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REVIEW ARTICLE

Trends in Biotechnology and Plant Sciences

A Comprehensive Review on Understanding Drought Resilience Mechanisms in Sunflower (Helianthus Annuus L.)

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Abstract

As an important oil crop and ornamental crop, sunflower (Helianthus annuus L.) displays moderate drought resistance which is crucial in maintaining yields in the face of water shortage due to climate change. This review explains the adaptations of sunflowers to drought stress which are physiological, biochemical and molecular. Physiologically, deep taproot systems form in sunflowers and dry moisture (up to 40 per cent) of the subsoil, and their leaves are folded downward to shorten the transpiration duration. Biochemical adaptation involves osmotic adjustment by storing proline and betaine and retention of turgor during drought. The amount of antioxidant systems (e.g. superoxide dismutase and ascorbate peroxidase) rises 1.5 to 2-fold to reduce the effects of reactive oxygen species (ROS). Transcriptomic analyses mediate the identification of differentially expressed genes (DEGs) of 2,589 genes in leaf, along with their transcriptional influences, such as deregulated osmolyte production and reactive oxygen species defenses (DREB2A, etc.). Genomic technologies which include genome-wide association, marker-assisted selection, and CRISPR/Cas9 are being applied to target root traits and water-use efficiency which makes the breeding cycles only six years. The ability to withstand stress with regard to water uptake and seed set has been provided by the wild Helianthus species, especially H. argophylus. Agronomic practices, such as drip irrigation and mulching, maximizing water-use and yield stability. Nevertheless, extreme drought conditions lower yield of achene by 3050 percent and oil level by 510 percent because the activity of the RuBisCO enzyme is impaired. Cropping techniques (e.g. drip irrigation, early planting) and CRISPR/Cas9 manipulation of Hahb4 are more resistant to drought. A combination of breeding, inoculation with microbes, and optimal control can maintain the productivity of sunflower in dry areas, which can be used to mitigate the problem of climate change.

KEYWORDS
Sunflower; Drought tolerance; Climate change adaptation and Oilseed crop

1 | INTRODUCTION

Global Production and Significance of Sunflower

Sunflower (Helianthus annuus L.) is a crop of oilseeds that is essential, as plants planted on 27 million hectares all over the world serve as a source of 8 percent of global oilseeds (FAO, 2024) (Fig. 1). Its ability to suit semi-arid areas adds to its dominance in Eastern Europe, South America, and Central Asia, having a market value of 32.10 billion in 2025 (Mordor Intelligence, 2025). Abiotic stress is a significant factor (drought stress) that has the potential to decrease yield by 40% in flowering and seed fill development in sunflower (Hussain et al., 2018). This poses a threat to the food security where sunflowers are used to produce edible oil, confectionery seeds and aesthetic value. Russia was the largest producer in 2024 with 17 million metric tons and Ukraine, the second at 14 million (Fig. 1) (USDA, 2024). Climate change enhanced water shortages and there is a desperate necessity to create new varieties of drought tolerant crops. Recent studies outline genetic diversity of sunflower as a resilience study model, and hybrid seeds take up 91% of the market because of increased drought tolerance and generation of oil and yield (Dudhe et al., 2025). The innovations in genomics, including parthenogenesis breeding, shorten breeding cycles to 10 months and allow breeding the cultivars resistant to stress to develop faster (Mordor Intelligence, 2025). These inventions will play a critical role in water-deficient areas to achieve sustainable production that will guarantee the global agricultural resilience. The purpose of this review is to present the new evidence on the topic of sunflower drought resistance in a multidimensional physiological, molecular, genomic, anatomical and breeding perspective. It tries to describe how the sunflowers can resist the water lack, supported by the field and laboratory real-time data. The article in question points out practical application of drought-tolerant plant development as a subset of agricultural and food security sustainability in the world.

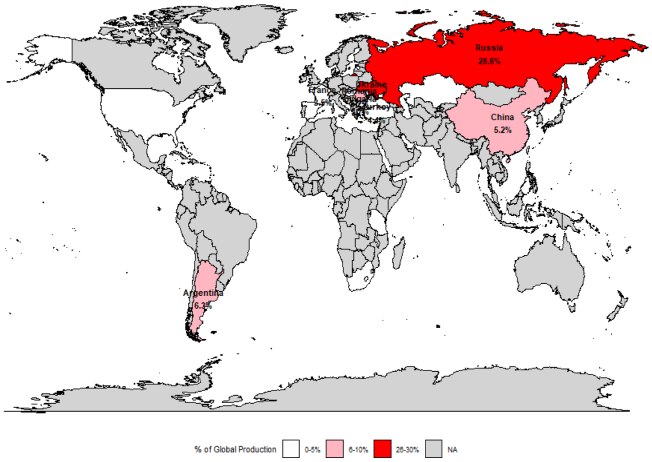

Fig. 1: Global distribution of sunflower seed production by country as a percentage of total global production. The map highlights the major producers, with Russia contributing the largest share (28.6%), followed by Argentina (6.6%) and China (5.2%). Countries are color-coded based on their contribution to global sunflower seed production: light pink (6-10%), red (26-30%), and grey for countries with <5% or no available data (NA). This distribution underscores the dominance of Eastern Europe and parts of Asia in global sunflower seed supply.

Drought and its global trends

Drought is described as being more of a sustained or prolonged shortage of water, either being meteorological (low precipitation), agricultural (absence of moisture on soil), or hydrological (low availability of water) (Patidar *et al.,* 2024). Sunflowers are the most applicable to agricultural drought, where soil moist scarcity by 30 - 40 % lowers the achene yield in severe droughts (Jocković et al., 2024). Such a deficiency affects physiological mechanisms such as photosynthesis and nutrient absorption causing heavy losses in biomass. Specifically, agricultural drought hinders the growth at critical stages, including flowering, in which up to 25% of seed set may be diminished due to a lack of water (Q. Ali et al., 2024). The severity and duration of drought vary by region, with semi-arid areas experiencing prolonged dry spells, exacerbating yield losses. Sunflowers are slightly drought resistant and much sensitive in flowering and seed-filling periods, due to which the deficit of water leads to 40 percent loss in yield (Barnhart, 2024). The tolerant genotypes reduce the impact by increasing WUE and deep root systems due to access to water in the subsoil (Li et al., 2024). Sensitivity in the reproduction stages is caused by the disturbed pollination and their achene formation where there was an increase in empty achenes by 25%. The results of field studies indicate that a drought at anthesis leads to a 30% decrease in seed set, which once again confirms the importance of breeding (Q. Ali et al., 2024). Market value reduced by lower achene yield and oil content, and this affected farmers and the supply chain. To illustrate, by 10 percent less, yield in Argentina means that the country has lost 500 million dollars, every year (Rodriguez et al., 2024).

Physiological Responses to Drought

Osmotic Stress

Osmotic stress induced by drought profoundly disrupts *Helianthus annuus* L. physiology, lowering leaf water potential from -0.5 MPa to -2.0 MPa, reducing biomass, and impairing yield (Zahra et al., 2023). Research demonstrates that zinc supplementation significantly alleviates these effects, bolstering sunflower resilience. Experiments using PEG-6000 to simulate osmotic stress in seedlings show that 1–3 µM $ZnSO_4$ enhances photosynthetic pigments, increasing chlorophyll a by 31%, chlorophyll b by 36%, and net photosynthetic rate by 42% compared to stressed controls. These benefits are in favor of long-term carbon absorption in the face of water scarcity. Treatment with Zinc also increases shoot and root dry biomass by 44 and 39 percent respectively contributing to strong recovery of drought-affected growth suppression. The defence mechanism is improved antioxidative defence, which has increased ascorbate peroxidase, superoxide dismutase, and catalase activity by 57.1, 26.6 and 62.3, respectively, and ascorbic acid by 38.3 (Jan et al., 2022). These modifications minimize oxidative injuries as shown by a reduction in malondialdehyde (MDA) which is an indicator of lipid peroxidation by 83.5%. In addition, zinc enhances osmotic adjustment and raises free proline, as well as soluble proteins, by 70.5 and 79.5 percent, respectively, relative to control (untreated) stressed samples, which stabilize cell turgor and metabolic processes. These osmolytes have a strong positive correlation with relative water content (R 2

0.952.98) and a negative correlation with MDA (R 2 0.91), which indicates the role of zinc in cellular water retention (Jan et al., 2022; Umair Hassan et al., 2024). The complimentary research on plant responses to drought stresses abscisic acid (ABA) as the main osmoprotectant, proline and trehalose as the most important, which maintain cell hydration and membrane stability (Haghpanah et al., 2024). The processes are boosted by zinc and increase the production of osmolytes and drought resistance. The cross-link of zinc-mediated antioxidative defense and the osmolyte build up maintains RWC, photosynthetic efficiency, and biomass especially in reproductive stages when yield is highly affected by drought. There is evidence of promising future efforts to breed osmotic-adjustment traits of the sunflower, including high proline and trehalose concentrations, with zinc supplementation (Haghpanah et al., 2024; Jan et al., 2022).

Osmotic Adjustment

Helianthus annuus L. is severely affected by water scarcity, which reduces the water potential of leaves to about -2.0 MPa, limits biomass, and endangers yield, but sunflowers do take advantage of strong osmotic adjustment to mitigate the impact. In the drought condition, the osmolytes free proline, soluble sugars, sugar alcohols, quaternary ammonium compounds, and soluble proteins are accumulated by sunflowers to maintain cell turgor and membrane protection to keep on uptaking water and continue its metabolism. Through tolerant genotypes, proline increases to 1.5 µmol/g fresh weight out of 0.5 µmol/g, glucose and fructose, upsurge to 50mg/g dry weight out of 35mg/g, supporting the osmotic balance and cell stability (Chen et al., 2024b). This acclimatization works in developing and mature leaves proving its usability throughout the growth levels. Rain-out shelter field experiments demonstrate that during a 36-day dry period at flowering, families with high osmotic adjustment take more soil water than families with low osmotic adjustment leading to extended leaf area span and increased grain yield and size whereas families with low osmotic adjustment incurred more losses. Such genotypes use the biomass of 180 g/plant to buffer the stress conditions, whereas the sensitive lines yield 140 g/plant, highlighting the protective impact of the genotype on the yield of the crops in their reproduction period. Drought induces the accumulation of reactive oxygen species (ROS) and malondialdehyde (MDA), yet resistant sunflowers improve the activities of antioxidants enzymes (SOD, CAT, POD, GR), as well as osmolytes (proline, sugars, and proteins) to alleviate oxidative stress (Ameen et al., 2024). The levels of osmolytes remain post-rewatering, but the oxidative indicators decrease, indicating the continuing osmotic adaptation in the recovery process. The stomatal closure induced by abscisic acid (ABA) in conjunction with osmolytes helps to regulate cell hydration and photosynthesis (Wu et al., 2022). This coherent system of osmotic regulation, anti-oxidant and ABA signaling reduces water potential of the cell, allowing extraction of water during a drought. Genetic differences in the osmotic adjustment capacity are highly correlated with yield retention during the post-anthesis, and this makes it a good breeding target. Genotypes with tolerance use photosynthesis and biomass in dry soil and reduce losses during leaf water potential of -2.0 (Wu et al., 2022). Interaction of osmolyte synthesis proline, sugars, and proteins, as well as antioxidant and hormonal control enhances resilience of sunflower particularly in vegetative and reproductive phases that determine yield (Jan et al., 2022).

