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Salt and Drought Stress Responses in Date Palm (Phoenix dactylifera L.): A Physiological, Biochemical, and Comparative Genome Analysis"

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Abstract

Drought and salinity are the two most critical environmental stresses negatively affecting plant productivity and quality with overlapping mechanisms. The majority of plant species are sensitive to these constraints that, over the past decades, increased as result of climatic changes. Salt and drought affected lands are increasing at an alarming rate and already reached about 62 million hectares (20%) of the world’s irrigated land, mainly in arid and semi-arid areas. Date Palm is a recognized important nutritious fruit crop whose production is ultimately affected by environmental threats (particularly salinity and drought) that are lowering yield and fruit quality. This review is focused on the current knowledge of the impact that drought and salt stresses singularly or in combination have on date palm growth, fruit yield and quality traits. Agronomic and stay green attributes, hormonal impact and biotechnological approaches have been explored. It was also put in light the important role of osmo-protectants, mineral and ion homeostasis, exogenous protectants, antioxidant compounds, antioxidant activities, transgenic approaches, breeding strategies, functional genomics and omics technology on inducing salinity and drought tolerance. Lastly, we have delineated perspectives and technologies to better salinity resistance of plants, examining all those aspects with the perspective of providing important knowledge to optimize the future cultivation of date palm.

Keywords: Date Palm; Drought; Eco-physiological traits; Nutrients; Omics technologies; Osmotic adjustment; Salinity; Salt-tolerant genotypes;

1 INTRODUCTION

Drought and salinity are two of the most significant abiotic stresses that impact crop production, growth, yield, and quality worldwide. Drought and salinity stresses reduce crop productivity, leading to economic losses and food insecurity. Therefore, there is the need to individuates crop varieties that can withstand these stresses maintaining the productivity under adverse conditions (Hussain et al., 2018 a, b, 2019, 2020; Cuong et al., 2020). A significant food insecurity has been developed due to long term drought and shortage of fresh water resources in several parts of the world, especially, in Sub-Saharan Africa and Arabian Peninsula that ultimately, caused shortage of cereals, grain crops, oil-seeds, vegetables and fruit trees (Lawal, 2021). Salinity is causing significant threats to arable land globally, affecting soil structure and biodiversity and causing soil erosion, and water scarcity (Arif et al., 2020; Hussain et al., 2016; 2020). The new climatic scenario with high temperatures, heat waves and floods, is exacerbating drought and salinity processes (Parvez et al., 2020). Therefore, it is necessary to evaluate the physiological, morphological, biochemical and genetic responses of plants to these abiotic stresses that can occur singularly or in combination, and with diverse entity depending on the area of incidence (Cuong et al., 2020). Stress can be partially or completely removed by a physical barrier or timing of behavior and/or appearance, stress tolerance can be, instead, achieved using either repair or prevention techniques (Munns and Tester, 2008). In arid and semiarid regions, salinity and drought remain the principal constraints for crop growth and for the development of countries whose economy is mainly based on agriculture.

Salinity is causing serious threat to agriculture, decreasing the productivity of cereals, legumes and fruit crops. Nevertheless, considerable advances have been made regarding the identification of resistance varieties and germplasm (Colmer et al., 2005). Food insecurity will likely rise without any attempt to adapt to climate changes, considering the increasing food demand. Climate changes are impacting not just food supply, but also food quality, food access and utilization, affecting particularly the nutritional properties of the crops. Additionally, since 1950, heat waves have been happening more often, and drought is occurring more frequently and taking a turn for the worse

Considering the growing exigency of recovering saline and drought lands for cultivating more food crops the principal objective is to individuate salt and drought tolerant plants able to make productive marginal stressed lands (Hussain et al. 2016). Screening and selection of plant genotypes with salinity and drought tolerance have been carried on for different fruit crops such as *Eugenia jambolana* (Jaman), *Zizyphus jujuba* (Ber), *Grewia asiatica* (Falsa*), Psydium guajava (*guava) (Qureshi and Rashid, 1988); *Psydium guajava, Syzygium cumini, Carrisa carandas, Achras zapota, Sapindus laurifolius, Zizyphus mauritiana* (Singh, 1994) and olive cultivars (Agizi Aksi, Agizi Shami, Teffahi) (Hassan et al., 2000). Among the fruit crops, *Eugenia jambolana* (Jaman), *Zizyphus jujuba* (Ber) and *Grewia asiatica* (Falsa*)* were highly salt-tolerant while *Psydium guajava (*guava) was moderately tolerant to salinity (Qureshi and Rashid, 1988).

Date palm (*Phoenix dactylifera* L.), belonging to the Palm family (*Arecaceae*) is an important fruit and cash crop, in Arabian Gulf countries, Asia and Africa (FAO, 2006). Molecular techniques such as omics technologies, DNA fingerprinting and genetic engineering have been used around the globe to improve the quality and the environmental adaptability of date palm (Ait-El-Mokhtar et al. 2019). Date palm is rich of several essential minerals, micronutrients and carbohydrates (Al-Farsi and Lee, 2008) as well as phytochemicals including, flavonoids, phenolic acids, anthocyanins, tannins and carotenoids (Echegaray et al. 2023). Due to its high content of fiber and antioxidant compounds (contained in its fruit) with recognized beneficial effects on human health, date palm is increasing its economic and nutritional importance and its cultivation is now wide spreading around the world with a global production estimated at eight million tons per year (Table 1).

As a result, date fruits have been and continue to be used in the local medicines to treat common health problems. Thus, is of paramount importance, to individuate date palm varieties able to perform well under drought and salinity stresses maintaining a high yield and even more a high nutritional value (Hussain et al., 2016).

This review wants to spotlight yield reduction and physiological disorders caused by drought and salinity in order to better evidence the limits and tradeoffs of these two constraints. The role of osmo-protectants, ion homeostasis, exogenous protectants, and antioxidants in contrasting these stresses was also provided. Finally, different management options useful to reverse the declining trend of date palm growth and yield have been discussed with the aim to increase long-term fruit and yield stability. Agronomic practices, as well as sustainable use of non-conventional water resources, integrated nutrient management, breeding tools, functional genomics, resource conservation and omics technologies to preserve/improve, in a sustainable way, date palm cultivation in marginal and stressed area have been extensively analyzed.

2 METHODOLOGICAL APPROACHS

The present review represents a methodological tool to provide answers, useful to evaluate theory or evidence in this field. It was carried out considering the relevant literature and the research projects, using different sources and search engines including Centre for Agriculture and Bioscience International (CABI), Scopus, Google Scholar, Elsevier Science Direct and Web of Science databases). The keywords used for the data collection includes: drought stress; eco-physiological traits; salinity stress; nutrient assimilation; omics technologies; osmotic adjustment; salt-tolerant genotypes; management. The manuscripts published up to 2021 with empirical results were selected to draft this review.

3. DROUGHT STRESS EFFECT ON DATE PALM

Drought stress can have significant impacts on the physiological and metabolic pathways of date palm trees, ultimately leading to reduced yield and fruit quality. The severity of these impacts can vary depending on a range of climatic factors (such as temperature, rainfall, and solar radiation).
Accumulation of reactive oxygen species (ROS), which can cause oxidative damage to cellular components such as proteins, lipids, and nucleic acids, is a primary symptom of drought stressful conditions. This can ultimately lead to reduced photosynthetic activity and deteriorating chlorophyll synthesis, as mentioned by Al-Muaini et al. (2019). In addition to these effects, drought stress can also affect other aspects of date palm physiology, such as root growth, nutrient

uptake, and water use efficiency. To mitigate these impacts, various strategies can be employed, including irrigation management, soil amendments, and genetic improvement through breeding and biotechnology.

Drought stress can cause disruption in the chlorophyll fluorescence and photosynthetic system of date palms, leading to changes in carbon partitioning at molecular and cellular levels. These changes can result in modifications to the composition of membrane proteins and lipids in the photosynthetic apparatus (Elshibli et al., 2016). One consequence of these changes is the reduction in the efficiency of photosynthesis, which can lead to reduced yield and quality of date fruits. Additionally, drought stress can also affect the synthesis and accumulation of carbohydrates and other metabolites in the plant, which can further impact growth and productivity (Cornic et al., 2006; Alikhani-Koupaei et al., 2018; Ahmed Mohammed et al., 2020).

To mitigate the effects of drought stress on date palms, it is important to implement strategies that help the plant to cope with water scarcity, such as irrigation management, mulching, and use of drought-tolerant cultivars. Additionally, improving the efficiency of photosynthesis and carbon partitioning through genetic improvement and biotechnological approaches can also represent a beneficial (Ahmed Mohammed et al., 2020). Date palm can tolerate low tissue water potential through osmotic adjustment, which involves the accumulation of compatible solutes, such as sugars and amino acids, to maintain cell turgor and function under water stress conditions. This can reduce transpiration and increase stomatal adjustment, which help the plant to store water (Al-Khateeb et al., 2019; Hussain et al., 2020).

