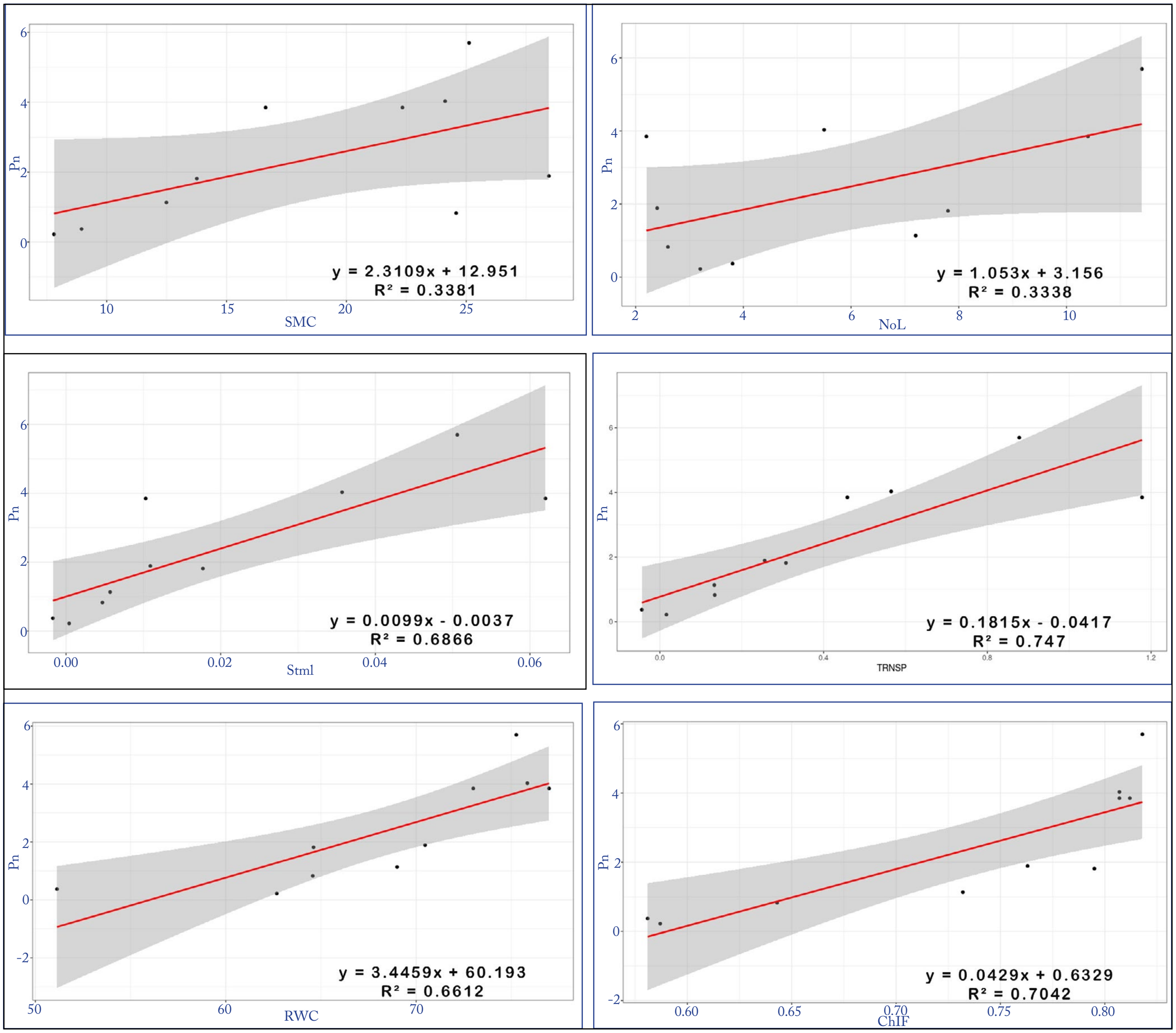

Figure 3: Relationships between photosynthesis and (a) soil moisture content, (b) number of leaves, (c) stomatal conductance, (d) transpiration rate, (e) relative water content and (f) Chlorophyll fluorescence. The red line represents the regression line and the shaded regions represent the 95% confidence levels for prediction