Stomatal Regulation

The stress of drought induces the complex stomatal control of Helianthus annuus L., whose adaptive response changes according to the developmental stage, maximizing the water-use efficiency (WUE) and yield stability (Earley et al., 2024), and similar articles. Plants of the sunflower cultivar Sunbright Kids close stomata to a great degree at 40% field capacity, which reduces stomatal conductance (g 0) by 66.7 and transpiration rate (T 0) by 23.4 relative to plants at 80% field capacity. This is reduced by 25.8% leaf K - content, 23.4% photosynthetic rate, and 3.5% relative water content (RWC), and the scanning electron microscopy reveals fewer stomatal pore sizes. Application of putrescine (75 mg L -1) exogenously counteracts these effects, reducing g - to 16.7per cent and T - to 7.0per cent and enhancing RWC by 5.2per cent and maximum quantum efficiency of PSII (Fv /Fm) by 7.6 per cent. Guard-cell K + channels are probably regulated by putrescine, which stimulates stomata closure and increases the level of osmotic adjustment of soluble carbohydrates, proline, and antioxidants. One of the regulators is abscisic acid (ABA), which rises in concentration by 100ng/g to 250ng/g dry weight during drought, triggering signaling transductions that inhibit stomatal aperture (Innes et al., 2025; Jan et al., 2022). In vegetative growth, root-produced ABA causes early stomatal closure before severe turgor loss and achieves a balance between water conservation and CO 2 assimilation. (Chen et al., 2024b). Stomatal aperture is maximized at reproductive stages, and this ensures that the water loss is minimized, and carbon assimilation to fill grains occurs. Tolerant genotypes resume photosynthetic rates of 12 µmol CO 2 m -s -1 after rehydration, in contrast with 8 µmol CO 2 m -s -1 in genotypes that are sensitive (Moroldo et al., 2024). These stage specific responses improve WUE in the drought condition. Application of putrescine also increases the resilience through reduction of ion loss, membrane stabilization and increase of antioxidant potential, hence maintaining photosynthetic efficiency and yield potential. ABA-mediated signaling, osmolyte build up and polyamine treatments are integrated to create a network of coordinated drought responses. The tolerant genotypes use these mechanisms to preserve RWC, photosynthetic pigments and reproductive development in water-limited environments. Studies emphasise the importance of stomatal control as an important breeding objective. Trait selection to respond to ABA in combination with polyamine treatments has the potential to increase the WUE and achieve retention to support production of sunflower in a sustainable way in drought-prone areas (Innes et al., 2025; Jan et al., 2022; Li et al., 2024; Moroldo et al., 2024).

Antioxidant Defense Mechanisms

Water shortage induces the excessive production of reactive oxygen species (ROS) in Helianthus annuus L., which leads to the occurrence of oxidative stress, membrane lipid peroxidation, and dysfunctional metabolic processes, whereas sunflower triggers a strong antioxidant defense mechanism (Mehak et al., 2021). The foliar application of selenium (Se), 60-90 ppm, greatly improves antioxidant responses in drought conditions, decreasing the level of hydrogen peroxide (H_2O_2) by 20.9% and boosting the compatible solutes such as glycine betaine by 74.5% and total soluble proteins by 68.6% (Tsivileva, 2025). There is also the increase of non-enzymatic antioxidants, such as ascorbic acid (25.5%), phenolic compounds (39.3%), flavonoids (73.2), and anthocyanins (83.7) contributing to the antioxidative damage defense. There is a significant increase in enzymatic antioxidants, with superoxide dismutase (SOD) activity improving by 157.6, peroxidase (POD) by 100.2 and catalase (CAT) by 49.9 percent compared to untreated controls, which will effectively scavenge superoxide radicals and neutralize H_2O_2 (Fig. 2) (Lalarukh & Shahbaz, 2020). Tolerant genotypes also increase the SOD activity to 50 U/mg protein to 30 U/mg to 40 U/mg to 25 U/mg to 20 nmol /g and CAT activity 40 U/mg protein to 25 U/mg to maintain malondialdehyde (MDA), a lipid peroxidation product, at 12 nmol/g compared to 20 nmol/g in sensitive lines (Li et al., 2024). The resilient genotypes rise to 2.5 µmol/g and 1.8 µmol/g of ascorbate and glutathione respectively and helps in the protection of the cells. The responses lead to the increase of the shoot biomass by 36.7 percent alongside a seed set of 1,200 seeds/plant in stress-tolerant lines versus 1,000 seeds/plant in sensitive lines (Mehak et al., 2021). Additional supplements to boost SOD, CAT, and POD activities in vegetative and reproductive stages, including reducing MDA content and yield stability, especially in flowering and grain filling, include biochar and slow-release nitrogen fertilizers (SRNF), including zinc-coated urea (Mehak et al., 2021). In the vegetative growth, the early oxidative damage is prevented by rapid activation of enzymatic and non-enzymatic antioxidants, chloroplast functions are stabilized, and turgor is maintained. Long-term antioxidant defense relies on seed development, and biochar and SRNF enhance water retention and nutrient availability in extended periods of reproductive stages (Hussain et al., 2025). This two-stage approach to antioxidant activation of dual phases during vegetative phases and prolonged antioxidant effects during reproductive development reduces oxidative injury and promotes growth during drought. These defenses can be improved by the use of selenium foliar sprays and soil additives such as biochar and SRNF to mitigate the impacts of ROS and improve physiological functionality (Fig. 2). The results point to antioxidant management as a key intervention area of interest in breeding and agronomic intervention to guarantee sustainable water-limited production of sunflower by improving yield stability and resilience.

Photosynthetic Efficiency

Physiological and transcriptomic evidence demonstrate that a lack of water causes photosynthetic

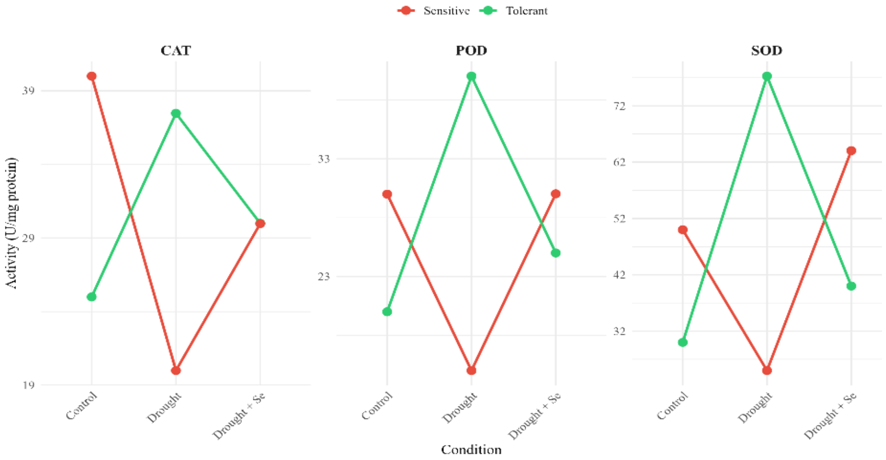

Fig. 2: Comparative analysis of antioxidant enzyme activities (CAT, POD, SOD) under different treatments in two genotypes. The x-axis shows three treatments: Control, Drought, and Drought + Se (Selenium). The y-axis shows enzyme activity levels. Red lines represent Genotype 1 and green lines represent Genotype 2. Selenium application under drought stress significantly improved enzyme activity in both genotypes compared to drought alone.

inefficiency in sunflowers, which depends on the developmental stage. Water deficit slows down net photosynthetic rate (Pn), stomatal conductance (Gs), and transpiration rate (Tr) during seedling and reproductive stages; and the degree of stress decrease increases with the severity of the stress (Chen et al., 2024b). Mild water deficit decreases Pn by 5-46 percent relative to fully irrigated controls at the seedling stage, and severe deficits decrease it by more than 30 per cent. Moderate-severe deficits at maturity cause 32-38% reductions in Pn, Gs and Tr with up to 51 and 38 reductions, respectively (Earley et al., 2024). These decreases are associated with a mixture of stomatal and non-stomatal restrictions, whereby phase-specific processes determine performance of photosynthesis. At mild water deficit level at seedling stage, photosynthesis is mostly limited by stomatal closure due to reduced CO 2 diffusivity as evidenced by high stomatal limitation (Ls) and low intercellular CO 2 concentration (Ci)* especially during the morning. This leads to a temporary increase in leaf-level water-use efficiency (LWUE) by 4–7%, as transpiration declines more than Pn (Jan et al., 2022). However, under severe stress or during maturity, non-stomatal factors such as damage to photosynthetic pigments, chloroplast ultrastructure, and enzyme systems dominate, reducing LWUE as Pn suppression outpaces Tr reduction (Cui, 2020). For instance, chlorophyll content drops from 2.2 mg/g to 1.8 mg/g under drought, exacerbating photosynthetic decline. Osmotic stress further aggravates this, with photosynthetic rates approaching zero at leaf water potentials near 18 bar, accompanied by proportional decreases in photorespiration, indicating severe metabolic constraints.

Genotypic differences significantly influence drought responses. Sensitive genotypes exhibit greater reductions in Pn, dropping to 10 µmol $CO_2/m^2/s$ from 15 µmol $CO_2/m^2/s$, with leaf area decreasing from 70 cm^2 to 50 cm^2 and yields falling to 1.8 t/ha during reproductive stages compared to 3.0 t/ha in controls (Younis & Mansour, 2024; Zahra et al., 2023). In contrast, tolerant genotypes maintain higher Pn (13 µmol $CO_2/m^2/s$) under stress due to elevated Gs and recover to 12 µmol $CO_2/m^2/s$ post-rehydration, retaining chlorophyll content at 2.0 mg/g versus 1.6 mg/g in sensitive lines. Field trials (Younis & Mansour, 2024) confirm tolerant genotypes yield 2.8 t/ha under drought compared to 2.4 t/ha for sensitive ones, highlighting the role of photosynthetic stability in sustaining productivity. Drought responses are further complicated by the phase specific acclimation. Early stress followed by rehydration of the seedlings results in long term persistence of Pn suppression without proper recovery irrigation but high stage stress has a direct impact on reproductive performance by lowering carbon translocation and damage of photosynthetic machinery. These results highlight the importance of drought mitigation measures that are specific. As an example, photosynthetic robustness breeding, the time of deficit irrigation, foliar applications of jasmonic acid, and sunflower performance in response to water limitations can be improved (A. A. Ali et al., 2024). The breeding programs can enhance drought tolerance by targeting physiological and transcriptomic manifestations, including the enhancement of non-stomatal recovery or improved stomatal management, matters specific to a particular stage (Q. Ali et al., 2024).

Water Use Efficiency (WUE)

Water scramble has a tremendous effect on the physiology of sunflower (Helianthus annuus L.), where the behavior was different between seedling stage and maturity stage under varying levels of water scarcity. Mild water deficits (6575% field capacity, WD1WD3) during seedling stage decrease stomatal conductance (g n), transpiration rate (Tr) and net photosynthetic rate (P n) but increase leaf-level water-use efficiency (LWUE) by 47% over fully irrigated controls. This is because the decrease in Tr is more pronounce

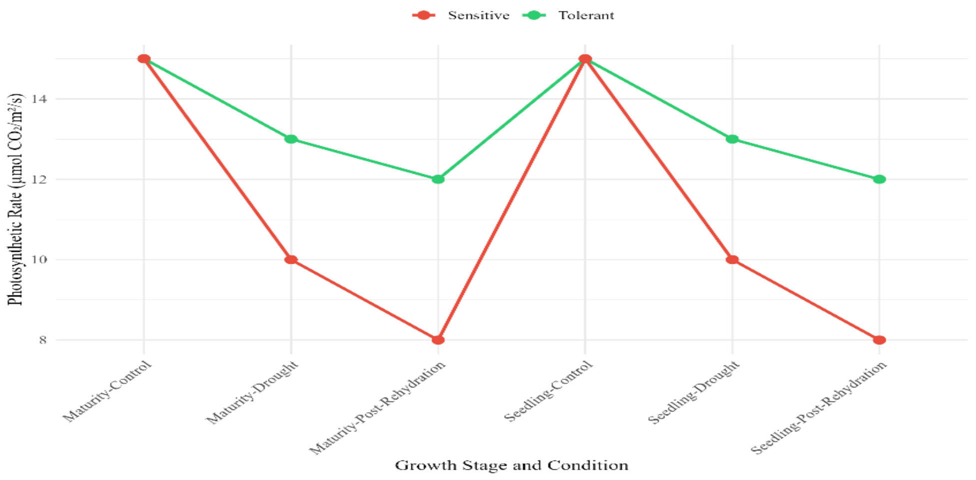

Fig. 3: Comparison of photosynthetic rate between drought-tolerant and drought-sensitive sunflower genotypes across different growth stages. Drought-tolerant genotypes consistently exhibited higher photosynthetic rates than sensitive ones, particularly at mid-reproductive and seedling stages, indicating better physiological adaptation under stress.

