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Correlation of Proline Accumulation With Increased Efficiency Water Use (WUE) in Plants in Drought Stress

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ABSTRACT

Drought stress is an abiotic stress that threatens global agricultural productivity by triggering complex adaptive responses in crops, including the accumulation of proline as a compatible osmolyte. This article analyzes the correlation between proline accumulation and increased water use efficiency (WUE) in drought-stressed plants through a comprehensive literature review of publications in 2019-2025. The results of the analysis revealed a consistent positive correlation where the increase in proline concentration correlated with the optimization of WUE through osmotic adjustment mechanisms and stomata regulation. Temporal dynamics show a critical phase of correlation occurs when the moisture content of the media decreases substantially, triggering progressive proline accumulation. The molecular mechanism involves the integration of proline biosynthesis with photosynthesis modulation and stomata regulation that maintains the rate of carbon dioxide assimilation with minimization of water loss. Genotypic variability in proline accumulation implies the potential for plant breeding to develop drought-tolerant varieties with superior WUE. This paper contributes to the development of drought stress mitigation strategies based on an understanding of physiological and biochemical mechanisms for global food security in the era of climate change.

Keywords: Drought stress; Proline accumulation; Water Use Efficiency (WUE)

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INTRODUCTION

Global climate change has increased the frequency and intensity of drought events that are seriously threatening agricultural productivity around the world. Drought is widely recognized as one of the most critical abiotic stressors because it inhibits plant growth, disrupts key physiological processes, and causes significant yield loss in various agricultural systems. In addition to limiting water availability, water deficits also trigger a complex set of plant responses at the morphological, physiological, biochemical, and molecular levels. In the context of global food security, a deep understanding of the mechanisms of plant adaptation to drought is critical to designing effective mitigation and breeding strategies (Sitaresmi et al., 2023).

To overcome the water deficit, plants have developed a variety of adaptive mechanisms that improve their ability to survive under drought conditions. One of the most common biochemical responses is the accumulation of proline, which is an amino acid that serves as a compatible osmolyte. Increased proline levels play a role in osmotic adjustment thereby helping cells maintain turgor under conditions of low water potential, as well as acting as protective molecules that stabilize proteins and cell membranes, capture reactive oxygen species (ROS), and engage in stress signaling pathways that regulate gene expression responsive to stress. Increased proline accumulation has been widely reported in a wide range of plant species experiencing drought stress, thus supporting its use as an important biochemical indicator in the assessment of plant tolerance to drought (Sitaresmi et al., 2023)

Water Use Efficiency (WUE) is a physiological parameter that describes the ratio between carbon assimilation through photosynthesis and water loss due to transpiration, thus serving as an important indicator in evaluating plant performance under conditions of water limitation. Increased WUE in drought-stressed plants is generally related to more efficient stomata regulation, adjustment of carbon metabolism, as well as the accumulation of protective metabolites, such as proline. Various studies have confirmed a positive correlation between proline accumulation and increased WUE, where plants with high proline content tend to show better water use efficiency. In corn plants, for example, proline supplementation is reported to be able to increase WUE while suppressing oxidative stress. However, the molecular mechanisms underlying these relationships are still not fully understood, and there is still debate over whether proline plays a direct role in improving photosynthesis efficiency and stomata regulation, or whether its contribution is indirect through protection against oxidative stress, including photosystem II (PSII) protection, stabilization of antioxidant proteins and enzymes, regulation of stomata closure, and maintenance of the integrity of photosynthetic systems (Hatfield & Dold, 2019)

Drought stress occurs when the availability of water in the soil is insufficient to meet the transpiration needs of plants, resulting in a water deficit in plant tissues. This condition triggers a series of physiological and biochemical changes that start from the closure of the stomata, a decrease in stomatal conductance, and a reduction in the rate of photosynthesis. The closure of the stomata is an initial response to minimize water loss through transpiration, but the consequence is a decrease in the diffusion of CO_2 into the leaves that inhibits photosynthetic activity. At the cellular level, dryness causes disruption to membrane structure, protein denaturation, and excessive production of ROS that can damage DNA, lipids, and vital enzymes. Proline is a cyclic amino acid that has the unique property of being a compatible osmolyte, which is a compound that can accumulate in high concentrations without interfering with normal cell metabolism. Proline biosynthesis in plants occurs primarily through the glutamate pathway, which is catalyzed by the enzymes Δ1-pyrroline-5-carboxylate synthetase (P5CS) and pyrroline-5-carboxylate reductase (P5CR). Recent research shows that proline accumulation not only plays a role in osmotic adjustment to maintain cell turgor, but also has a multifaceted function in the stress response (Nahar et al., 2022)

