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REVIEW OPEN ACCESS

Unveiling sunflower morphological and phenological adaptations to drought stress☆

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Abstract – Drought stress significantly threatens crop productivity worldwide, requiring a comprehensive understanding of plant adaptations to alleviate its adverse effects. Sunflower, as an important source of edible oil, is greatly affected by drought in different developmental stages. This review investigates the morphological aspects and phenological adaptations of sunflower under drought conditions. Through a detailed description of morphological and phenological changes in sunflower, induced by drought, we aim to unravel the plant's strategies for coping with water scarcity. In addition, the study describes genetic background of drought tolerance in sunflower, as well as insight about valuable genetic resources. Finally, we have described drought mitigation mechanisms known in sunflower, through morpho-physiological adaptations and agricultural practices which can alleviate the effect of drought. As a future strategy this research emphasizes the importance of genetic diversity in cultivating drought-resilient sunflower, using modern breeding techniques through genomic selection and omic's technologies as a promising strategy in the face of escalating water limitations and development of drought tolerant and tenacious sunflower.

Keywords: Sunflower / drought / adaptation / resources

Résumé – La sécheresse menace de manière drastique la productivité des cultures dans le monde entier, ce qui nécessite une compréhension globale des adaptations des plantes à cette contrainte afin d'en atténuer les effets néfastes. Le tournesol, en tant que source importante d'huile alimentaire, est fortement affecté par la sécheresse à différents stades de son développement. Cette revue étudie les aspects morphologiques et les adaptations phénologiques du tournesol en conditions de sécheresse. Grâce à une description détaillée des changements morphologiques et phénologiques du tournesol, induits par la sécheresse, nous cherchons à comprendre les stratégies de la plante pour faire face à la pénurie d'eau. En outre, l'étude décrit les déterminants génétiques de la tolérance à la sécheresse chez le tournesol, et donne un aperçu des ressources génétiques exploitables. Enfin, nous décrivons les mécanismes d'atténuation des effets de la sécheresse connus chez le tournesol, par le biais d'adaptations morpho-physiologiques et de pratiques agricoles. Pour le futur, en vue d'obtenir des tournesols résistants à la sécheresse dans un contexte de forte contrainte hydrique, cette étude souligne l'importance de mobiliser la diversité génétique, en utilisant des techniques de sélection modernes par le biais de la sélection génomique et de technologies omiques prometteuses

Mots clés : Tournesol / sécheresse / adaptation / ressources

☆ Contribution to the Topical Issue "Adaptation au changement climatique / Adapting to climate change".

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Highlights

Drought emerges as a growth and yield-limiting factor for crops, affecting crucial stages like emergence, flowering, pollination, and grain-filling across a range of crops. A detailed description of drought-induced morphological and phenological changes in sunflower, complemented by the genetic background of drought tolerance in sunflower and providing insight into valuable genetic resources, with the application of modern breeding techniques through genomic selection and omic technologies can be very useful in the breeding process of drought tolerant sunflower.

1 Introduction

The increasingly frequent and severe climate fluctuations have profound impacts on the atmosphere, leading to sudden temperature changes. These shifts, noted by the occurrence of intense storms and hail, have significant adverse effects on crop cultivation. Heat waves resulting in elevated temperatures cause heightened transpiration and increased water requirements for plants. Coupled with irregular rainfall distribution, these conditions give rise to shorter or prolonged drought periods, causing a substantial decrease in agricultural crop yields. Despite various factors, both biotic and abiotic, that present constraints on crop production, insufficient water availability stands out as one of the most prevalent limitations affecting productivity in field conditions (Arslan *et al.*, 2020). The scarcity of water is a critical factor influencing plant growth and development, especially considering that water constitutes 90–95% of fresh biomass (Razzaq *et al.*, 2017; Seleiman *et al.*, 2021). Drought emerges as a growth- and yield-limiting factor for crops, affecting crucial stages like flowering, pollination, and grain-filling across a range of crops. On a global scale, it is estimated that a significant proportion, up to 83%, of economic losses attributable to drought are linked to agriculture. The associated costs amounted to US$ 29 billion in semi-arid and arid regions between 2005 and 2015 (Cvejić *et al.*, 2023).

Sunflower (*Helianthus annuus* L.) is one of the most important sources of edible oil worldwide. It has been acknowledged that areas under sunflower production are increasing (Domenco *et al.*, 2022). Due to its qualitative properties, sunflower oil is considered a premium quality oil for human nutrition, so it is essential to produce sustainable sunflower oil. Moreover, due to its ability to grow in different agroecological conditions and its moderate drought tolerance, sunflower may become the oil crop of preference in the future, especially in light of global environmental changes (Miladinović *et al.*, 2019). Although sunflower is proposed as a model crop because of its high ability to adapt, sunflower is highly sensitive to water shortage at different stages, which is undoubtedly reflected in a drastic yield loss (Kaya *et al.*, 2016; Razzaq *et al.*, 2017). Drought can cause as much as 80% of yield reduction during anthesis (Pekcan *et al.*, 2015). Differences in water availability have a pronounced negative effect on the phenotypic expression of various traits in sunflower (Barnhart *et al.*, 2022). There are well-documented studies about the adverse effects of drought on important agro-morphological and physiological properties of sunflower such as head and stem diameter, plant height, root-to-shoot ratio, leaf water potential, leaf area index, total chlorophyll content as well as significantly reduced seed yield caused by lower seed weight and lower oil yield during seed filling phase (Maury *et al.*, 2000; Hossain *et al.*, 2010; Vanaja *et al.*, 2011; Keipp *et al.*, 2020). Hence, to ensure the sustainable production of sunflower oil, it is crucial to understand the effect of drought on various aspects of the crop and know about the physiological, biochemical, and genetic basis of drought at the molecular and crop levels (Hussain *et al.*, 2018).