However, even with these adaptive mechanisms, drought stress can still significantly reduce growth, yield, and quality of date palm. This is because drought stress can impact many plants physiological and biochemical processes contemporarily, including photosynthesis, respiration, and nutrient uptake, which in turn lead to reduced biomass accumulation, lower fruit yields, and poorer fruit quality (Al-Khateeb et al., 2019).

To minimize the impact of drought stress on date palms, it is important to implement effective irrigation management strategies that optimize water use efficiency and minimize water losses through evaporation and runoff. Additionally, other management practices such as mulching, crop rotation, and the use of drought-tolerant cultivars can also help to mitigate the effects of drought stress on date palms (Al-Khateeb et al., 2019).

At the morphological level, plants can modify their root systems to explore deeper soil layers in search of water, or they can reduce leaf area and leaf thickness to reduce transpiration rates. At the physiological level, plants can regulate stomatal conductance, which is the major determinant of water loss through transpiration. Plants can also accumulate compatible solutes, such as sugars and amino acids, to maintain cell turgor and function under water stress conditions (El Rabey et al., 2015).

At the biochemical and metabolic levels, plants can activate various signalling pathways that trigger the expression of genes involved in stress tolerance, such as genes encoding heat shock proteins, chaperones, and enzymes involved in osmotic adjustment. Additionally, plants can modify their metabolism to accumulate specific compounds, such as proline, which can act as osmo-protectants and protect cellular structures from damage during drought stress.

Finally, when drought stress conditions are alleviated, plants can reset their standard cellular operation by reversing many of the changes that occurred during stress, such as reducing the accumulation of compatible solutes and re-establishing normal metabolic pathways.

Osmotic stress, caused by drought conditions, can have negative effects on plant growth and nutrient uptake, by decreasing their ability to take up nutrients such as nitrogen (N) and phosphorus (P), which are essential nutrients. When a plant is exposed to osmotic stress, such as from high salinity or drought, water becomes scarce, and the plant needs to conserve it. One way it does this is by reducing the number of open stomata on its leaves, which in turn reduces the uptake of nutrients through the roots.

Nitrogen is essential for plant growth and development, and it is required for the production of chlorophyll, the molecule that enables photosynthesis. Phosphorus is also critical for plant growth and it is necessary for energy transfer within the plant, as well as for the synthesis of DNA and other important molecules (Ebrahimi et al., 2021).

In addition to affecting macro-nutrient uptake, osmotic stress can also impact the uptake of micro-nutrients, such as iron, zinc, and manganese, which are required in smaller quantities but are nonetheless essential for plant health.

Meddich et al. (2015) investigated the efficacy of indigenous fungal isolates and of three selected *Glomus mycorrhizal fungi* in improving the tolerance to water stress in date palm seedlings of the Bouffgouss variety.

El Rabey et al. (2015) evidenced 47 differentially expressed proteins in leaves of Sagie date cultivar 3-month-old for 30 days under drought stress. Under PEG induced osmotic stress, Djibril et al. (2005) demonstrated in two date palm varieties (Nakhla hamra and Tijib), that epicotyl length, primary root length, secondary root number and proline content increased. Nakhla hamra variety resulted more tolerant than Tijib. The different response of the two cultivars was ascribed to the greater proline content and root length of NHH in respect to Tijib. In short, the authors evidenced and confirmed previous findings showing that the variety can play a central role in preserving from specific abiotic stress. Several marker-assisted breeding tools such as proline accumulation have been recognized as vital in inducing drought stress tolerance in date palm. It was demonstrated like an osmolyte or an antioxidant able to rectify water stress.

The stomatal closure and water shortage can impose significant negative effects on photosynthetic process and Calvin cycle enzyme activation. This led to plant growth reduction, inflorescence development and fruiting (Ashraf and Harris, 2013; Farooq et al., 2009). Drought decreased photosynthetic carbon assimilation, and chlorophyll content (*a* and *b*) causing the collapse of photosynthetic pathway (Chaves, 2009). Figure 1 synthesizes the influence of drought stress on photosynthesis.

4. DROUGHT STRESS ON DATE PALM FRUIT YIELD AND QUALITY

Fruit yield and quality of date palm can be affected by water scarcity and the response can be related to the type of cultivar or variety and can be different on quality and productivity. Several researchers demonstrated that fruit quality was directly related to fruitlet mass. The availability and accumulation of carbohydrates in the individual fruit was responsible to attain fruit mass (Génard et al., 2008; Serra et al., 2016). Ahmed Mohammed et al. (2020) showed that the innovative sub-surface irrigation (SSI) system improved date palm fruit quality and production while significantly reduced the amount of water used. This irrigation strategy may be useful to optimize water use efficiency reducing its waste.

One such strategy is deficit irrigation, which involves applying water at levels below crop water requirements. Studies have shown that moderate deficit irrigation can improve water use efficiency and increase date palm fruit yield, without negatively affecting fruit quality (Singh et al., 2014). Other strategies include using efficient irrigation systems such as drip or micro-sprinkler irrigation, which can reduce water losses due to evaporation and runoff, and using soil moisture sensors to optimize irrigation with the aim to avoid over- or under-watering. In addition to these irrigation strategies, it may also be beneficial to incorporate practices that improve soil water retention and reduce water loss through evaporation, such as mulching and soil amendments. Overall, by implementing these water management practices, date palm growers can improve the water use efficiency of their crops and reduce their dependence on irrigation water in water-scarce areas.
Recently, Ghazzawy et al. (2023), studying how water stress affected date palm productivity, concluded that at the fruit ripening stage, water stress had a limited effect on the yield of the tree (kg/tree) and on skin separation of the date fruits, but stimulated the ripening of the fruits. Mattar et al. (2021) showed that an irrigation deficit on date palm trees, grown in arid regions, either with fresh water or with brackish water improved fruit quality but negatively affected yield. Conversely, Al-Mansor et al (2021) showed that the date palm has the ability to withstand water stress, even if it negatively affected the production. The authors demonstrated that, in order to obtain a high production, 100% of irrigation should be used, but the use of RDI at a rate of 0-75% of ETc in the period that cover from the beginning of the flowering stage to the beginning of the Kamari stage, and from the end of the Khalal stage and the beginning of the Rutub stage to the end of the season and harvesting of fruits, could be useful for the production and for saving 5%-39% of water Drought tolerance mechanisms.

Drought stress affect plant production in many regions of the world (Ahmed Mohammed et al., 2020), causing an early inhibition of floral development with consequent sterility of growing plants (Stanton et al., 2000; Achard et al., 2006; Su et al., 2013). This is generally a dose-dependent effect (Li et al., 2007). Under extreme drought conditions, date palm (*Phoenix dactylifera* L.) has the potential to survive (El Rabey et al., 2016). Waxy, thick cuticle and pinnately leaves sheltered with many spines provide insulation to the tip growing points in date palm. Deep root systems also contribute to increase the survival of date palm under limited supply of water (Sané et al., 2005). Different varieties of date palm can have distinct tolerant potential to mitigate the drought adverse effects. For the survival of plants under stress, early initiation of flowers is the major mechanism usually referred as stress escape (Sherrard and Maherali, 2006). It is a classical mechanism in plants where life cycle is completed rapidly prior to upcoming the stress. Under limited water supply, metabolic process becomes fast in plants. High metabolic rate of plants resulted in rapid division and expansion of cells (Kooyers, 2015). During this process, plants shift from vegetative growth phase into reproductive phase and start the initiation of flowering. Stress activates transcriptional induction of twin sister of FT (TSF) and floral promoters FT dependent on gene GIGANTEA and plant stress hormone abscisic acid (ABA) during long days. However, in short day, ABA and drought activate floral repressors, restricting the transcription of FT and TSF (Riboni et al., 2013).

Figure 3 shows drought escape possibility of date palm tree. Solute accumulation resulted in osmotic adjustments of cells by decreasing the osmotic potential. An increase in water gradient influx, improved the water content of tissues by preserving cell turgor. During the whole drought period, such osmotic adjustments in the cells, regulated the physiological activity for the completion of plant life cycle (Kramer and Boyer, 1995). For the maintenance of turgor compatible active solute (CAS) accumulation is very important. These CAS includes sugar alcohols, soluble sugars, glycine-betaine, proline, organic acids, potassium, calcium and chloride ions that are highly soluble, non-toxic even at high cytosolic concentrations. Accumulation of compatible active solutes protects plants from the negative effects of reactive oxygen species. Furthermore, they also stabilized the membrane, maintained the proteins and enzyme structures and adjusted the turgor (Serraj and Sinclair, 2002; Sané et al., 2005; Yaish, 2015). Water molecules, during reduced osmotic potential of cells, played an imperative role in maintaining the cell turgor and the activities of cytoplasm and organelles under drought stress. As demonstrated by Subbarao et al. (2000) and Shareef et al. (2021), such conditions allow an optimum plant growth, photosynthesis and assimilate partitioning to fruit filling, additionally, the significant decrease in leaf water volume during the active accumulation of solutes in cytoplasm is a key phenomenon which causes osmotic adjustment of cells. Maintenance of turgor and attraction of water molecules via accumulation of solute mitigates the adverse effects of drought in plants (Abobatta, 2019). The osmotic adjustment facilitates the better translocation of pre-anthesis carbohydrates during the formation of fruits (Subbarao et al., 2000). Fig. 5 shows the mechanism of drought tolerance due to osmotic molecule accumulation in the date palm tree.