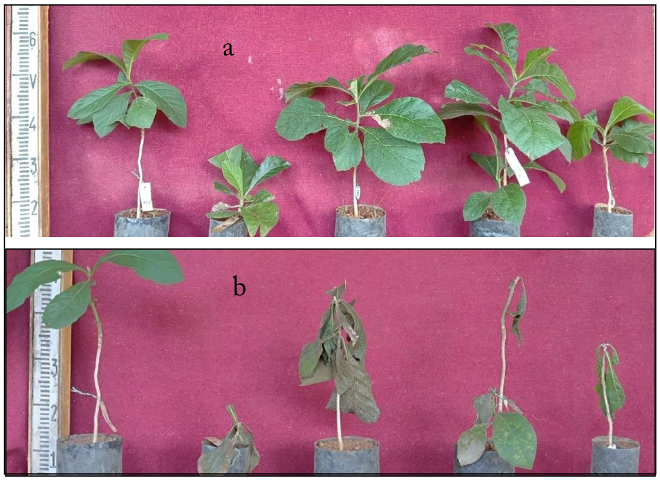

Plate: Plants under normal (a) and drought conditions (b) showing withering of leaves

content drastically drops as it loses water (Elsheery and Coa 2008). Depending on the severity of the drought, relative water content can recover as the plant regains hydration. Husen (2010) reported a reduction of about 50% in RWC under water-stress conditions.

The initial high photosynthesis rate suggests optimal conditions for photosynthesis at the start of the observation period. The decline from days 9 and 10 indicates that the plants are experiencing increasing stress, possibly due to water limitation or other adverse conditions affecting their photosynthetic activity. The photosynthesis rate starts to recover on reirrigation, indicating that the plants are beginning to regain their photosynthetic function, possibly due to the alleviation of stress conditions or adaptation mechanisms kicking in. Reduced photosynthesis and stomatal activities are frequently observed under drought stress in trees (Rajarajan et al., 2022; Galeano et al., 2019). Decreases in stomatal conductance and net photosynthesis during drought stress are fairly, but their underlying mechanisms remain poorly understood (Niinemets 2016). Stomatal closure limits the amount of CO_2 absorption, which reduces photosynthesis, and plants store water (Borah et al., 2019; Wang et al., 2022). This reduces gas exchange, which, in turn, affects photosynthesis and can lead to leaf wilting and an increase in leaf temperature (Liu et al., 2010). In normal conditions, transpiration rates were relatively high and contributed to the plant's cooling. The decrease in transpiration rate during drought further supports the plant's effort to conserve water and mitigate water loss during drought stress. Reduced transpiration can lead to increased temperature and abridged nutrient transport. Additionally, photo-inhibition may occur during the stress period, which could harm the photosynthetic apparatus of plants (Niinemets 2016). When the plants were re-watered, their stomata restarted work by opening again, repairing or replacing any damaged photosynthetic components, which will result in a partial or complete recovery of photosynthetic rates (de Sousa Leite et al., 2022).

Chlorophyll fluorescence happens when chlorophyll absorbs light and re-emits as fluorescence, which helps assess plants' photosynthesis efficiency (Hwang et al., 2023). The current study examines how drought stress affects teak seedlings, paying special attention to the Photosystem II efficiency (Fv/Fm values) (Taria et al., 2020). The decreased Fv/Fm values show that the photosynthetic efficiency is most likely due to physiological adjustments brought on by water scarcity (Alam et al., 2018). In contrast to these results, Rajarajan et al. (2022) reported reduced Fv/Fm values in *Pongamia pinnata* under drought stress (0.22 to 0.58), among different accessions. Chlorophyll is essential for photosynthesis as it absorbs light energy. The amount of chlorophyll in a plant indicates the condition of its chloroplasts and its capacity for photosynthesis (Tezcan et al., 2019). A high chlorophyll indicates healthy chloroplasts and active photosynthesis (Khaleghi et al., 2012). Chloroplast damage during a drought can lower a plant's chlorophyll content by decreasing photosynthetic efficiency and greenness. In drought conditions, chlorophyll values exhibited slight decreases or increases in response to water-stress (Li et al., 2006). Findings align with results from studies by Liu et al. (2011), Galeano et al. (2019), Borah et al. (2019), and Hassan et al. (2021), indicating a reduction in chlorophyll levels with escalating water stress. The decline in chlorophyll content is commonly regarded as a characteristic manifestation of oxidative stress, potentially stopping pigment photo-oxidation, chlorophyll degradation, and/or deficiency in chlorophyll synthesis (Smirnoff, 1993).