The main objective of this review is to summarize sunflower morphological and phenological characteristics for adaptation to drought stress and to point to future perspectives for an efficient breeding strategy (Fig. 1). Identifying and categorizing key morphological characters for adaptation is important, emphasizing traits like root architecture, leaf morphology, stomatal behavior and phenological phase important to avoid drought stress. We will explore the genetic background underlying morphological adaptations in response to drought stress. We will emphasize current breeding strategies for drought tolerance in sunflower focusing on the role of genetic resources, prioritizing morphological and phenological traits as key targets and identifying mitigation mechanisms of sunflower to adapt to drought stress. Finally, by summarizing key findings, the review will offer insights for developing drought-tolerant sunflower hybrids.

2 Drought-induced morphological changes in sunflower

The impact of drought is that the plant is forced to modify its architecture to be able to bring the necessary physiological processes to an end and produce seeds to enable survival in order to adapt to the imposed situation. Disturbance in the water regime, as well as the efficiency of water use by the plant, caused by drought, induce morphological changes that are most often manifested in reduced size and number of leaves, reduction in plant height (dwarf plants), limiting root growth (Xiong *et al.*, 2020; Seleiman *et al.*, 2021). Drought-induced changes in plant architecture are also manifested in sunflower crop, affecting their growth, development, and overall health. Although, due to its anatomy, primarily the root, the sunflower copes better with drought compared to some other field crop species, sunflowers are sensitive to water deficit, and drought conditions can lead to various negative effects.

In sunflower drought causes numerous morphological changes in the above-ground plant architecture, such as plant height, stem diameter, leaf length and width, petiole length, number of leaves, as well as head diameter (Sarvari *et al.*, 2016; Pekcan *et al.*, 2016, 2022). Under controlled conditions, drought stress was observed to reduce the head diameter of sunflower plants by up to 50% (Kaya, 2016). Another study investigated the induced drought tolerance in sunflower and

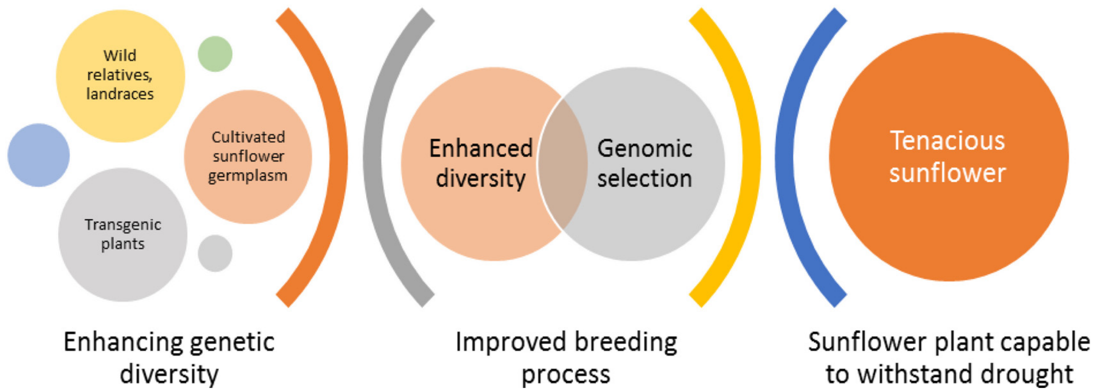

Fig. 1. Pathway for improving sunflower tolerance to drought.

found that drought at the head formation or achene-filling stage significantly decreased plant height and head diameter (Blanchet *et al.*, 2018). Furthermore, a study on sunflower genotypes subjected to water deficit revealed that drought stress affected plant height and stem diameter (Ghaffari and Hoseinlou, 2013). Negative effect of different drought treatments on sunflower seed development affected development of sunflower achene with decreased pericarp thickness and modified embryo metabolism (Vancostenoble *et al.*, 2022). Different studies have shown that drought stress affects various leaf traits of sunflower, as well, including specific leaf areas, leaf transpiration, and leaf number (Janzen *et al.*, 2023). The reduction in number and size of leaves during vegetative phase of sunflower is considered as one of the main indices that plants are facing drought stress (Shiranirad, 2000). As a total leaf surface area per unit ground area represents leaf area index (LAI) it is closely related to drought tolerance in the context of plant physiology and sensitivity to water deficit. Drought stress reduces the number and growth rate of leaves, diminishing LAI and photosynthesis (Hussain *et al.*, 2018; Havrlentova *et al.*, 2021; Shafiq *et al.*, 2021). The extremely unfavourable influence of drought on the morphological and agronomic properties of sunflower inbred lines, with the reduction of traits up to 90%, is described in the study of Pekcan *et al.* (2022).

As outlined in earlier studies, root morphological traits (depth, orientation, branching number, diameter, density) as well as fresh and dry root weight and also total dry matter are significant indicators of drought tolerance in sunflower (Rauf and Sadaqat, 2008; Rauf *et al.*, 2009; Geetha *et al.*, 2012; Nagarathna *et al.*, 2012). Drought decreases root length and root length density but increases root diameter (Janzen *et al.*, 2023). Drought-induced changes in root morphology and increased root mortality contribute to a decrease in root biomass, which is less than the decrease in shoot biomass, resulting in a higher root-to-shoot mass ratio (Kaya, 2016). Drought treatments in sunflower induce elongation in the root but inhibit the shoot growth and causes a decrease in fresh and dry root and plant weight, as well as a reduction in chlorophyll and carotenoid content (Rauf *et al.*, 2009; Manivannan *et al.*, 2014). Capacity for deep root growth may improve root acquisition of water when ample water at depth is available (Comas *et al.*, 2013). Anatomical traits (especially xylem features) also play a central role in plant growth, resource allocation, and acquisition of soil resources such as water and nutrients (Lynch and Brown, 2012). Vessel diameter, as well as the number of xylem vessels, affects root hydraulic conductivity and can affect plant productivity under drought (Zimmermann, 1983). Passioura (1983) indicated that a reduction in root xylem diameter can reduce total plant hydraulic conductance and limit plant maximum growth potential. These morphological changes in the root are important for the plant's adaptation to drought conditions and may need to be considered in terrestrial biosphere models to improve climate-biosphere predictions (Beyaz, 2022).

