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Decipher the Role of Phytohormones and Polyamines in Modulating Root Architectural Dynamics and Root Biochemical Adaptations of Maize Seedlings under PEG-induced Water Deficit Stress

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ABSTRACT

Background: The study aimed to characterize the effects of seed priming with phytohormones and polyamines on root morphological architecture and root biochemical activities in maize seedlings under water deficit stress during early growth stages. Drought stress is one of the most critical abiotic constraints affecting maize productivity. Particularly during the seedling stage, root establishment is vital for later growth and yield. Root morphological architecture and root biochemical efficiency serve as a key regulator in determining the plant's capacity to access water and nutrients under stress conditions. Among various strategies to improve drought resilience, phytohormone and polyamine seed priming has become a viable and sustainable and cost-effective method and ecofriendly approach to enhance early seedling vigor.

Methods: Maize hybrid COH(M) 8 seeds were primed using optimal concentrations of various phytohormones and polyamines and are compared with control (non-primed) and hydroprimed and control seeds. The primed and uniformly germinated seedlings, along with the control, were grown in test tubes containing Hoagland nutrient solution under a -0.4 MPa PEG induced water deficit stress. An evaluation of root morphological architecture and root biochemical parameters was subsequently carried out to assess the influence of optimized seed priming treatments under water deficit stress. The morphological architecture traits recorded included root length, fresh and dry root weight, root depth, root width, maximum number of roots, root bushiness, root area and root volume which provided insights into growth responses. In addition, a comprehensive set of root biochemical parameters was quantified to elucidate the functional mechanisms underlying stress tolerance. These comprised invertase activity, sucrose synthase activity, ATPase activity, membrane leakage, root activity and root carbohydrate content. When taken as a whole, these measures offered a comprehensive understanding of the connection between metabolic efficiency and root structural characteristics during drought.

Result: Significant decreases in root morphological architecture and root biochemical characteristics were brought about by PEG-induced water deficit stress; the decrease was more noticeable in non-primed seeds. These effects were lessened by seed priming with phytohormones and polyamines, which increased root development and metabolic activity. Superior root characteristics and root biochemical efficiency demonstrated that melatonin @ (150 µM) and serotonin @ (100 µM) provided the maximum tolerance across treatments. Their strong correlation suggests that root development and root biochemical activity could be used as selection criteria for drought resistance in maize seedlings.

Key words: Drought, Maize, Phytohormones and polyamines, Root architecture, Root biochemical activity.

INTRODUCTION

Maize (*Zea mays* L.) is the world's third most significant cereal crop, after wheat and rice. It can be grown in a wide range of soil types and climates. Maize is extremely susceptible to drought, especially in the early stages of development, even though it has a C4 photosynthetic pathway that allows for excellent water usage efficiency. The uptake of water and nutrients is significantly influenced by the morphological and biochemical properties of roots. However, in drought conditions, root growth is frequently severely hindered, which limits cell division, elongation and nutrient uptake, thereby decreasing overall plant vigor and resilience (Chassot and Richner, 2002).

Seed priming with phytohormones and polyamines has aroused as a promising and cost-effective approach for improving seedling establishment and enhancing root development under drought stress conditions. Various phytohormones, including melatonin, serotonin, salicylic acid and brassinolides, play important roles in stimulating cell expansion, promoting lateral root formation and increasing water absorption through mechanisms similar to auxin signaling. In addition, polyamines such as spermine

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and spermidine contribute to stress tolerance by maintaining cellular homeostasis, strengthening antioxidant defense systems and regulating osmotic balance (Sarropoulou *et al.,* 2012). Several current studies have demonstrated the effectiveness of these compounds in improving drought tolerance in maize. For instance, melatonin-based seed priming has been shown to alleviate oxidative damage, increase the activity of antioxidant enzymes and improve seedling biomass under polyethylene glycol (PEG)-induced water stress conditions (Cao *et al.,* 2021). Likewise, spermidine treatment has been reported to enhance root growth characteristics, including root length, surface area and overall root vigor, thereby improving maize seedling performance under both controlled and field drought environments (Dong *et al.,* 2022).