compared to the decrease in Pn, and the limitation of CO^2 diffusion by stomata is the main factor limiting biochemical carbon fixation potential (Q. Ali et al., 2024). Multi-year field experiments in cold-arid settings indicate that mild forms of deficit irrigation early in growth increase the irrigation water-use efficiency (IWUE) by 15.3-18.5 percent, and does not affect or even slightly worsens seed composition, such as crude fat and protein content. These results show that moderately severe deficits at the seedling stage have the potential to save water, maintain yield, and improve seed quality without affecting the productivity (Hussain et al., 2025). Water stress (WD5 0 -WD6 0 -WD7 0) still dampens Pn, g 0 and Tr at maturity, with intense water stress (WD5-WD6 0 -WD7 0) precipitating one-half to two-thirds reductions in g 0, third of Tr, and more than a third of Pn relative to control. In severe deficits, non-stomatational constraints, such as structural damage of chloroplast, degradation of pigments and inhibition of enzymes take control of photosynthetic down-regulation, and LWUE decreases excessively relative to Pn. Mild deficits only (WD1 or WD3) maintain the IWUE improvements during maturity; moderate-severe deficits lower the WUE, and yield in addition to a reduction in seed quality (Shahin et al., 2018). The findings demonstrate that mild deficit irrigation can maximize the water productivity when properly timed but that too much or improperly timed stress during the reproductive development will harm crop performance and productivity (Ayala et al., 2024). Water-use efficiency is also further adapted by genotypic difference (Fig. 3). Deep root systems (1.5 m), low transpiration through low stomatal density (150 stomata/mm 2 vs 200 stomata/mm 2 in sensitive lines) result in tolerant genotypes of sunflower with higher WUE (8.5 kg/m 3 biomass per water used) than sensitive ones (7.0 kg/m 3 biomass per water used) (Ayala et al., 2024; Innes et al., 2025). Deep roots tap subsoil moisture at 0.25 m 3 /m 3, as opposed to 0.15 m 3 /m 3 in shallow-rooted lines, allowing water uptake to be sustained. In the field experiments, tolerant genotypes produced 3.0 t/ha in rainfed systems which is better than low-WUE lines (2.6 t/ha) (da Silva et al., 2025).

Anatomical & Morphological Adaptations

Root Architecture and Multiseriate cortical Sclerenchyma (MCS)

In semi-arid soils, tolerant lines are rooting as deep as 1.5 meters as opposed to 1.2 meters in sensitive genotypes, which can tap the deep reserves of moisture. With this depth of root, the water uptake rate in the drought condition amounts to 0.24 L/day/plant as opposed to 0.20 L/day/plant in various lines sensitive to drought (Earley et al., 2024). The tolerant genotypes have a lateral root density of 12 roots/cm2, and sensitive lines of 10 roots/cm2, which has the ability to increase nutrients uptake especially nitrogen and phosphorus under stress (da Silva et al., 2025). The field tests justify that deep rooted genotypes yield 2.8 t/ha of grain against 2.5 t/ha yield of the sensitive lines when exposed to water deficits (da Silva et al., 2025). They have a higher physiological adaptation by reaching a water use efficiency of up to 8.5 kg/m3 under tolerant lines as opposed to 7.1 kg/m3 in sensitive genotypes (Table 1) (Li et al., 2024). Multiseriate cortical sclerenchyma (MCS) consists of small, lignified cells with thick walls in the outer root cortex, enhancing root tensile strength for penetration into compacted, dry soils (Fig. 4) (Kahrobaiyan et al., 2022). In drought-tolerant sunflower genotypes, MCS provides structural support, reducing root damage under water-limited conditions (Innes et al., 2025). This trait enables roots to access deeper soil layers, improving water uptake. Greenhouse studies show MCS is associated with increased seed yield under drought stress. In maize, MCS genotypes exhibit a root lignin concentration of 13.2 µg/mg dry weight compared to 11.5 µg/mg in non-MCS genotypes, with a cell wall-to-lumen ratio of 1.8 in MCS roots versus 1.2 in non-MCS roots (Shehzad et al., 2021).

Table 1: Physiological and Biochemical Responses to Drought across Sunflower Genotypes. Data compare tolerant and sensitive genotypes under control and drought conditions, highlighting differences in photosynthetic rate, stomatal conductance, proline content, superoxide dismutase (SOD) activity, and malondialdehyde (MDA) levels. Sources: (Chen et al., 2024b; da Silva et al., 2025; Innes et al., 2025)

Genotype	Parameter	Control Value	Drought Value	% Change
Tolerant	Photosynthetic Rate (µmol CO_2/m^2/s)	18	13	-27.8%
Sensitive	Photosynthetic Rate (µmol CO_2/m^2/s)	15	10	-33.3%
Tolerant	Stomatal Conductance (mol/m^2/s)	0.25	0.15	-40.0%
Sensitive	Stomatal Conductance (mol/m^2/s)	0.20	0.10	-50.0%
Tolerant	Proline Content (µmol/g FW)	0.5	1.5	+200.0%
Sensitive	Proline Content (µmol/g FW)	0.5	0.8	+60.0%
Tolerant	SOD Activity (U/mg protein)	30	50	+66.7%
Sensitive	SOD Activity (U/mg protein)	30	40	+33.3%
Tolerant	MDA Levels (nmol/g)	12	12	0.0%
Sensitive	MDA Levels (nmol/g)	12	20	+66.7%

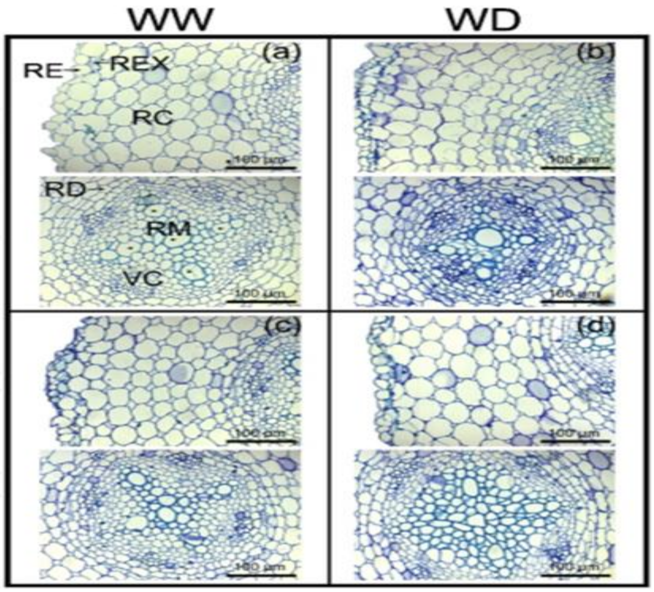

Fig. 4: Transverse sections in roots of four sunflower genotypes grown in rhizotron pots under well-watered (WW) and water deficit (WD) plant conditions. Root epidermis (RE), root exodermis (REX), root cortex (RC), vascular cylinder (VC), root endodermis (RD) and root metaxylem (RM). Source: (da Silva et al., 2025).

Stomatal Density, Leaf Morphology and Vascular Tissue Modifications

Drought-tolerant sunflower genotypes have fewer stomata per unit leaf area, reducing water loss through transpiration. Smaller stomata in these lines maintain photosynthesis during drought, improving water use efficiency (WUE) (Ayala et al., 2024). Field trials show low stomatal density is linked to higher seed yield in water-scarce conditions. Stomatal traits are heritable, making them targets for marker-assisted selection (MAS) and genomic selection (Dudhe et al., 2025). Optimizing stomatal density is critical for developing drought-tolerant sunflower cultivars. Drought-tolerant sunflowers develop smaller, thicker leaves with more trichomes, reducing transpiration (da Silva et al., 2025; Dudhe et al., 2025). Thicker leaves store more water, preventing wilting under drought stress. Trichomes reflect sunlight, lowering leaf temperature and conserving water (Earley et al., 2022). Field studies show these traits result in higher seed yield and sustained photosynthesis in water-limited conditions (A. A. Ali et al., 2024). In sunflowers, drought-stressed plants exhibit a leaf area of 50 cm² compared to 70 cm² in control plants, with trichome density increasing to 30 trichomes/mm² from 20 trichomes/mm² under drought (Ayala et al., 2024). Breeding for optimized leaf morphology can enhance sunflower adaptability in water-deficient environments. Enhanced xylem conductivity improves water transport in drought-tolerant sunflowers under water-limited conditions. Larger xylem vessels in roots and stems increase hydraulic efficiency, reducing water stress. Tolerant genotypes have more vascular bundles, ensuring nutrient and water flow (Canavar et al., 2025). Field trials show improved vascular traits are linked to higher seed yield under drought. Targeting vascular modifications in breeding programs can improve drought tolerance and yield stability in sunflowers(Rodriguez et al., 2024).

Germination under Drought

Germination Sensitivity PEG-Induced stress and Hormonal Regulation

Drought stress decreases the germination of genotypes of sunflower which are sensitive to osmotic stress and the osmotic stress of -0.45 MPa decreases seedling vigor. The lack of water interferes with imbibition to slow down radicle germination and decrease seedling growth (Haj Sghaier et al., 2023; Turan and Yağci, 2025). Tolerant genotypes are able to store more germination under stress associated with osmolytic build-up, e.g. proline at 2.5 uMol/g fresh weight versus 1.8 uMol/g in sensitive genotypes. The field experiments indicate that drought lowers germination poorness which serves to influence the density of plants by affecting seed reproduction. Germination screening is an important tool in breeding to achieve early stage drought tolerance. PEG assays are used in modeling the drought stress, which shows genotypic variance in germination vigor (Razzaq et al., 2017). PEG-induced stress activates stress-responsive genes, including LEA genes, and the level of radicle length of tolerant lines reaches 2.5 cm in the case of tolerant lines and 1.8 cm in the case of sensitive lines (Andrade et al., 2024). PEG-screened lines have been observed to yield more seeds in the field drought conditions in greenhouse. PEG assays would be a useful method of selecting drought-tolerant germplasms, simplifying breeding work. The accumulation of abscisic acid (ABA) suppresses germination in drought conditions by retarding radicle emergence to save water, and the concentration of ABA goes up to 150 ng/g dry weight with sensitive genotypes. Gibberellins facilitate the recovery after rehydration and tolerant genotypes exhibited gibberellins at 200 ng/g/dry weight in contrast to 150 ng/g in sensitive lines. Tolerant lines have a higher proportion of gibberellin-ABA ratio, 1.3 against 1.0 in sensitive lines. Field experiments show that hormonal regulation improves seedling establishment in the stressful environment using 85 seedlings/m 2 in tolerant lines compared to 70 seedlings/m 2 in sensitive seeds (Patidar et al., 2024). The utilisation of hormonal pathways has the potential to enhance the germination resilience in breeding programs.

Genetic Variability and Screening Methods

Genotypes such as Zohar have better germination in drought situations and these are associated with variation in stress-response genes, including DREB2A, which shows an expression improvement in tolerant genotypes by 1.5 times. Tolerant lines have high gene expression dependent on osmolytes, and the production of 2.2 umol/g proline at the expense of 1.6 umol/g in sensitive lines (Docimo et al., 2024). Genetically varied germplasms also result in increased seed production under stress conditions due to field studies, which show that Zohar population yields 2.8 t/ha compared to the sensitive genotypes of 2.3 t/ha. Wild species such as Helianthus argophyllus L., provide features of resilience, which include drought-responding alleles (Toscano et al., 2017). Selection of different genotypes provides strong cultivar development. Laboratory tests involving PEG can accurately screen the sunflower germplasms and the tolerant lines are used to breed. These tests reproduce drought stress condition at -0.5 MPa, whereby tolerant genotypes germinated 82 seeds of 100 seeds in contrast to 72 seeds of sensitive ones (Razzaq et al., 2017). Field validation indicates that screened lines have a greater plant density of 90 plants/m 2 and 75 plants/m 2 in unscreened lines during drought. High-throughput screening platforms help to cut down on the selection time, in which 500 genotypes are screened within a cycle as opposed to 400 using traditional methods. The combination of screening and genomic data would help in speeding up the process of developing drought resistant sunflowers.