A better understanding of root morpho-anatomical traits and how traits are related is essential in order to increase crop productivity under different drought conditions. Since drought tolerance has been intensively researched in the last decade, and plant breeders have identified physiological traits resulting from drought responses, it is necessary to utilize a precise phenotyping platform, which is being widely used in such studies (Fita *et al.*, 2015; Kooyers, 2015; Blum and Tuberosa, 2018; Martignago *et al.*, 2020). Recently, such an approach was initiated by the Institute of Field and Vegetable Crops from Novi Sad via the SMARTSUN and CROPINNO projects, which, using modern methods of precise root phenotyping (Fig. 1) along with genotypic and epigenetic research, examines the mechanisms of adaptation of sunflower to extreme abiotic factors, primarily drought. The aim was to assess the potential of existing sunflower genotypes to tolerate drought conditions using high-throughput root phenotyping in rhizotrons (Radanović *et al.*, 2022, Cvejić *et al.*, 2023a, Dedić *et al.*, 2023). In work of Cvejić *et al.* (2023a), root morphological traits were assessed using rhizotrons under well-watered control (70% volumetric water content) and drought stress (41–50% volumetric water content), followed by root digital image analysis using a WinRhizo scanner. The study revealed that several root morphological traits, including fresh and dry root mass, root width, primary root length, total length of the root system, volume, surface area, and diameter, can indicate a differential response to drought. Generally, the tested genotypes exhibited a reduced growth rate and a significant decrease in measured parameters, except for the average diameter of the root system, under reduced water availability conditions compared to growth under well-watered control. By phenotyping sunflower roots in rhizotrons and selecting appropriate root traits, drought-tolerant genotypes

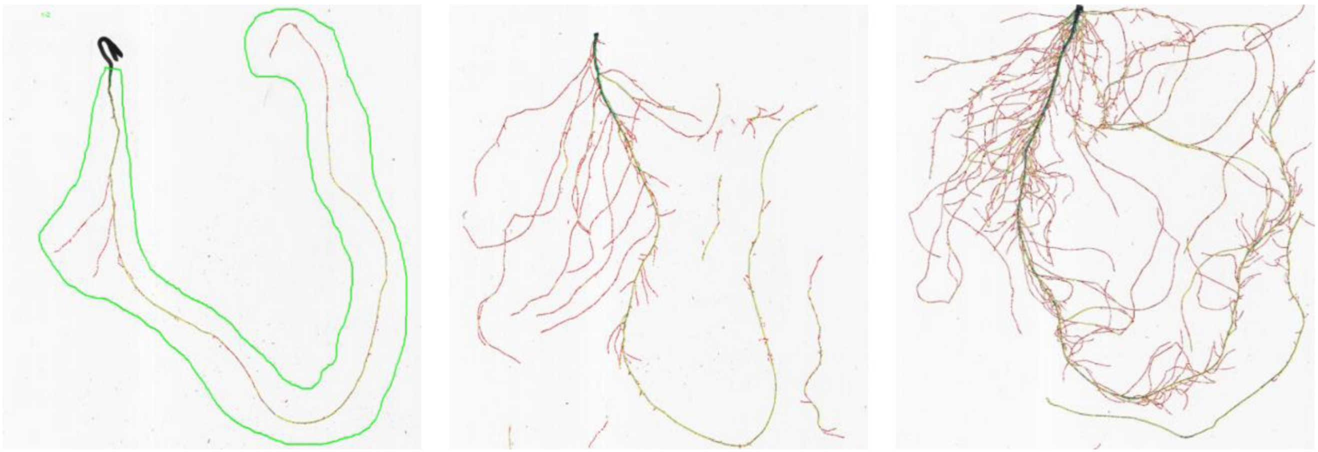

Fig. 2. Sunflower roots grown under 42, 50 and 70% water content in rhizotrons.

Table 1. Sunflower genes related to drought.

Gene responsible	Function	Reference
SDI genes (*HaElip1*, *HaDhn1*, and *HaDhn2*)	Drought adaptive response	Ouvrard *et al.* (1996)
HaABRC5	Upregulated in response to drought	Liu *et al.* (2004)
ABA-responsive genes (*HaLTP*, *HaDHN1*, *HaACCO2*, and *HaTIP7*)	Partial rootzone drying (PRD)	Aguado *et al.* (2014)
Tonoplast Intrinsic Proteins (TIPs) genes (*HaTIP7* and *HaTIP20*)	Regulation of turgor pressure of cells	Safdar *et al.* (2023)

that can withstand water stress conditions can be identified, directing breeding efforts towards a greater focus on these traits (Fig. 2).

3 Drought-induced phenological changes in sunflower

Drought-induced phenological changes in sunflower can vary depending on the timing and severity of the drought (Janzen *et al.*, 2023). Phenotypic responses differ between early and late drought stress. Early-stressed sunflowers show reduced overall growth but become highly water-acquisitive during recovery, resulting in overcompensation and higher growth rates. Late-stressed sunflowers, on the other hand, are smaller and more water-efficient.

