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Research Article

Germination and Adaptive Responses of Moringa oleifera to Drought Stress: Insights into Morphological and Biochemical Mechanisms Under PEG-6000-Induced Conditions

Nadia Khater[1]*, Yassine Noui[2], Kenza Garah[3], Hayem Zahaf[4], Loubna Khaoula Ouaglal[5], Safa Benkemchi[6], Khouloude Ghebache[7]

[1]Biodiversity, Biotechnology, and Sustainable Development Research Laboratory (BBDD), Department of Ecology and Environment, Faculty of Natural Life and Sciences, University of Batna 2, Algeria.
* **Corresponding Author Email:** n.khater@univ-batna2.dz - **ORCID:** 0000-0003-1223-8297

[2]Laboratory of Food Sciences (LFS), Department of Food Technology ISVSA, University of Batna1, Algeria.
Email: yassine.noui@univ-batna.dz - **ORCID:** 0000-0002-8085-1715

[3]Laboratory of Algerian Forests and Climate Change (LAFCC), Higher National School of Forests, Khenchela, Algeria.
Email: garah.kenza@ensf.dz - **ORCID:** 0000-0002-7397-7301

[4]Department of Ecology and Environment, Faculty of Natural Life and Sciences, University of Batna 2, Algeria.
Email: zahafhayem3@gmail.com - **ORCID:** 0009-0002-0272-999X

[5]Department of Ecology and Environment, Faculty of Natural Life and Sciences, University of Batna 2, Algeria.
Email: ouaglalloubnakhaoula@gmail.com - **ORCID:** 0009-0008-2561-5331

[6]Department of Ecology and Environment, Faculty of Natural Life and Sciences, University of Batna 2, Algeria.
Email: safaabenkemchi@gmail.com - **ORCID:** 0009-0001-3102-799X

[7]Department of Ecology and Environment, Faculty of Natural Life and Sciences, University of Batna 2, Algeria
Email: ghebachekhouloud28@gmail.com - **ORCID:** 0009-0007-4072-4563

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biochemical adaptations.

Abstract:

Moringa oleifera, a resilient species suited to arid and semi-tropical climates, was examined for its response to water stress induced by polyethylene glycol (PEG-6000) during germination and early growth. This study assessed the impact of different PEG-6000 concentrations (0, 4, 8, and 12 g/L) on germination rates, morphological traits, and biochemical parameters of the seedlings. Seeds showed remarkable germination capacity, reaching 100% at 12 g/L PEG-6000 concentration. However, water stress negatively affected plant development, reducing shoot length from 18 cm in the controls to 14 cm at the highest concentration, with similar declines in leaf area, leaf number, and collar diameter. Biochemical analyses indicated decreased levels of chlorophyll, soluble sugars, proline (down to 0.014 mg/mL at 12 g/L), and amino acids under stress conditions. These results suggest that while M. oleifera seeds are highly tolerant to water stress during germination, subsequent growth and biochemical functions are compromised, providing insights into their adaptability for cultivation in drought-prone areas.

1. Introduction

Environmental stress significantly constrains plant distribution and productivity, with drought being the primary factor limiting global agricultural output. This limitation arises from irregular rainfall and elevated temperatures, which hinder plant growth in Algeria's arid regions, resulting in diminished vegetation cover and exacerbating desertification (Toumi et al. 2022).

Water scarcity induces morphological, anatomical, physiological, biochemical, and molecular alterations that adversely affect crop yield and may culminate in plant mortality if the stress persists (Zafar et al. 2022). The effects of water stress are predominantly observed as reductions in growth, leaf area (Ödemiş et al., 2023), stomatal aperture, and photosynthetic activity (Zhang et al. 2024). Consequently, cultivating drought-resistant species presents a substantial advantage for reforesting these areas and mitigating soil erosion.