Recent evidence provided by Manavalagan *et al.* (2023) further supports the beneficial role of seed priming in drought stress management. The study showed that priming treatments alleviated the inhibitory effects of polyethylene glycol (PEG)-induced water deficit on maize germination and seedling vigor, emphasizing the value of priming techniques for promoting robust early growth and improving drought resilience in maize.

Despite these promising results, studies associated to compare the relative efficacy of phytohormones and polyamines in improving root morphology and root biochemical traits under PEG-induced drought stress remains limited. Addressing this knowledge gap, the present research was undertaken to assess and compare the impact of phytohormones (Melatonin, serotonin, salicylic acid, brassinolides) and polyamines (Spermidine, spermine) on root morphological and root biochemical responses of maize seedlings exposed to PEG-induced water deficit stress (Fig 1).

MATERIALS AND METHODS

The current study used genetically pure COH(M) 8 hybrid maize seeds as its experimental material and was carried out at Tamil Nadu Agricultural University, Coimbatore during 2023-2024. *In vitro* testing was used to assess how seed priming affected the root morpho-architectural characteristics and root biochemical activities of COH(M)8 during drought stress under temperature 25±2°C with photoperiod 16 h light and 8 h darkness. The light intensity used was 1200 lux with RH OF 60-70 %. Drought stress was simulated in the laboratory using PEG 6000 (polyethylene glycol). To standardize the stress level, different osmotic potentials *viz.,* -0.2 MPa, -0.4 MPa, -0.6 MPa, -0.8 MPa, -1.0 MPa were tested. The ideal osmotic potential for causing drought stress was determined to be -0.4 MPa based on 50% seedling mortality seen on seventh day (Manavalagan *et al.,* 2023).

The optimum concentrations of 6 seed priming compounds were standardized by testing different levels of each compound melatonin (50 µM, 100 µM, 150 µM, 200 µM), serotonin (50 µM, 100 µM, 150 µM, 200 µM), spermine (50 µM, 100 µM, 150 µM, 200 µM), spermidine (50 µM, 100 µM, 150 µM, 200 µM), salicylic acid (50 ppm, 75 ppm, 100 ppm, 150 ppm) and brassinolides (0.1, 0.2, 0.5, 1.0 ppm). The optimized concentrations were melatonin (150 µM), serotonin (100 µM), spermine (50 µM), spermidine (50 µM), salicylic acid (100 ppm) and brassinolides (0.5 ppm), which is selected based on highest germination percentage and seedling vigour in comparison with hydropriming and non-primed control. To evaluate the influence of seed priming on root morpho-architecture and root biochemical responses under drought stress, seeds primed with the optimized concentrations of phytohormones and polyamines were subjected to simulated drought conditions (-0.4 MPa PEG 6000).

A factorial completely randomized design (FCRD) with four replications was used for the experiment. Melatonin (150 µM), serotonin (100 µM), spermine (50 µM), spermidine (50 µM), salicylic acid (100 ppm) and brassinolides (0.5 ppm) and distilled water (hydropriming) were used to prime 100 surface sterilized seeds for 12 hours using a 1:1 weight by volume seed to solution ratio. After priming, the seeds were cleaned with distilled water and allowed to dry in the shade at room temperature in order to restore their initial moisture content (Manavalagan *et al.,* 2025).

Primed seeds with optimal concentrations employing phytohormones and polyamines were subjected to drought stress conditions in order to investigate the impact of seed priming on root morphological architecture and root biochemical activity under drought stress.

The primed and control (non-primed) seeds were placed on germination paper to allow for radicle emergence. Once radicle emergence occurred, uniformly germinated seedlings were carefully transferred on a sponge inside a 180 ml test tube, which contained the Hoagland nutrient solution with simulated drought stress by adding PEG 6000 of -0.4 MPa. The seedlings were allowed to grow for 15 days in the nutrient medium and each treatment was replicated for five times.