Drought stress can significantly impact the growth and development of sunflowers, leading to observable changes in their phenological stages, such as delayed germination, delayed vegetative growth and flowering, shortened flowering duration, and seed filling. In an effort to complete their life cycle before the drought becomes too severe, sunflowers may exhibit early maturity (Debaeke *et al.*, 2021). Drought conditions alter the balance of plant hormones, such as abscisic acid (ABA) (Du *et al.*, 2018; Vancostenoble *et al.*, 2022). These hormonal changes can influence the transition from vegetative to reproductive growth, potentially promoting earlier flowering and seed development.

Premature leaf senescence, induced by drought, plays important role in adaptive strategy of several species, where the plant undergoes an accelerated aging process, leading to the yellowing and eventual death of leaves (Munne-Bosch and Alegre, 2004). When water is limited, plants may prioritize water conservation by shedding older leaves through senescence. By sacrificing older leaves, the plant reduces transpiration (water loss through leaf pores), conserving water for essential physiological processes. As leaves senesce, nutrients from the dying tissues are mobilized and redistributed to other parts of the plant, especially to developing seeds (Tan *et al.*, 2023). This nutrient remobilization is a survival strategy to ensure that essential nutrients are redirected to plant areas where they are most needed for reproduction and survival. Abiotic stress may accelerate the senescence (aging) of leaves and other plant tissues (Tan *et al.*, 2023). This premature aging can lead to a decline in overall plant health and productivity.

4 Genetic background of sunflower drought tolerance

Genetic tolerance to drought in sunflower is a complex trait influenced by multiple genes and their interaction with the environment. Sunflower have evolved several mechanisms to cope with drought stress and genetic diversity within sunflower germplasm plays a crucial role in determining drought tolerance. It possesses various drought-responsive genes, including those encoding proteins involved in stress signal transduction, transcription factors and proteins that protect against oxidative damage (Tab. 1). Earlier, Ouvrard *et al.* (1996) isolated six different cDNAs from two sunflower lines, corresponding from transcripts up-regulated by water stress, and designated them as sdi (sunflower drought-induced). Comparison of transcripts between two lines enabled authors to identify three sdi genes (*HaElip1*, *HaDhn1* and *HaDhn2*) differently accumulated in the tolerant line. Cellier *et al.* (1998)

used the same sunflower genetic material to study the correlation of phenotypic adaptation and gene expression under drought conditions. They concluded that *HaElip1* was not correlated with drought adaptive response. Furthermore, although both transcripts, *HaDhn1* and *HaDhn2*, belong to the dehydrin family of proteins, researchers found that the accumulation of *HaDhn1* transcripts was even in tolerant and sensitive lines, suggesting that the accumulation of *HaDhn1* in tolerant plants is triggered by additional factors. Advances in molecular genetics have allowed isolation and identification of specific genes associated with drought/salinity tolerance in sunflower crop, and better understanding the physiological response at a molecular level. By applying differential display using reverse transcription polymerase chain reaction (DDRT-PCR) Liu *et al*. (2004) identified *HaABRC5* gene, expressed in lower rates in leaves, seedling shoots and roots, upregulated in response to drought, salinity and abscisic acid (ABA). Aguado *et al*. (2014) conducted an extensive study in order to evaluate gene expression in sunflower root and leaf organs under different irrigation treatments. They concluded that previously described ABA-responsive genes (*HaLTP*, *HaDHN1*, *HaACCO2* and *HaTIP7*) by Ouvrard *et al*. (1996) were responsive to partial rootzone drying (PRD) treatment. Unlike, *HaELIP1* was unresponsive to PRD treatment in leaves, suggesting that *HaELIP1* gene expression in roots and leaves could potentially be used to identify the primary response to water deficit in the root and the secondary response caused by water deficit in the leaves (Aguado *et al*., 2014).

The most recently published study investigated the molecular mechanisms of drought tolerance at different stages of sunflower development (Shi *et al*., 2023). A comprehensive study outlined that four of evaluated traits (germination rate, germination potential, germination index and root-to-shoot ratio) can be a useful for sunflower breeding for drought tolerance. Also, 33 QTLs associated with drought tolerance were identified on eight chromosomes of which chromosome 13 is the most important due to the presence of many QTLs associated with drought tolerance (Shi *et al*., 2023). An under-researched area regarding sunflower responses to drought conditions is certainly the role of aquaporins. Aquaporins are water cell proteins present in the plasma membrane and in the vacuolar membrane (Johansson *et al*., 2000). A large number of isoforms of these complex molecules are present in plants, some of which are constitutive elements, while others are regulated by environmental conditions during plant growth and development, as well as by the influence of stress (Johansson *et al*., 2000; Kapilan *et al*., 2018). A recent study reported the expression patterns of Tonoplast Intrinsic Proteins (TIPs) which is important in understanding their role in plant growth, development, and stress responses (Safdar *et al*., 2023). TIPs are localized in the vacuolar membrane and play a key role in regulating the turgor pressure of cells due to their ability to control water movement between cytosol and vacuolar compartments (Afzal *et al*., 2016). A root-specific RB7-type TIP genes have been identified in sunflower. Similarly, the upregulated expression of *HaTIP7* and *HaTIP20* observed in sunflower roots upon water deprivation indicated their role in drought stress responses (Sarda *et al*., 1999). Expression patterns of genes of Tonoplast Intrinsic Proteins (TIPs) in drought enhancement of sunflower were explored using semi-quantitative polymerase chain reaction (semi q-PCR) and real-time polymerase chain reaction (q-PCR) analysis (Safdar *et al*., 2023). Results indicated that selected *HaTIPs* showed differential expression and indicated an upregulation of expression of *HaTIP-RB7* and previously described *HaTIP7* in drought tolerant entries (Safdar *et al*., 2023).