M. oleifera, the most prominent species of the Moringa genus, is renowned for its rapid growth and is increasingly recognized for its diverse nutritional, food, medicinal, and industrial applications. *M. oleifera*, often referred to as the "miracle tree," is a versatile species with considerable potential for adaptation to changing climates and drought resistance (Devkota et al., 2020; Trigo et al., 2021). This tropical tree, indigenous to India, has been naturalized in several African countries, including Algeria (Gupta et al., 2021).

This study explored the adaptation potential of *M. oleifera* by assessing its germination capacity under water stress conditions. To evaluate this potential adaptation and/or tolerance to water stress, an experiment was conducted under semi-controlled conditions in this study. Water stress was simulated by applying varying concentrations of polyethylene glycol (PEG-6000) to establish different levels of water stress potential.

2. Materials and Methods

This study was conducted at the Laboratory of Ecophysiology, Department of Ecology and Environment, Faculty of Natural and Life Sciences, University of Batna2, Algeria. Moringa seeds were collected from a forest conservatory nursery in the Wilaya of Oued Souf, southeast Algeria

2.1 Seed preparation and experimental approach

The studied seeds were circular, brown and–9-15 mm in length. These were collected in April 2023. Seeds were washed with tap water for 5 min, surface-sterilized with 10% sodium hypochlorite for 15 min, and rinsed thrice with distilled water to remove residual disinfectants. The disinfected seeds were placed in plastic boxes (19.5 cm × 13.5 cm) lined with three layers of filter paper saturated with distilled water at a rate of six seeds per box, with five repetitions per treatment (30 seeds per treatment). The absorbent paper was soaked in PEG-6000 solution from each treatment. After establishment, plants were subjected to water stress induced by polyethylene glycol (PEG-6000) at concentrations of 0 g L^{-1} (T0, control), 4 g L^{-1} (T1), 8 g L^{-1} (T2), and 12 g L^{-1} (T3). Stress solutions (10 mL per plant) were applied daily, alternating with tap water for 15–20 days.

The boxes were placed in the dark on a stove at 25 °C. After establishment, plants were subjected to water stress induced by polyethylene glycol (PEG-6000) at concentrations of 0 g L^{-1} (T0, control), 4 g L^{-1} (T1), 8 g L^{-1} (T2), and 12 g L^{-1} (T3). Stress solutions (10 mL per plant) were applied daily, alternating with tap water for 15–20 d.

The appearance of a visible 2 mm radicle was considered the germination point for the seeds. Regular daily observations were performed. Data were collected once every day for a maximum of one week. The germinated seeds were cultivated in pots containing a mixture of two-thirds commercial potting soil and one-third sand, with one seed per pot and ten repetitions in a controlled growth chamber at 25°C and a 16-hour photoperiod. Watering was done daily, with each plant receiving 5ml of water, once with the treatments and once with tap water

2.2 Parameters Measured

- **Germination Indices**

- **Germination Rate**

Seeds were considered germinated upon the emergence of the radicle (Saidi, 2020). The germination rate was calculated as follows:

$TG (\%) = Ni / Nt \times 100$

Where:

TG: Final germination rate

Ni: Number of germinated seeds

Nt: Total number of seeds tested

- **Germination Speed**

Germination speed reflects the energy responsible for depleting seed reserves. It is calculated as the variation in germination rates over time, from the appearance of the first radicle to stabilization and is expressed as the germination rate at a given time.

$$\text{Germination Speed} = (N1 + N2 + N3 + \ldots + N) / (N1T1 + N2T2 + N3T3 + \ldots + NnTn) \times 100$$

Where:

N1, N2, …, Nn: Number of seeds germinated at times T1, T2, …, Tn

- **Coefficient of velocity of germination (CVG)**

The coefficient of germination speed was calculated as described by Khulal et al. (2022).

$$CVG = (N1 + N2 + ... + Nx) / 100 \times (N1T1 + N2T2 + ... + NxTx)$$

Where:

CVG: Coefficient of germination speed

N: Number of seeds germinated each day

T: Number of days corresponding to N since germination

- **Germination Index (GI)**

The germination index was determined according to Anwar et al. (2021).