Several defense mechanisms are responsible for drought tolerance upregulating antioxidant productions when water availability is limited, playing a pivotal role in date palm stress tolerance (Benhiba et al., 2015; Helaly et al., 2017; Sakran et al., 2018).

Few studies are reported on omics of drought in date palm. El Rabey et al. (2016) studied genes involved in salinity and drought stressed date palm cultivar “Sagai”. Out of 47 expressed genes found, 13 were responsive to salinity and drought, seventeen were reactive to salinity and the remaining 7 were responsive to drought only. Few DGE (ribulose-1,5- bisphosphate, carboxylase/oxygenase, oxygen-evolving enhancer protein 2, chroloplastic-like and cytochrome P450) were down-regulated under drought, with a consequent deactivation of photosynthetic pathway.

In addition, it was observed that date palm plants produced higher concentration of phenolic compounds and flavonoids under limited availability of water. Non-enzymatic antioxidants play a vital role in scavenging the ROS in drought stress conditions (Ashraf et al., 2011). The role played by non-enzymatic antioxidant system is not well understood because no enough data have been published in the literature, this review is highlighting this information to provide concise knowledge to researchers working in this field.

At the time of plant development, chloroplasts are important organelles and represent the place in which biochemical process of photosynthesis occur via optimum functioning of chlorophyll a molecule that is directly involved in the conversion of light energy to chemical energy. This is the main aspect of stay green mechanism (Condon et al., 2004). The effect of stay green phenotype through its active photosynthetic apparatus in spike, under drought, is mainly relevance in tribe

Triticeae. Limited research works are available yet (Raven and Griffiths, 2015). Awns derived from lemma usually grow as bristle-like structures, having rough or smooth surface along stomata. It contributes in manufacturing of photo-assimilates (Toriba and Hirano, 2014). Extended and active stay green depends upon delay and accelerate senescence in plants under limited water availability to compensate yield, enhancement in seed formation, and decrease in organ sterility (Gregersen et al., 2013; Dolferus, 2014). Figure 4 shows a stay green tolerance mechanism in the date palm tree. Majorly four stay green categories are so far identified. Late senescence's that starts and proceed with normal rate (type A). Senescence that starts as per schedule, but proceeds with a slow rate (type B). The retention of chlorophyll that is indefinite, and the senescence proceeds normally under the chlorophyll layer (type C). Leaves that remain green with an active photosynthesis, but with a very slow ensconcing (type D) (Thomas and Howarth, 2000; Thomas and Ougham, 2014).

To mitigate drought stress, the role of phytohormone is very important and vital. Drought stress significantly changes the sensors of phytohormone in the plants. Among the different phytohormones some of the most important are abscisic acid (ABA), jasmonic acid (JA), salicylic acid (SA), auxins (IAA), ethylene (ET), gibberellins (GAs), brassinosteroids (BRs) and cytokinin's (CKs) (Kazan, 2015; Ullah et al., 2018).

(1) Abscisic Acid

Plants produce a significant amount of ABA under osmotic stress which activates the expression of genes strictly correlated to the physiological changes that allow plants adapting to drought stress (Yamaguchi-Shinozaki and Shinozaki, 2006; Safronov et al., 2017). As stress starts, signals are sent to the plasma membrane to produce ABA. Following the ABA synthesis in the plastids, xanthoxin into ABAIs transformation occurred in cytoplasm (Seo and Koshiba, 2002). Vascular tissues in the plants transport ABA to different cells specially to guard cells (Kuromori et al., 2010). Under osmotic stress condition, to maintain, cellular turgor, minimizing the negative effects of limited availability of water, plants reduce the transpiration rate through the closure of stomata. Thus, low stomatal conductance can be considered a potential indicator of mitigation of drought stress in plants. Baloch et al. (2011), Elshibli et al. (2016) and Müller et al. (2017) showed a negative correlation of drought stress with the rate of transpiration and stomatal conductance. When the potential of leaf cells decreases, ABA sent a signal to the guard cells for their closing. The closure of guard cells results in the minimum conductance of stomata which in turn decreases the water losses through transpiration. However, some exceptions can occur in which two conductors of stomata are also associated with the rate of photosynthesis in the plants (Von Caemmerer et al., 2004). In short, these findings on ABA role can be useful for breeding program to obtain plants with more responsive guard cells to water shortage or high salinity.

(2) Jasmonic Acid

Jasmonates are well known to play a critical role in defense against abiotic stresses in different tissues and especially in flowers. It is synthesized in plastids, peroxisome, and cytosol at cellular level. Jasmonate ZIM-domain (JAZ) proteins have imperative JA signaling pathways. JA increases the development of root, scavenging of ROS and stomatal closure under drought stress (Munemasa et al., 2007; Riemann et al., 2015). It was observed that 12-OPDA (12-oxo Phytodienoic acid) plays a vital in the eco-physiological attributes of cellular plant functionality, especially in the leaf stomata (opening and closing) because it is a JA precursor (Bosch et al. 2014). In addition, elevated levels of 12-oxo-phytodienoic acid (OPDA) have been associated with minimum stomatal aperture which provides tolerance against drought. Conversion of OPDA to JA was inhibited by osmotic stress and then OPDA either worked with and without ABA to provide the drought tolerance through closure of stomata (Savchenko et al., 2014; Kazan, 2015).

The study of Waheed et al. (2022), evidenced that applying JA to Grewia asiatica plants experiencing moderate drought stress had beneficial effects on their antioxidant activity, plant performance, and growth. The plants were exposed to 100% and 60% of their field capacity, and JA was applied only when the plants were experiencing moderate drought stress, as indicated by an average stem water potential of 1.0 MPa. The researchers monitored physiological and biochemical measures over a 14-day period. Compared to untreated plants, the JA-treated plants displayed significant improvements in plant growth, with a 15.5% increase, and in CO2 assimilation (AN) and stomatal conductance (GS), with increases of 43.9% and 42.7%, respectively, on day 3. The study also found that the activities of the three antioxidant enzymes, ascorbate peroxidase (APX), glutathione peroxidase (GPX), and superoxide dismutase (SOD), were significantly increased in JA-treated plants compared to untreated plants. The APX, GPX, and SOD activities of drought-stressed JA-treated plants increased by 87%, 78%, and 60%, respectively, on day 3.

In this context, Beniušytė et al. (2023) showed that a single application of JA to pine seedlings in several genetic families led to an increase in antioxidant enzyme activities, total phenol content, and carotenoid content, with a level of response that correlated positively with the JA concentration used. There was some variation in the response of different genetic families, many of them showed a significant increase in these measures compared to the untreated group.

(3) Ethylene

Ethylene biosynthesis is regulated by different levels of control, including transcriptional, post-transcriptional, translational, and post-translational mechanisms. The transcriptional regulation of ethylene biosynthesis genes is mediated by various transcription factors and other regulatory proteins. In addition, post-transcriptional and translational mechanisms, such as alternative splicing, RNA interference, and protein modification, also play important roles in regulating ethylene biosynthesis (Fatma et al., 2022). Environmental stress, such as high temperature, drought, salinity, flooding, and pathogen infection, can trigger ethylene biosynthesis and signaling in plants. Although, ethylene has been widely studied relatively to the plant senescence process, its role in drought-induced senescence is not so much known. It has been proved that under drought, ethylene provoked leaf abscission and as result water losing decreased (Aeong et al., 1997). Under water deficiency, ethylene synthesis was paralleled by an enhancement and subsequent reduction in ACC, indicating that water stress caused the de novo synthesis of ACC synthase, the rate-controlling enzyme of ethylene biosynthesis pathway. Furthermore, ethylene and its metabolic process are significant to trigger plant responses to flooding and water deficiency (Voesenek and Bailey-Serres, 2009; Habben et al., 2014). It induces a signal transduction network that finishes with the synthesis of some transcription factors that control gene activation/repression along all the stress period. Ethylene has been shown to have a regulatory role in the production of various secondary metabolites in plants, such as alkaloids, glucosinolates, and terpenoids (Baharudin et al. 2023). The effects of ethylene on secondary metabolite production can be either positive or negative, depending on the type of metabolite and the specific environmental conditions.

(4) Auxins

Production of auxin mostly occurred in younger leaves, developed seeds and leaf primordia which is conserved in plants. Mostly auxin is transported via cell-to-cell transport in case of short distance movement while phloem for large distance transport (Chai & Subudhi 2016). It significantly promotes the elongation of roots which played an important role in better uptake of water and drought tolerance (Wolters and Jürgens, 2009).