5 Genetic resources for drought tolerance

Overcoming the negative impact of drought on productivity and the creation of tolerant sunflower genotypes has become one of the strategic goals in sunflower breeding (Cvejić *et al*., 2023). Breeders use all available resources and methods to increase genetic variability and, thus, the chance to create a highly productive genotype.

Creating high-performing sunflower hybrids by utilizing existing collections is the most practical and advisable approach for developing genotypes tailored to specific climatic conditions. This involves conducting crosses between established parental lines and introducing new germplasm that carries potentially valuable traits for drought tolerance. The focus of activities in this domain also includes broadening the genetic foundation of plant species through cross-breeding genotypes with different genetic bases from existing collections and more concentrated genotypes from the traditional gene pool, encompassing domestic and domesticated varieties of wild relatives.

In addition, developing new germplasm resources with new background allelic diversity is proving to be instrumental in determining genes that contribute to basic adaptive traits (Kilian *et al*., 2021). Moreover, the widespread practice of interspecific hybridization serves as a means of transferring beneficial traits from wild relatives to cultivated breeding lines. This process, which constitutes the initial stage of the pre-breeding process, ultimately leads to the development of new genotypes.

During domestication, cultivated sunflower lost some drought survival mechanisms found in wild relatives (Seiler *et al*., 2017). In breeding for drought tolerance, the most widely used *Helianthus* species are *H. argophyllus* and *H. anomalus* (Baldini and Vanozzi, 1999; Seiler, 2007). Among wild relatives *H. anomalus* is distinguished with large achene and relatively high oil content, which makes it desirable for breeding purposes and was identified as a target species, particularly for abiotic stress tolerance and adaptation to extreme soil properties (Seiler *et al*., 2006; Seiler, 2007; Kantar *et al*., 2015). The wild annual *H. argophyllus* Torrey & Gray found in sandy beaches of Texas and Florida, with an annual rainfall of 50–100 cm, has been extensively used for sunflower drought tolerance. The drought tolerance mechanisms of *H. argophyllus* were compared with four susceptible cultivated lines in the greenhouse with varying irrigation regimes (Baldini *et al*., 1993). Under drought conditions, *H. argophyllus* was shown to have higher photosynthetic rates, higher transpiration efficiency, and less leaf area reduction. The greater water content of leaves helped maintain greater photosynthetic activity, which led to a greater dehydration avoidance capability due to its well-developed root system enabling improved water uptake. Similar field experiments conducted by Martin *et al*. (1992) also indicated that *H. argophyllus* had a lower transpiration, a more efficient stomatal control and osmotic adjustment, and the benefits of a

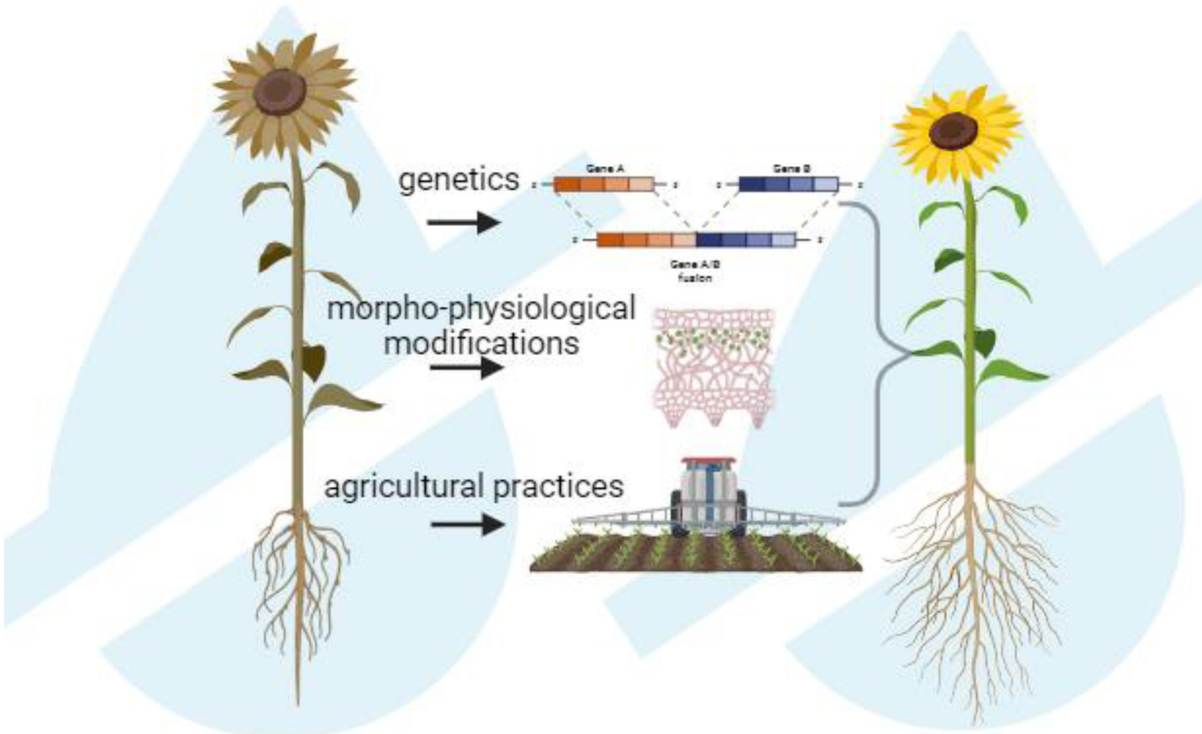

Fig. 3. Integrated approach for drought tolerant sunflower.