Proline is an important amino acid that plays a vital role in the adaptation of plants to environmental stress. It acts as an osmoprotectant, helping to maintain cellular turgor and prevent dehydration in plants exposed to stress (Mansour, 1998). It also functions as an energy or reducing power sink (Verbruggen et al., 1996), scavenger of reactive oxygen species (ROS) and their derivatives (Hong et al., 2000; Bashir et al., 2007), and serves as a source of carbon and nitrogen under stress conditions (Peng et al., 1996). Drought conditions led to a significant increase in proline content, indicating that drought stress induced the accumulation of proline in teak plants (Galeano et al., 2019). A notable decline in proline content from drought to the recovery phase suggests a recovery process, with proline levels decreasing as conditions improve.

Glycine betaine is another osmoprotectant that helps to maintain osmotic balance and cell turgor under stress conditions (Noctor et al., 1997; Hassan et al., 2021). There was a noteworthy increase in glycine content under drought conditions compared to normal conditions (Annunziata et al., 2019; Tran et al., 2018). Increased glycine betaine levels can protect cell osmotic balance and protect cellular structures (Zouari et al., 2018). The glycine content was reduced during the recovery phase compared to the drought stress (Castro-Duque et al., 2020). MDA is an indicator of oxidative cell membrane damage. It displays the extent of lipid peroxidation, which may jeopardize the integrity of the membrane (Khaleghi et al., 2019; Wang et al., 2022). All teak accessions experienced cell membrane damage from ROS during water stress, as evidenced by the elevated MDA level. The teak accessions exhibited an increased MDA content in their leaves following drought treatment (Husen 2010; Hassan et al., 2021). The ability to prevent or repair membrane damage during dehydration processes MDA is essential for preserving membrane integrity (Yang et al., 2009; Rawat et al., 2021).

Under stressful circumstances, soluble sugars function as an energy source and help to preserve osmotic balance and cell turgor. Because sugars sustain turgor and supply energy for metabolic processes when photosynthesis is restricted, drought stress can increase total soluble sugar levels (Rosa et al., 2009). Soluble sugars are highly sensitive to environmental stresses, and their levels can vary depending on the species (Rosa et al., 2009). During drought, there was a trend of increased soluble sugar content for most accessions compared to normal conditions, indicating a potential metabolic response to water stress. Several studies have reported similar findings, showing increased soluble sugar content in response to drought stress (Zhang et al., 2020; saandez et al., 2021). The protein content in plant cells is necessary for enzymatic reactions, structural support, and stress response and is represented by total soluble protein levels (Wu et al., 2022). Total soluble protein may rise in response to drought stress as plants produce stress-related proteins to shield cellular structures and sustain metabolic processes (Zhongcheng et al., 2019). Plants produce specific proteins in response to drought stress, such as chaperones, late embryogenesis abundant (LEA) proteins, and antioxidant enzymes. Other studies reported similar findings, showing increased protein content in response to drought stress (Gurrieri et al., 2020; Hassan et al., 2021; Zonouri et al., 2014).

4. CONCLUSION

The research successfully identified the critical period for drought stress in teak seedlings, occurring on the 9th and 10th days of water withholding. The study demonstrated that drought stress significantly impacted physiological and biochemical markers, aiding in understanding teak's adaptation mechanisms. The findings suggested that teak seedlings exhibited a pronounced drought escape mechanism by shedding leaves and reducing transpiration. The recovery phase showed partial restoration of physiological functions, highlighting the resilience of teak under rehydration.

5. REFERENCES

Alam, B., Singh, R., Uthappa, A.R., 2018. Different genotypes of Dalbergia sissoo trees modified microclimate dynamics differently on the understory crop cowpea (*Vigna unguiculata*) as assessed through ecophysiological and spectral traits in agroforestry system. Agricultural and Forest Meteorology 249(2), 138–148. http://dx.doi.org/10.1016/j.agrformet.2017.11.031.

Anjum, S.A., Xie, X., Wang, L.C., Saleem, M.F., Man, C., Lei, W., 2011. Morphological, physiological and biochemical responses of plants to drought stress. African Journal of Agriculture Research 6(9), 2026–2032. http://dx.doi.org/10.5897/AJAR10.027.