(5) Gibberellins

Gibberellins (GAs) have been extensively studied due to their crucial role in regulating various plant growth and developmental processes, including seed germination, fruit development, and senescence. In addition to their physiological functions, GAs have also been used in agriculture for crop improvement, such as increasing seed and fruit size, promoting germination, and enhancing yield. Recent researches showed that GAs is involved in many other processes beyond their traditional functions. For instance, GAs have been implicated in responses to biotic and abiotic stresses, such as drought, salinity, and pathogen attack. They are also involved in regulating root development, nodulation, and nutrient uptake. Furthermore, GAs plays a role in regulating secondary metabolites, including flavonoids, alkaloids, and terpenoids, which have various pharmacological properties. Understanding the mechanisms of GA biosynthesis, metabolism, and signaling is essential for improving crop yields and enhancing plant resilience to environmental stresses (Castro-Camba et al., 2022). GA3 has been shown to improve fruit quality characteristics such as size, shape, color, and firmness, and enhance the accumulation of secondary metabolites such as flavonoids, phenolic acids, and antioxidants. However, the response of plants to GA3 application varies depending on the concentration, frequency, and timing of application, as well as the specific plant species and environmental conditions. Overdosing of GA_3 can lead to negative effects such as reduced root growth, delayed flowering, and decreased seed yield. Therefore, proper management and application of GA_3 is necessary to achieve maximum benefits without causing any negative impacts on plant growth and development (Bagale et al., 2022).

(6) Cytokinins

Cytokinins (CKs) are growth phytohormones that play a key role in the mitigation of environmental stresses, growth regulation and development of organs (Lubovská et al., 2014; Li et al., 2016). Different studies showed that CKs have dual effect against drought (Zwack and Rashotte, 2015; Li et al., 2016). Intensity and duration of drought stress influence the synthesis of CKs in plants (Zwack and Rashotte, 2015). Rivero et al. (2007) showed a positive influence of CKs on the plants under drought induced stress. Conversely, a negative impact of CKs on osmotic tolerance has been showed in different studies (Werner et al., 2010; Nishiyama et al., 2011; 2013).

(7) Brassinosteroids

Brassinosteroids (BRs) regulate gene expression and protein synthesis, affecting many physiological processes such as seed germination, flowering, senescence, photosynthesis, and chlorophyll synthesis. They are able to maintain the stability of antioxidant enzymes by regulating the genes required for their stimulation. Brassinosteroids (BRs) and auxins were initially thought to regulate these processes independently, recent studies evidenced instead, that they can interact each other to regulate plant growth and development such as seed germination, root and shoot growth, and fruit development. BRs have been shown to enhance the response of plant tissues to auxins, leading to increased cell expansion and elongation. The molecular mechanisms underlying the interplay of BRs and auxins are complex and involve various signal transduction pathways. Studies demonstrated that BRs can enhance the activity of auxin-responsive genes by promoting the expression of transcription factors that are involved in regulating these genes (Bashri et al., 2022). Brassinosteroids can be utilized as biostimulants to induce drought stress resistance and to better plant performance (Trevisan et al., 2020). These compounds are able to mitigate drought stress, by enhancing the photosynthesis and biomass, powering antioxidant enzymes and stimulating the expression of connected genes.

5 SALINITY STRESS EFFECT ON DATE PALM

Salinity effects have been investigated both in vitro and in vivo on different levels of tissue organization such as callus induction and fast-growing phase, and different stade palm date life cycle as seed germination, seedling stage (one-three-month-old) and adult plants, (Al-Mansor et al. 2001). The results suggested that in vitro screening for salinity tolerance in date palm can give data without external perturbation. Callus induction using immature embryos may offer the potential of selection from the pre-existing date palm gene pool for enhancing salt tolerant cultivars or individuals even if this cannot be conclusive. The callus growth of the cultivar Barhee was demonstrated to be completely inhibited under a salinity of 125 mM (Al-Khayri, 2004). Low salt concentration (25 mM) stimulated date palm callus growth, while the increasing salinity decreased palm date callus growth. Na/ K ratio was positively correlated to proline accumulation and was the reason of the increased callus growth under low salinity concentration (AL-Khayri, 2004). The in vitro responses of date palm (*Phoenix dactylifera* L.) callus of Hillawi cv. to different concentration of sodium chloride (NaCl) (68.45; 137 and 205.34 mM) was studied by Abass (2016) at the proliferation stage. His results showed as NaCl treatment at high concentrations decreased callus growth. Fresh and dry biomass were significantly reduced; compared to untreated callus. The decrease in growth was accompanied with an enhancement of brown color. A stimulatory effect on callus growth was observed only at a NaCl concentration of 68.45 mM. An accumulation of free proline and hydrogen peroxide was observed increasing NaCl concentrations, whereas the activity of catalase decreased. Results related to RAPID analysis detected DNA polymorphism evidenced appearance and disappearance of fragments compared to the control callus. This result suggested a genetic rearrangement which could be the reason of the observed morphological and biochemical changes in date palm callus under saline stresses.

The findings of Al-Khateeb et al. (2020) evidenced that salt adaptation in date palm is associated with improved growth, physiological performance, ion concentrations, and K+/Na+ ratios. The SA regenerants showed better tolerance to salt stress compared to SNA regenerants and the control. Additionally, the inverse nonlinear correlation between the leaf Na+ concentration and net photosynthesis in the SNA regenerants implies that high Na+ accumulation in leaves negatively affects photosynthetic activity. The strong linear relationship between leaf K+ contents and stomatal conductance in SA regenerants indicates that high K+ concentrations in leaves may facilitate stomatal opening, which could contribute to enhanced gas exchange and improved photosynthetic activity.

Subsequently, Ait-El-Mokhtar et al. (2020) carrying on research on date palm seedlings, evidenced that leaf water content increased after salinity treatment when date seedlings were grown with mycorrhizal fungi. Taken all together these results put in light the importance of biotic and abiotic coadjutant in increasing date palm seedling resistance to salinity.

Salinity generally decreases soil water potential causing “osmotic stress” (Munns and Gilliham, 2015). Several researches highlighted that under salt stress, leaf water relations and leaf osmotic potential were reduced and in turn reduced leaf biomass, plant growth and yield (Jabeen and Ahmad, 2012; Hussain et al., 2020; Hussain et al., 2019; Hussain et al., 2018; Mishra and Tanna 2017; Hussain et al. 2020).

The study of Djibril et al. (2005) showed that non-tolerant date palm cultivars responded to salinity stress by increasing epicotyl length, primary root length, secondary root number, and proline content. In contrast, the study by Al-Qurainy et al. (2020) demonstrated that the response to salinity stress varied between date palm cultivars, with root length being more affected than shoot length, and with the Ajwa cultivar showing greater tolerance to salinity compared to Mabroom. In Table 2 is reported the impact of salt stress on growth, eco-physiological traits and yield stability of different varieties of date palm.

Regarding the effects of salinity, several reports indicated (Mehta et al., 2010, Kalaji et al., 2018a; Hussain et al., 2016; Hussain et al., 2020) that during salt stress, chloride and sodium ions accumulated in leaves, roots, branches and tree trunk and successively translocated to other growth tissues such as shoots, twigs, young newly emergent leaves and flowers (Paludan-Müller et al., 2002) causing diverse and severe damage with harmful impact on the growth, physiological processes and plant photosynthesis.

Alhammadi and Kurup (2012) showed that date palm variety can approach with different tolerant mechanism to salinity stress. The excess of sodium in some date palm varieties can be accumulated in leaves and the extent can depend on the date palm variety. Additionally, a salt exclusion mechanism can be also adopted by other varieties with a consequent reduction in Na^+ translocation to the shoots.

Salinity impacts the rate of photosynthesis with consequence on fruit size, number of date fruits on the bunch and fruit yield per tree. In the most of the fruit trees, the fruit size is directly correlated to fruit dry matter accumulation from photosynthetic leaf tissues towards the date fruit part. High temperature exacerbated the salinity effects inducing significant reduction in photosynthetic ability, yield and fruit volume in date palm. Tripler et al. (2007) reported that yield and transpirations in date palms (cv. Medjool) were highly decreased after increasing salinity and boron in lysimeters. Conversely, Youssef and Award (2008), documented that seedling growth, plant performance and photosynthesis were stimulated in date palm following salinity treatment via increasing stomatal conductance and chlorophyll contents. Several researchers reported that salt stress impacted photosynthesis, shifting the source-sink relationship, plant growth and tolerance (Sever et al., 2018). The degradation of xanthophyll pigments caused by salinity could be responsible of the inhibition of photosynthesis for the greater reactive oxygen species (ROS) accumulation (Duo et al., 2018; Hussain et al., 2020), In short, the data evidence that the different responses of the cultivars to salinity can be the results of the activation of different metabolic pathways.