denser root system. The better adaptation of wild relatives of sunflower to drought conditions is also reflected in the fact that the ratio of dry and fresh mass, as well as the osmotic potential of the leaf, remains the same, while in cultivated sunflower these values decrease (Sobrado and Turner, 1983). Also, smaller leaf area is associated with better adaptation to drought conditions. Therefore, regarding smaller leaf area, some wild relatives of sunflower, with such characteristics, such as *H. praecox*, *H. nuttalli*, *H. strumosus*. *H. grosseserratus*, *H. maximiliani* and *H. pauciflorus* indicate a better adaptation to dry conditions (Jocković, 2023). Divergent selection based on physiological parameters for drought tolerance on F1, F2 and F3 progenies of a cross between a cultivated line and *H. argophyllus* has been proven effective (Baldini and Vannozzi, 1998, 1999), with a high level of drought tolerance and yield potential combined in improved sunflower cultivars. This efficiency is likely to rely on the ability of the breeder to select adequate parameters with respect to individual cross combinations. Several other sunflower wild relatives, widely adapted to drought conditions, can be used as a potential source for tolerant genes, such as *H. mollis*, *H. deserticola*, *H. hirsutus*, *H. maximiliani*, *H. niveus*, *H. tuberosus*, *H. hirsutus* etc (Baldini and Vannozzi, 1999; Škorić, 2009; Vassilevska-Ivanova *et al*., 2014; Bowsher *et al*., 2016). The most recent study of Hussain *et al*. (2023) demonstrated efficient use of *H. argophyllus* in development of drought tolerant cultivated sunflower germplasm.

6 Drought mitigation mechanisms

Successful cultivation of sunflowers in an increasingly challenging environment with frequent occurrences of dry periods during the growing season requires combining all available genetic tools (Jocković *et al.,* 2021) and the application of agricultural measures in order to reduce the negative impact of the mentioned stress (Fig. 3).

6.1 Morpho-physiological adaptations

Sunflower crop has several mechanisms (morphological and physiological) that help them mitigate the effects of drought and adapt to arid or water-limited environments. These mechanisms are also known under term "plasticity" which refers to the plant's ability to exhibit adaptive changes in its morphology, physiology and behaviour to cope with water scarcity. Understanding the plasticity of sunflower under drought stress is important for developing drought-resistant genotypes through breeding programs. Morphological and physiological adaptations allow sunflower to adapt to drought conditions and improve their chances of survival. It's important to note that the specific responses can vary depending on the severity and duration of the drought, as well as the genetic background of the sunflower genotype. Additionally, some sunflower genotypes are more drought-tolerant than others due to selective breeding and genetic modifications. Considering that the phenotype represents the realization of a genotype in certain environmental conditions, the increased genetic variation of plant architecture is of great importance to maximize the productivity within the conditions in which the plant is grown (Radanović *et al*., 2018).

Root Architecture: Sunflowers with deep and extensive root systems can better access soil moisture in deeper layers, which can help them withstand periods of drought. Genetic factors influence root development, and breeding for improved root architecture can enhance drought tolerance. Cultivated sunflower has the potential to trap soil moisture reserves that are inaccessible to many other crops and root traits such as root length and diameter, root length density, root volume, fresh and dry root weight and total dry matter are significant indicators of sunflower root drought tolerance (Hladni *et al*., 2022). Rauf *et al.* (2009) evaluated sunflower root characteristics under different water regimes and results indicated that drought had a repressive effect on root weight and shoot length while elevating effect on root length and root-to-shoot ratio. However, there is a lack of useful data about morphological and physiological root parameters of sunflower that can be useful in breeding as it requires knowledge about root traits and their effect on sunflower productivity, while it is known that depth-efficient roots for more water uptake are one of the indicators of physiological drought tolerance (Hladni *et al*., 2022).

Osmotic Adjustment: Osmotic adjustment is a mechanism that allows plants to maintain turgor pressure and cell integrity by accumulating compatible solutes, such as sugars and proline, in response to water deficit. Genetic factors influence the plant's ability to perform osmotic adjustment, helping it survive and recover from drought stress. As an additional measure, it is proven that application of 5 μM of ABA under water deficit enhances sunflower water relation and osmotic adjustment, which improves accumulation of compatible solutes and achene yield (Safdar *et al*., 2020).

Reduced Plant Growth: Drought stress limits water availability for various metabolic processes, including photosynthesis. As a result, the plant may experience reduced vegetative growth. This reduction in growth is a certain adaptation in order to conserve energy and water, which ultimately results in shorter and more compact plants. It is associated with the regulation of plant hormones such as gibberellin. Gibberellins (GAs) are plant hormones that play a crucial role in various aspects of plant growth and development, including stem elongation, seed germination, and flowering (Hedden and Thomas, 2012; Davière and Achard, 2013). In conditions of water scarcity, the plant may reduce gibberellin levels as a strategy to conserve water and limit unnecessary growth. This can result in shorter internodes and overall reduced stem elongation. It is proven that a reduction in gibberellin activity also increases plant tolerance to abiotic stress, such as drought (Mariotti *et al*., 2022). Similarly, in tomato, transgenic plants with induced dwarfism via alterations in GA biosynthesis were characterized by reduced leaf expansion and internode elongation, with a positive effect on drought stress (Li *et al*., 2012).

Lower dormancy: Detrimental effect of drought stress on sunflower during seed development enhanced tolerance to different biotic stresses such as water stress, water, hypoxic, cold and salt stresses accompanied with induced lower dormancy (Vancostenoble *et al*., 2022).