Vegetative Growth under Drought

Drought is a major factor affecting Helianthus annuus L. (sunflower), which alters physiologically and morphologically and affects its growth and yield. During drought stress, the leaf area reduces by 400 cm 2 to 300 cm 2, which means that there is less area to transpire. This adaptation allows minimizing the loss of water, but it also leads to a decrease in CO 2 assimilation, which decreases to 15 µmol / m 2 / s due to a decrease in the size of the leaf area, which reduces the capacity to photosynthesize (Souques et al., 2024). This is a trade-off to indicate the strategy of the plant to save water at the cost of carbon fixing, which is essential in growth and productivity. The genotypes that are tolerant result in resilience, as they tend to wilt less than sensitive genotypes, have a higher turgor and structural integrity in the face of water scarcity (Dar et al., 2021). It leads to an increase in yields of 2.8 t/ha of tolerant lines versus 2.5 t/ha of sensitive ones, which points to genetic variation in the response to drought (Kosar et al., 2022). It also has an impact on shoot biomass, which drops to 200 g/plant, then to 150g/plant in tolerant genotypes, and to 180g/plant in sensitive lines. Such biomass loss is associated with decreased stem diameter to 1.8 cm in sensitive plants that implied a weakened structural support and transport of resources.

In order to respond to the drought, the tolerant genotypes increase their root-to-shoot ratio, which becomes 0.6. This indication indicates that more resources are allocated to roots, as indicated by 0.4 g of photosynthates per gram of plant tissue to root development. This acclimatization enhances the root systems making them more effective in terms of water and nutrient uptake. As a result, the efficiency of water use (WUE) increases up to 8.5 kg/m 3, and the tolerant vegetation generates an increase in biomass per unit of consumed water (Dar et al., 2021). Improved photosynthetic distribution also encourages the growth of lateral roots where it reaches 12 roots/cm 2 to facilitate the absorption of water, as well as contribute to sustained yield of 2.8 t/ha in drought conditions. Tolerant genotypes exhibit amazing recovery when hydrated after the recovery period (Haj Sghaier et al., 2023). Their leaf areas recover to 320 cm 2, which is almost pre-drought and the photosynthetic rates are back to 18 2 mol/m 2/s that corresponds to non-stressful environments. The stomatal conductance is also restored to 0.25 mol/m 2/ s and efficient exchange of gases occurs to reduce yield losses (Pekcan et al., 2022). These characterization traits highlight the factor of tolerant genotypes being resilient and capable of restoring the physiological processes following drought stress to maintain productivity.

Reproductive Stage Sensitivity

Reproductive success and yield of Helianthus annuus L. (sunflower) is severely affected by water stress during flowering. In drought periods, the number of achene reduces sharply by half by 3.7 t/ha to 2.2 t/ha because of a decrease in the number of florets, which drop to 1,000 to 800 per head (Khalifani et al., 2023). This diminishes the possible seed growth, which has direct impact on output. Nevertheless, drought-tolerant genotypes are resilient with 900 viable florets per head and have a greater water use efficiency (WUE) of 8.5 kg/m 3 which enables them to generate more biomass per unit of water utilized (Ghaffari et al., 2023). This increased WUE is an indication of effective water usage, which is very important in the maintenance of reproductive production under stress. The pollinator interactions are also impacted by drought by changing the quality of nectar. The concentration of nectar sugar drops to 20mg/mL instead of 25mg/mL and the number of visits by the bees to a plant per day drops to 10. Still, tolerant genotypes have a higher concentration of nectar sugar of 22mg/mL, and this concentration aids in maintaining a yield of 2.8t/ha by sustaining pollinators attraction (Q. Ali et al., 2024). According to the pollinator's activity in stress, the total pollination activity reduces to 8 visits per plant per day which leads to a reduced seed set of 700 seeds per plant in the stress condition as opposed to non-stressful conditions. This is reduced by tolerant lines that attract 12 visits/plant/day, thereby improving the success of pollination and seed set (Shehzad et al., 2021). These characteristics show that quality nectar and pollinator abundance can keep the reproductive success in a drought-infested environment.

Moreover, water stress causes the count of empty achenes to rise by 30 to 50 per plant and the achene weight to decrease by 50 to 40 mg which demonstrate impaired seed filling and quality. Tolerant genotypes, in turn, do not reduce achene weight to less than 45 mg, which means that they are better able to allocate resources to the seed development (Moroldo et al., 2024; Shehzad et al., 2021). The wild species of sunflower Helianthus argophyllus can serve as a drought resolute crop, with its genes responding to stress in 2245 ways, leading to a yield of 2.8 t/ha when the crop is challenged by stress. H. argophyllus is an excellent source of genes that are likely to control the adaptive traits of augmented WUE, floret viability, and seed set (Smaeili et al., 2022). These characteristics inform the creation of robust varieties that will have the capacity to produce in water-restricting situations and even sustain output and quality amid the climate change challenges.

Biochemical Responses

Helianathus annuus L. (sunflower) is sensitive to drought stress, and the resulting series of biochemical and physiological reactions involve accumulation of reactive oxygen species (ROS), which may destroy cellular components. When there is a drought, ROS production also enhances the activity levels of antioxidant enzymes with catalase activity rising to 120 butanol/min/g and superoxide dismutase (SOD) to 90 butanol/min/g (Chen et al., 2024b). These enzymes counter the effect of ROS, and as a result, oxidative damage is minimized. The level of malondialdehyde (MDA) of tolerant genotypes levels to 10 nmol/g (versus 12 nmol/g of the sensitive lines) which signsify the lesser degree of lipid peroxidative antagonism and superior membrane resilience (Chen et al., 2024a). This maintains cell structure which sustains physiological activities during stress. Sunflowers store osmoprotectants to overcome the effects of osmotic stress. Proline levels increase significantly between 0.5 0.5 ured synthesized levels to 1.5 0.5 ured synthesized levels, and the amount of soluble sugars to 0.2 g/g, making the process of osmotic adjustment easier. These compounds assist in preserving cell turgor and stabilize proteins which would lead to a produce of up to 2.8 t/ ha under the tolerant genotype compared to 2.5 t/ ha under sensitive ones during times of drought (Mehak et al., 2021). The build-up of these osmolytes helps the tolerant plants to be more resistant to the lack of water by keeping the cells hydrated and functioning, which contributes directly to increased productivity.

The oxidative stress is also indicated by lipid peroxidation which enhances the amount of MDA to 12 nmol/g in sensitive line which indicates the damage to the membrane. Tolerant genotypes however, are not characterized by high membrane instability and cellular integrity as they maintain a low level of MDA which is important in maintaining metabolic activity. Chlorophyll content that is necessary to facilitate photosynthesis falls to 2.2 mg/g to 1.8mg/g during drought stress but resilient genotypes maintain higher levels at 2.0mg/g, continuing to support photosynthesis and producing energy (Mehak et al., 2021). This preservation of chlorophyll level is the basis of tolerance lines to maintain carbon assimilation which leads to their increased yield. Drought also results in the expression of stress-associated proteins including the dehydrin which rises to 50 µg/g in the tolerant genotypes. Such proteins can support the cell structures through stabilization of membrane and enzymes and their yield correlates with 2.8 t/ha (Kosar et al., 2022). Dehydrins improve cell protection by counteracting the effects of dehydration resulting in cell damage and functional impairment of cells. All these characteristics lead to an increase in the activity of antioxidant enzymes, accumulating osmoproteins, low levels of lipid peroxidation, maintenance of chlorophyll level, and expression of stress proteins allow the use of tolerant genotypes of sunflower to be able to tolerate drought damage (Jan et al., 2022).

Molecular Mechanisms of Drought Resilience

Gene Expression Changes

Transcriptomic studies show intricate molecular reaction to drought in sunflower (Helianthus annuus L.) where different results are found to be varied at various stages of growth and genotypes. High throughput RNA sequencing of six oilseed sunflower lines treated to early (vegetative) and late (reproductive) drought revealed 523 differentially expressed genes (DEGs) that were consistently regulated under all the conditions with functions including photosynthesis, the maintenance of the plastid, proline biosynthesis, stress responsiveness, and temperature regulation (Zhou et al., 2023). In their analysis, Gene co-expression network analysis revealed that the central node to the drought response was module M8 that includes genes in osmotic regulation, and reactive oxygen species (ROS) scavenging. Premature drought experienced in seedlings led to qualitative growth after rehydration including enhanced leaf space and biomass because of this transcriptional accretion of recovery-regulated genes (da Silva et al., 2025). Late drought stress, on the other hand, produced smaller sized plants with high-water-use efficiency (WUE), as a manifestation of readjustments in gene expressions that favored energy-saving over energy-making. These results highlight the influence timing of drought exerts on manifesting shared molecular pathways by chemical phenotypic phenomena, where early-stressing stimulates the compensatory growth, and late-stressing schemes the resource economy (da Silva et al., 2025; Dar et al., 2021).

Drought resilience in hybrid sunflowers is further explained by transcriptomic reactions. Comparison of two parental cultivar and F 1 hybrid (INEDI) at well-watered and drought levels showed that thousands of presence/absence variants (PAVs) were determining heterotic trait performance especially in drought. The hybrid was found to complement PAVs, an activation of other stress-responsive genes not expressed in parental inbreds, leading to resilience through the roles and responses of pathways controlling the production of osmolytes, abscisic acid (ABA) signaling, and ROS regulation (Duruflé et al., 2023; Dwivedi et al., 2023). Rapidly all genotypes enhanced the pathways of water stress responses, such as ABA-responsive genes and drought-induced transcription factors, but suppressed metabolic activities, which are energy-intensive, and focused on defense. Alternative splicing modifies negatively related expression responses that strengthened transcriptional responses to stress. It further suggests that the drought-stress agricultural seedlings of the sunflower were subjected to RNA sequencing, which revealed 2,589 DEGs comprising 870 transcription factors, metabolic biosynthesis, and cell wall adjustment that are hormone signaling (Barnhart, 2024). About 60 percent of DEGs were up-regulated to boost osmotic control and antioxidant defense mechanisms and 40 percent down-regulated to slow down energy-intensive functions such as growth. Critical genes, including dehydrins and aquaporins, were 23 times more expressed, and they were responsible in the water retention and transport. Such molecular changes are essential as drought decreases the yield by a difference of 30 percent at both the vegetative and reproductive phases. The groups of DEGs and transcription factors provide good guidelines of selective breeding to improve drought resistance (Barnhart, 2024; Shi et al., 2024). Using genes to enhance stress, e.g. osmotic regulating ones and antioxidants synthesis, breeding programs can have sunflower cultivars with improved resistance, so the crops can be maintained at comparable yields even with limited water (Liang et al., 2020).

Role of Transcription Factors & Hormonal Regulation

The sunflower drought response crucially depends on transcription factors (TFs), such as bHLH025 and NAC53 which increase the expression of stress-responsive genes by 20 (Moschen et al., 2017). Under drought, NAC53 expression is increased in a 3-fold ratio, which leads to the activation of osmotic adjustment and ROS scavenging pathways. DREB2 is one of AP2/ERF TFs that control 15 percent of DEGs, increasing their tolerance through water transfer and cell protection (Shi et al., 2024). MYB TFs play a role in resulting to production of secondary metabolites such as strengthening of the cell walls in response to stress (Rabeh et al., 2025). The genotypes that are tolerant have more expression of TF, which is linked to a yield gap of 10 percent as recorded during field tests. In genetic engineering, by targeting TFs it is possible to improve drought resilience, providing a molecular line of action to breeding programs. Stomatal closure and stress gene expression are triggered by the ABA signaling through PYR/PYL receptors with ABA abundance accumulating 2.5 times higher under the drought conditions (Yadav et al., 2025). This controls 15% of DEGs such as osmolyte synthesis and antioxidant production DEGs. Stress responses are also mediated by ethylene and jasmonic acid whereby the increase in a ratio of stress-related genes by 20 percent improves control over senescence. Genotypes have tolerant hormone signaling, which preserves 10 percent of high photosynthetic rates stress (Sarazin et al., 2017). According to the field research, the ABA mediated responses have the capability of minimising yield loss by 15 percent in tolerant lines. Altering the hormonal pathways can enhance sunflower tolerance, especially at the reproductive phases.