Al Kharusi et al. (2019) demonstrated that salinity stress affects the growth and metabolism of date palm cultivars differently. The two cultivars (Umsila and Zabad) responded differently to salinity stress with Umsila being more tolerant. The study showed that Umsila had a better-developed root system, more efficient water uptake, and accumulated more osmo-protectants such as soluble sugars, proline, glycine betaine, and lignin, which helped in mitigating the harmful effects of salinity. The study also highlighted the importance of an efficient photosynthetic system in inducing salinity tolerance in date palm and confirmed the role of the cultivar in abiotic stress tolerance.

In two-years (2017-2018) of field experiment, Shareef et al. (2021), exposed the date palm (cv. Sayer) to the salt stress (10 ds m^{-1}) and evaluated the different physiological and biochemical parameters. They showed an increase in plant height, number of new leaves, total chlorophyll, and relative water content while hydrogen peroxide, malondialdehyde, and electrolyte leakage decreased and evidenced also a significant reduction in the absorption of sodium, chloride while potassium increased. They ascribed the salinity tolerance of Sayer cultivars to a less absorption of NaCl which in turn caused minor damage to the plant metabolism.

In soil, the excess of salts represents the main constraint caused by salinity. The excess of salts can significantly low plant growth, development and yield causing high osmotic potential which in turn inhibits water and minerals uptake causing cellular dehydration and lowering leaf water potential that impede numerous physiological and cellular processes affecting plant metabolism and decreasing crop yield (Ghadiri et al., 2004).

The optimal growth was observed under saline environment (3000 ppm of NaCl), as compared to control. Meanwhile, relative growth rate and biomass was reduced by increased salinity from 6000, and 12000 ppm (Al-Hammadi, 2006). Several marker-assisted breeding tools such as proline accumulation, demonstrated like an osmolyte or an antioxidant can contrast the water uptake deficiency.

Numerous authors studied the role of anti-stressors in modulating salinity tolerance in date palm. Award et al. (2006), found that Khalas, a variety of date palm, was able to better tolerate salinity due to modulation via different anti-stress molecules such as salicylic acid, vitamin E, acetyl salicylic acids and gamma aminobutyric acid. Al-Absi, et al. (2023) documented that date palm, following salinity stress, had different eco-physiological traits (ion homeostasis, scavenging ROS, and osmotic adjustment) that partially counteracted the salt stress. Some genes such as PdGLX1, PdPIP1;2, PdDJ-1, and PdVIK have been shown to play a role in enhancing methylglyoxal detoxification activity and decreasing the accumulation of reactive oxygen species under salinity stress. However, the extent of tolerance mechanisms was specific for each cultivar, highlighting the need for more research to identify and understand the genotypic variation in salt adaptation among the different date palm cultivars.

Numerous authors showed also the role of cultivars in contrasting salinity stress. Alhammadi and Edward (2009), concluded that there were differences in salt tolerance between date palm cultivars and that were related to the ability of roots to use salt exclusion mechanisms. It is important to understand the mechanisms underlying salt tolerance in date palms in order to develop more effective strategies for breeding salt-tolerant cultivars and for managing salt-affected soils in date palm cultivation. Al-Khateeb and Al-Khateeb (2007) demonstrated that five cultivars of date palm had significant difference in salinity tolerance. They showed how the K+/Na+ ratio was crucial in reducing the negative effects of salinity and demonstrated the importance of this ratio in promoting salt stress tolerance in seedling growth. The addition of AM fungi and compost increased P, N, K, and Ca and decreased sodium uptake. The excessive uptake of different ions by the plants can be related to an initial growth decrease and to a subsequent yield reduction under salinity (Tripler et al. 2011). In salt affected marginal soils, sodium, chloride and sulphate represent the main toxic ions (Munns and Tester, 2008).

The study by Al Kharusi et al. (2019a, b) provided more insights into the mechanisms of salt tolerance in date palm. The thicker Casparian strip in roots is known to prevent the uptake of toxic ions helping to maintain ion homeostasis. Higher proline, nutrient elements (K^+ and Ca^{+2}), carbohydrates, and glycine betaine were found more in the root tissues of Umsila than Zabad date palm, under salinity (Al Kharusi et al., 2019b). The leaf water potential was highly reduced in both varieties, mostly in Zabad. An opposite trend was observed in leaf relative water content. In this regard, the better capacity of Umsila to retain potassium than sodium in leaf and root tissues in respect to Zabad has been related to its better tolerance to salinity considering that K+ represents the cation most affected by sodium toxicity. A significant decrease in leaf ion contents (P, N, K, and Ca) was also observed by Ait-El-Mokhtar et al. (2020) on date palm exposed to high salinity (240 mM NaCl), compared to salt unexposed plants

Serrat et al. (2020) and Al-Dakheel et al. (2022) highlighted the importance of the varieties in determining the level of salinity tolerance in date palms. The study found that some varieties, such as Lulu and Barhi, were highly tolerant to salinity stress, while others, such as Shagri, Khnizi, Nabtat Saif, Ajwat Al Madinah, Khalas, and Maktoumi, had lower salinity tolerance and lower yield potential. Lulu and Barhi were the two high-yielding varieties with high salinity tolerance while Khisab, Sukkari, Jabri, Shahla, showed a 50% yield reduction at 10 dS m−1 ECw. Their study suggested that salinity tolerance is linked to specific morphological and physiological responses of date palm varieties to salinity stress.

Salt accumulation in plant tissues may affect the essential nutrient availability, absorption, uptake, transport and partitioning in the whole plant inducing a nutritional imbalance (Munns and Gilliham, 2015; Hussain et al., 2020) and consequently affecting the normal plant growth, development and yield. The excess of salt buildup in soil rhizosphere can cause severe nutritional imbalance in date palm because impede the absorption and translocation of some essential macro and micronutrient as potassium, calcium, nitrogen, phosphorus, magnesium, iron, manganese, copper and zinc, that are necessary to regulate plant metabolic functions. However, K+ accumulation can compete with sodium alleviating its stress through ionic balance (Munns et al., 2020). Date palm can adjust its growth and development through phenotypic plasticity, metabolic and genes regulation. These regulation mechanisms may contribute to induce salt tolerance through salt exclusion and/or compartmentalization.

UV exposure, contributed to create ion unbalance, affecting differently the absorption of nutrients by date palm. Al-Enezi et al. (2012) showed as the uptake of phosphorous, sodium, calcium, cobalt and manganese were significantly enhanced by long term UV exposure while the absorption of other nutrients such as copper, sulfur, nitrogen and potassium were significantly reduced suggesting as the combination of salinity and light conditions can influence nutrients uptake.

Several authors reported that sodium stress can impact photosynthetic machinery, causing inhibition of CO_2 intake and assimilation. The compounds most affected by severe salinity were xanthophylls and proteins of PSI and PSII, involved in the electron transport rate (Degl'Innocenti et al., 2009; Qados, 2011; Sudhir et al., 2005; Hussain et al. 2018; Hussain and Al-Dakheel, 2018). Generally, there is a significant increase in Na and Cl contents in leaves/roots after seawater exposure, and it was noted that high quantity of solutes (sugars, alcohols, nitrogen) is produced and accumulated in roots under salinity. The authors concluded that date palm seedlings were tolerant towards seawater exposure to some extent, and highly tolerant to flooding. Al Kharusi et al. (2019) comparing two different palm date varieties evidenced that salt stress reduced photosynthesis in all the tested varieties even if the variety Umsila, under salinity showed, a more stable photosynthesis a root system more structured. These results suggested that the major salt resistance of Umsila could be related to the root modifications and to the greater content of sugars that worked osmolytes to maintain osmotic potential. The impact of salt stress on the photosynthetic process of date palm is reported in Figure 2. Al-Qurainy et al. (2020) showed that efficiency of PSII photochemistry (F_v/F_m) of two target cultivars (Ajwa and Mabroom) was not affected at 50 mM NaCl after a 60-day of treatment. However, F_v/F_m was significantly decreased at higher salinity concentration (100 and 150 mM NaCl) compared to un salinized cultivars. The physiological plasticity of the different components of the photosynthetic apparatus was different under salinity in the date palm. The photosynthesis and gas exchange attributes were highly decreased while NPQ and PSII photochemistry remained un-affected. Ait-El-Mokhtar et al. (2020) showed that photosynthetic efficiency was highly decreased by salinity treatment. The treatment with AMF and/or compost significantly higher F_v/F_m and photosynthetic pigments as compared to the untreated plants, increasing the tolerance to salinity.