Leaf senescence: Drought stress can alter hormonal signals in the plant, affecting the usual progression of senescence and causing premature leaf senescence, where older leaves die off to reduce water loss and allocate resources to younger, more vital parts of the plant. Some hormones, such as abscisic acid (ABA), play a role in regulating senescence and might be influenced by drought conditions (Abhilasha and Choudhury, 2021; Gupta *et al.,* 2022).

Reduced leaf size and petiole length: From the aspect of tolerance to drought, leaf area and petiole length represent one of the key criteria when selecting cultivated sunflower genotypes (Merrien *et al*., 1982; Blum, 1996). Sunflower often reduces the size of leaves in response to drought. This is an adaptive response to minimize water loss through transpiration. Smaller leaves have a reduced surface area, which decreases the rate of water loss. A higher LAI usually means more leaves and, therefore, a larger surface area for transpiration (the loss of water vapor from plant leaves). In drought conditions, excessive transpiration can lead to water stress and reduced plant performance. However, some plants with a high LAI are also capable of fine-tuning their stomatal conductance (the opening and closing of stomata on leaves) to reduce water loss and improve drought tolerance.

Leaf curling or rolling: Sunflower can exhibit this phenomenon caused by various biotic and abiotic factors, among which is certainly drought (personal observations). It is a common adaptive mechanism in plants caused via changes in a water potential (Ali *et al.,* 2022). This helps to reduce the water loss through transpiration and enhance the accumulation of dry matter (Lang *et al.,* 2004).

Cuticle and stomatal regulation: The cuticle, a waxy layer covering the leaves, and stomata, small pores on the leaf surface, play essential roles in regulating water loss through transpiration. Genetic variation can affect the thickness and composition of the cuticle and the control of stomatal opening and closing, which can impact a sunflower's ability to conserve water during drought. Sunflower regulates the opening and closing of stomata (small pores on the leaf surface) to control water loss where long-term water deficit leads to limitation of photosynthesis in leaves (Panković *et al.,* 1999). In response to drought, plants tend to close their stomata to limit water vapor loss through transpiration. This, however, can also reduce carbon dioxide uptake for photosynthesis.

Plant trichomes: As outlined by Jocković (2023) their presence increases the tolerance to abiotic stress such as drought, by lowering the leaf temperature, keeping moisture on the leaf surface and reducing the absorption of solar energy and UV radiation (Benz and Martin, 2006; Galmés *et al*., 2007). In a study of Aschenbrenner *et al*. (2013) the presence of non-glandular trichomes (NGT) was recorded on the vegetative organs (stem and leaf) of sunflower (*Helianthus annuus* cv. Giganteus). Likewise, in the research of Jocković (2023) dense indumentum was recorded on both, abaxial and adaxial, leaf epidermis, within the wild relatives *H. argophyllus*, *H. mollis*, *H. nuttalli*, *H. strumosus* and *H. grosseserratus* which may be used as a potential sources of genes for this trait for the breeding of cultivated sunflower for drought tolerance.

Photosynthetic efficiency: Genetic variation can impact a sunflower ability to maintain photosynthetic activity during drought stress (Arslan *et al.,* 2020). Sunflower genotypes with genes that enable them to continue photosynthesis under limited water conditions are more likely to survive and produce seeds. Drought-tolerant plants often have mechanisms to maintain photosynthesis even under water stress.

Early flowering: Usually, sunflower genotypes adjust their flowering time in response to water availability (Buriro *et al.,* 2015). They may start flowering earlier in the season if they sense water scarcity, increasing their chances of reproducing before the drought becomes severe. Drought stress sometimes delays the onset of flowering in sunflower. Delaying flowering allows the plant to redirect resources toward essential functions, such as root development and water uptake, before allocating resources to reproduction.

Early maturing sunflower hybrids exhibit different responses to drought stress. When subjected to drought at an earlier growth stage, sunflowers show reduced overall growth but become highly water-acquisitive during recovery irrigation, resulting in overcompensation and higher growth rates. In contrast, sunflowers stressed later in their growth stage are smaller and more water use-efficient. Transcriptomic responses to drought stress are similar across different timing and severity levels, with shared differentially expressed genes related to photosynthesis and plastid maintenance. However, phenotypic responses diverge between early and late drought, with early-stressed sunflowers showing higher aboveground biomass and leaf area, while late-stressed sunflowers are smaller and more water use-efficient (Janzen *et al*., 2023).

Flower and seed production: In extreme drought conditions, sunflower may reduce or even abort flower and seed production to prioritize survival. This is a last-resort strategy to conserve energy and water for essential physiological processes.

Stay green nature in sunflower is considered as an indicator of drought tolerance (Hilli and Immadi, 2021). Drought stress negatively impacts the performance of sunflower, but foliage application of 5-aminolevulinic acid (5-ALA) improves sunflower performance under drought stress by improving stay green and antioxidant enzyme activities (Almeida *et al*., 2020). The specificity of the green trait is reflected in the fact that it enables plants to have an extended photosynthesis interval, which, especially in conditions of drought and heat stress, enables a longer period of grain filling, and thus a higher yield (Kamal *et al*., 2018). The spraying of zinc sulphate (ZS), potassium phosphite (KPhi), and the hydrogen sulphide (H2S) donor sodium hydrosulphide (NaHS) mitigates the deleterious effects of water deficit on sunflower plants by maintaining higher water potential, lower leaf malonaldehyde content, and increased activity of the antioxidant enzyme peroxidase (Shi *et al*., 2023).