Annunziata, M.G., Ciarmiello, L.F., Woodrow, P., Dell'Aversana, E., Carillo, P., 2019. Spatial and temporal profile of glycine betaine accumulation in plants under abiotic stresses. Frontiers of Plant Science 10, 230. https://doi.org/10.3389/fpls.2019.00230.

Ashwath, M.N., Santhoshkumar, A.V., Kunhamu, T.K., Hrideek, T.K., Shiran, K., 2023. Epicormic shoot induction and rooting of *Tectona grandis* from branch cuttings: influence of growing condition and hormone application. Indian Journal of Ecology 50(1), 38–46. http://dx.doi.org/10.55362/IJE/2023/3849.

Barrs, H., 1968. Determination of water deficits in plant tissues. Water Deficits and Plant Growth: 235–368. Determination of Water Deficits in Plant Tissues | CiNii Research.

Bashir, F., Mahmooduzzafar, Siddiqi, T.O., Iqbal, M., Alam, M., 2007. The antioxidative response system in soybean plants exposed to Deltamethrin, a synthetic pyrethroid insecticide. Environmental Pollution 147(1), 94–100. https://doi.org/10.1016/j.envpol.2006.08.013.

Bates, L.S., Waldren, R.P., Teare, I.D., 1973. Rapid determination of free proline for water-stress studies. Plant and Soil 39(1), 205–207. https://doi.org/10.1007/BF00018060.

Borah, N., Borua, P.K., Roy, S., Saikia, S.P., 2019. Physiochemical studies in seedlings of teak (*Tectona grandis* Linn. f.) of north east India about drought resistance for selection of improved germplasm. Journal of Tropical Forest Environment 9(2). https://doi.org/10.31357/jtfe.v9i2.4465.

Brunner, I., Herzog, C., Dawes, M.A., Arend, M., Sperisen, C., 2015. How tree roots respond to drought. Frontiers of Plant Science 6, 547. https://doi.org/10.3389/fpls.2015.00547.

Castro-Duque, N.E., Chávez-Arias, C.C., Restrepo-Díaz, H., 2020. Foliar glycine betaine or hydrogen peroxide sprays ameliorate waterlogging stress in cape gooseberry. Plants 9(5), 644. https://doi.org/10.3390/plants9050644.

Coleman, H.D., Brunner, A.M., Tsai, C.J., 2021. Synergies and entanglement in secondary cell wall development and abiotic stress response in trees. Frontiers of Plant Science 12, 639769. https://doi.org/10.3389/fpls.2021.639769.

De Sousa Leite, T., da Silva Dias, N., de Freitas, R.M.O., Dombroski, J.L.D., de Sousa Leite, M., de Farias, R.M., 2022. Ecophysiological and biochemical responses of two tree species from a tropical dry forest to drought stress and recovery. Journal of Arid Environment 200, 104720. http://dx.doi.org/10.1016/j.jaridenv.2022.104720.

Elsheery, N.I., Cao, K.F., 2008. Gas exchange, chlorophyll fluorescence and osmotic adjustment in two mango cultivars under drought stress. Acta Physiological Plantarum 30, 769–777. http://dx.doi.org/10.1007/s11738-008-0179-x.

Galeano, E., Vasconcelos, T.S., Novais de Oliveira, P., Carrer, H., 2019. Physiological and molecular responses to drought stress in teak (*Tectona grandis* Lf). PLoS One 14(9), e0221571. https://doi.org/10.1371/journal.pone.0221571.

Genty, B., Briantais, J.M., Baker, N.R., 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochimica et Biophysica Acta (BBA)-Gen. Subjects 990(1), 87–92. https://doi.org/10.1016/S0304-4165(89)80016-9.

Grieve, C.M., Grattan, S.R., 1983. Rapid assay for determination of water-soluble quaternary ammonium compounds. Plant Soil 70(2), 303–307. http://dx.doi.org/10.1007/BF02374789.

Guo, X.Y., Zhang, X.S., Huang, Z.Y., 2010. Drought tolerance in three hybrid poplar clones submitted to different watering regimes. Journal of Plant Ecology 3(2), 79–87. https://doi.org/10.1093/jpe/rtq007.

Gurrieri, L., Merico, M., Trost, P., Forlani, G., Sparla, F., 2020. Impact of drought on soluble sugars and free proline content in selected Arabidopsis mutants. Biology 9(11), 36. https://doi.org/10.3390/biology9110367.

