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Mechanisms of drought tolerance in Moringa: Strategies for mitigation and adaptation - Review

Vijayaragavan V[1], Sumathi T[2*], Irene vethamoni P[3], Ravichandran V[4] & Raju M[5]

[1]Department of Vegetable Science, Horticultural College and Research Institute, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

[2]Turmeric Research Centre, Tamil Nadu Agricultural University, Bhavanisagar 638 451, Tamil Nadu, India

[3]Department of Horticulture, Horticultural College and Research Institute, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

[4]Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

[5]Centre for Water and Geospatial Studies (CWGS), Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

*Email: sumathi.t@tnau.ac.in

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Abstract

Moringa oleifera, often called the "miracle tree," is renowned for its resilience to harsh environmental conditions, particularly drought. This review explores the mechanisms by which Moringa tolerates drought stress, making it a vital crop in arid and semi-arid regions. Morphological, physiological, biochemical and molecular adaptations attribute the tree's drought tolerance. Key mechanisms include an extensive root system that enhances water uptake, efficient water use through stomatal regulation and the accumulation of Osmo protectants such as proline. Additionally, Moringa activates antioxidant enzymes that mitigate oxidative stress under drought conditions, safeguarding cellular integrity. Molecular responses play a significant role as well, with the upregulation of drought-responsive genes and stress-related proteins that enhance the tree's ability to cope with water scarcity. These adaptive traits not only contribute to Moringa's survival but also improve its productivity under water-limited conditions. Beyond its environmental resilience, Moringa holds significant socioeconomic value. Its rich nutritional content, medicinal properties and potential for income generation make it a critical crop for addressing food security and poverty, especially in developing regions. This review highlights the importance of promoting Moringa cultivation as a sustainable agricultural practice in drought-prone areas. In conclusion, understanding and leveraging Moringa's drought tolerance mechanisms can contribute to climate change mitigation and adaptation strategies. Expanding its cultivation could lead to more resilient agricultural systems, providing both environmental and socioeconomic benefits. Continued research is essential to optimize its use and ensure its widespread adoption in vulnerable regions.

Keywords

climate change; drought; grafting: Moringa; physiology

Introduction

Moringa oleifera Lam., a mono-generic species of the family Moringaceae, is a deciduous tree that originated in Asia and is native to India, with its origin found in humid sub-tropical regions of sub-Himalayan regions of Northern India (1), but it is widely cultivated in many arid countries. It has been cultivated in various agricultural systems, including monocropping, intercropping and agroforestry. It is a drought-tolerant and valuable species with the potential as an ecological solution in agroforestry systems, aiding in reducing the negative impacts of drought and enhancing soil quality in arid areas (2). In South Africa, it is intercropped with vegetables, fruit trees and medicinal and aromatic plants (3). Moringa is also used in alley cropping in Ghana (4). It is extensively cultivated for its tender pods, leaves and flowers marking its significance as a miracle tree.

Moringa is known as an anti-malnutrition plant, with all parts of the plant like Moringa leaves, Moringa flowers, Moringa seeds and Moringa pods, being edible. Additionally leaves, stems, bark and roots possess medicinal properties. Moringa is often referred to as "A Mother's Best Friend" due to its extensive nutritional and medicinal benefits (5). The entire Moringa plant is generally used for industrial purposes, although the roots can be used as a substitute for horseradish; the wood is used in the paper industry; the powdered seeds are used in bio water clarifiers in place of coagulants for chemicals like aluminium sulphate and the oil extracted from the seed kernels is known as ben oil and is used to make biolubricants (6). Moringa is generally recognized for its resistance to pests and diseases, but it is affected by a few, Moringa tree defoliator *Noorda blitealis* (7) and powdery mildew (8). This review focuses on the detailed views of the Moringa's drought tolerance mechanism along with its associated adaptative strategies, in the morphology, physiology, biochemical and molecular levels occurring in the plant during drought stress and their mitigation strategies thereby making the plant grow on a large scale in drought-affected areas for a sustainable future.

Impact of moringa in socio-economic status

Moringa has gained importance in socio-economic development, especially in rural areas of drought-affected and impoverished countries (9). It plays a critical role in providing food during lean seasons and droughts, especially when households face limited food options. It is recognized as a famine food in arid regions like Niger, Kenya and Ethiopia (10).

Moringa is a crucial livelihood strategy and source of income in countries like Ghana, Ethiopia, Kenya, Burkina Faso, Zimbabwe, Senegal and Niger (11). In Ghana's Bono East Region, Moringa cultivation contributes to income generation and job creation, making it a valuable poverty-reduction strategy (10). Beyond improving nutrition and health for smallholder farmers in developing countries, Moringa has enhanced their livelihoods and incomes (12). Promoting indigenous vegetables like Moringa is beneficial for health, food security and income generation across Africa (13). Although Moringa grows in drought-prone areas, its growth is affected by drought.