Due to the complexity of the drought tolerance manifestation and the large number of morphological and physiological characteristics involved, the selection of parameters used in individual genetic and breeding studies often relies on the contrasting characteristics of the parents involved. A "stay-green" trait has been specifically mentioned by Škorić (2016) for its relatedness to drought tolerance, earlier confirmed by Vranceanu (2000) as an effective criterion for selection of drought tolerance in sunflower. Drought tolerance lines with stay-green characteristics have been shown to have increased RuBisCo proteins, therefore higher photosynthesis, and higher quantum yield of photosynthesis in the leaves, supporting the use of stay-green trait for drought tolerance selection.

6.2 Agricultural practices

Successful drought management for sunflower requires a combination of agricultural practices defined by specific growing conditions. Local climate, soil type and severity of drought are important parameters that influence the selection of strategic measures aimed at reducing the negative impact of drought. One of the first strategic decisions for sunflower production in drought-prone environments is the selection of hybrids specifically adapted to thrive in water-limited conditions. Plant breeders have developed drought-resistant sunflower hybrids through selective breeding (Jocković *et al*., 2019; Gul *et al*., 2021). Drought-tolerant sunflower genotypes develop more root systems, enabling more efficient uptake of available water (Killy *et al*., 2016). Also, choosing the sowing date when the risk of drought is lower can reduce the negative effects of crop exposure to water deficit (Krstić *et al*., 2023). Appropriate planting density is important from two aspects: 1) optimize crop competition for water and nutrients and 2) a dense canopy with a high LAI can provide shade to the soil surface, reducing evaporation and keeping the soil cooler. This can help conserve soil moisture and make it available for the plant during dry periods. As additional measures that can mitigate the negative effect of drought, it is recommended, depending on the possibility, to incorporate organic matter into the soil to improve water-holding capacity and, if possible, implement irrigation during critical stages such as emergence, flowering and seed filling. Seed priming techniques with different solutions have been proven to be as efficient strategy for improving germination parameters in drought conditions in many crops (Sadeghi *et al*., 2011; Eskandari and Kazemi, 2011; Čanak *et al*., 2014; Jocković *et al*., 2018). A recent study by Wasaya *et al*. (2021) emphasizes the use of β-aminobutyric acid (BABA) via foliar application in the vegetative and reproductive stage of sunflower as a mitigation strategy. It has been determined that foliar application of BABA significantly improved 1000 seed weight (TSW) and seed yield (SY) of sunflower (Wasaya *et al*., 2021). More recently, there are studies about successful exogenous application of organic compound such as trehalose which demonstrated significant improvement in sunflower plants under drought stress (Kosar *et al*., 2020, 2022). Similarly, foliar application of stigmasterol, a brassinosteroids (BRs) group of growth regulators, mitigates the negative effect of drought on sunflower by improving growth and development (Hanafy and Sadak, 2023).

7 Future strategies

Enhancing genetic diversity: Maintaining genetic diversity within sunflower germplasm is crucial for breeding drought-tolerant varieties. Different sunflower genotypes may exhibit v exhibit varying levels of drought tolerance, and breeding programs can utilize this diversity to develop improved varieties. Sunflower wild relatives and local landraces can be a fruitful source of desirable genes thanks to their adaptation to different habitats.

Modern breeding techniques: This is a controversial topic, but genetic engineering techniques can be used to introduce drought-tolerant genes from other plants or organisms into sunflower. This technique has already been used for the development of drought-tolerant transgenic wheat plants (Khan *et al.*, 2019). Combining genes from different crops (organisms) may provide a more efficient mechanism to combat drought conditions. Genome editing, as a rapidly evolving field, could provide the means to solve challenges related to sunflower drought resilience by enhancing traits related to plant architecture and adaptation to the environment (Miladinović *et al.*, 2021). However, regulatory and environmental concerns need to be addressed when employing transgenic approaches.

Genomic selection and other −omics technologies: Genomic selection involves predicting the genetic value of plants based on their entire genome rather than individual markers. This approach can improve and accelerate the breeding process for drought tolerance by considering the complex interactions between multiple genes. Furthermore, exploitation of available genetic resources comprising wild relatives and landreces in combination with genome-wide association studies and genomic selection could accelerate introduction of drought-resilience related traits into cultivated sunfower (Hladni *et al.*, 2022). There is also growing evidence that epigenetic mechanisms may have a role in increasing crop resilience to specific stresses and therefore may find their application in sunflower breeding for drought tolerance (Varotto *et al*., 2020). Due to complex nature of sunflower drought tolerance, using only one −omics approach could not be sufficient to develop novel drought-tolerant genotypes. Hence, efficient integration of different tools by using multi-omics approach to drought tolerance is a promising strategy for further efforts in creation drought-tolerant sunflower (Hladni *et al.*, 2022). the contribution of new high-throughput phenotyping facilities and the role of crop modeling for evaluating water stress patterns and explore the performance of candidate ideotypes (and new genotypes) on a wide range of environments (present and future).

Phenotyping and crop modelling: The contribution of new high-throughput phenotyping facilities and the role of crop modelling in evaluating water stress patterns are crucial components of advancing agricultural research, particularly in the context of exploring the performance of candidate ideotypes and new genotypes across diverse environments, both present and future. High-throughput phenotyping facilities allow researchers to collect vast amounts of data on plant traits in a short period. This includes information on growth patterns, morphology, physiology, and responses to environmental stresses like water scarcity. Crop models allow researchers to simulate different environmental scenarios, including variations in temperature, precipitation, and soil conditions. This enables the assessment of how candidate ideotypes and genotypes might perform under both current and future climate conditions.

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Conflicts of interest

The authors declare that they have no conflicts of interest related to this article.

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