Renzetti et al. (2024) conducted a comprehensive meta-analysis of transgenic plants expressing proline metabolic genes and found that proline accumulation exerts significant beneficial effects on a wide range of physiological and morphological parameters under drought and salinity stress. The study reveals that the benefits of proline may be more related to proline metabolism itself than just proline accumulation, with a major role in redox regulation and interaction with accumulated ROS predominantly in stressful conditions. WUE is defined as the ratio between gross primary productivity to evapotranspiration, or at the leaf scale as the ratio between the rate of CO_2 assimilation to the rate of transpiration. WUE reflects the efficiency of crops in producing biomass or crop yields relative to the amount of water used.

demonstrate that exogenous application of proline improves the morpho-physiological response and yield of drought-stressed maize crops under different irrigation systems. The results showed that proline significantly increased water productivity and WUE, indicating that proline plays a role not only in stress tolerance but also in optimizing water use. This increase in WUE is attributed to proline's ability to stabilize membranes, protect enzymes, and increase antioxidant enzyme activity that facilitates better stomata conductance and higher CO_2 diffusion through the leaves (Ibrahim et al., 2022)

Correlation between proline accumulation and WUE has been observed in various plant species with varying mechanisms. revealed that proline accumulation in woody plant seedlings showed a nonlinear pattern of drought stress duration, with the highest accumulation occurring at about 70 days of drought treatment. The study also identified that the effects of drought on proline accumulation were greater in deciduous species than coniferous species, and higher in species with orthodox seeds, suggesting that proline's response to drought was mediated by the functional characteristics of the plant. The molecular mechanisms linking proline accumulation to increased WUE involve several complex pathways, including protection against oxidative damage, stabilization of protein and membrane structures, as well as regulation of the expression of stress-responsive genes such as the abscisate hormone biosynthesis (ABA) gene. Various studies have explored the relationship between proline and plant responses to drought stress in various species and environmental conditions. conduct a comprehensive evaluation of the impact of drought stress on grain productivity and WUE on various rice cultivars, as well as assess genotypic variability in response to water stress. The results showed that drought-tolerant rice cultivars had higher proline accumulation and better WUE, indicating a positive correlation between the two parameters. The study also identified that genotypic variability in proline and WUE responses to drought could be leveraged for crop breeding programs in developing more drought-tolerant varieties with superior water use efficiency (Joanna et al., 2023; Hussain et al., 2022).

Conducted a comparative study on three tropical perennial crops to understand different adaptation strategies to drought stresses (He et al., 2024). The study found that Clerodendrum paniculatum species that accumulated high amounts of proline exhibited drought tolerance strategies through strong osmotic adjustments, while Melastoma malabathricum species that accumulated lower prolines relied on avoidance strategies through tight stomata closure to minimize water loss. These findings suggest that proline's role in drought tolerance is species-specific and may involve different mechanisms depending on the adaptation strategies adopted by each species. The study also found a strong linear correlation between the rate of photosynthesis and the conductance of the stomata, as well as between the conductance of the stomata and the rate of transpiration, which collectively affects the WUE at the whole plant level. In the context of applied agriculture, the results of field experiments over two consecutive seasons investigating the effects of deficit irrigation integration, soil amendment, and proline application on WUE, yield, and quality of seedless Crimson grapes. The study showed that proline at 500 ppm as a foliar application, combined with irrigation at 75% of field capacity and the addition of soil amendments, resulted in the highest WUE while maintaining optimal fruit quality.