Drought conditions severely affect Moringa species by reducing growth, leaf production and overall yield. Water stress limits nutrient uptake, leading to stunted growth and decreased biomass. The height of *M. oleifera* is 281.45 cm compared to *M. ovalifolia,* which grows slowly at 113.2 cm in arid and semi-arid regions in Namibia (14). Reduced water availability impairs physiological processes, such as photosynthesis and chlorophyll synthesis, lowering productivity in *M. peregrina* populations (15). Drought can also reduce the seed oil content of *M. oleifera* (16). In severe cases, drought stress results in poor flowering and fruiting, affecting seed production and the overall health of the plants, especially in sensitive species (17).

Nutritional powerhouse and health-boosting superfood

Moringa is a cost-effective and nutritionally rich alternative to many commercial vegetables. Its leaves are packed with dietary polyphenols, such as flavonoids, terpenoids and essential minerals that boost health (18). Additionally, Moringa is abundant in compounds like α and β-carotene, γ-tocopherol, ascorbic acid, β-cryptoxanthin, luteolin and violaxanthin, which can serve as nutritional supplements and improve the shelf life of various food products (19). Moringa seed oil also contains unsaturated fatty acids, offering significant health benefits.

Immature Moringa pods contain approximately 20.7% protein and 46.8% fiber. The amino acid content is 30.0% in pods, 44.0% in leaves and 31.0% in flowers. Both immature pods and flowers have similar levels of palmitic, linolenic, linoleic and oleic acids (20). Moringa leaves are rich in essential minerals like calcium, potassium, zinc, magnesium, iron and copper, along with vitamins A, B, C, D and E (21). Dried leaves contain seven times more vitamin C than oranges, four times more calcium than milk, four times more vitamin A than carrots and three times more potassium than bananas (22). Additionally, Moringa leaves are richer in iron than many commercial vegetables, including spinach (*Spinacia oleracea* L.) (23).

Moringa powder is frequently used to fortify foods. Moringa leaf supplements can help protect against oxidative stress and iron deficiency (24). Due to its high protein, vitamin and mineral content, Moringa is added to various foods as a fortification ingredient, such as beverages, bread, dairy products, pastries and snacks, to enhance their nutritional value (25). Additionally, fortified Moringa leaf powder as a complementary food has been found to significantly improve the hemoglobin levels of infants aged 8-12 months after four months of feeding (26).

Moringa is abundant in pharmacological properties, including anti-inflammatory, antibacterial, antioxidant, diuretic, antiulcer, anticancer, anticonvulsant, antipyretic, hepatoprotective, antihypertensive, anthelmintic, antiviral and antispasmodic effects. Extracts from Moringa seeds and pods, which contain thiocarbamate, glycosides, isothiocyanate and β-sitosterol, have been shown to effectively reduce blood pressure (27). The abundance of antioxidant properties in *M. oleifera* affirms its traditional medicinal use globally for chemo-preventive and cancer treatment applications (28). *M. oleifera* extract elevates high -density lipoprotein and reduces low density lipoprotein, preventing atherosclerosis and cardiovascular complications in diabetes patients (29). *M. oleifera* contains a wide range of metabolites that contribute to its hypoglycemic effects, making it promising for diabetes treatment (30). Moringa leaves are abundant in antioxidants like gallic acid, chlorogenic acid, ellagic acid and ferulic acid, along with flavonoids such as kaempferol, quercetin and rutin, capture free radicals and bind metals for enhanced health benefits (31). This valuable crop, under drought conditions, undergoes changes in nutritional composition, which is a potential loss to our diet (32).

M. oleifera, while known for its high nutritional content, also contains many antinutritional agents which may decrease nutrient absorption and bioavailability. Phytates, which comprise about 2.5%, bind to important minerals such as iron, zinc and calcium, decreasing their absorption (33). Trypsin inhibitors disrupt protein digestion by inhibiting the action of trypsin, an enzyme required for protein metabolism. Oxalates can form insoluble compounds with calcium, lowering its bioavailability and potentially causing kidney stones. Tannins are polyphenolic chemicals that limit protein digestibility by creating complexes with proteins. Saponins can influence cell membrane permeability, thus restricting nutrient absorption and contributing to a bitter taste, making Moringa products less appealing. Small concentrations of cyanogenic glycosides can produce cyanide, which poses a risk if consumed in large quantities. However, cooking methods such as boiling and blanching significantly reduce these compounds, enhancing nutrient absorption and making Moringa a highly beneficial food source (34).

Genetic diversity and breeding in moringa

Developing plants that can withstand drought stress requires germplasm, which is a representation of the genetic diversity of plant species (Fig. 1). It provides important features that help breeding programs develop robust varieties that can tolerate water scarcity and support sustainable agriculture in adverse geographical areas. Despite its many uses and morphological differences, there are very few collected accessions and active germplasm banks for Moringa. Databases on wild or domesticated Moringa accessions are few. In India, the Horticultural College at Tamil Nadu Agricultural University is a premier research institution specializing in Moringa breeding, particularly germplasm collection, preservation and variety enhancement. There are 85 accessions available for commercial production in different agroecological zones (35). Currently, the World Vegetable Centre has approximately 93 accessions sourced from Tanzania, Taiwan, Thailand, the United States, the Philippines, India, Nigeria, Malaysia and Cambodia. Height, branching patterns, bearing habits, leaflet size and shape and pod length are all different across these cultivars (Table 1).