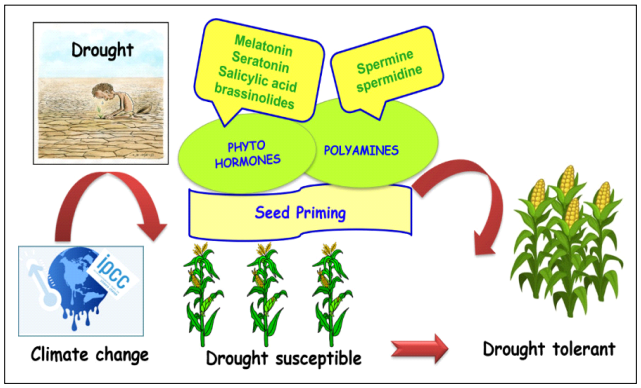


Fig 1: Schematic diagram summarizing the proposed mechanism by which melatonin and serotonin improve drought tolerance.

15 days after sowing, observations on root morphological architecture parameters *viz*., length, fresh and dry biomass, depth, width, maximum number of roots, root bushiness, root area, root volume was observed using GiA roots software (Fig 2), which is an acronym for general image analysis of roots, which was used to automate and simplify the thorough examination of root networks (Galkovskyi *et al.,* 2012). Also the root biochemical assays included root activity (mg g^{-1} h^{-1} FW) (Comas *et al.,* 2000), root carbohydrate content (g glucose equiv. g^{-1} DW) (Nelson, 1944; Somogyi, 1926), root membrane leakage (%) (Huang *et al.,* 2005), root invertase (nmol g^{-1} FW), root sucrose synthase (µmol g^{-1} FW) (Appeldoorn *et al.,* 1997) and root ATPase activity (mg g^{-1}) (Forbush, 1983) were experimented.

Statistical analysis

The R-based program GRAPES (v1.0.0) was used to statistically analyze root morpho architectural and root biochemical characteristics. Analysis of variance (ANOVA) and Pearson's correlation coefficients between the attributes were evaluated. ANOVA was led to assess treatment effects. Mean comparisons under drought stress conditions were carried out using post-hoc tests-duncan's multiple range test (DMRT) to find significant variances between treatments.

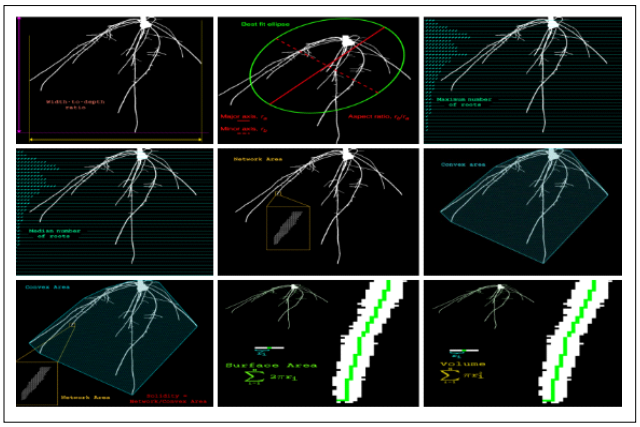


Fig 2: Root system architecture traits image in GiA roots.

RESULTS AND DISCUSSION

The outcomes of the present investigation revealed that, the root morphological architecture and root biochemical activity of maize hybrid COH(M) 8 under simulated drought stress conditions were considerably impacted by seed priming with various phytohormones and polyamines. Drought stress adversely affected root growth and metabolic activities of maize seedling. However, considerable variation was observed among the treatments in their ability to mitigate stress effects. For every root growth and root biochemical parameter, our analysis of variance and mean comparison data amply demonstrated the variations between the priming treatments (Fig 3).