Based on the description above, this paper examines several things such as: (1) how the quantitative correlation pattern between the level of proline accumulation and the water use efficiency component in drought-stressed plants with varying intensity and duration, (2) how the temporal dynamics of proline accumulation and WUE changes during drought stress progression, and in which phase the correlation between the two parameters reaches the most significant level, and (3) how the underlying molecular mechanisms cordate proline accumulation and increased WUE, specifically related to the transcription regulation of genes involved in proline biosynthesis, photosynthesis, and stomata regulation. Based on the formulation of the problem, this study aims to quantify and analyze the correlation between the level of proline accumulation and various components of WUE in plants experiencing drought stress with varying intensity and duration, as well as identify the dose-response relationship pattern between proline concentration and water use efficiency. In addition, this paper also examines the characterization of the temporal dynamics of proline accumulation and changes in WUE during drought-stress progression from the initial phase to the advanced phase, identifies the critical phases in which the correlation between proline and WUE is strongest, and evaluates the recovery capacity of plants after rewatering.

METHODS

This paper investigates and analyzes the correlation between proline accumulation and increased water use efficiency in drought-stressed plants, by searching scientific articles from various reliable literature sources including international journals indexed *by Scopus*, *Web of Science*, *ScienceDirect*, and *Google Scholar* With a publication time limit in 2019? until 2025 to obtain up-to-date and relevant information. Keywords used in literature searches include "*proline accumulation*", "*water use efficiency*", "*drought stress response*", "*osmotic adjustment*", "*stomatal conductance*", and other related term combinations related to the research topic. The literature reviewed includes experimental research articles, review articles, and other scientific publications that present empirical data on the physiological, biochemical, and molecular mechanisms related to the role of proline in increasing WUE in various plant species under drought conditions. The selection of literature is based on the relevance of the topic, the quality of the research methodology, and the contribution to the understanding of the WUE proline correlation mechanism that is the focus of this study. Furthermore, the data obtained were analyzed descriptive-comparatively by identifying, extracting, and synthesizing important information from each literature collected.

The extracted data included the mechanisms of proline biosynthesis and accumulation, physiological parameters of WUE such as photosynthesis rate, transpiration rate, and stomata conductance, as well as causal or correlational relationships between proline concentrations and WUE components under various drought-stress conditions. Synthesis was carried out by comparing findings from various studies to identify patterns of consistency, species-specific variability, temporal dynamics of proline and WUE responses, as well as the molecular mechanisms underlying these correlations. A narrative approach is used to present the results of the analysis coherently by integrating physiological, biochemical, and molecular perspectives from the literature studied. This literature review also identifies the remaining knowledge gaps and formulates the theoretical and applicable implications of the findings that have been published regarding the optimization of water use efficiency through modulation of proline accumulation in plants facing water deficit conditions (Zulfiqar et al., 2023; Ghosh et al., 2021).

RESULT AND DISCUSSION

Quantitative Correlation Pattern Between Proline Accumulation and Water Use Efficiency Components

A consistent pattern of positive correlation was seen between the level of proline accumulation and the water use efficiency component in various plant species experiencing drought stress of varying intensity and duration. A comprehensive study on the detection of drought stress in tea plants reveals that the accumulation of biochemical compounds such as proline, antioxidant enzymes, and stress-related hormones such as abscisic acid plays a crucial role in the plant's adaptation to drought conditions, which directly affects photosynthesis capacity and transpiration rate as key components of WUE. Studies on glutinous rice plants demonstrated that the proline content of all varieties increased substantially when water application was lowered, which correlated with a decrease in chlorophyll content while maintaining the physiological viability of the plant through osmoregulatory mechanisms. This phenomenon indicates that proline functions as a protective molecule that facilitates the continuity of essential metabolic processes even under conditions of significant water deficit. (Anjarsari et al., 2025; Sobir et al., 2018).

Further investigation of the mechanism of proline accumulation in eggplant plants showed that proline accumulation occurs gradually from the initial phase of drought stress when the moisture content of the medium decreases substantially, and undergoes a progressive escalation along with the intensification of the stress duration accompanied by a decrease in density and percentage of open stomata to reduce the rate of excessive transpiration. This response pattern implies that proline accumulation is an integrated adaptive strategy that synergizes with stomata regulation to optimize the balance between carbon assimilation and water loss. Studies on various genotypes of eggplants that experience salinity stress also confirm that abiotic stress causes a consistent increase in proline accumulation as stress intensity increases, despite decreases in other morphological and physiological characters, suggesting that proline is a biochemical indicator sensitive to the level of stress experienced by plants. This quantitative correlation is strengthened by the finding that plants with higher proline content show superior resistance to drought stress, as the higher the proline content, the more tolerant the plant is to water deficit conditions, making the presence of proline a reliable indicator of plant resistance (Harahap, 2025).