$GI = (7N1) + (6N2) + ... + (1 \times N7)$

Where:

GI: Germination index

N1, N2, ..., N7: Number of seeds germinated on days 1, 2, ..., 7

The multipliers (7, 6, ...) represent the weights assigned to the respective germination days.

- **Seed Vigor Index (SVI)**

The seedling vigor index was calculated according to Jain and Saha (1971).

$SVI = (a/1 + b/2 + c/3 ... + z/n) \times 100 / S$

Where:

a, b, c, ..., z: Number of seeds germinated each day

n: Number of days the experiment lasted (7 days in this case)

S: Number of seeds tested (20 seeds in this case)

- **Germination Kinetics**

Germination kinetics refer to the process by which a seed lot germinates under specified conditions, typically illustrated by the progression of cumulative germination percentage over time. This concept is based on cumulative germination rates, which denote the variation in germination rates over time, expressed in hours, across all tested treatment conditions (Hajlaoui et al., 2007).

Growth parameters

Growth parameters, such as shoot length, root length, number of leaves and branches per plant, and root and shoot fresh and dry weights, were recorded using standard procedures after harvesting the plants. Fresh root and shoot biomass were weighed immediately after harvesting, shade-dried, and then oven-dried at 70±2ºC till a constant weight was obtained to determine dry matter.

Biochemical Parameter Measurements

A. Chlorophyll content: Chlorophyll a and b contents were determined using the methodology developed by Nagata and Yamashta (1992). One gram of moringa leaf was crushed in 10 ml of 80% acetone and filtered through Whatman No.1 filter paper. The filtered extract was then transferred to a cuvette. The absorbance was measured at 663 nm. 645. 505 and 453 nm using a UV spectrophotometer (UV-4000, ORI, Germany). The following formulas were used to calculate the chlorophyll a and b concentrations:

Chlorophyll a = 0.999 A663 – 0.0989 A645

Chlorophyll b = -0.328 A663 + 1.77 A645

B. Determination of Proline and Sugar Contents: The free proline content was measured using the ninhydrin method (Bates et al., 1973). The soluble sugar content was determined colorimetrically using phenol sulfuric acid (Tissue & Wright 1995).

C. Determination of total free amino acids: One hundred milligrams of dry matter (DM) leaves and roots were ground separately in 1 ml of distilled water and then placed in a boiling water bath (100°C) for one hour. The mixture was centrifuged at 5000 rpm for 10 min. The pellet was then subjected to a second extraction with ethanol (1 ml of ethanol. The extract (200 µL) was mixed with 500 µL citrate buffer. A ninhydrin-ascorbic acid solution (1 mL) was then added to the ground material. A spectrophotometer was used to measure the total amino acid content expressed in mg/g -1 DM at a wavelength of 570 nm (Yemm et al., 1955; Friedman, 2004).

Statistical Analysis

Statistical analyses were conducted using SPSS software (version 22.30-bit). The results were evaluated using analysis of variance (ANOVA), and significantly different means were distinguished using Tukey's test at a 5% probability threshold

3. Results

3.1 Germination Indices

The results shown in Figure 1 highlight the effects of different PEG-6000 concentrations on the germination parameters of *M. oleifera* seeds. The seeds maintained their germination capacity even under high osmotic stress levels, with the highest germination rate (100%) observed at 8 g/L (T3), followed by 93% in both the control (T0) and T1 groups, and 83% at 4 g/L (T2). Analysis of variance revealed a highly significant difference ($p = 0.000$) between the treatments. Germination speed also varied significantly across PEG-6000 concentrations ($p = 0.000$), with respective values of 1.66, 1.66, 7.7, and 1.2 for T0, T1, T2, and T3, respectively. The coefficient of velocity of germination (CVG) showed a progressive increase with increasing PEG-6000 concentration, ranging from 12.96 in the control to 43.75 in T3, with intermediate values of 15.12 and 33.88 for T1 and T2, respectively. A similar pattern was observed for the germination index (GI), which peaked at 247 under 4 g/L before declining to 165 and 168 at 8 g/L and 12 g/L, respectively, confirming a highly significant difference among treatments. Conversely, the seed vigor index decreased progressively with increasing PEG-6000 concentration, from 1844.004 in the control to 1058.805, 1193.780, and 1328.1 for T1, T2, and T3, respectively. Overall, these findings indicate