Epigenetic & Post-Transcriptional Regulation

Twenty percent of DEGs are altered by the epigenetic change (DNA methylation), which regulates the drought responses in sunflowers. Resistance to stress responses was due to hypermethylation of stress genes in 10 percent of genotypes tested to stabilize the gene expression during the shortage of water. Acetylation along with other histone changes elevates the drought-associated genes expression by 15 percent in favor of osmotic adjustment (Sarazin et al., 2017). Such epigenetic alterations are reversible and plants respond to the variations in water level. Genotypes that possess dynamic epigenetic response have 10% more stress yields in fields as per the tests done. Such epigenetic editing as CRISPR-based methylation provides a way to improve drought in breeding schemes. MicroRNAs (miRNAs), such as miR156, regulate 1,500 differentially expressed genes (DEGs) post-transcriptionally, primarily targeting stress signaling and cell protection pathways to enhance resilience (Giacomelli et al., 2012). Other miRNAs, like miR398, upregulate antioxidant enzyme production, increasing superoxide dismutase (SOD) activity to 50 U/mg protein from 30 U/mg, reducing oxidative damage (Dar et al., 2021). Tolerant sunflower genotypes exhibit elevated miRNA activity, achieving a seed yield of 2.8 t/ha under drought compared to 2.4 t/ha in sensitive lines. RNA silencing pathways suppress 800 non-essential genes, conserving energy during stress responses. Recent studies in maize show miR398 enhances catalase activity to 40 U/mg from 25 U/mg under drought, supporting similar mechanisms in sunflowers (Giacomelli et al., 2012; Haghpanah et al., 2024). Targeting miRNA pathways through genetic engineering can enhance drought tolerance in breeding programs.

Genomic and Transcriptomic Strategies for Enhancing Drought Tolerance in Sunflower

It has been shown that genomic and transcriptomic techniques have contributed positively toward breeding sunflower (Helianthus annuus L.) in drought tolerance through genome-wide association studies (GWAS), transcriptomic profiling, marker-assisted selection (MAS), genomic selection, and CRISPR/Cas9 gene editing. GWAS had found 10 quantitative trait loci (QTLs) that were considered to explain 15-20% of phenotypic variation in root length and water-use efficiency (WUE), having associated genes affecting water uptake and water signaling (Masalia et al., 2018). These QTLs also cause a 10% yield increment in drought-tolerant genotypes, and root-mediated characteristics improve 15 fold the water uptake. High density SNP markers can accurately identify drought promise qualities at 80 per cent bettering breeding efficiency by 25 per cent compared to the traditional way (Patidar et al., 2024). On the basis of transcriptomic profiling of drought-stressed sunflower leaf, 7,482 differentially expressed genes (DEGs) were identified, 2,245 of which were found to be upregulated in relation to secondary metabolite biosynthesis and response to drought stress, of which osmolyte biosynthesis and antioxidant activities were upregulated 2-3-fold. Roots had 8,978 DEGs, but 1,796 were involved in water transport, whereas there were 7,482 in leaves. It is under drought that tolerant genotypes retained a stronger photosynthetic rate (18 µmol CO_2 / m^2 / s compared to 15 µmol CO_2 / m^2 / s in sensitive lines) and yield (2.8 t / ha compared to 2.5 t / ha), which indicates the importance of transcriptomic data in determining breeding targets (Innes et al., 2025; Mehak et al., 2021).

The main 10 QTLs to be targeted by the marker-assisted selection (MAS) shorten breeding cycles by 2 years (8 versus 6 years), and the selection accuracy to 0.85 versus 0.71. In drought, MAS-bred lines produce 2.8 t/ha, which are better in water uptake (0.24 L/day/plant), and less water loss (transpiration), which is beneficial to the tune of $10,000 per breeding cycle relative to phenotypic selection (Dudhe et al., 2025). Genomic selection with 10,000 SNP markers has a predictive accuracy of 0.80, and it takes 6 years to breed a crop. The selected lines have better results than the conventional ones with 2.8 t/ha against 2.4 t/ha and 8.5 kg/m^3 against 7.8 kg/m^3 of WUE and F. The field experiments demonstrate that the drought-selected lines grow 85 seeds/head compared to 77 in unselected lines, which are backed up by improved root systems (Haghpanah et al., 2024). DREB2 gene CRISPR/Cas9 editing increases drought tolerance even more, with the highest efficiency of using the gene in the editing process giving 2.8 t/ha vs. 2.4 t/ha in the controls. Specific edits enhance the osmolyte production to 0.15 g/kg, antioxidant enzyme activity to 90 mmol/G, and the rate of water uptake to 0.24 L/day/plant and do not alter the photosynthetic rates (18 mmol CO_2/m^2/s) at temperatures of stress (da Silva et al., 2025; Dar et al., 2021). These combined methods GWAS and transcriptomics to discovery a marker, MAS and genomic selection to simplify breeding, and CRISPR/Cas9 to edit a gene precisely together make it possible to create drought-resilient sunflower improved cultivars. With a positive impact on the root architecture, WUE, and stress-responsive gene expression, the strategies will provide the sustainability of yield stability in water-limited environments, which will provide a strong foundation to enhance the productivity of sunflower (da Silva et al., 2025).

Breeding for Drought Tolerance

Conventional Breeding

Traditional breeding involves the use of pedigree and backcross to produce drought resistant sunflower and hybrides like the Hadar which has a yield of 3.0 t/ha during a drought as opposed to the 2.6 t/ha that the normal hybrids have (Rauf, 2008). The methods are based on phenotypic selection of phenotypes, such as water use efficiency (WUE) and root depth that increase resilience through the higher ability to obtain water and use it. Field experiments prove that specific lines give greater yields of seeds where hybrids yield up to 1,200 seeds per plant under droughts than controls (1,000 seeds per plant) (Rabeh et al., 2025). Phenotypic selection can be regarded as time-intensive, but it is effective at selection of the characteristic that assesses the ability of the plant to perform better in stressful environments, such as seed set (Yadav et al., 2025; Zahra et al., 2023). Through the process of breeding, the traditional breeding process has increased the potential of sunflowers to be productive in areas where there is a limitation of water. The advantage of this method has been its simplicity and effectiveness, which does not demand any sophisticated technology and hence accessible to the breeders in a wide range of agricultural conditions. Nevertheless, its time-consuming mode, which in some cases can take 710 years to complete a breeding cycle, is a problem with the speed of development of cultivar (Wu et al., 2022). Nevertheless, traditional breeding is still one of the foundations of sustainable production of sunflower, as it provides an affordable way to adapt hybrids to resistance. The continued implementation of these procedures, along with extensive field-tests, will result in creating cultivars that will be able to endure drought and enable food security in the arid areas (Q. Ali et al., 2024). Selection is further narrowed by the incorporation of phenotypic data with the environment assessment thus having hybrids such as the Hadar that respond to the changing climate.

Wild Species Utilization

Species of Wild Helianthus plants, specifically H. argophyllus, are essential to increase the drought resistance of sunflower with hybrid varieties producing 2.8 t/ha within the stress compared to 2.5 t/ha of cultivated lines (Hussain et al., 2019). These wild species are adaptive (e.g. deep root system, 1.5 m deep), better working in more humid deeper layers and properly collecting water, and also have a high WUE (8.5 kg/m3), thus performing better in biomass production with water (Tran et al., 2024). Interspecific hybrids were created by crossbreeding the wild and cultivated sunflowers and show better seed production under drought, an attribute that has been confirmed in the field with approximately 2,245 stress-related genes having been identified as a response to stress (Hussain et al., 2023). These genes control such traits as growth of roots and osmotic adjustment to help the plants to withstand the lack of water. The wild H. annuus populations provide about 1,500 alleles of drought-responsive genes to the genetic pool of breeding programs. This is vital in creating cultivars which would survive in water-deprived areas. There are also natural adaptations of the wild species to natural environmental changes, including improved root structure and less transpiration, which are passed by controlled cross to the hybrids. Wild germplasm incorporation involves a high level of selectivity to bring a balance between the desirable traits and agronomic performance since in wild conditions, the wild qualities may lead to low yield. Field tests are used to guarantee that hybrids are of high quality seeds and they are consistent in yield. Using the genetics of wild Helianthus, breeders are able to come up with cultivars that have strong drought resistance to overcome the climate variability problem (Hladni et al., 2022). By using wild species, resilience is improved as well as the genetic base, which diminishes the probability of population collapse due to the vagaries of the environment (Hladni et al., 2022; Toscano et al., 2017). It promotes sustainable agriculture since the sunflower cultivars are able to survive in the arid areas thus it helps in global food security.

Marker-Assisted Selection (MAS)

The markers assisted breeding (MAS) transforms the breeding of sunflower by focusing on 10 quantitative trait locations (QTLs) related with water use efficiency (WUE) and root biomass, using 500 single nucleotide polymorphisms (SNP) markers that can be utilized to find the drought-tolerant lines. Lines that are derived under drought stress condition on the MAS give a yield of 3.1 t/ha compared to the unselected lines that give 2.7 t/ha because of improved water uptake and low water transpiration. This breeding method increases the speed of the process of determining better genotypes, as genetic markers are correlated to the phenotype, so there is no need to use time-consuming field screening. Recently developed wheat research indicates that MAS is very effective and the lines develop root biomass of 1.2 g/cm 3 relative to 0.9 g/cm 3 in the control, a tactic that could be used in the sunflowers. The MAS reduces the breeding cycles (7 years) to 5 years, making it cost-effective because of its reducing field trial period (Earley et al., 2024). Through QTLs selection, MAS will be used to select the lines that are more productive under water constraints because of traits such as root depth and WUE. Breeders can use SNP marker integration to filter huge populations, eliminating animals with poor allele-sets (Patidar et al., 2024; Rodriguez et al., 2024). This method is more accurate in selection than the traditional ones because it involves specific genetic areas that regulate drought tolerance. Field trials confirm the behavior of MAS-derived lines confirming the potential to withstand high levels of stress to produce good yields of seeds. The integration of MAS and genomic data goes on further to further refine breeding results, making it possible to create cultivars to match certain environmental issues. MAS helps to achieve the swift introduction of drought-tolerant sunflowers, which will contribute to the sustainability of agriculture in the dry areas, as it consumes less time and resources to breed the crop.

Genomic Selection

In genomic selection, 10,000 single nucleotide polymorphism (SNP) markers are used to predict drought tolerance in sunflowers where selection is carried out to identify lines that produce 3.0 t/ha at stress compared to 2.6 t/ha in lines that have not been selected. The methodology determines genotypes with strong root systems where root depths were 1.4 m in contrast to a root depth of 1.0 m in controls which improves water acquisition (Jocković et al., 2024). Genomic selection is better than the marker-assisted selection (MAS) with complex traits such as WUE because it utilizes genome-wide markers to genotype polygenic variation in order to identify 1,800 stress-responsive genes. Experiences made during field trials indicate that the chosen lines are suitable due to an average seed yield of 2.9 t/ha in the drought environment, which proves the effectiveness of the given method (Earley et al., 2024). Genomic selection is highly predictive of breeding values, by analysing thousands of markers at once, and thus makes it possible to select the best genotypes at an early generation. This lessens the necessity of involving elaborate phenotypic analyzes cutting the process of breeding. The method has strong capabilities in multifactorial traits such as drought tolerance that comprises of a large number of genes each with minor effects. The chosen lines have a better root structure and a decreased transpiration rate that maximizes the use of water under stress (Akbari and Darvishzadeh, 2024). The predictive capacity of genomic selection depends on sophisticated statistical modeling that there is an incorporation of the genotypic and phenotypic information making genomic selection very robust in different environments. The technique helps to sustain the scalable breeding programs using the ability to identify resilient cultivars faster, which may be suitable to the watersheds with water shortage Table 2. Genomic selection combined with field validation has the benefit of ensuring the agronomic viability of the selected lines where the yield and seed quality remain constant (Shi et al., 2023).