To enhance both abiotic stress resistance and yield potential, a combination of traditional and modern molecular breeding methods is necessary. Marker-assisted selection is commonly used in plant breeding for germplasm characterization, gene pyramiding, purity checks, diversification analysis, multi-trait introgression and trait stacking across various commercial crops using DNA markers. Using molecular markers like SSR markers found substantial genetic diversity in 161 Moringa accessions worldwide with origin in the Indo-Pakistan region (36). Genetic variation in ten individual Moringa plants was investigated using ten primers of each inter-simple sequence repeat (ISSR) and start codon targeted (SCoT) markers (37). The efficacy of molecular techniques (ISSR, SCoT, ITS barcoding) in assessing genetic diversity in 23 Moringa genotypes from Kerala, Tamil Nadu and Karnataka. Emphasizing their importance, seven cytochrome P450 markers were utilized for genetic conservation and plant improvement in Moringa (38). Advanced SNP markers were employed to assess genetic diversity in Moringa populations under consistent clustering of genotypes across various analysis tools underscoring the significance of acknowledging unique seed origins (39).

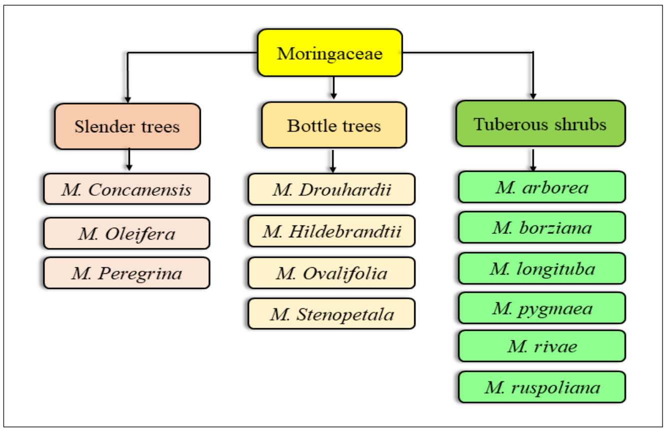

Fig. 1. Classification of Moringa species.

Table 1. Summary of botanical features of different Moringa species

Sl. No.	Species	Geographic Distribution	Availability status	Special feature	Drought tolerance	Reference
1	*M. drouhardii*	Madagascar	Least concern	base is swollen to facilitate the storge of water	Highly drought tolerance	(96)
2	*M. oleifera*	Himalayan tracts of northern India	Least concern	Deciduous to evergreen, semi spreading to upright tree shape. Flowers throughout the year	Drought resistant	(96)
3	*M. hildebrandtii*	Madagascar	Critically endangered	large leaves, scented flowers and fast growth	Highly drought tolerance	(97)
4	*M. stenopetala*	Kenya, Ethiopia	Data deficient	The species is grown in mixed multi-storey stands with food crops and used for fodder purpose	Drought resistance	(98)
5	*M. ovalifolia*	Namibia, Angola	Near threatened	Withstand harsh climatic conditions	Drought resistance	(99)
6	*M. concanensis*	India, Pakistan, Bangladesh	Data deficient	Fast growing species with rich source of plant micro and macro nutrients, proteins	Drought resistance	(100)
7	*M. peregrina*	Arabia, Red Sea area	Least concern	Development of root tubers during the seedling stage.	Drought tolerance	(101)
8	*M. arborea*	Kenya, Ethiopia, Somalia	Data deficient	Deciduous tree with a robust white succulent trunk and is abundant in micronutrients.	Drought tolerance	(102)
9	*M. longituba*	Kenya, Ethiopia, Somalia	Data deficient	Rich in micronutrients	Drought tolerance	(103)
10	*M. rivae*	Kenya, Ethiopia, Somalia	Near threatened	Many primary branches and predominant in arid regions	Drought tolerance	(103)
11	*M. pygmaea*	Kenya, Ethiopia, Somalia	Data deficient	Short shrub with Large tuberous rootstock	Drought tolerance	(104)
12	*M. borziana*	Kenya, Ethiopia, Somalia	Least concern	Single straggling type with tuberous root	Drought tolerance	(103)
13	*M. ruspoliana*	Kenya, Ethiopia, Somalia	Data deficient	Largest leaflets with high dry mass protein content	Drought tolerance	(102)

Prospects of moringa as a drought-tolerant crop

Rising greenhouse gases like carbon dioxide levels alter the climate, leading to elevated temperatures and changing the pattern of rainfall. This reduces water resources for plants, leading to intensified droughts. Drought is typically characterized by a lack of rainfall over a prolonged period, which leads to insufficient water supply. Drought harms agricultural soils, causing degradation, biodiversity loss, reduced yields, impacting surface and groundwater levels, affecting soil fertility and microbiology (40). Unlike many other agricultural plants, Moringa grows quickly and is resilient to harsh environmental factors. Moringa can grow in a variety of environments, including high temperatures, shaded locations and altitudes of up to 1000 meters. This plant prefers temperatures between 25 and 35 ^{0}C, but may survive up to 48 ^{0}C for short periods or in shaded areas (41).