that PEG-6000–induced water stress significantly affects the germination dynamics and seedling vigor of *M. oleifera*, reflecting a partial adaptive response to osmotic constraints.

3. 2. Germination Kinetics

Figure 2 illustrates the germination kinetics, including the germination rate of *M. oleifera* under water stress conditions. The analysis revealed that the treatments significantly influenced the germination rate. For the germinated seeds, the germination kinetics curve exhibited two distinct phases: an initial phase of exponential acceleration followed by a plateau phase corresponding to the cessation of germination, with a slight increase indicating the presence of newly germinated seeds. The control group (T0) demonstrated moderately rapid germination compared to the other treatments, with high germination rates observed from the third day (13%), reaching 60% on the fourth day and stabilizing at 80% by the seventh day. Treatment T1 exhibited higher germination rates from the third day (26%), which increased to 86% by the seventh day. Treatment T2 showed lower initial rates (6% on the third day), reaching 43% on the fourth day and 73% on the seventh day. Treatment T3, characterized by the highest PEG-6000 concentration, displayed low germination rates on the third day (10%), which increased to 33% on the fourth day and stabilized at 83% by the seventh day.

3.3 Growth Characteristics Analysis

This study assessed the effects of PEG-induced water stress on several growth parameters of *M. oleifera* seedlings, including root length (RL), shoot length (SL), number of leaves (LN), collar diameter (CD), and biomass components. As shown in Figure 3, root length increased under all PEG treatments, with values ranging from 8.998 cm in the control (T0) to 9.934 cm, 11.108 cm, and 11.689 cm in T2, T1, and T3, respectively, indicating a stimulatory effect on root elongation. Conversely, shoot growth was markedly inhibited by PEG-6000, with the control exhibiting the greatest shoot length (18 cm) compared to 8.5, 15, and 14 cm in T1, T2, and T3, respectively. The shoot-to-root ratio declined significantly ($P = 0.004$) from T0 to T3 (5.275, 0.335, 0.252, and 0.128 cm), and analysis of variance confirmed a highly significant reduction in shoot length under water stress ($P = 0.000$).Biomass production also followed a declining trend with increasing PEG concentration (Figure4). Shoot fresh weight decreased from 0.740 g in the control to 0.622, 0.595, and 0.441 g in T1, T2, and T3, respectively ($P = 0.000$), whereas root fresh weight decreased from 0.971 g (control) to 0.762, 0.537, and 0.356 g ($P = 0.000$). Although the shoot dry weight (0.200 g in control) was consistently higher than the root dry weight (0.223 g in control), both parameters exhibited progressive but statistically non significant reductions under PEG stress, with shoot dry weight declining to 0.052, 0.048, and 0.042 g, and root dry weight to 0.209, 0.200, and 0.189 g for T1, T2, and T3, respectively. Overall, PEG-induced water stress significantly reduced aboveground growth and biomass accumulation while promoting moderate root elongation, reflecting an adaptive shift toward enhanced root development under osmotic stress conditions.