6 SALINITY STRESS ON DATE PALM FRUIT YIELD AND QUALITY

Soil and water salinity, in tropical and sub-tropical regions impact soil fertility and crop productivity with severe reduction of yield and quality of fruit trees and crop. Suitability of fruit quality for human consumption depends upon the composition of amino acids, glucose and carbohydrates in the fruits. Although date palm can be grown on nutrient poor, sandy and marginal and salt affected lands, however, nutritional qualities are considered to be highly degraded following long-term salinity exposure. Salt stress has a negative impact on amino acids, glucose and carbohydrates in various date palm cultivars (Hamad et al., 2015; Jana et al., 2019; Safronov et al., 2017; Ait-El-Mokhtar et al., 2020; AL-Temimi 2020). Moreover, salt stress decreased the number of fruit bunches per tree, and number of fruits (Al-Muaini et al. 2019). According to reports from Marcar et al. (1995), salinity tolerance in date palm depended upon variety and environmental conditions. Date palm fruit yield was significantly decreased at a salt concentration of 10000 ppm. The date palm plants can successfully grow in arid and hot climate under saline environment. They require sun light and are resistant to heat, withstanding temperature up to 50oC for short periods. They can tolerate low temperatures but do not grow below 10oC. Such plants do not set and develop fruit until temperature is above 25^{o}C. At the time of fruiting, the temperature should be high (45-50^{o} C) and humidity should be low (Qureshi and Barrett- Lennard, 1998). The cv. Medjool showed poor performance in terms of fruit yield under salinity (8 - 12 dS m^{-1}) with a reduction of 35 – 50% (Tripler et al., 2011). Shareef et al. (2020) documented that foliar application of traditional and nano-fertilizers in saline environment enhanced in date palm the number of fruit bunches, bunches weight, fruit weight. The indole acetic acid and gibberellic acid were also increased compared to the unfertilized palm. The biochemical attributes such as fruit ripening rate, dry mass, total soluble solids, peroxidase, superoxide dismutase, and abscisic acid content were also increased in fertilized than unfertilized trees. Date palm varieties showed differential responses in biomass, fruit yield, remote sensing traits and in nitrogen/carbon stable isotopes, in dry leaves of palm trees irrigated with water at different salinity.

Recently, Serret et al. (2020), showed negative correlation between carbon isotope composition and fruit yield and biomass. However, nitrogen isotope composition did not show correlation between yield and biomass.

7 SALINITY TOLERANCE MECHANISMS

The major mechanisms of date palm adaptations to salinity involve osmoregulation and osmo-protection, ion homeostasis, antioxidant defense system and hormonal regulations. Al-Khurasi (2017) reported that efficient modulation of oxidative stress, photosynthetic activities and Na^+ exclusion in the leaf play important role in adaptation of date palm in saline conditions. The researcher identified two groups, salt tolerant and salt sensitive cultivars, while working on several date palms. Among all, Manoma and Umsila belonged to the category of tolerant cultivars due to reduced levels of reactive oxygen species, higher exclusion of Na^+ and higher root and shoot weight. These traits accounted for their superior tolerance to conditions of high salinity. Higher accumulations of ions and osmo-protectants (proline, sugars, glycine betaine and lignin) increased its potential when grown under salinity conditions. Taken all together these results provided good insights in salt tolerance modulations of date palm (Al-Khurasi et al., 2019).

Under salinity, the physiological studies demonstrated that Na^+, Cl and K^+ levels control stress mechanism (Alrasbi et. Al., 2010). Based on previous studies, it can be recommended that the specific cultivars of date palm can be watered with saline water at the vegetative stage. To support this notion, Youssef and Awad (2008) conducted research to evaluate the physiological responses of date palm cultivars under different salinity levels (subjected to seawater treatments at 1, 15, and 30 mS cm^{-1}) using a 5-Aminolevulinic acid-based fertilizer. Their findings revealed that with the increasing amount of saline stress the accumulation of Na^+ ions enhanced by three folds when compared to control and 30 mS cm^{-1} salinity level. Furthermore, they found that the electrolyte leakage caused also the disruption of membrane integrity. Their statistical correlation found a strong relationship between chlorophyll (chl) *a*/*b* ratio and assimilation rate at all salinity levels. However, salinity did not influence carboxylation efficiency of the RuBiSco enzyme. Henceforth, it is proved that selected cultivars (Khunaizy, Khalas and Abunarinjah) can be watered with saline water, even if a prominent decline could be expected if the EC of irrigation water exceeds 9 dS m^{-1} that may reach up to 50% with water EC 18 d S m^{-1} (Alrasbi et al, 2010).

Extensive studies on the physiological and molecular basis provided the deeper insights to understand the protective mechanisms used by the crops to escape from the drastic outcomes of salt induced oxidative damage (Horie et al., 2009). Some plant species like halophytes and extremophiles developed various kinds of protective processes that allow them to complete their life cycle even under high saline conditions (Flowers and Colmer, 2008). Among all the protective mechanism, foremost is the control of ion concentrations in plant organs. The major mechanisms involved in salt stress tolerance of plants are summarized below;

8 OSMOREGULATION AND OSMOPROTECTION

At cellular level, the most important and key phenomenon of the plants to reduce the effects of salinity induced drought stress is the osmotic adjustment. Osmotic adjustment or osmoregulation is considered as the most important process during the stress tolerance in plants (Greenway and Munns, 1980; Neocleous and Vasilakakis, 2007). It includes the accumulation of sugars, proline, ions, glycine betaine, and organic acids. Normally, these molecules are involved in the protection of plant cells from the negative effects of reactive oxygen species and ultimately stabilize the proteins and membranes (Hasegawa et al., 2000; Hussain et al., 2015). Ion homeostasis and osmoregulation are the central part of the adaptive mechanisms when subjected to saline stress (Flowers and Colmer, 2008). In halophytes the osmotic adjustment is maintained by the hyper accumulation of osmolytes and Na^+ and Cl^- ions (Yeo, 1983; Glenn et al., 1999). The osmolytes are primarily located in the cytoplasm, the ions in the vacuoles. The main role of the osmolytes is to mitigate the oxidative damage induced by salt stress and to protect the macromolecular sub-cellular structures from free radicals that are produced under abiotic stresses. Higher contents of osmolytes in plants can have a strong positive correlation with enhanced stress tolerance by scavenging the free radicals and promoting the protective enzymes (Szabados et al., 2011). Plenty of evidences from the repeated studies involving molecular, morphological, physiological, genetic and biochemical approaches strongly revealed that osmolytes (glycine betaine, polyamines, choline-O-sulfate, dimethyl-sulfonio-propionate, and b-alanine betaine), amino acids (ectoine and proline) and alcohols and sugars (sorbitol, mannitol, fructan, trehalose, and D-ononitol) are the main regulators of plant stress tolerance against saline and water deficit stresses (Kumar, 2015).

9 ION HOMEOSTASIS

Among the many strategies to escape from the negative effects of salt stress, the re-establishment of ion-homeostasis is one of the most important mechanisms. Under stressful environments, the movement of Na^+ is crucial since it inhibits many enzymes so it is vital to maintain its level in the cytoplasm for preventing its hyper accumulation in the cytosol because it is highly involved in the osmotic adjustment regulation by acting as an osmolyte. This strategy is commonly found in halophytes plants (Zhu, 2001). In a latest study, Al-Harrasi et al (2020) provided insight into the molecular mechanisms underlying salinity tolerance in date palm. The identification of a novel Na+/H+ antiporter gene in date palm (PdNHX6) and its characterization in transgenic Arabidopsis and yeast cells was significant, as NHXs are known to play a crucial role in the ion homeostasis under salt stress. The study also highlighted the importance of oxidative stress in salt tolerance and suggested that PdNHX6 may be a potential candidate gene for improving salt tolerance in crops. Additionally, they demonstrated that PdNHX6 might modulate the proton pumping into the vacuole. Despite the promising enhancement of Na+, a balanced Na^+/K^+ ratio was maintained in transgenic Arabidopsis lines under salt stress conditions. Taken all the findings together, this research highlighted that PdNHX6 is prominent regulator of Na^+/K^+ ratio and of pH homeostasis in vacuoles.

In addition to glutathione, ascorbate is also a crucial antioxidant involved in salt stress tolerance. Ascorbate, also known as Vitamin C, scavenges reactive oxygen species and protects the cell from oxidative damage caused by salt stress. Like glutathione, the ascorbate-glutathione cycle plays an important role in detoxifying reactive oxygen species.

Furthermore, the expression of antioxidant enzymes such as catalase (CAT) and peroxidase (POD) is known to be upregulated during salt stress. These enzymes play a crucial role in the detoxification of reactive oxygen species and protect the plant from oxidative damage caused by salt stress (Hussain et al., 2016).

Osmolytes, small organic molecules that accumulate in plant cells in response to environmental stresses, such as salinity, also help to protect the plant from the negative effects of oxidative stress. The osmolytes produced by plants include proline, glycine betaine, and sugars. These osmolytes are able to stabilize cell membranes, maintain water balance, and scavenge reactive oxygen species, thereby promoting salt stress tolerance in date palm and other plants. Under salt stress, the growth and chemical compositions of date palm seedlings differed significantly. Plant height, number of leaves, and fresh and dry weights were decreased following salt stress (Darwesh, 2023).

10 HORMONAL REGULATIONS

Comparatively few studies have been found on the hormonal regulation of salt stress in date palm. However, the exogenous spray of ABA hormone was demonstrated to mitigate the effects of salinity. ABA is a hormone widely studied over the years and it was found upregulated in the roots of plants under saline conditions. It has also been found that ABA has a central role in controlling the ions balance in the vacuoles (Chen et al., 2001; Gurmani et al., 2011). Along with ABA, some other compounds like brassinosteroids (BR) and salicylic acid (SA) having hormonal characteristics are also involved in salt tolerance responses (Clouse and Sasse,1998; Fragnière et al., 2011).