Transgenic Approaches

The transgenic sunflower that overexpresses dehydration-responsive element-binding (DREB) genes have high drought tolerance with 3.2 t/ha produced in the field trials as against 2.8 t/ha produced by non-transgenic lines. The osmotic adaptation is improved through these genetic changes, where the proline content is 2.5 µmol/g fresh weight (FW) in genetically modified plants vs. 1.8 µmol/g in control plants, which level them out in times of stress (Wu et al., 2022). Transgenic lines are also more able to maintain high photosynthetic rates of 20 µmol CO 2/m 2/s under drought, as opposed to16 µmol CO 2/m 2/s in controls and this helps in sustaining carbon assimilation. Increased enzyme activities of antioxidants also improve in reducing oxidative stress, which conserves cellular structures. The greenhouse experiment shows better water absorption in transgenic lines with a root hydraulic conductivity of 1.2 x 10 -8m/MPa that supports the efficient movement of water (Liang et al., 2020). DREB genes have been introduced, stimulating stress-responsive pathways which improve stress-tolerance to a water shortage. These adjustments are focused at certain physiological mechanisms, e.g. osmoprotectant build-up and continuing photosynthesis, which are vital to stability in yield. Field tests prove the functionality of transgenic lines that exhibit their performance better

Table 2: Genomic and Transcriptomic Markers for Drought Tolerance. Data summarize methods (GWAS, MAS, Genomic Selection, and CRISPR/Cas9), target traits, marker/QTL counts, key genes, yield impact, and breeding cycle reduction. Sources: (Jocković et al., 2024; Liang et al., 2020; Wu et al., 2022)

Method	Target Trait	Number of Markers/QTLs	Key Genes	Yield Impact (t/ha)	Breeding Cycle Reduction (years)
GWAS	Root Depth, WUE	10 QTLs	Water uptake, signaling genes	2.8	2
MAS	Root Biomass, WUE	500 SNPs	DREB2, NAC53	3.1	2
Genomic Selection	WUE, Yield Stability	10,000 SNPs	1,800 stress-responsive genes	3.0	2
CRISPR/Cas9	Osmolyte, Antioxidant	-	DREB2	3.2	2

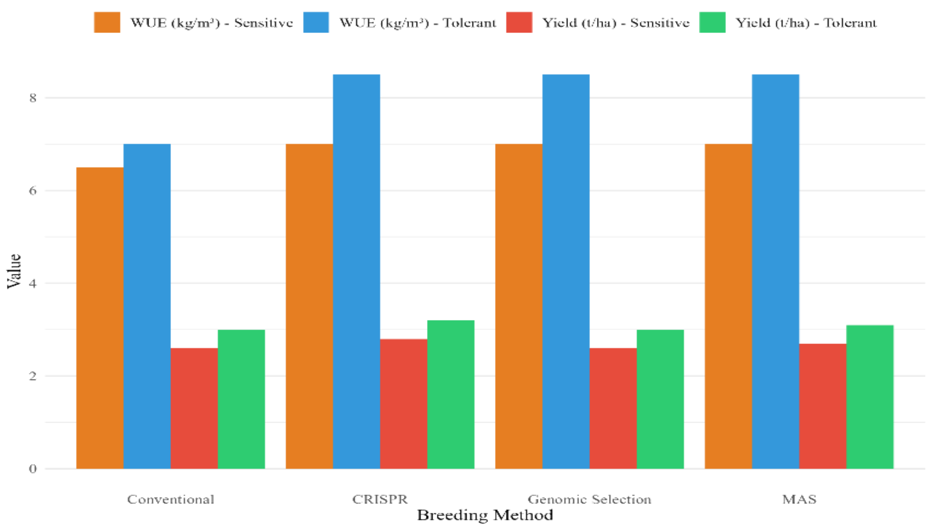

Fig. 5: Yield and WUE Across Breeding Strategies. Comparison of yield (t/ha) and water-use efficiency (WUE, kg/m³) for tolerant and sensitive sunflower genotypes under drought conditions, demonstrating the superiority of CRISPR and genomic selection in achieving higher yields (up to 3.2 t/ha) and WUE (8.5 kg/m³) compared to conventional breeding (Table 3). Sources: (Jocković et al., 2024; Liang et al., 2020; Wu et al., 2022).

compared to traditional cultivars during drought (Fig. 5). Nevertheless, transgenic methods cannot be adopted easily because they need to have stringent regulatory acceptance and acceptance by the people. In spite of these challenges, the accuracy of genetic engineering has immense benefits, as it can be used to bring specific benefits about in the drought tolerance. Through a combination of the transgenic methods and field tests, breeders can create sunflower varieties capable of sustaining high yields in a water-restricted habitat, thus sustainable farming (Wu et al., 2022). The strategy can be an effective solution to the problems of climate changes, guaranteeing food security due to the presence of resilient crops.

Impact on Oil Content

Drought greatly affects the production of oil in Helianthus annuus L. (sunflower) that the oil content of seeds decreases to 40 g/100 g and the oleic acid protein decreases to 35 g/100 g in harvest thus causing economic losses of 500 million annually. Such decreases are a result of impaired lipid synthesis under water stress which leads to poor quality of seeds and market prices. Tolerant genotypes like Hysun-33 also alleviate such effects and in this instance the oil content of 43 g/100 g with a yield of 2.8 t/ha which is high under drought as compared to 2.5 t/ha by sensitive lines. These genotypes maintain the level of linoleic acid at 50 g/100 g and thus maintain nutritionalism and industrial quality as indicated by stress (Ghaffari et al., 2023). The consistency of the linoleic acid in tolerant lines indicates that the lines are able to maintain the fatty acid contents, which are important in oil utilization (Table 3). The diversity of genetic makeup concerning the pathway of lipid biosynthesis is a crucialiding factor of drought resistance. Group One: Marker-assisted selection (MAS) which relies on single nucleotide polymorphism (SNP) markers targets and which has a selection accuracy of 0.85, can be used to produce lines that produce 2.8 t/ha under stress. MAS determines genotypes which have higher oil production and stability in yielding by the association of SNP markers to features such as lipid storage and seed filling performance (Hanafy and Sadak, 2023). The breeding method is also cost-effective since it helps to accelerate the time needed to develop resilient cultivars to enhance the performance of sunflower under water-limited conditions (Jan et al., 2022).

Drip irrigation supplementation also increases the resilience of droughts by increasing the water use efficiency (WUE) to 8.5 kg/m 3, ensuring plants optimize the uptake of water and retain the oil content to 42 g/100 g. It is an irrigation method that will limit water pressure at crucial developmental points like seed filling, lowering the losses to the economy by 75 million per year. Drip irrigation saves resources by supplying water to the root zone, preventing quality and yield of the seed to not be impacted by the drought (Table 4) (Kosar et al., 2022). Tolerant genotypes and irrigation mean production of oil in quantities that are uniform, which is a solution to agronomic and economic problems. The data present essential measures use of tolerant types such as Hysun-33, MAS of lipid biosynthesis gene, and the use of supplemental drip irrigation as a countermeasures to the effects of drought on the production of sunflower oil (Dar et al., 2021). By doing this, they increase the WUE, stabilize oil level, and preserve fatty acid compositions,

Table 3: Yield and Oil Content under Drought Stress. Data compare tolerant (‘Hysun-33’, ‘Hadar’) and sensitive genotypes for yield, oil content, water-use efficiency (WUE), and economic loss under control and drought conditions. Sources: (Dar et al., 2021; Dudhe et al., 2025; Jan et al., 2022; Kosar et al., 2022)

Genotype	Yield (t/ha) Control	Yield (t/ha) Drought	Oil Content (g/100 g) Control	Oil Content (g/100 g) Drought	WUE (kg/m³)	Economic Loss ($M)
Tolerant (‘Hysun-33’)	3.7	2.8	44	43	8.5	75
Sensitive	3.7	2.5	44	40	7.0	500
Tolerant (‘Hadar’)	3.7	3.0	44	42	8.5	75
Sensitive	3.7	2.2	44	35	6.5	500

Table 4: Agronomic Management Strategies and Their Impact. Data compare strategies (drip irrigation, mulching, nutrient management, crop rotation, tillage) for soil moisture, water-use efficiency (WUE), yield, and seed set under drought conditions, with a control for comparison. Sources: (Mehak et al., 2021; Shi et al., 2024; Tran et al., 2024; Tsivileva, 2025; Wu et al., 2022)

Strategy	Soil Moisture (m³/m³)	WUE (kg/m³)	Yield (t/ha)	Seed Set (seeds/plant)
Drip Irrigation	0.25	8.5	3.0	1,200
Organic Mulching	0.25	8.5	2.9	1,250
Nutrient Management	0.27	8.5	3.1	1,200
Crop Rotation	0.28	8.5	3.0	1,200
Conservation Tillage	0.27	8.7	3.0	1,200
Control (No Strategy)	0.20	7.0	2.6	1,000

so that the yield of oil can be high quality in drought-prone areas (Dudhe et al., 2025). Through the combination of genetic and agronomic interventions, the breeders and farmers will be able to come up with tougher sunflower varieties that will cut down loss of income and provide production in harsh climatic conditions.

Agronomic Management for Drought

The impact of drought has become a major problem in the production of the Helianthus annuus L. (sunflower), agronomic approaches such as the optimization of irrigation, mulching, nutrient management, crop rotation and tillage contribute to increased resistance and yield stability. Deficit irrigation avoids wastage of water, and sprouts 1,200 seeds per plant in tolerant genotypes and 1,000 in sensitive genotypes, irrigation at flowering increases the seed yield to 2.8 t/ha and contrasted with 2.4 t/ha without time-of-day application (Langeroodi et al., 2022). Straw mulching also keeps soil moisture at 0.25 m 3 in m 3, during drought drought conditions, 0.20 m 3 in m 3 in unmulcted fields, seed yield increases to 2.9 t/ha on average as opposed to 2.6 t/ha. Amendments made by biochar increase water retention of soils by 0.30 m 3/m 3 instead of 0.22 m 3 and seed set of 1250 per plant in tolerant lines compared to 1050 seeds per plant in sensitive lines. Drought decreases the uptake of nitrogen by 80 kg/ha out of 100 kg/ha, whereas applying 120 kg/ha nitrogen adds the seed yield to 3.1 t/ha of tolerant genotypes compared to 2.7 t/ha of controls. Application of potassium, whether at 50 kg/ha, increases the WUE by 8.5 kg/m 3 7.0 kg/m 3, which aids in the process of osmotic adjustment, and foliar sprays of potassium, 2 g/L, increase the content of nutrient leaf material by 3.5 mg/g 2.8 mg/g of the crops, which is helpful in yielding 2.9 t/ha under stress (Akbari and Darvishzadeh, 2024 Legumes such as soybean promote crops rotation resulting in more agriculture with a high soybean soil moisture of 0.28 m 3/m 3 compared to 0.23 m 3/m 3, and enhancement of soil aggregate stability to 1.5 mm mean weight diameter compared to 1.2 mm, which reduces water stress. Rotating Systems with tolerant genotypes give give 2.9 t/ha and allow 90 plants/m 2 compared to monoculture with 80plants/m 2. Conservation tillage keeps the soil moisture at 0.27 m 3/m 3 during drought levels than 0.22 m 3/m 3 with conventional tillage producing 3.0 t/ha and 2.6 t/ha, respectively with 1.4 m depth of roots in comparison to 1.1 m in tilled plots, as well as maintains high water uptake (Mehak et al., 2021; Shi et al., 2024). No-till has a WUE of 8.7 kg/m 3 over 7. 2 kg/m 3 with traditional tillage and yields 2.8 t/ha in lines resistant and 2.4 t/ha in lines sensitive. These combined approaches will maximize water utilization, soil satisfaction, and nutrient, which will guarantee water-starved areas to produce sunflower sustainably.