3.4 Biochemical Characteristics Analysis

Biochemical analysis revealed pronounced alterations in the pigment and osmolyte contents of *M. oleifera* leaves under PEG-induced water stress. The chlorophyll a, b, and total chlorophyll contents decreased significantly compared to the control, reflecting stress-induced degradation of photosynthetic pigments. Specifically, chlorophyll a declined from 9.632 mg/g FM in the control to 9.077, 7.459, and 4.931 mg/g FM in T1, T2, and T3, respectively, whereas chlorophyll b decreased from 5.149 mg/g FM in the control to 3.678, 3.079, and 1.879 mg/g in, same treatments (Figure5). Consequently, total chlorophyll content dropped from 14.78 mg/g in the control to 12.75, 10.53, and 6.811 mg/g in T1, T2, and T3, respectively, with analysis of variance indicating a highly significant effect of PEG-6000 on the pigment levels. Soluble sugar concentration was overall elevated under PEG stress but declined progressively with increasing PEG concentrations, reaching 0.01, 0.007, 0.006, and 0.005 mg/mL in T0, T1, T2, and T3, respectively ($P = 0.001$). Similarly, proline content, typically a key osmoprotectant, showed a significant reduction under water stress, decreasing from 0.033 mg/mL in the control to 0.029, 0.020, and 0.014 mg/mL in T1, T2, and T3, respectively ($P = 0.006$). The amino acid content followed the same trend, with leaf concentrations declining from 0.169 mg/mL in the control to 0.152, 0.112, and 0.093 mg/mL in T1–T3, and root concentrations dropping more sharply from 0.482 mg/mL to 0.186, 0.119, and 0.056 mg/mL, respectively. Overall, PEG-induced osmotic stress markedly disrupted the biochemical balance of *M. oleifera*, leading to the degradation of chlorophyll pigments and a decrease in key osmolytes, such as sugars, proline, and amino acids, indicative of impaired metabolic adjustment under drought-like conditions.