It is resilient to long dry seasons and grows well in areas with annual rainfall ranging from 250 to 1500 mm. However, drought is one of the factors that can negatively impact plant growth (42). The Moringa tree requires minimal management, establishes itself easily and adapts well to arid climates (43). Moringa's resilience during moderate droughts is largely due to its long, tuberous taproot, which reaches deep into the soil to access water from deeper layers, unlike many commercial crops (44). Instead of relying on direct rainfall, the tree stores water in its roots and succulent tissues for use during dry periods. However, despite its ability to endure water stress, Moringa is not classified as a true drought-tolerant species, as it lacks certain biochemical mechanisms, like osmotic adjustment, found in other drought-resistant plants. Moringa instead exhibits effective water stress avoidance strategies, such as isohydric behavior (45). Also, severe drought significantly reduces the key morphological and yield-attributing growth parameters like plant height, the number of branches per plant, as well as the fresh and dry weights of leaves and shoots (46).

Morpho-physio-biochemical changes in Moringa

Drought increases in root formation reflects an adaptive strategy aimed at minimizing water loss through leaves while improving water absorption through an increased number of roots (32). The leaves of *M. oleifera* are arranged alternately, compound and bipinnate, with 2 to 6 pairs of opposite pinnate, each bearing 3 to 5 pairs of opposite leaflets. The terminal leaflet is larger, ovate to elliptic and has a rounded apex and base. The leaflets are mostly smooth and glabrous, while the petiole is covered with fine pubescent hairs. Under drought conditions, Moringa leaves may become thinner as the plant loses water, reducing cell turgor pressure. This is an adaptive response to minimize water loss by decreasing leaf surface area, a common drought-tolerance mechanism (48). It induces profound morphological alterations and physiological shifts in Moringa, disrupting their normal growth patterns, causing lower germination rates, reduced leaf area, disrupted stomata responses (49) and reduced levels of chlorophyll. Severe and prolonged drought results in a continuous decline in leaf water content (50).

Physiological changes involve basic plant functions like photosynthesis and stomatal movements. Net photosynthetic rate, maximal quantum yield, stomatal conductance and transpiration rate decreased in drought conditions, ultimately resulting in a reduction in plant metabolism and production status (51). Moringa plants may not show symptoms of the sentence. The efficiency of PSII, regulated by the quantum yield (Fv/Fm), predicts plant responses to environmental conditions. Drought stress decreases PSII efficiency, leading to photoinhibition and damage, but reduced Fv/Fm also helps plants minimize photosynthetic activity as a protective response to stress (52) (Fig. 2). Moringa plants quickly and strongly close their stomata due to the accumulation of abscisic acid (ABA). Photosynthesis remains unaffected in Moringa during drought stress because the plant produces isoprene, which helps leaves manage water stress through its antioxidant or membrane-stabilizing effects. This also signals the activation of the MEP pathway, providing additional protection to photosynthesis