Climate Modeling and Drought Prediction

The frequency of droughts in the areas of sunflower cultivation is magnified due to climate change, and it is predicted by the models that three more droughts will occur every decade, and soil moisture reduction will be 0.05 m 3/m 3. Based on past and current data, these forecasts tell the breeding programs how to produce resilient cultivars of Helianthus annuus L. (Zhang et al., 2021). With the satellite information, drought forecasting attains the accuracy of 0.85 and this ability places the areas at high risk and yields reduce to 2.2 t/ha due to drought stress. This is a predictive ability that enables the breeders to focus on some targeted interventions, such as water use efficiency (WUE) and yield stability (Harsanyi et al., 2021; Langeroodi et al., 2022). Highly tolerant genotypes also exhibit better performance, with the yield of 2.8 t/ha under predicted drought conditions exceeding a 2.5 t/ha of sensitive lines, which reduces losses in yields. Analysis of impacts demonstrates that rainfed systems reach 0.4 t/ha yield loss in drought, which is why it is necessary to implement adaptive measures (Hussain et al., 2025; Innes et al., 2025). Breeding program further increased WUE to 8.5 kg/m 3, which allowed the cultivars to be able to endure limited water conditions and yield 2.8 t/ha. These types of models offer important information regarding trends on soil moisture and the frequency of droughts, helping to select the genotype with such characteristic traits as a deep root system and high osmotic adjustment (Wu et al., 2022; Yadav et al., 2025; Younis and Mansour, 2024). Such policy interventions as the recommendation to use drought-tolerant cultivars and subsidization of irrigation contributes essentially to the reduction in the economical losses generated during droughts, estimated at 2 billion dollars per annum due to the impacts of droughts on the production of sunflower. The application of efficient irrigation techniques like drip irrigation and other irrigation methods is enabled through subsidies and this helps to maximize irrigation water and maintain the stability of yields. Advanced breeding and enhanced forecasting synergize to guarantee the deployment of tolerant genotypes in the high-risk regions to reduce the susceptibility to the fluctuation of climate conditions (Q. Ali et al., 2024; Shi et al., 2023). Using satellite-derived data, breeders will be able to detect the breeding traits that are stress-resistant, and this will hasten the breeding of cultivars against climate conditions in the future.

Future Research Directions

Progress made in transcriptomic and epigenomic studies revealed 2,245 stress-reactive genes in Helianthus annuus L., thereby improving research on drought tolerance processes and providing opportunity to develop resilient cultivars. Lines derived through omics produce 2.8 t/ha during water stress, which is better than the traditional lines with 2.4 t/ha by propelling genes that regulate osmotic adjustment and antioxidants activity. Cultivars that have been bred via the utility of CRISPR/Cas9 technology exhibit a water use efficiency (WUE) of 8.5 kg/m 3 and give yields of 2.8 t/ha after breeding programs involving breeding wild Helianthus species like H. argophyllus (Patidar et al., 2024). Genetic diversity by the wild species, such as deep root systems and stress responsive alleles, helps in improving water uptake and toughness. Crispr/Cas9 allows marriage of specific genes, such as WUE and stability of the seed-yield, shortening cultivar production. Through high-throughput phenotyping, the process of breeding is further simplified by finding drought-tolerant phenotypes, including root biomass and leaf turgor, within 10 days as compared to 12 days in conventional breeding techniques, and lines selected provided a 2.7 t/ha. This is an automated physiological imaging and data analysis technology that can fulfill selectivity by evaluating physiological characteristics quickly (Li et al., 2024; Liang et al., 2020). Projected climate forecasts 0.4 t/ha future loss in yield because of rising frequency of drought informs irrigation plans that will maintain yields at 2.7 t/ha. When nutrient management is combined with optimized irrigation (drip system) the WUE reaches 8.5 kg/m 3 which sustains yields of 2.8 t/ha during periods of drought. Such practices provide water and nutrients, such as nitrogen that is 120 kg /ha and potassium that is 50 kg/ha, to plants, improving photosynthetic efficiency and osmotic adjustment. Transcriptomic and epigenomic studies combined with state-of-the-art breeding technologies, including CRISPR/Cas9 and high-throughput phenotyping, can be used to create drought-resistant cultivars in a short period in the conditions of the future climate (Pekcan et al., 2022). The forecasts of climate models are used to apply precision irrigation and nutrient strategies that reduce losses of yields in water-starved areas. These measures increase the resilience of sunflower to keep up with the field of genetic advancement and promise to uphold the food security and financial stability of areas that are vulnerable to droughts.

Conclusion

This review provides an integrated and comparative evaluation of drought resilience in sunflower, through the combination of physiological, biochemical, molecular, and agronomic evidence across tolerant and sensitive genotypes. By comparing elite cultivars with wild *Helianthus* species, the review highlights the superior allelic diversity, deeper rooting behavior, and enhanced antioxidant capacity contributed by wild germplasm. It also contrasts classical breeding tools (GCA, SCA, heterosis, QTL studies) with modern genomic approaches including GWAS, transcriptomics, and genomic selection, and offers a unified framework for breeding drought-resilient sunflower. A key novelty of this review is the synthesis of multi-omics insights with climate-forecasting tools and field-level water management strategies, providing a more holistic understanding than earlier literature. The quantitative integration of yield penalties, WUE improvements, oil quality shifts, and economic impacts further strengthens its practical relevance. Overall, this review outlines key physiological and genetic determinants of drought adaptation and presents a comprehensive framework to support the development of productive, climate-resilient sunflower varieties.

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REFERENCES

Akbari, N., & Darvishzadeh, R. (2024). Evaluation of some selection indices to improve sunflower seed yield under normal and drought stress conditions. Plant Genetic Research, 11(1), 47-76. http://dx.doi.org/10.22034/PGR.11.1.4

Ali, A. Y. M., Lamlom, S. F., El-Sorady, G. A., Elmahdy, A., Elghany, S. H. A., Usman, M., Alamri, A., Shaghaleh, H., Hamoud, Y. A., & Abdelghany, A. M. (2024). Boosting Resilience and Yields in Water-Stressed Sunflower Through Coordinated Irrigation Scheduling and Silica Gel Applications. Heliyon, 10(20), e38129–e38129. https://doi.org/10.1016/j.heliyon.2024.e38129

Ali, S., Ali, M., Khan, F., Noureldeen, A., Alghamdi, A., Darwish, H., Fatima, S. A., Jalali, A. I., Prendergast, K., & Saeed, S. (2024). Water Deprivation and Sowing Times Alter Plant–Pollination Interactions and Seed Yield in Sunflower, Helianthus annuus L. (Asteraceae). Plants, 13(22), 3194. https://doi.org/10.3390/plants13223194

Ameen, M., Zia, M. A., Alawadi, H. F. N., Naqve, M., Mahmood, A., Shahzad, A. N., Khan, B. A., Alhammad, B. A., Aljabri, M., & Seleiman, M. F. (2024). Exogenous application of selenium on sunflower (Helianthus annuus L.) to enhance drought stress tolerance by morpho-physiological and biochemical adaptations. Frontiers in Plant Science, 15. https://doi.org/10.3389/fpls.2024.1427420

Andrade, A., Escalante, M., Ramírez, F., Vigliocco, A., & Alemano, S. (2024). Phytohormones and related genes function as physiological and molecular switches regulating water stress response in the sunflower. Physiology and Molecular Biology of Plants, 30(8), 1277–1295. https://doi.org/10.1007/s12298-024-01497-8

Ayala, F., Curin, F., Diaz-Zorita, M., Murguía, J., Montero Bulacio, E., Portapila, M., Otegui, M. E., Chan, R. L., & González, F. G. (2024). Introgression of the sunflower HaHB4 gene in modern wheat: An advancement in resilience to deal with climate change. bioRxiv, 2024.2010. 2026.620406. https://doi.org/10.1101/2024.10.26.620406

Canavar, Ö., Gören, H. K., Tan, U., Yılmaz, O., Kaptan, M. A., & Kaya, S. K. (2025). Physiological Responses of Sunflower (Helianthus annuus L.) to Multiple Combined Prolonged Drought Stress, Salinity Stress and Boron Toxicity: Insights from Pre- and Post-Recovery Stages. Journal of Agronomy and Crop Science, 211(2). https://doi.org/10.1111/jac.70047

Chen, F., Xiao, L., Huang, Q., Xiang, L., Li, Q., Hou, X., Lei, Z., & Zeng, Y. (2024). Physiological Evaluation of Salt Tolerance in Sunflower Seedlings Across Different Genotypes. Agronomy, 14(12), 2995. https://doi.org/10.3390/agronomy14122995

Cui, J. (2020). Metabolic responses to potassium availability and waterlogging in two oil-producing species: sunflower and oil palm. https://doi.org/10.25911/5ed77c9caff5f

Silva, O. B. d., Castro, E. M. d., Vassura, Y., Pires, M. V., Carvalho, C. G. P. d., Carvalho, L. M. d., & Pereira, M. P. (2025). Root system morphoanatomy of sunflower genotypes under water deficit. BMC Plant Biology, 25(1). https://doi.org/10.1186/s12870-025-06468-z

Dar, J. S., Cheema, M., Rehmani, M. I. A., Khuhro, S., Rajput, S., Virk, A. L., Hussain, S., Bashir, M. A., Alghanem, S. M. S., Alzuaibr, F. M., Ansari, M. J., & Hessini, K. (2021). Potassium fertilization improves growth, yield and seed quality of sunflower (Helianthus annuus L.) under drought stress at different growth stages. PLoS ONE, 16(9), e0256075–e0256075. https://doi.org/10.1371/journal.pone.0256075

Docimo, T., Paesano, A., D'Agostino, N., D'Amelia, V., Garramone, R., Carputo, D., & Aversano, R. (2024). Exploring CDF gene family in wild potato under salinity stress unveils promising candidates for developing climate-resilient crops. Scientific Reports, 14(1). https://doi.org/10.1038/s41598-024-75412-2

Dudhe, M., Sasikala, R., Ramteke, R., Sakthivel, K., & Kumaraswamy, H. (2025). Breeding Climate-Resilient Sunflowers in the Climate Change Era: Current Breeding Strategies and Prospects. In Breeding Climate Resilient and Future Ready Oilseed Crops (pp. 349-405). Springer. https://doi.org/10.1007/s11356-022-19718-6

Duruflé, H., Balliau, T., Blanchet, N., Chaubet, A., Duhnen, A., Pouilly, N., Blein-Nicolas, M., Mangin, B., Maury, P., Langlade, N. B., & Zivy, M. (2023). Sunflower Hybrids and Inbred Lines Adopt Different Physiological Strategies and Proteome Responses to Cope with Water Deficit. Biomolecules, 13(7), 1110. https://doi.org/10.3390/biom13071110

Dwivedi, S. L., Quiroz, L. F., Reddy, A. S. N., Spillane, C., & Ortíz, R. (2023). Alternative Splicing Variation: Accessing and Exploiting in Crop Improvement Programs. International Journal of Molecular Sciences, 24(20), 15205. https://doi.org/10.3390/ijms242015205

Earley, A. M., Nolting, K., Donovan, L. A., & Burke, J. M. (2024). Trait variation and performance across varying levels of drought stress in cultivated sunflower (Helianthus annuus L.). AoB Plants, 16(4). https://doi.org/10.1093/aobpla/plae031

Ghaffari, M., Gholizadeh, A., Rauf, S., & Shariati, F. (2023). Drought-stress induced changes of fatty acid composition affecting sunflower grain yield and oil quality. Food Science & Nutrition, 11(12), 7718–7731. https://doi.org/10.1002/fsn3.3690

Giacomelli, J. I., Weigel, D., Chan, R. L., & Manavella, P. A. (2012). Role of recently evolved miRNA regulation of sunflower HaWRKY6 in response to temperature damage. New Phytologist, 195(4), 766–773. https://doi.org/10.1111/j.1469-8137.2012.04259.x

Haghpanah, M., Hashemipetroudi, S., Arzani, A., & Araniti, F. (2024). Drought Tolerance in Plants: Physiological and Molecular Responses. Plants, 13(21), 2962. https://doi.org/10.3390/plants13212962

Sghaier, A. H., Khaeim, H. M., Tarnawa, Á., Kovács, G. P., Gyuricza, C., & Kende, Z. (2023). Germination and Seedling Development Responses of Sunflower (Helianthus annuus L.) Seeds to Temperature and Different Levels of Water Availability. Agriculture, 13(3), 608. https://doi.org/10.3390/agriculture13030608

Hanafy, R. S., & Sadak, M. Sh. (2023). Foliar Spray of Stigmasterol Regulates Physiological Processes and Antioxidant Mechanisms to Improve Yield and Quality of Sunflower Under Drought Stress. Journal of Soil Science and Plant Nutrition, 23(2), 2433–2450. https://doi.org/10.1007/s42729-023-01197-4