Molecular Mechanisms Underlying the Correlation of Proline and WUE

The molecular mechanism linking proline accumulation to increased WUE involves complex regulatory pathways that integrate proline biosynthesis, photosynthesis modulation, and stomata regulation through a coordinated network of transcriptional signals. Proline is synthesized through metabolic pathways catalyzed by key enzymes in cytoplasm and chloroplasts, and serves as an osmoregulator that maintains cell turgor by lowering the osmotic potential of the cytoplasm without interfering with enzyme function and membrane structure, thus maintaining the continuity of photosynthesis and metabolic processes even in water deficit conditions. This osmoregulatory mechanism directly contributes to the increase in WUE by allowing plants to maintain a relatively high rate of carbon dioxide assimilation despite the reduction in transpiration rates due to partial closure of the stomata, thereby increasing the ratio of productivity to water consumption (Violita, 2021).

The integration of technologies in water management such as sensor-based precision irrigation systems and *the Internet of Things* demonstrates that optimizing water distribution according to the specific needs of the growth phase of plants can increase productivity and significantly reduce water use, which conceptually reflects the function of proline in optimizing water use efficiency at the molecular and cellular levels. The parallels between external water management and internal regulation through proline accumulation underscore the importance of a holistic approach in improving WUE that integrates agronomic strategies with an understanding of plant physiological and biochemical mechanisms. Stomata regulation is a crucial component in the proline-WUE correlation mechanism, where proline accumulation facilitates the maintenance of stomata guard cell turgor so that plants can modulate stomata aperture more precisely and responsively to changes in environmental water status, allowing for optimization of carbon dioxide diffusion by minimizing water loss (Lokot Muda Harahap, 2025; Asbur et al., 2025)

Differences in functional characteristics between species and genotypes in proline accumulation capacity and WUE responsiveness to drought indicate the existence of exploitable genetic variability for crop breeding programs targeting improved drought tolerance and water use efficiency. Studies on different species show that there are differences in the amount of proline accumulation in different types of plants during drought stress depending on the genetic and physiological characteristics of the plant, suggesting that genotype selection with superior proline accumulation capacity can be an effective strategy in developing drought-tolerant varieties. These molecular implications are reinforced by the finding that more efficient irrigation techniques such as drip and sprinkler irrigation show higher water use efficiency than traditional methods, underlining that WUE optimization requires an integrative approach that combines precision irrigation technology with the utilization of plant genotypes that have superior adaptive physiological and biochemical mechanisms (Rusmayadi et al., 2023).

CONCLUSION

A consistent positive correlation occurred between proline accumulation and increased water use efficiency in drought-stressed plants. The analysis demonstrated that the elevation of proline concentration correlates with the optimization of the WUE component through osmotic adjustment mechanisms, cellular membrane protection, and precise modulation of stomata aperture. Temporal dynamics indicate that a critical phase of the proline-WUE correlation manifests when the moisture content of the medium decreases substantially below a certain threshold, triggering proline accumulation that facilitates the maintenance of cell turgor and metabolic continuity. The molecular mechanisms underlying this correlation involve a complex integration between proline biosynthesis, photosynthesis regulation, and stomata regulation that allows plants to maintain the rate of carbon dioxide assimilation by minimizing water loss. The genotypic variability in proline accumulation capacity implies the potential utilization of genetic diversity for the development of plant varieties with superior drought tolerance and water use efficiency, contributing to global food security in the era of climate change.

Therefore, further experimental studies that integrate transcriptomic and metabolomics analysis are needed to uncover the genetic regulatory pathways that link proline accumulation with comprehensive WUE optimization. The development of applicative strategies through molecular marker-based breeding programs targeting genotypes with superior proline accumulation capacity needs to be intensified to produce drought-tolerant plant varieties. The implementation of precision irrigation technology integrated with an understanding of the physiological mechanisms of proline accumulation can be a holistic approach to increase agricultural productivity in areas with limited water resources, supported by institutional capacity strengthening and public-private partnership schemes to facilitate the adoption of technology by farmers.

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