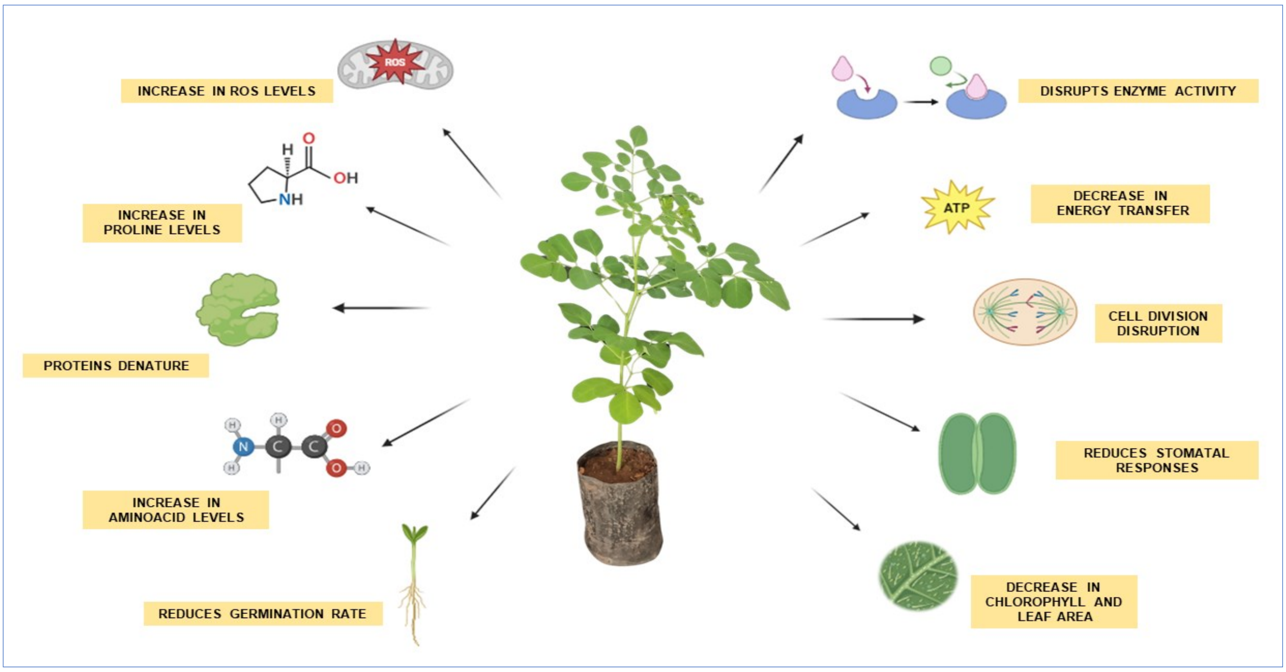

Fig 2. Schematic illustration of changes involved in Moringa under drought stress (created with BioRender.com).

under water-limited conditions (45).

Moringa exhibits tight isohydric behaviour during drought, similar to hygrophytes, but absence of osmolyte accumulation (carbohydrates and proline), resulting in leaf loss (53). Drought induces nutrient deficiencies by reducing root nutrient absorption capacity due to limited root functionality, affecting water and mineral uptake. Excessive accumulation of secondary metabolites, such as phenolic compounds, total flavonoids and condensed tannins, along with osmotic regulators such as proline and soluble sugars, occurs in response to osmotic stress caused by water deficiency (54). These Osmo protectants and antioxidant compounds are present in all plant parts but mostly in leaves (55). This intricate interplay between drought stress and plant responses underscores their adaptive strategies to endure water scarcity.

Osmolytes play a vital role in scavenging reactive oxygen species (ROS) in *M. oleifera*, particularly under stress conditions like drought or high salinity. Osmolytes such as proline, glycine betaine and sugars accumulate in the plant cells during stress, helping maintain cellular osmotic balance. In addition to this, they act as antioxidants, neutralizing harmful ROS generated during stress. ROS, like hydrogen peroxide (H_2O_2) and superoxide radicals ($O_2^{\bullet -}$), can damage proteins, lipids and DNA. Osmolytes mitigate this by stabilizing proteins and membranes, protecting cells from oxidative damage and aiding in maintaining redox homeostasis, thus enhancing stress tolerance in Moringa (56).

Drought is likely one of the most evident factors influencing the chemical composition of *M. oleifera* seed oils. It affects the seed weight, oil yield, degree of unsaturation, oxidative stability and fatty acid composition, which are particularly susceptible to drought. Notably, the oil yield is the most significantly impacted by drought compared to the other growth characteristics (16). *M. oleifera* seed variety PKM-1, the content and properties of Ben seed oil vary significantly, primarily depending on the species and environmental conditions (57).

Antioxidant enzymes play a vital role in reducing reactive oxygen species (ROS) production and protecting against oxidative damage (58). In *M. oleifera*, enzymes like superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) are key to ROS scavenging, contributing to the plant's drought resistance. Under 25% field capacity stress, the activities of SOD, CAT, APX, glutathione reductase (GR) and glutathione peroxidase (GPX) in Moringa leaves were significantly enhanced by 76.15%, 66.74%, 43.26%, 79.30% and 22.2%, respectively (52). The antioxidant activity of *M. oleifera* leaves is strongly influenced by agroclimatic conditions and seasons. Cold region plants showed higher antioxidant activitycompared to those from temperate areas. Similarly, antioxidant activitywas at its highest in December (a cold month) and lowest in June (a hot month), with only a few exceptions. Environmental temperature is a key factor in determining antioxidant activitylevels (59) (Fig. 3).

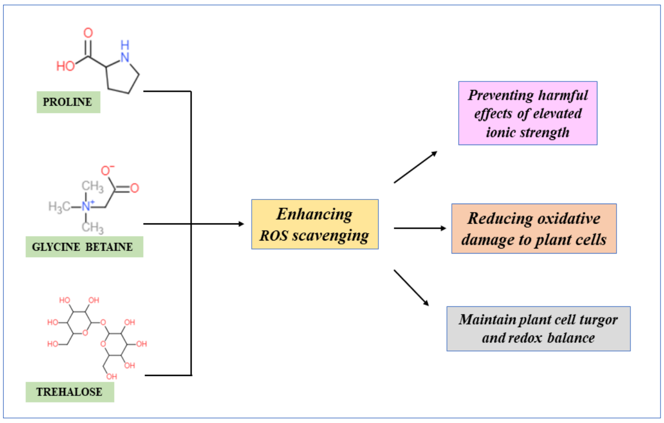

Fig 3. Role of Moringa osmolytes in scavenging ROS.