Using specific phytohormones and polyamines to prime seeds, markedly alleviated osmolyte [PEG] simulated drought stress inhibition of maize root growth, with melatonin (150 µM) which preserved the root morphological and root biochemical attributes even when there is water deficit stress condition (Singh *et al*., 2020). Among the various treatments, melatonin primed seeds recorded the highest root length (28.9 cm), fresh root weight (0.845 g) and dry root weight (0.121 g), followed closely by serotonin (100 µM) (27.6 cm, 0.811 g and 0.093 g, respectively), whereas control recorded comparatively lower values of (18.5 cm, 0.324 g and 0.021 g) (Fig 4 and 5), indicating that melatonin enhanced both elongation and biomass accumulation; this likely reflects melatonin's auxin-like activity that promotes cell elongation and cell wall loosening, thereby facilitating root extension and mass gain

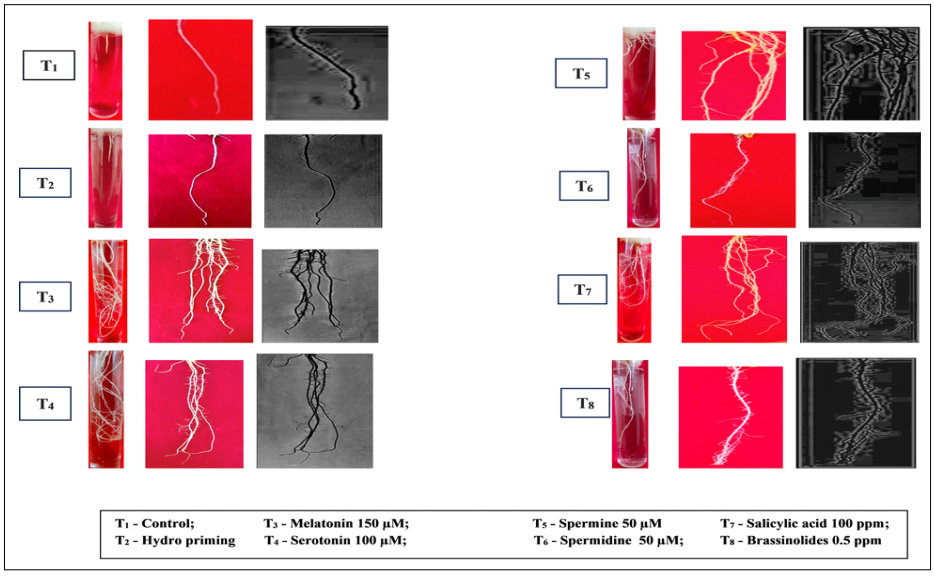


Fig 3: Root system architecture of maize seedlings primed with phytohormones and polyamines.

(Bleiss and Ehwald, 1993; Mukherjee *et al.,* 2014). Serotonin also played a crucial role in promoting root elongation and lateral branching (Pelagio-Flores *et al.,* 2011). Correspondingly, melatonin primed seeds also developed greater root depth (3452 cm) and width (3.51 cm) followed by serotonin treated seeds (3316 cm, 3.23 cm), while the control exhibited the lowest values (2291 cm, 1.98 cm) (Fig 6 and 7), which is consistent with melatonin enhancing root penetration and lateral expansion through modulation of auxin transport and root meristem activity (Hernández-Ruiz and Arnao, 2008). Root branching traits were similarly enhanced with melatonin which is observed with maximum root number (753) and root bushiness index of (1.52), followed by serotonin (745, 1.48 respectively). In contrast, the control seedlings had the lowest root number (532) and bushiness (1.37) (Fig 6 and 7). This is also again, a pattern that supports the hypothesis that both melatonin and serotonin influence auxin-mediated lateral root initiation and subsequent branching patterns (Hernández-Ruiz and Arnao, 2008; Pelagio-Flores *et al.,* 2011).