11 MANAGEMENT FOR IMPROVING DROUGHT AND SALT RESISTANCE OF DATE PALM

Date palm is able to alter its developmental activities, physiology, metabolic processes, and gene-expression to mitigate the stress adversity. Several management activities can be adopted to combat salinity and drought stresses. As well as several salt and drought tolerant varieties can be selected using advance breeding techniques i.e. Tissue Culture, Biotechnology, Mutation and Genetic Engineering to be used in adverse conditions. Among the good agronomic practice deep ploughing before transplanting date palm suckers represents a good practice in reducing salt accumulation especially in area where water for irrigation is saline (Al-Wahaibi et al., 2007).

Mulching is practiced to reduce soil evaporation, to conserve soil moisture, to maintain soil temperature and to reduce salt accumulation. Previously, Al-Wahaibi et al., (2007) proposed few centimeter layers of chopped date palm residues (leaf or trunk) on the soil, to significantly reduce soil evaporation to keep the soil moisture high. In this case, orchard was irrigated with brackish water but the soil EC was found minor than the orchard without mulch (Al-Rasbi, 2010). Therefore, mulching technique can be adopted to improve the resistance to salinity and drought conditions by helping early roots establishment, rapid growth and development to withstand against salinity stress and unfavorable soil physical properties.

Soil enrichment with organic matters (farm manures, crop residues, composts, green manure, industrial waste etc.) can be a solution for water infiltration and improvement of soil against salinity. During organic matter decomposition, numerous ions are released in soils this phenomenon keeps the soil aggregated and leads towards higher porosity and less soil evaporation; and end up with cut down surface salt concentration. Many researches proved that the addition of organic matter to soils was the best technique for reclamation of soils and the better way to control soil EC and pH (Al-Rasbi, 2010; Al-Dakheel et al. 2022). However, the application of organic matters, should be adopted according to the soil type, soil salinity level and water and irrigation methods.

Traditionally, inter-cropping is practiced in date palm orchards. With changing climatic regime and use of saline water, there is a direct need to select suitable crops for inter-cropping. Selected crops (wheat, barley, sorghum, pearl millet, tomato, spinach etc.) should be relatively salt tolerant or cultures with low water requirements (Hussain et al., 2016). Leguminous crops can be used in rotation because they improve soil properties (nitrogen fixation, soil microorganisms and soil metabolic activity) and it is generally adopted to conserve soil water moisture for improving plants vigor. However, cover crop may improve soil and water quality (Hussain et al., 2016).

Selection of variety is also a good practice to be adopted. Al-Mulla et al. (2013) screened different varieties for salinity and proposed that Khalas was variety which has ability to perform well at higher level of salinity. The benefit of the date palm is its difference among cultivars or multiple genotypes developed from seeds (Al-Doss et al., 2001). Some date palm producing countries follow traditional breeding methods and face problems related to germplasm recognition, sex determination, agronomic characteristics, abiotic stress and biotic stress. Traditional breeding and biotechnological tools incorporate genetic variants that would quickly produce new genotypes that resist biotic and abiotic stress with superior fruit quality. Different breeding programs and researchers are focused on individuating suitable resistant cultivars able to produce good quality fruits also in stress condition. Conventional breeding and the use of innovative biotechnological methods will offer potential solutions to the necessity of grow date palm under abiotic stress conditions (Sedra, 2011).

Previously, Al-Khateeb (2019) investigated the role of PdMT2A gene in the tolerance of date palm seedlings to salt stress. The results showed that the overexpression of PdMT2A gene significantly improved the growth of transgenic seedlings under salt stress compared to wild-type seedlings. The transgenic seedlings had higher shoot and root length, fresh and dry weight, and chlorophyll content. The transgenic seedlings also had lower levels of Na^+ and higher levels of K^+ and Ca^{2+} ions. The study concluded that the overexpression of PdMT2A gene enhances the salt stress tolerance in date palm seedlings by maintaining ion homeostasis and reducing the oxidative stress.

Al-Harassi et al. (2020a) worked on novel tonoplast Na+/ H+ antiporter gene (PdNHX6) from date palm, which conferred the tolerance in Arabidopsis against salinity. Novel genes were functionally characterized in mutant yeast cells and Arabidopsis plants in order to test the behavioral responses of transgenic organisms against salinity. The study suggests that PdNHX6 plays a role in regulating K+ and pH homeostasis of the vacuoles, which is an essential mechanism for salt tolerance in plants. The overexpression of PdNHX6 in Arabidopsis plants resulted in improved salt stress tolerance, greater chlorophyll retention, and healthier Na+/K+ ratio despite the increase in Na+. The localization of PdNHX6 in the tonoplast surrounding the central vacuole further supports its involvement in the salt tolerance process.

In another research, Khan et al. (2020). reported that combined application of silicon (Si) and gibberellic acid (GA_3) can improve heat stress tolerance in date palm by up-regulating certain antioxidant enzymes and activating heat shock proteins, while also down-regulating genes related to the ABA signaling pathway. This suggests that Si and GA3 may have a synergetic effect on improving plant growth and development under heat stress conditions.

In plants, the abiotic stress response is governed by the regulatory mechanism of genes involved in various biological pathways and signaling cascades. Omics approaches characterize the pool of plant’s biomolecules and their function that play a critical role in homeostasis and signaling to alter stress effectively (Parida et al., 2018). To date, various omics-based approaches, including transcriptome, proteomics, metabolomics, etc., have been widely used to provide novel insights into the regulatory mechanism involved in plant response to abiotic stress factors and utilize this information in plant improvements.

Previous studies have been conducted on NGS based profiling of proteomics and metabolomics techniques used to unveil salinity response (Radwan et al., 2015, Yaish et al., 2015, Müller et al., 2017, Safronov et al., 2017, Yaish et al., 2017, Al-Harrasi et al., 2018, Jana et al., 2019). A comparative study conducted on salt treated and healthy date palm seedlings of “Deglet Beida reported differential gene expression (DGE) in young roots, down-regulation of Na^+ uptake and transport genes, and up-regulation of ABA signaling pathway (Radwan et al., 2015). Other

DE genes may strengthen the cell wall by diverting flux from phenylproponoid pathways into lignin biosynthesis. Yaish et al., 2017 worked on RNA seq of salt treated and healthy seedlings and found DGE in both ones. Genes expressed in the leaves were involved in photosynthesis, starch and sucrose metabolism, and oxidative phosphorylation, while genes expressed in the roots had a role in tryptophan, purine and thiamine metabolism.

Furthermore, Jana and Yaish (2020) investigated the effect of glutathione peroxidase genes in stressed date palm. They used PdGPXI-5 because PdGPX genes family has a significant impact in maintaining the cellular redox balance; in case, it enhances the ability to scavenge ROS in date palm cells. These ROS are generated under various abiotic stresses. Therefore, PdGPX genes family would be futuristic approach to characterize the date palm varieties that can naturally overexpress these genes. Moreover, these can be used to generate transgenic date palm tree for novel abiotic stresses. This technique may improve the production of most economic fruit trees under abiotic stresses.

Recently, Al-Hassi et al. (2020b) worked on date palm under stress conditions and identified MAP kinase kianas kinase (MAPKKK) genes. From this, they functionally characterized a salt-inducible vascular highway 1-interacting kinase (PdVIK). PdVIK encoded from date palm genome possesses an ankyrin repeat domain and kinase domain. PdVIK improves tolerance to salinity and oxidative stresses when overexpress itself in yeast. However, authors concluded that overexpression of PdVIK resulted in morphological improvement into better root growth in comparison to wild accessions under stress. Physiologically, this gene can control the ionic uptake process in yeast and stimulate proline accumulation in stressed transgenic plants. These results provide evidence that PdVIK can play a role in date palm under stress.

12 CONCLUSION AND FUTURE PERSPECTIVE

Even though date palm is widely distributed and cultivated worldwide for its nutritious and economic importance; abiotic stresses represent a threat for its sustainable production chain (both market and agribusiness development).

Previously, studies were mainly focused on an efficient use of agronomic practices (deep ploughing, mulching, intercropping/cover cropping), but in a changing climatic scenario, the evidence on the physiological traits or remote sensing that govern the reaction to the abiotic stresses in date palm can provide basic information for breeding program.

Genomics and omics offer a set of methods for the identification of specific loci in different varieties that can be applied to identify variation among cultivars in traits such as abiotic stress resistance, to better understand the varietal adaptation capability against changing climate threats. This allows to understand their different roles in crop genomes and to link the genomic changes to phenotypic traits of great agronomic importance. All this, will be critical to growing high-yielding, climate-resilient and highly nutritious fruits for the growing human population.

Understanding in toto how date palm responds to both stress and highlighting the different mechanisms of response to the two different stresses will enable to better manage date palm cultivation contributing to increase crop yield and fruit quality under the diverse stresses.