Molecular mechanisms of moringa under drought

The Moringa plants not only have biochemical and physiological changes but also undergo a series of molecular changes to combat drought conditions. Drought stress signaling encompasses crucial stages: signal perception, transduction and responsiveness and so activating physiological and metabolic reactions for rapid protective mechanisms in response to drought (60). Plant cells recognize stress stimuli through membrane receptors, triggering second messengers like calcium ions, inositol phosphate, ROS, cyclic nucleotides, sugars and nitric oxide. These messengers activate signaling pathways, transmitting signals efficiently (61). The combined effect of all these components helps the plants combat drought stress. Under drought stress, the plants enact molecular adaptations for water management, modulating gene expression at the transcriptional level. Upregulation, downregulation and stress protein accumulation enhance drought tolerance through signaling pathways, including dehydration-responsive element-binding genes (62) (Fig. 4).

M. oleifera exhibits a heightened expression of genes PER43, CATA2 and GPX2 under drought causing antioxidant activity. Genes involved in ethylene biosynthesis and signalling, including DREB1A, ETO1, RAP27, ACS8, CRL5 and ACCO, also display notably elevated expression levels in Moringa leaf tissues to withstand drought stress (63). The decrease in *M. oleifera* growth due to drought was associated with a reduction in the relative 2S albumin gene *Mo-CBP3-1* expression in plant leaves and roots (64). The *BAK 1* gene plays a major role in the brassinosteroid signal transduction pathway, transducing the BR signal, thereby helpful for the developmental process for Moringa (65). The APX gene family has been identified as a key player involved in drought tolerance in *M. oleifera*. In response to interactions with endophytic fungal consortia, the genes *MolHSF3, MolHSF19* and *MolAPX* genes were highly expressed in *M. oleifera* under drought stress. As antioxidants released by fungi increase antioxidant capacity, effectively mitigating drought-induced oxidative stress in the roots of *M. oleifera* (66). Trehalose-6-phosphate synthase (TPS), crucial during drought,

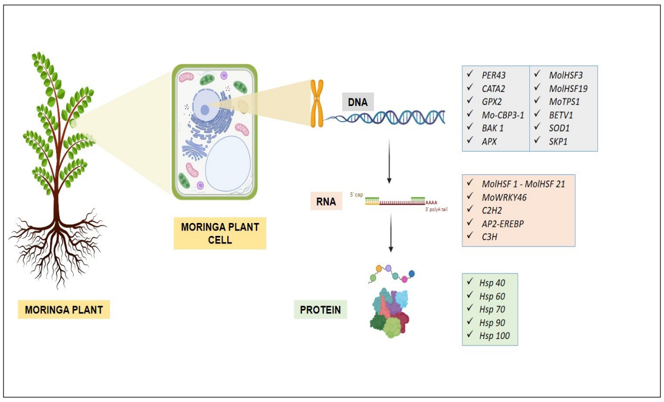

Fig 4. Various molecular components involved in drought regulation in Moringa.

biosynthesizes trehalose, serving as a signalling molecule and Osmo protectant. It modulates carbon metabolism and is demonstrated by the *MoTPS1* gene in *M. oleifera* (67). The *BET V1* gene is a specific gene family present in *M. oleifera* (65) and is a potential factor related to the binding of many ligands, including ABA, lipids and steroids. The binding of ligands like abscisic acid (ABA) plays a crucial role in plant stress adaptation, particularly during drought. When a plant experiences water stress, it synthesizes more ABA, which binds to receptors in guard cells surrounding stomata. This triggers a signal cascade that causes the stomata to close, reducing water loss through transpiration. At the same time, ABA-binding activates stress-responsive genes that enhance water-use efficiency and other protective mechanisms. This rapid physiological adjustment helps plants conserve water and survive adverse conditions, making ligand binding a key element in stress adaptation (45).

Heat shock transcription factor (HSF) *MolHSF1-MolHSF21* family of genes plays an important role in drought tolerance in *M. oleifera*. These transcription factors regulate the expression of genes involved in stress responses and contribute to the plant's adaptation to water-deficit conditions (68). Heat shock proteins like Hsp70 (molecular chaperons, 25 copies in *M. oleifera* genome), Hsp40 (J-proteins, 52 copies), Hsp60 (chaperonins, 17 copies in *M. oleifera* genome), Hsp90 (three copies), Hsp100 (Clp proteins, nine copies in *M. oleifera* genome) and small heat shock proteins (27 sHsps copies in *M. oleifera* genome) (65).