In addition, enhanced overall root architecture in melatonin primed seedlings exhibited maximum root area (132.5 cm^2) and root volume (1.35 cm^3), followed by serotonin. These improvements suggest a robust root system with enhanced water and nutrient acquisition capacity (Manonmani *et al*., 2025) (Table 1) (Fig 7), which implies improved soil exploration capacity and potential water and nutrient uptake, mirroring stimulatory effects reported for melatonin in other species such as cucumber, cherry and sunflower (Mukherjee *et al.,* 2014; Sarropoulou *et al.,* 2012). Seed priming treatments showed significant influence on root biochemical parameters under drought stress (Fig 4-7).

Melatonin and serotonin priming maintained higher metabolic and stress buffering activity of roots under drought. Thus, melatonin (45.5 mg g^{-1} h^{-1} FW) and serotonin (43.2) recorded the highest root activity, compared to control (25.1) which indicated better metabolic activity and nutrient uptake efficiency and also indicating greater respiratory and nutrient-uptake capacity likely driven by preserved mitochondrial function and enhanced energy metabolism

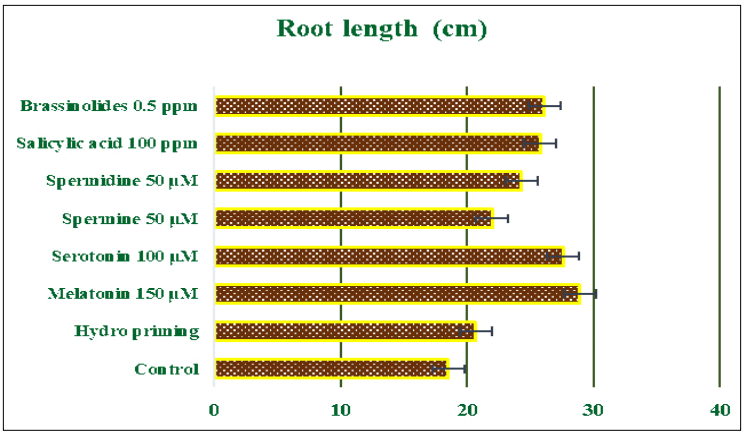


Fig 4: Effect of seed priming with phytohormones and polyamines on root length (cm) of maize COH (M) 8 under simulated drought stress condition.

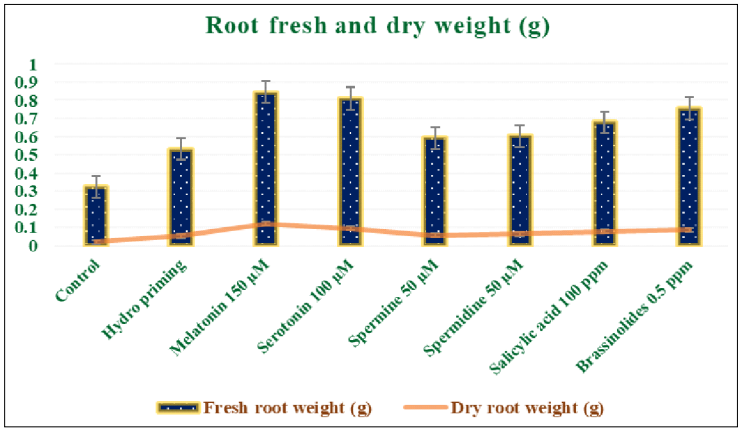


Fig 5: Effect of seed priming with phytohormones and polyamines on root fresh and dry weight (g) of maize COH (M) 8 under simulated drought stress condition.

in primed roots (Altaf *et al.,* 2022) (Fig 8). Melatonin primed roots accumulated more carbohydrate content (0.088 g glucose equiv. g^{-1} DW), followed by serotonin (0.085), suggesting that priming improved osmotic adjustment and carbon reserve availability under water deficit, which supports continued growth and osmoprotection (Fig 9) (Zahedi *et al*., 2024).

Table 1: Effect of seed priming with phytohormones and polyamines on root area of maize COH(M) 8 under simulated drought stress condition.