Harfouche, A., Meilan, R., Altman, A., 2014. Molecular and physiological responses to abiotic stress in forest trees and their relevance to tree improvement. Tree Physiology 34(11), 1181–1198. https://doi.org/10.1093/treephys/tpu012.

Hassan, M.A.E., Santhoshkumar, A.V., Hrideek, T.K., Jijeesh, C.M., Joseph, J., 2021. Variability in drought response among the plus tree accessions of *Tectona grandis* (Linn f..) from the provenances of Kerala, South India. Acta Physiological Plantarum 43(3), 1–12. http://dx.doi.org/10.1007/s11738-021-03215-3.

Hedge, J.E., Hofreiter, B.T., 1962. Carbohydrate chemistry. Academic Press, New York, pp. 17–22. doi: 10.12691/jfnr-3-3-14. Accessed on 25th September 2023.

Hernandez, J.O., An, J.Y., Combalicer, M.S., Chun, J.P., Oh, S.K., Park, B.B., 2021. Morpho-anatomical traits and soluble sugar concentration largely explain the responses of three deciduous tree species to progressive water stress. Frontiers in Plant Science 12, 738301. https://doi.org/10.3389/fpls.2021.738301.

Hiscox, J.D., Israelstam, G.F., 1979. A method for the extraction of chlorophyll from leaf tissue without maceration. Canadian Journal of Botany 57(12), 1332–1334. https://doi.org/10.1139/b79-163.

Hong, Z., Lakkisneni, K., Zhang, K., Verma, D.S.P., 2000. Removal of feedback inhibition of ^1- pyrroline-5-carboxylate synthetase results in increased proline accumulation and protection of plants from osmotic stress. Plant Physiology 122, 1129–1136. https://doi.org/10.1104/pp.122.4.1129.

Husen, A., 2010. Growth characteristics, physiological and metabolic responses of teak (T*ectona grandis* Linn. f..) clones differing in rejuvenation capacity subjected to drought stress. Silvae Genetica 59(1-6), 124–136. https://doi.org/10.1515/sg-2010-0015.

Hussain, H.A., Hussain, S., Khaliq, A., Ashraf, U., Anjum, S.A., Men, S., Wang, L., 2018. Chilling and drought stresses in crop plants: implications, cross talk, and potential management opportunities. Frontiers of plant science 9, 393. https://doi.org/10.3389/fpls.2018.00393.

Hwang, Y., Kim, J., Ryu, Y., 2023. Canopy structural changes explain reductions in canopy-level solar-induced chlorophyll fluorescence in *Prunus yedoensis* seedlings under a drought stress condition. Remote Sensing Environment 296, 113733. https://doi.org/10.1016/j.rse.2023.113733.

Khaleghi, A., Naderi, R., Brunetti, C., Maserti, B.E., Salami, S.A., Babalar, M., 2019. Morphological, physiochemical and antioxidant responses of *Maclura pomifera* to drought stress. Scientific Reports 9(1), 19250. https://doi.org/10.1038/s41598-019-55889-y.

Khaleghi, E., Arzani, K., Moallemi, N., Barzegar, M., 2012. Evaluation of chlorophyll content and chlorophyll fluorescence parameters and relationships between chlorophyll a, b and chlorophyll content index under water-stress in *Olea europaea* cv. Dezful.

World Academy of Science, Engineering and Technology 6(8), 636–639. https://doi.org/10.5281/zenodo.1082211.

Li, R.H., Guo, P.G., Michael, B., Stefania, G., Salvatore, C., 2006. Evaluation of chlorophyll content and fluorescence parameters as indicators of drought tolerance in barley. Agricultural Sciences in China 5(10), 751–757. https://doi.org/10.1016/S1671-2927(06)60120-X.

Liu, C., Liu, Y., Guo, K., Fan, D., Li, G., Zheng, Y., Yu, L., Yang, R., 2011. Effect of drought on pigments, osmotic adjustment and antioxidant enzymes in six woody plant species in karst habitats of southwestern China. Environmental and Experimental Botany 71(2), 174–183. https://doi.org/10.1016/j.envexpbot.2010.11.012.

Liu, C.C., Liu, Y.G., Guo, K., Zheng, Y.R., Li, G.Q., Yu, L.F., Yang, R., 2010. Influence of drought intensity on the response of six woody karst species subjected to successive cycles of drought and rewatering. Physiologia Plantarum 139(1), 39–54. https://doi.org/10.1111/j.1399-3054.2009.01341.x.