C3H transcription factors, with some copies being reported to respond to drought stress, have two copies under positive selection (65). *lamu*_GLEAN_10016878 and *lamu*_GLEAN_10011614 are the two genes identified in *M. oleifera.* The functional annotation of gene *lamu*_GLEAN_10016878 indicates its role as a *Myb/SANT-like DNA binding domain*. The *Myb/SANT-like DNA binding domain* plays a pivotal role in plants under drought stress. It acts as a regulatory element, influencing gene expression and contributing to adaptive responses during water scarcity. *Gene lamu_GLEAN_10011614*, a conserved *ribosomal protein S6e*, is vital for pre-18S RNA and ribosome maturation and protein synthesis machinery. *S6e* has two nucleolar binding sequences (Nobis) and multiple nuclear localization signals (NLS) with phosphorylation sites acting as switches in cellular processes (65).

Propagation technology - combating drought stress

Yet another technique involves the Propagation practices in Moringa, such as using well-established cuttings or root divisions, to enhance drought tolerance (69). These methods ensure the continuity of desirable genetic traits, promoting resilience to water scarcity. Moringa plants originating from drought-resistant parent material are better equipped to withstand water stress, resulting in improved survival and productivity under challenging environmental conditions (70). Vegetative propagation enhances drought tolerance by allowing plants to reproduce without seeds, ensuring genetic continuity and preserving traits adapted to arid conditions. Moringa is a highly cross-pollinated crop and seeds are highly heterogeneous and quickly lose their viability. Hence, vegetative propagation methods are used to produce genetically identical plants for the parents to adapt to the drought conditions, which can protect the emerging Moringa seedlings from stressful environments (71). Vegetative propagation gives rapid multiplication; preservation of desirable traits like drought tolerance and early maturing are the key components. Moringa utilizes various propagation methods, including sexual (seeds) and asexual (cuttings, air layering, grafting) techniques. Asexual propagation is commonly employed for efficient multiplication, emphasizing resilience and adaptability (72).

Limb cuttings for Moringa propagation are much preferred for cultivation due to easy availability and successful root development. Moringa limb cuttings contribute to drought tolerance by preserving genetic traits that enhance water stress resilience. This propagation method ensures the continuity of desirable characteristics, promoting Moringa's adaptability and survival in arid conditions. Drought-tolerant parents will produce seedlings that are genetically identical to them, hence transferring the drought-resilient to the seedlings and enabling them to withstand stressful environments (73).

Grafting is a swift alternative to slow breeding, boosting short-term stress tolerance in crops. It minimizes losses from factors like low soil temperature and high salinity, offering advantages for drought tolerance and increased yields (74). An annual high-leaf-producing Moringa type like PKM 1 with abundant benefits was grafted onto perennial rootstock for improved drought tolerance. Grafting onto Moolanur Moringa rootstock showed drought tolerance ability by high peroxidase and catalase activity (75). Grafting Moolanur with PKM 1 resulted in a high success percentage within 40 days, indicating its suitability as a perennial rootstock (76). At 40 days, Moolanur perennial Moringa rootstock, with a thickness of 0.51 cm, outperformed other stages. This stage is optimal for successful grafting with an annual Moringa scion cv. PKM 1 (77). The preliminary work for analysis of the drought is being undertaken in a pot culture study and grafted seedlings showed a higher drought tolerance capacity.

External applications stimulate drought tolerance

With an aim of sustainable agricultural solutions, harnessing the potential of Moringa growing even in drought conditions has gained prominence. Exploring the external application of extracts holds promise in fortifying Moringa against drought stress.

Applying ascorbic acid (250 mg/L) externally to Moringa trees is successful in reducing the effects of drought. Through the use of substances like humic acid (1000 mg/L) and seaweed extract (1000 mg/L), reducing the negative effects of water stress and increasing the tolerance of Moringa plants can be achieved economically and environmentally (78). ZnO nanoparticle application boosts enzyme activity, aiding drought tolerance in Moringa (79). Additionally, zinc and boron improve the chemical composition of leaf samples and seed oil (80). Foliar application of trehalose effectively mitigates drought stress in Moringa plants (81). ACC deaminase, found in plant-associated bacteria, mitigates ethylene effects in drought stress. It breaks down ACC, reducing ethylene levels. *Trichoderma gamsii and Fusarium proliferatum* induce drought tolerance in *M. oleifera* (63). Melatonin foliar treatment enhances the growth and yield of *M. oleifera* under drought stress (58). L-Phenylalanine enhances drought tolerance in *M. oleifera* by increasing photosynthetic pigments, IAA, foliage yield components and nutritional values, along with boosting antioxidant activities (82).

Glycine betaine, an Osmo protectant, maintains cellular water balance. Applying Glycine Betaine effectively mitigated drought stress in *M. oleifera*, improving growth and yield (83). The foliar application of potassium mitigated the negative impact of drought on plants and enhanced the continued uptake of nutrients in Moringa (17). Applying benzyl amino purine (BAP) externally enhanced the growth of Moringa plants, including increasing shoot length, root length, leaf count and photosynthetic pigments, particularly in drought conditions (47). Glutathione is an antioxidant that plays a role in plant growth, cell division and elongation, which protects cells. Glutathione spraying treatment gave the highest concentration of macro and micronutrient and protein content in Moringa leaves in drought (84). All these will lead to enhanced production of Moringa even under drought stress.