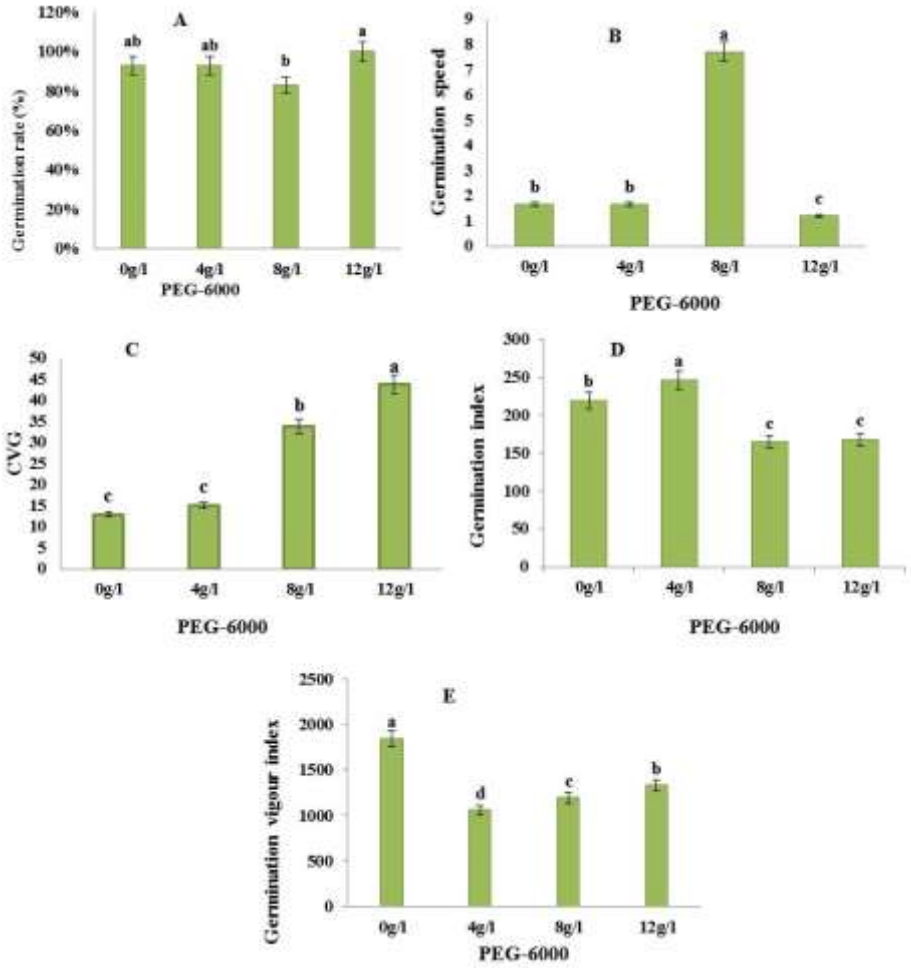

Figure 1. *Germination rate (A), germination speed (B), coefficient of velocity of germination (C), Germination Index (D), and germination vigor index (E) of M. oleifera seeds under the effect of different PEG concentrations. Means showing different letters are statistically different ($p<0.05$)*

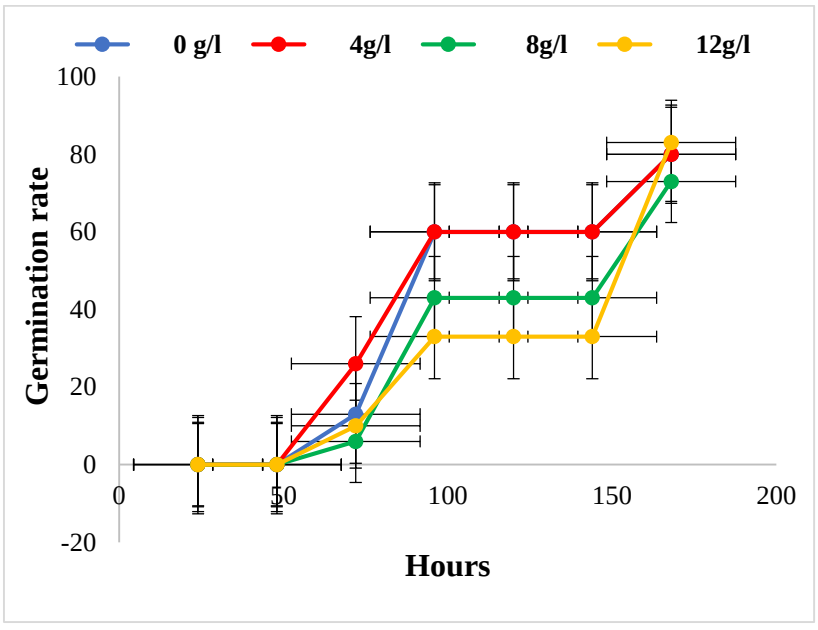

Figure 2. *Germination kinetics of M. oleifera seeds under water-stress conditions.*

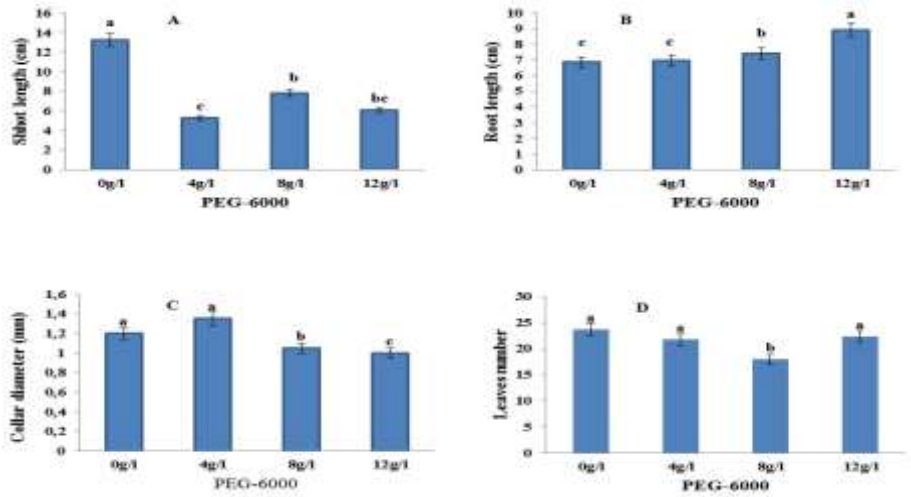

Figure 3. *Changes in the growth characteristics (A=shoot length; B=root length; C=collar diameter; D=number of leaves) of M. oleifera under drought conditions. Means showing different letters are statistically different (p<0.05)*