Lowry, O., Rosebrough, N., Farr, A.L., Randall, R., 1951. Protein measurement with the Folin phenol reagent. Journal of Biological Chemistry 193(1), 265–275. https://doi.org/10.1016/S0021-9258(19)52451-6.

Mansour, M.M.F., 1998. Protection of plasma membrane of onion epidermal cells by glycine betaine and proline against NaCl stress. Plant Physiology and Biochemistry 36(10), 767–772. https://doi.org/10.1016/S0981-9428(98)80028-4.

Minocha, R., Majumdar, R., Minocha, S.C., 2014. Polyamines and abiotic stress in plants: a complex relationship. Frontiers of Plant Science 5, 175. https://doi.org/10.3389/fpls.2014.00175.

Moya, R., Bond, B., Quesada, H., 2014. A review of heartwood properties of *Tectona grandis* trees from fast-growth plantations. Wood Science and Technology 48, 411–433. http://dx.doi.org/10.1007/s00226-014-0618-3.

Muthulakshmi, E., Amrutha, S., Sivakumar, V., Ghosh Dasgupta, M., 2023. Development of physiological indices for screening dehydration tolerance in Eucalyptus clones under nursery conditions. New Forest 54(6), 1103–1118. http://dx.doi.org/10.1007/s11056-022-09958-2.

Niinemets, U., 2016. Uncovering the hidden facets of drought stress: secondary metabolites make the difference. Tree Physiology 36(2), 129–132. https://doi.org/10.1093/treephys/tpv128.

Peng, Z., Lu, Q., Verma, D.P., 1996. Reciprocal regulation of 1-pyrroline-5-carboxylate synthetase and proline dehydrogenase genes controls proline levels during and after osmosis stress in plants. Molecular Genetics and Genomics 253, 334–341. https://doi.org/10.1007/pl00008600.

Preciado-Rangel, P., Reyes-Pérez, J.J., Ramírez-Rodríguez, S.C., 2019. Foliar aspersion of salicylic acid improves phenolic and flavonoid compounds, and also the fruit yield in cucumber (*Cucumis sativus* L.). Plants 8(2), 44. https://doi.org/10.3390/plants8020044.

Rajarajan, K., Sakshi, S., Taria, S., 2022. Whole plant response of *Pongamia pinnata* to drought stress tolerance revealed by morpho-physiological, biochemical and transcriptome analysis. Molecular Biology Reports 49(10), 9453–9463. https://doi.org/10.1007/s11033-022-078.

Rawat, N., Singla-Pareek, S.L., Pareek, A., 2021. Membrane dynamics during individual and combined abiotic stresses in plants and tools to study the same. Physiologia Plantarum 171(4), 653–676. https://doi.org/10.1111/ppl.13217.

Rosa, M., Prado, C., Podazza, G., Interdonato, R., González, J.A., Hilal, M., Prado, F.E., 2009. Soluble sugars: Metabolism, sensing and abiotic stress: A complex network in the life of plants. Plant Signalling Behaviour 4(5), 388–393. https://doi.org/10.4161/psb.4.5.8294.

Seleiman, M.F., Al-Suhaibani, N., Ali, N., 2021. Drought stress impacts on plants and different approaches to alleviate its adverse effects. Plants 10(2), 259. https://doi.org/10.3390/plants10020259.

Sinacore, K., Breton, C., Asbjornsen, H., Hernandez-Santana, V., Hall, J.S., 2019. Drought effects on *Tectona grandis* water regulation are mediated by thinning, but the effects of thinning are temporary. Frontiers in Forests and Global Change 2, 82. https://doi.org/10.3389/ffgc.2019.00082.

Smirnoff, N., 1993. The role of active oxygen in the response to water deficit and desiccation. New Phytologist 125, 27–58. https://doi.org/10.1111/j.1469-8137.1993.tb03863.x.

Sneha, C., Santhoshkumar, A.V., Sunil, K.M., 2012. Effect of controlled irrigation on physiological and biometric characteristics in teak (*Tectona grandis*) seedlings. Journal of Stress Physiology and Biochemistry 8(3) 196–202. https://sciup.org/14323663.