Drought Screening methods

Polyethylene glycol (PEG) is widely used in controlled environments to simulate drought conditions. By reducing the water potential in the growth medium, PEG creates osmotic stress, mimicking drought. Varying PEG concentrations can induce different levels of stress, allowing researchers to evaluate plant physiological and biochemical responses, such as growth reduction, changes in water use efficiency (WUE) and alterations in chlorophyll content (85). Mannitol is an osmotic agent that also mimics drought conditions by inducing water stress in plants. In *M. oleifera*, mannitol-induced drought stress in micro-propagated plants leads to significant reductions in shoot and root length, as well as decreases in fresh and dry weights of both shoots and roots. This stress simulates water deficit conditions, allowing researchers to evaluate plant tolerance mechanisms and understand the sensitivity of *M. oleifera* to drought (86).

Field capacity represents water-holding capacity after excess water has drained from the soil. By manipulating field capacity (100%, 70%, 40%), researchers can simulate varying degrees of drought stress. This approach is particularly useful for assessing the drought tolerance of different plant genotypes or treatments under pot experiment conditions (87). Monitoring parameters like growth, yield and physiological responses The photosynthetic CO_2 assimilation, stomatal conductance, transpiration, vapor pressure deficit, internal carbon concentration, chlorophyll a, chlorophyll b and total chlorophyll and stem diameter, height and number of leaves were measured under these varying conditions, providing valuable insights for the ability of the plant to cope with water scarcity in Moringa (88).

The integration of PEG-induced osmotic stress, varying field capacities and Mannitol water treatment provides a robust framework for screening drought tolerance in plants. This approach can help identify strategies to improve crop resilience, optimize water use and sustain productivity under water-limited conditions, making it highly relevant for developing drought-tolerant cultivars and innovative water management practices.

Research gap

Although Moringa phytochemicals have many positive potentials, there are issues with the plant's potential for toxicity (89). Phytochemicals are tannin, estrogene, pectinesterase, moringine and moringinine. When taken in too many amounts, the poisonous substances found in *M. oleifera*, such as alkaloids and other phytotoxins, may cause paralysis of the nerves and other adverse effects (90). No conclusive scientific evidence proving the adverse effects of Moringa consumption; it is recommended to consume it in smaller doses to ensure safe use and minimize any potential risks. Additionally, further in-depth research is needed to fully understand its potential toxicity, effectiveness and safety.

Plant species with a broad geographic distribution, like Moringa, are exposed to diverse environmental conditions, leading to the evolution of various morphological and phytochemical traits. Moringa, a cross-pollinated tree species with 28 diploid chromosomes, exhibits significant variation in its morphological, physiological and quantitative characteristics (91). The tree's forms range widely, from annual to perennial, deciduous to evergreen and semi-spreading to erect (92). Additionally, some Moringa trees bloom twice a year, while others flower continuously throughout the year (93). Developing new cultivars with high-yielding, continuous flowering and stress tolerance traits could further extend Moringa cultivation across a wider range of agroclimatic conditions.

Researchers have access to a valuable germplasm pool for breeding projects that aim to improve desired traits and quality because of the substantial genetic diversity seen in Moringa. However, progress in exploring second-generation qualities such as nutrition, flavour and bioenergy is slow compared to other well-studied plants with substantial breeding programs. The chemical compositional diversity in Moringa presents an opportunity for the development of cultivars with desired traits, such as the ability to lessen bitterness to suit consumer tastes (94). Furthermore, a significant production hurdle is bsusceptibility to pests and diseases, particularly spider mite infestations (*Tetranychus urticae*) that result in wilting and mortality (95). Therefore, boosting leaf yield, improving nutritional content, reducing bitterness and enhancing Moringa's tolerance to biotic and abiotic stress should be the main goals of breeding projects.

Conclusion

In conclusion, this review comprehensively explores diverse and innovative drought mitigation strategies adapted by Moringa oleifera, shedding light on the multifaceted approaches adopted across various disciplines. From molecular mechanisms involving key genes and signalling pathways to agronomic practices and technological innovations, a holistic understanding of drought response emerges. The integration of precision agriculture, crop breeding for stress resilience and harnessing advanced technologies showcase a promising trajectory for sustainable drought management. As climate change intensifies, these strategies not only provide immediate relief but also establish a foundation for long-term resilience in agriculture. This review serves as a valuable resource for guiding future research works on Moringa for drought screening technologies and being a valuable crop for changing the future.

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Authors' contributions

VV collected the research article and wrote and drafted the manuscript. ST corrected the manuscript. IP wrote the molecular mechanism aspects of drought. RV participated in editing the final manuscript. RM contributed a pictorial representation of the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

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