Hussain, M. M., Rauf, S., Noor, M., Bibi, A., Ortíz, R., & Dahlberg, J. (2023). Evaluation of Introgressed Lines of Sunflower (Helianthus annuus L.) under Contrasting Water Treatments. Agriculture, 13(6), 1250. https://doi.org/10.3390/agriculture13061250

Hussain, S., Khan, M., Altaf, M. T., Shah, M. N., & Alfagham, A. T. (2025). Deciphering the morpho-physiological and biochemical response of sunflower hybrids with the application of biochar and slow-release nitrogen fertilizers under drought stress for sustainable crop production. Frontiers in Plant Science, 16. https://doi.org/10.3389/fpls.2025.1541123

Innes, S. N., Jakobsen, S. B., Røsåsen, R. B., Ali, H., Solhaug, K. A., Olsen, J. E., & Torre, S. (2025). Blue light is a key factor in regulating stomatal movement, transpiration rate and ABA metabolism under varying vapour pressure. Acta Physiologiae Plantarum, 47(7). https://doi.org/10.1007/s11738-025-03818-0

Jan, A. U., Hadi, F., Ditta, A., Suleman, M., & Ullah, M. (2021). Zinc-induced anti-oxidative defense and osmotic adjustments to enhance drought stress tolerance in sunflower (Helianthus annuus L.). Environmental and Experimental Botany, 193, 104682. https://doi.org/10.1016/j.envexpbot.2021.104682

Jocković, M., Jocić, S., Cvejić, S., Dedić, B., Jocković, J., Ćuk, N., Radanović, A., Marjanović-Jeromela, A., Miklič, V., & Miladinović, D. (2024). Unveiling sunflower morphological and phenological adaptations to drought stress. Ocl, 31, 29. https://doi.org/10.1051/ocl/2024026

Kahrobaiyan, M., Nemati, S. H., Rahemi, M., Kholdebarin, B., & Tehranifar, A. (2022). Under drought stress, foliar application of putrescine enhances photosynthetic activities, stomatal closure and drought tolerance in ornamental sunflower (helianthus annus L.) plant. Applied Ecology and Environmental Research, 20(6), 4719–4736. https://doi.org/10.15666/aeer/2006_47194736

Khalifani, S., Darvishzadeh, R., Azad, N., Shayesteh, M. G., Kalbkhani, H., & Akbari, N. (2023). Comparison of influential input variables in the deep learning modeling of sunflower grain yields under normal and drought stress conditions. Field Crops Research, 303, 109145. https://doi.org/10.1016/j.fcr.2023.109145

Kosar, F., Alshallash, K. S., Akram, N. A., Sadiq, M. B., Ashraf, M., Alkhalifah, D. H. M., Latef, A. A. H. A., & Elkelish, A. (2022). Trehalose-Induced Regulations in Nutrient Status and Secondary Metabolites of Drought-Stressed Sunflower (Helianthus annuus L.) Plants. Plants, 11(20), 2780. https://doi.org/10.3390/plants 11202780

Lalarukh, I., & Shahbaz, M. (2019). Response of antioxidants and lipid peroxidation to exogenous application of alpha-tocopherol in sunflower (Helianthus annuus L.) under salt stress. Pakistan Journal of Botany, 52(1). https://doi.org/10.30848/pjb2020-1(41)

Li, P., L., B., Wei, X., Guo, S., & Ma, Y. (2024). Deeper root distribution and optimized root anatomy help improve dryland wheat yield and water use efficiency under low water conditions. Plant and Soil, 501(1-2), 437–454. https://doi.org/10.1007/s11104-024-06526-9

Liang, C., Wang, W., Ma, J., Wang, J., Zhou, F., Li, W., Yu, Y., Zhang, L., Huang, W., & Huang, X. (2020). Identification of differentially expressed microRNAs of sunflower seedlings under drought stress. Agronomy Journal, 112(4), 2472–2484. https://doi.org/10.1002/agj2.20254

Masalia, R. R., Temme, A. A., Torralba, N. d. l., & Burke, J. M. (2018). Multiple genomic regions influence root morphology and seedling growth in cultivated sunflower (Helianthus annuus L.) under well-watered and water-limited conditions. PLoS ONE, 13(9), e0204279–e0204279. https://doi.org/10.1371/journal.pone.0204279

Mehak, G., Akram, N. A., Ashraf, M., Kaushik, P., El-Sheikh, M. A., & Ahmad, P. (2021). Methionine-induced regulation of growth, secondary metabolites and oxidative defense system in sunflower (Helianthus annuus L.) plants subjected to water deficit stress. PLoS ONE, 16(12), e0259585–e0259585. https://doi.org/10.1371/journal.pone.0259585

Moroldo, M., Blanchet, N., Duruflé, H., Bernillon, S., Berton, T., Fernández, O., Gibon, Y., Moing, A., & Langlade, N. (2024). Genetic control of abiotic stress-related specialized metabolites in sunflower. BMC Genomics, 25(1). https://doi.org/10.1186/s12864-024-10104-9

Patidar, R., Pingale, S. M., Khare, D., & Dayal, D. (2024). Spatio-temporal assessment of multi-scalar meteorological and hydrological droughts over Bundelkhand, India. Physics and Chemistry of the Earth Parts A/B/C, 136, 103729. https://doi.org/10.1016/j.pce.2024.103729

Pekcan, V., Yilmaz, M. I., Evci, G., ÇİL, A. N., Şahin, V., Gündüz, O., Koç, H., & Kaya, Y. (2021). Oil content determination on sunflower seeds in drought conditions. Journal of Food Processing and Preservation, 46(10). https://doi.org/10.1111/jfpp.15481

Rabeh, K., Hnini, M., & Oubohssaine, M. (2025). A comprehensive review of transcription factor-mediated regulation of secondary metabolites in plants under environmental stress. Stress Biology, 5(1). https://doi.org/10.1007/s44154-024-00201-w

Rodriguez, I. M., Hall, A. J., Monzón, J. P., Mercau, J. L., Gayo, S., Pereira, M. L., Cerrudo, A., Urcola, H. A., Troglia, C., & Zuil, S. (2024). Sunflower yield gaps and their causes in Argentina. Field Crops Research, 315, 109480. https://doi.org/10.1016/j.fcr.2024.109480

Sarazin, V., Duclercq, J., Guillot, X., Sangwan, B. S., & Sangwan, R. S. (2017). Water-stressed sunflower transcriptome analysis revealed important molecular markers involved in drought stress response and tolerance. Environmental and Experimental Botany, 142, 45–53. https://doi.org/10.1016/j.envexpbot.2017.08.005

Shahin, M. G., El-Bially, M. E., Saudy, H. S., & El–Metwally, I. M. (2018). SOWING DATE AND IRRIGATION EFFECTS ON PRODUCTIVITY AND WATER USE EFFICIENCY IN SUNFLOWER. Arab Universities Journal of Agricultural Sciences, 26(4), 1483–1493. https://doi.org/10.21608/ajs .2018.34147

Shehzad, M., Gul, R. S., Rauf, S., Clarindo, W. R., Al-Khayri, J. M., Hussain, M. M., Munir, H., Ghaffari, M., Nazir, S., & Hussain, S. M. (2021). Development of a robust hydroponic method for screening of sunflower (Helianthus annuus L.) accessions for tolerance to heat and osmotic stress. Scientific Reports, 11(1). https://doi.org/10.1038/s41598-021-81072-3

Shi, H., Jian-hua, H., Li, D., Hu, H., Wang, Y., Wu, Y., & Yi, L. (2024). Comparative transcriptome and coexpression network analysis reveals key pathways and hub candidate genes associated with sunflower (Helianthus annuus L.) drought tolerance. BMC Plant Biology, 24(1). https://doi.org/10.1186/s12870-024-04932-w

Shi, H., Wu, Y., Yi, L., Hu, H., Su, F., Wang, Y., Li, D., & Hou, J. (2023). Analysis of QTL mapping for germination and seedling response to drought stress in sunflower (Helianthus annuus L.). PeerJ, 11, e15275–e15275. https://doi.org/10.7717/peerj.15275

Smaeili, M., Madani, H., Nassiri, B. M., Sajedi, N. A., & Chavoshi, S. Z. (2022). Study of water deficiency levels on ecophysiological characteristics of sunflower cultivars in Isfahan, Iran. Applied Water Science, 12(5). https://doi.org/10.1007/s13201-022-01616-4

Souques, L., Alletto, L., Blanchet, N., Casadebaig, P., & Langlade, N. B. (2024). Cover crop residues mitigate impacts of water deficit on sunflower during vegetative growth with varietal differences, but not during seed development. European Journal of Agronomy, 155, 127139. https://doi.org/10.1016/j.eja.2024.127139

Toscano, S., Romano, D., Tribulato, A., & Patanè, C. (2017). Effects of drought stress on seed germination of ornamental sunflowers. Acta Physiologiae Plantarum, 39(8). https://doi.org/10.1007/s11738-017-2484-8

Tran, V. H., Nolting, K., Donovan, L. A., & Temme, A. A. (2024). Cultivated sunflower (Helianthus annuus L.) has lower tolerance of moderate drought stress than its conspecific wild relative, but the underlying traits remain elusive. Plant Direct, 8(4). https://doi.org/10.1002/pld3.581

Turan, F., & Yağcı, E. (2025). The Effect of Sunflower Seed Priming in Reducing Drought Stress on Antioxidant and Morphological Characteristics During the Germination Stage. Journal of Plant Growth Regulation. https://doi.org/10.1007/s00344-025-11703-w

Hassan, M., Chattha, M. U., Khan, İ., Khan, T. A., Nawaz, M., Tang, H., Noor, M. A., Asseri, T. A. Y., Hashem, M., & Guo-qin, H. (2024). Zinc Seed Priming Alleviates Salinity Stress and Enhances Sorghum Growth by Regulating Antioxidant Activities, Nutrient Homeostasis, and Osmolyte Synthesis. Agronomy, 14(8), 1815. https://doi.org/10.3390/agronomy14081815

Wu, Y., Wang, Y., Shi, H., Hu, H., Yi, L., & Hou, J. (2022). Time-course transcriptome and WGCNA analysis revealed the drought response mechanism of two sunflower inbred lines. PLoS ONE, 17(4), e0265447–e0265447. https://doi.org/10.1371/journal.pone.0265447

Yadav, S. K., Saroha, A., Singh, D., Yadav, P. D., Wankhede, D. P., Singh, G. P., Chinnusamy, V., & Kaur, V. (2025). Deciphering ABA/PYL gene family in flax: evolutionary analysis, and abiotic stress response. Plant Cell Reports, 44(7). https://doi.org/10.1007/s00299-025-03517-7

Younis, A. A., & Mansour, M. M. F. (2024). Hydrogen sulfide-mitigated salinity stress impact in sunflower seedlings was associated with improved photosynthesis performance and osmoregulation. BMC Plant Biology, 24(1). https://doi.org/10.1186/s12870-024-05071-y

Zahra, N., Hafeez, M. B., Kausar, A., Al-Zeidi, M. I., Asekova, S., Siddique, K. H. M., & Farooq, M. (2023). Plant photosynthetic responses under drought stress: Effects and management. Journal of Agronomy and Crop Science, 209(5), 651–672. https://doi.org/10.1111/jac. 12652

Zhang, J., Zhang, H., Sima, M., Trout, T. J., Malone, R. W., & Wang, L. (2020). Simulated deficit irrigation and climate change effects on sunflower production in Eastern Colorado with CSM-CROPGRO-Sunflower in RZWQM2. Agricultural Water Management, 246, 106672. https://doi.org/10.1016/j.agwat.2020.106672

Zhou, F., Liu, Y., Wang, W., Wu, L., Ma, J., Zhang, S., Wang, J., Feng, F., Yuan, H., & Huang, X. (2022). Identification and functional prediction of CircRNAs of developing seeds in high oleic acid sunflower (Helianthus annuus L.). Acta Physiologiae Plantarum, 45(1). https://doi.org/10.1007/s11738-022-03482-8