Taria, S., Rane, J., Alam, B., Kumar, M., Babar, R., Anuragi, H., Rajarajan, K., Singh, N.P., 2020. Combining IR imaging, chlorophyll fluorescence and phenomic approach for assessing diurnal canopy temperature dynamics and desiccation stress management in *Azadirachta indica* and *Terminalia mantaly*. Agroforestry Systems 94, 941–951. https://link.springer.com/article/10.1007/s10457-019-00461-w.

Tezcan, A., Aslan, G.E., Kaman, H., 2019. Evaluation of drought stress on the chlorophyll content of the plants: A review of the Solanaceae family. Fresenius Environmental Bulletin 28, 4636–4641. https://doi.org/10.7717/peerj.15954.

Verbruggen, N., Hua, X.J., May, M.M., Van Montagu, M., 1996. Environmental and developmental signals modulate proline homeostasis: Evidence for a negative transcriptional regulator. Proceedings of National Academy of Science USA 93(16), 8787– 8791. https://doi.org/10.1073/pnas.93.16.8787.

Vishnu, M.V., Parthiban, K.T., Raveendran, M., Kanna, S.U., Radhakrishnan, S., Shabbir, R., 2022. Variation in biochemical, physiological and ecophysiological traits among the teak (*Tectona grandis* Linn. f) seed sources of India. Scientific Reports 12(1), 1–11. http://dx.doi.org/10.1038/s41598-022-15878-0.

Wang, Y., Wang, Y., Tang, Y., Zhu, X.G., 2022. Stomata conductance as a goalkeeper for increased photosynthetic efficiency. Current Opinion on Plant Biology 102310. https://doi.org/10.1016/j.pbi.2022.102310.

Wu, S., Tian, J., Ren, T., Wang, Y., 2022. Osmotic adjustment and antioxidant system regulated by nitrogen deposition improve photosynthetic and growth performance and alleviate oxidative damage in dwarf bamboo under drought stress. Frontiers of Plant Science 13, 819071. https://doi.org/10.3389/fpls.2022.819071.

Xiao, X., Yang, F., Zhang, S., Korpelainen, H., Li, C., 2009. Physiological and proteomic responses of two contrasting *Populus cathayana* populations to drought stress. Physiological Plantarum 136(2), 150–168. https://doi.org/10.1111/j.1399-3054.2009.01222.x.

Yang, F., Xu, X., Xiao, X., Li, C., 2009. Responses to drought stress in two poplar species originating from different altitudes. Biological Plantarum 53(3), 511–516. https://doi.org/10.1007/s10535-009-0092-1.

Zhang, P., Zhou, X., Fu, Y., 2020. Differential effects of drought on nonstructural carbohydrate storage in seedlings and mature trees of four species in a subtropical forest. Forest Ecology Management 469, 118159. https://doi.org/10.1016/j.foreco.2020.118159.

Zhou, Z.C., Li, G., Chao, W., Xu, F., Sun, X., Chen, Z., 2019. Physiological responses and tolerance evaluation of five poplar varieties to waterlogging. Notulae Botanicae Hortic. Agrobotanici Cluj-Napoca 47(3), 658–667. https://doi.org/10.15835/nbha47311440.

Zoghi, Z., Hosseini, S.M., Kouchaksaraei, M.T., Kooch, Y., Guidi, L., 2019. The effect of biochar amendment on the growth, morphology and physiology of *Quercus castaneifolia* seedlings under water-deficit stress. European Journal of Forest Research 138, 967–979. https://link.springer.com/article/10.1007/s10342-019-01217-y.

Zonouri, M., Javadi, T., Ghaderi, N., 2014. Effect of foliar spraying of ascorbic acid on cell membrane stability, lipid peroxidation, total soluble protein, ascorbate peroxidase and leaf ascorbic acid under drought stress in grapes. International journal of Advanced Biological and Biomedical Research 4(2), 349–354. https://www.ijabbr.com/article_9042.html.

Zouari, M., Elloumi, N., Labrousse, P., Rouina, B.B., Abdallah, F.B., Ahmed, C.B., 2018. Olive trees response to lead stress: Exogenous proline provided better tolerance than glycine betaine. South African Journal of Botany 118, 158–165. http://dx.doi.org/10.1016/j.sajb.2018.07.008.

Zulfiqar, F., Ashraf, M., Siddique, K.H., 2022. Role of glycine betaine in the thermotolerance of plants. Agronomy 12(2), 276. https://doi.org/10.3390/agronomy1202027.