Treatments (T)	Root area (cm^2)
T1- Control	105.3±0.12^{f}
T2 - Hydro priming	119.1±0.34^{f}
T3- Melatonin 150 µM	132.5±0.22^{a}
T4- Serotonin 100 µM	130.3±0.07^{b}
T5- Spermine 50 µM	126.7±0.44^{c}
T6- Spermidine 50 µM	120.2±0.54^{d}
T7- Salicylic acid 100 ppm	125.8±0.38^{c}
T8- Brassinolides 0.5 ppm	130.7±0.94^{b}

Membrane integrity was improved evidence by lower electrolyte leakage in melatonin (1.15%) and serotonin (1.18%) compared to control (2.11%) which points to better preservation of cellular membranes, likely *via* enhanced antioxidant defenses and stabilization of membrane lipids, a mechanism frequently proposed for both melatonin and polyamines (Altaf *et al.,* 2022) (Fig 9). Enzyme activities associated with carbohydrate metabolism and ion transport were also elevated in melatonin treatments (root invertase, root sucrose synthase and root ATPase activity of about 5.32 nmol g^{-1} FW, 5.14 µmol g^{-1} FW and 0.89 mg g^{-1}, respectively) with lower activities in control, indicating the priming sustained enzymatic systems that mobilize sugars and maintain ionic gradients required for growth under stress. Such upregulation in root enzymatic activity enhances sink strength of roots and supports osmotic and energetic demands during drought (Fig 10).

Correlation analysis of root morpho architectural and root biochemical traits

Correlation analysis showed that root architectural and biochemical characteristics work together to control drought

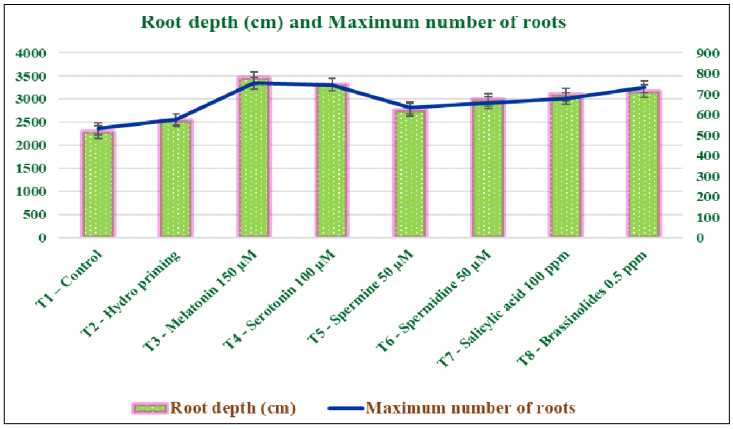


Fig 6: Effect of seed priming with phytohormones and polyamines on root depth and maximum number of roots of maize COH(M) 8 under simulated drought stress condition.

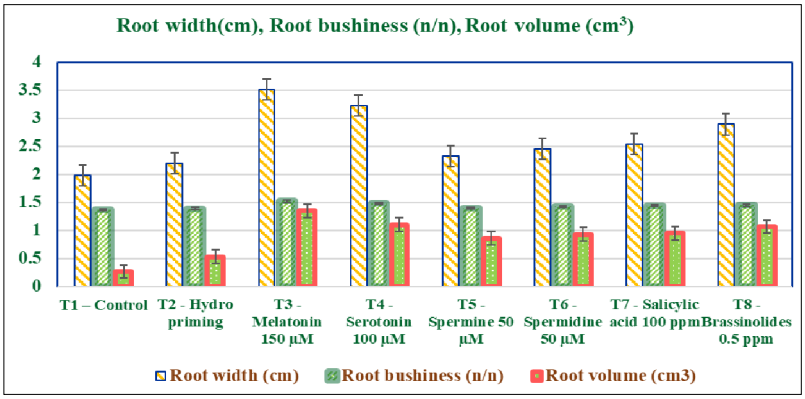


Fig 7: Effect of seed priming with phytohormones and polyamines on root width, root bushiness and root volume of maize COH(M) 8 under simulated drought stress condition.