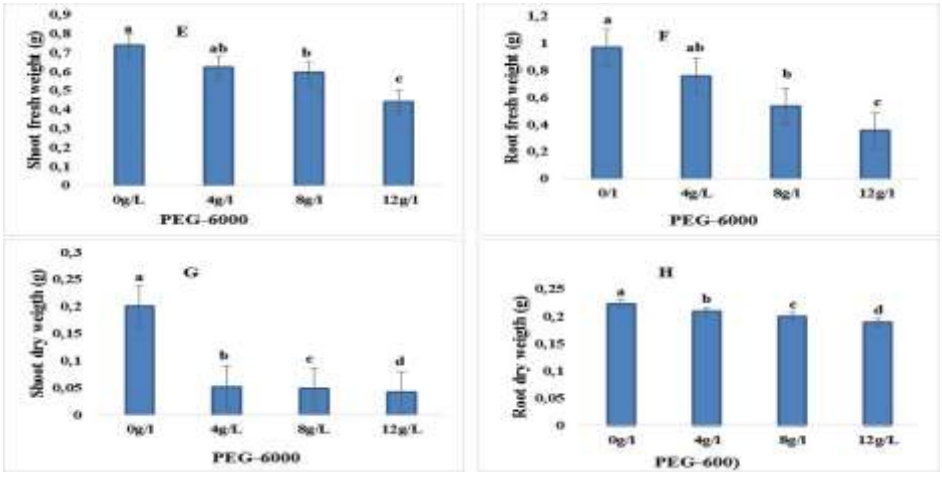

Figure 4 : *Changes in growth characteristics (A=shoot fresh weight; B=shoot dry weight; C=root fresh weight; D=root dry weight) of M. oleifera under drought conditions. Means with different letters are statistically different (p<0.05).*

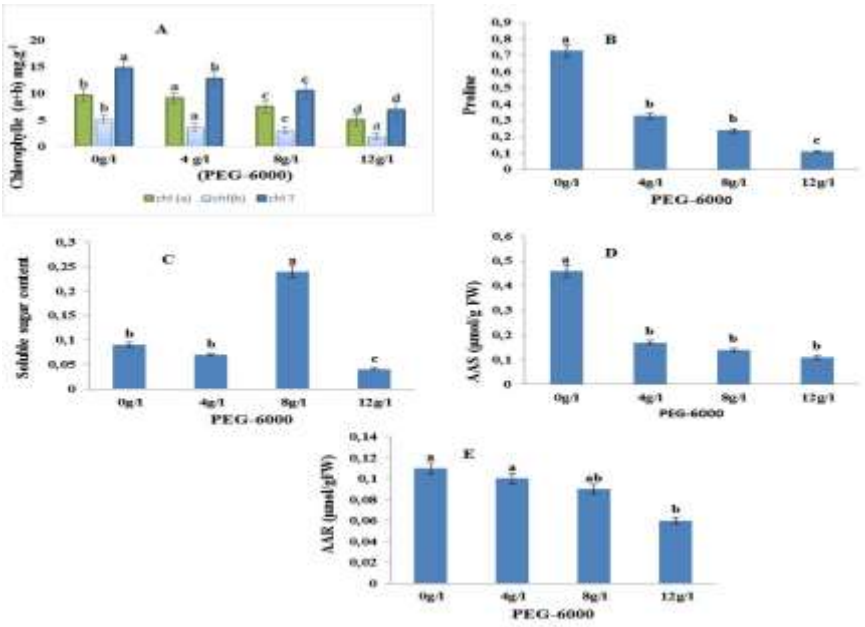

Figure 5: *Biochemical characteristics of M. oleifera seeds under the effect of different PEG concentrations: Chlorophylle a+b (A), proline (B), soluble sugar content (C), amino acid content in the stem (D), and amino acid content in the root (E). Means showing different letters are statistically different (p<0.05).*