tolerance in maize (Fig 11). A broad root system enhances soil exploration, water extraction and nutrient acquisition during moisture shortage, as evidenced by the substantial positive connections found between root length and root biomass, depth, width, bushiness, root number, volume, ATPase activity and carbohydrate content. Plant water status

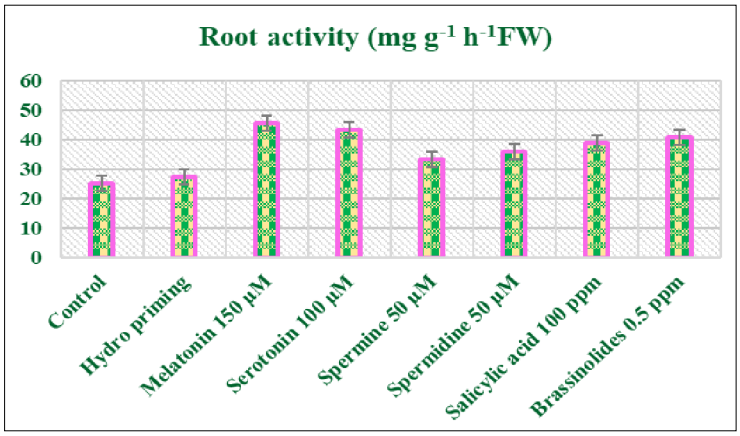


Fig 8: Effect of seed priming with phytohormones and polyamines on root activity (mg g^{-1} h^{-1} FW) of maize COH(M) 8 under simulated drought stress condition.

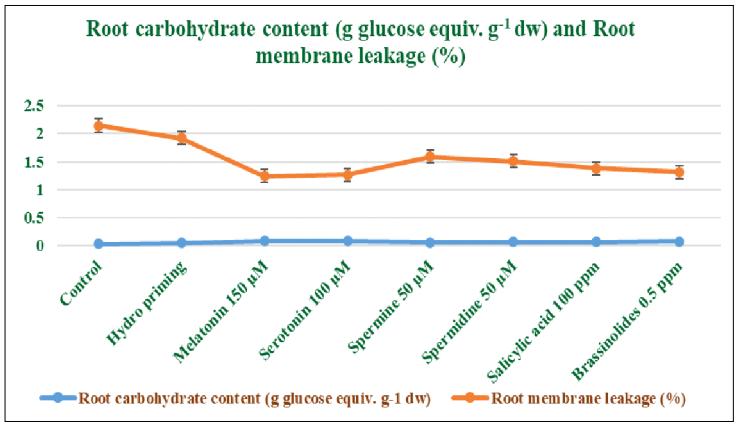


Fig 9: Effect of seed priming with phytohormones and polyamines on root carbohydrate content (g glucose equiv. g^{-1} dw) and root membrane leakage (%) of maize COH(M) 8 under simulated drought stress condition.

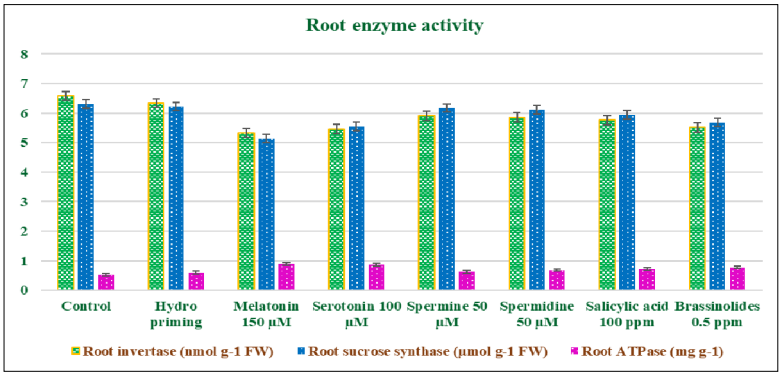


Fig 10: Effect of seed priming with phytohormones and polyamines on root invertase (nmol g^{-1} FW), root sucrose synthase (µmol g^{-1} FW), root ATPase (mg g^{-1}) of maize COH(M) 8 under simulated drought stress condition.

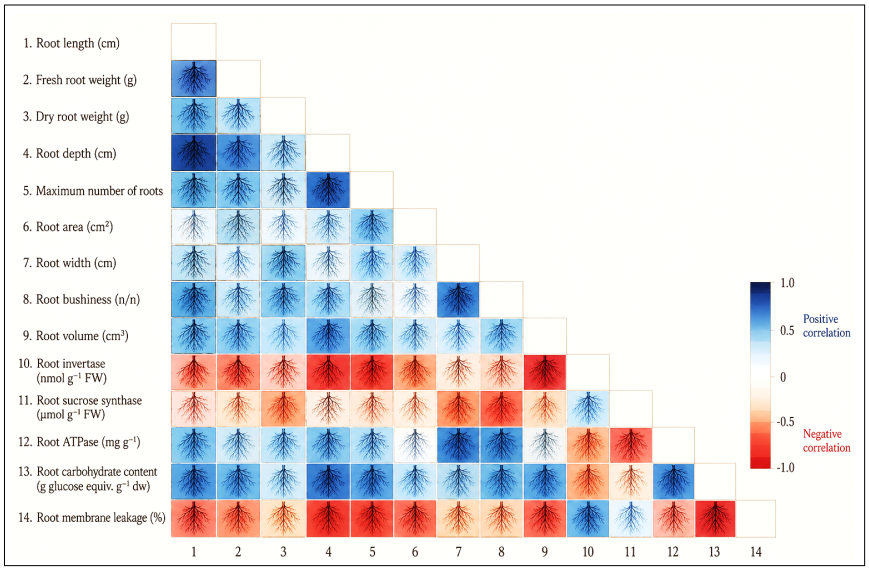


Fig 11: Correlation analysis of root morpho architectural and root biochemical traits of COH(M) 8 seeds under simulated drought stress condition.

in maintained and increased biomass accumulation is supported by this coordinated root development (Lynch, 2018; Uga *et al.,* 2013).

By promoting ion transport, nutrient uptake and osmotic adjustment, ATPase activity positively linked with root growth and preserved cellular metabolism during drought. A higher carbohydrate content supported root growth by providing energy and osmoprotection (Ruan, 2014). On the other hand, elevated invertase activity, sucrose synthase activity and membrane leakage hindered root growth by compromising carbon use, membrane stability and metabolic efficiency. In general, after melatonin and serotonin seed priming, increased ATPase activity and carbohydrate buildup improved root functioning and drought resistance in maize.

Although PEG-induced osmotic stress is a reliable and reproducible approach for simulating drought under controlled conditions, it does not fully represent the complexity of natural field drought. Therefore, the beneficial effects of phytohormone and polyamine seed priming observed in this study should be validated under greenhouse and field conditions. Nevertheless, the improved root architecture, carbohydrate metabolism, membrane stability and antioxidant defense indicate the potential of these priming agents as cost-effective seed enhancement technologies and provide useful physiological traits for breeding drought-resilient maize cultivars.

CONCLUSION

The current study concludes that seed priming with phytohormone and polyamines particularly melatonin and serotonin effectively improve the root morphological architecture and root biochemical activities of maize seeds even under drought stress. Therefore, future research should concentrate on clarifying the molecular mechanisms such as the signaling pathways and gene regulatory networks involved in drought stress responses that underlie the advantageous effects of these priming agents. Validation of these findings under different soil types, climatic conditions and field environments will also be essential to assess their practical applicability in agricultural production systems. Furthermore, investigating the combined effects of different phytohormones and polyamines, together with the use of advanced root phenotyping and imaging technologies, may provide deeper insights into the mechanisms of drought adaptation and facilitate the development of maize cultivars with enhanced drought resilience.

Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article. No funding or sponsorship influenced the design of the study, data collection, analysis, decision to publish, or preparation of the manuscript.

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