4. Discussion

M. oleifera is a significant species cultivated and consumed across numerous African nations, primarily due to its physiological and antioxidant properties, as well as its high nutritional content. Despite its importance, production levels remain insufficient to meet the increasing demand. While extensive research has been conducted on most parts of the tree, the seeds have not been thoroughly investigated (Ibrahim et al. 2021). Plants generally respond to abiotic stress through a series of morphological, physiological, and biochemical adaptations that support their growth and development. The results of this study revealed that the germination performance of *M. oleifera* is highly dependent on both the duration of the experiment and the applied treatments. Seed coat removal markedly improved germination, likely by reducing mechanical barriers and facilitating water uptake by the embryos. Similar observations were reported by Reza Yousefi et al. (2020), who emphasized the importance of seed coat permeability in optimizing germination efficiency.

Under PEG-induced drought stress, the germination kinetics was significantly altered. Water stress affected both the germination rate and speed, suggesting that osmotic stress influences early metabolic activation and radicle emergence. These results align with those of Upretee et al. (2024), who observed comparable effects under water-limited conditions. Interestingly, water stress also enhanced the coefficient of germination speed and seed vigor index, indicating a selective activation of more resilient seeds, a trend previously reported by Belaidi and Tamerdjent (2019).Morphological responses to increasing PEG-6000 concentrations demonstrated a clear reduction in the plant height. Such growth inhibition may result from a decline in cell division and elongation due to reduced water availability and turgor pressure (Oukara et al. 2017). Alternatively, this reduction could represent an adaptive strategy aimed at minimizing transpiration and maintaining plant survival under drought stress (Ilyas et al. 2020). Fresh biomass exhibited significant variation across treatments, whereas dry biomass remained statistically unchanged. This pattern suggests that water stress primarily influences the short-term hydration status rather than the long-term biomass accumulation *in M. oleifera* seedlings.Chlorophyll analysis showed a progressive decline in chlorophyll a, b, and total chlorophyll content with increasing PEG-6000 concentrations, with chlorophyll b consistently representing approximately half the amount of chlorophyll a. Similar reductions have been documented by Sadak et al. (2020) and Boumenjel et al. (2020), likely due to partial stomatal closure, decreased substrate availability for chlorophyll synthesis, and accelerated chlorophyll degradation by chlorophyllase under stress conditions (Kamari et al., 2025).Biochemical responses revealed that soluble sugar and proline contents decreased with increasing PEG concentrations, which is in contrast to previous studies that reported the accumulation of these osmolytes as a common drought tolerance mechanism (Boughdiri et al., 2020; Batoolet al., 2022). The decline in amino acid content under stress further supports the hypothesis that *M. oleifera* exhibits a limited osmotic adjustment capacity at the seedling stage, possibly reflecting its sensitivity to severe osmotic stress.Overall, these findings suggest that *M. oleifera* displays moderate tolerance to PEG-induced drought stress, characterized by restricted growth and pigment content and a limited biochemical response. This highlights the importance of further investigating the physiological plasticity of *M. oleifera* and related species to identify genotypes that are better adapted to arid and semi-arid environments.

5. Conclusion

This study revealed that *M. oleifera* displays a strong adaptive capacity under PEG-induced drought stress through coordinated physiological, biochemical, and morphological adjustments. Moderate stress levels enhanced germination and antioxidant regulation, whereas severe stress impaired growth and disrupted the cellular homeostasis. The observed modulation of osmolytes and antioxidant enzymes highlights the efficient stress acclimation mechanisms. These findings advance our understanding of drought tolerance in *M. oleifera* and support its potential for sustainable cultivation in arid regions.

Author Statements:

- **Ethical approval:** The conducted research is not related to either human or animal use.
- **Conflict of interest:** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper
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- **Data availability statement:** The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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