These knowledges will be valuable for numerous farmers and plant breeding for improving crop yield stability and production to increase the economic sustainability under changing climatic conditions in marginal environments.

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TABLE 1 Global date production (2018)

Country	Area harvested (ha)	Yield (hg/ha)	Production (mt)
Egypt	49,184	317,615	1,562,171
Saudi Arabia	116,125	112,195	1,302,859
Iran (Islamic Republic of)	171,647	70,153	1,204,158
Algeria	168,855	64,831	1,094,700

Iraq	147,900	41,554	614,584
Pakistan	100,611	46,880	471,670
Sudan	37,225	118,436	440,871
Oman	25,125	146,789	368,808
United Arab Emirates	38,117	90,542	345,119
Tunisia	57,329	42,096	241,333
Libya	32,500	54,225	176,229
China	13,876	114,078	158,294
China, mainland	13,876	114,078	158,294
Morocco	59,127	18,892	111,701
Kuwait	3,353	288,267	96,656
Yemen	13,736	35,024	48,108
Israel	4,733	94,190	44,580
United States of America	5,301	70,251	37,240
Turkey	2,610	136,332	35,577
Qatar	2,417	120,033	29,012
Mauritania	9,058	24,341	22,049
Chad	11,535	18,521	21,364
Jordan	3,146	62,257	19,588
Niger	6,648	29,387	19,537
Somalia	2,666	51,715	13,785
Albania	482	278,485	13,423
Bahrain	3,177	33,620	10,682
Mexico	1,573	56,888	8,946
Palestine	1,428	24,561	3,508

Syrian Arab Republic	370	81,081	3,000
Spain	465	35,226	1,638
Benin	683	21,075	1,439
Kenya	499	22,944	1,144
Mali	57	125,851	717
Cameroon	160	39,592	635
Namibia	141	25,397	357
Eswatini	98	32,007	312
Peru	141	19,433	274
Djibouti	*	*	117
Colombia	8	41,841	33
World	1,105,982	3,120,683	8,684,512

Source FAO (2020)

TABLE 2 Influence of salt stress on growth, ecophysiology, secondary metabolites and fruit yield of different varieties of date palm.

Variety	Salt stress	Decrease or increase over control	References
Succary	Deficit irrigation (I_{50}) saline water	Fruit yield and quality traits (Fruit moisture content, Total sugar and non-reducing sugar contents) were reduced.	Mattar et al. (2021)
Umsila	14 dS m^{-1}	Enhanced production of secondary metabolites, (+)-catechin, epicatechin, vitamins, and osmolytes such as the sulfonic amino acid taurine.	Al Kharusi et al. 2021
Zabad	4.8 dS m^{-1}	Enhanced production of secondary metabolites, (+)-catechin, epicatechin, vitamins, and osmolytes such as the sulfonic amino acid taurine.	Al Kharusi et al. 2021
Zabad	NaCl solution (240 mM)	Reduction in growth and photosynthetic pigmentation.	Al Kharusi et al. 2019
Umsila	NaCl solution (240 mM)	Accumulation of glutathione, phenolic compounds, flavonoids and proline. Acivation of superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX)	Al Kharusi et al. 2019
Zabad, Umsila, Nagal, Abunarenja, Fard, HilaliOmani, Nashukharma, Barni, Manoma, and Khalas	240 mM NaCl	Accumulation of salt in roots and shoots, reduced shoot potassium, leaf relative water content. Increased electrolyte leakage.	Al Kharusi et al. (2017)
Suksomboon Palm	up to 200 mM NaCl	Ca,Mg N and P contents in roots and shoots decreased in presence of increasing salinity	Alhammadi and Edward, (2009).
Cordia rothii Roem. and Schult. (Ehretiaceae)	4.3, 6.0, 8.2, 10.5, 12.8, and 14.6 dS m^{-1}	Germination & seedling growth decreased increasing salinity	Ramoliya and Pandey, 2003
Lulu	salinity concentrations (0, 0.6, 1.2, and 1.8%).	Growth retardation	Aljuburi (1992)
Khalas	salinity concentrations (0, 0.6, 1.2, and 1.8%).	Growth retardation	Aljuburi (1992)

Boman	salinity concentrations (0, 0.6, 1.2, and 1.8%).	Growth retardation	Aljuburi (1992)
Barhee	salinity concentrations (0, 0.6, 1.2, and 1.8%).	Growth retardation	Aljuburi (1992)
Khalas		Growth and yield reduction	Al-Wali et. Al. (2011)
Khalas', 'Khunaizy' and 'Abunarenjeh	6, 9, 12, 15 and 18 dS m^{-1}	Growth and yield reduction. Knunaizy was salt more salt tolerant.	Alrasbi et. al, 2010
Hayany	8.1 dS m^{-1}	microorganisms biofertilizer (EM) at 60 and 90 ml/palm/year and potassium sulphate at 1 and 1.5 kg/palm/year as well as their combinations in alleviating the adverse effect of salinity on productivity of "Hayany" date palm	Salma et al. 2014
Zaghloul		Potassium fertilization improved yield and fruit quality parameters	Harhash and Abdel-Nasser (2007)
Khalas		Potassium fertilization improved yield and fruit quality parameters	Shahin (2007)
Lulu	seawater treatments at 1-, 15-, and 30-mS cm^{-1} salinity levels in the presence or absence of 0.08% ALA-based (5-aminolevulinic acid-based) functional fertilizer commercially known as Pentakeep-v	Reduction in membrane integrity, chlorophyll pigments, and CO_2 assimilation rate, stomatal conductance, reduction in potassium uptake,	Youssef, and Awad (2008),
Medjool	1.8, 4, 8 and 12 dS m^{-1}	Tree growth and fruit yield was decresaed at higher salinity levels.	Tripler et al. (2011)
Mesalli, Razez, Khashkar and Bugal White	7.8, 11.7, 15.6, 19.5, 23.4 and 27.3 dS m^{-1}	plant height, collar girth and number of leaves, photosynthetic pigments. . The varieties responded differentially to the increasing salt concentration.	Kurup et al. (2009)
Boufeggous	(0 and 240 mM NaCl) with and without AMF inoculation.	Mycorrhizal plants showed higher plant height, leaf area and shoot and root dry weight, photosynthetic efficiency, leaf water potential, photosynthetic pigments, protein content, lipid	Ait-El-Mokhtar et al. (2019)

peroxidation under saline condition compared to non inoculated salt-affected plants

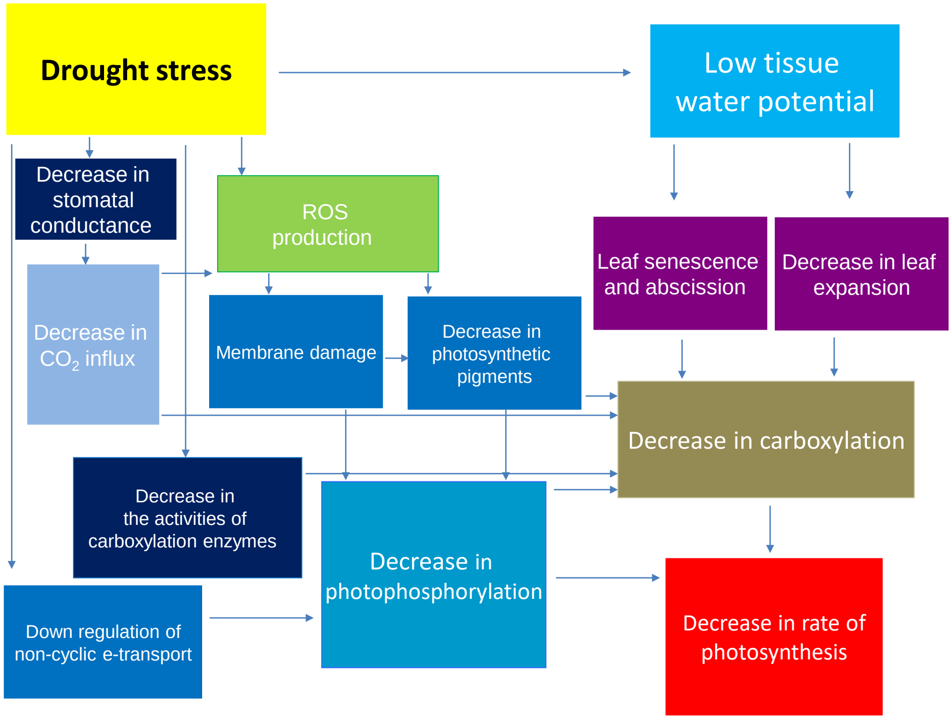

FIGURE 1 Influence of drought stress on photosynthetic pathway. Drought stress lowers the tissue water status, and decrease stomatal conductance, increasing ROS production, which in turn suppresses leaf development, accelerates leaf senescence and abscission, resulting in a decrease in photo-phosphorylation and carboxylation with a consequent reduction in the rate of photophosphorylation.

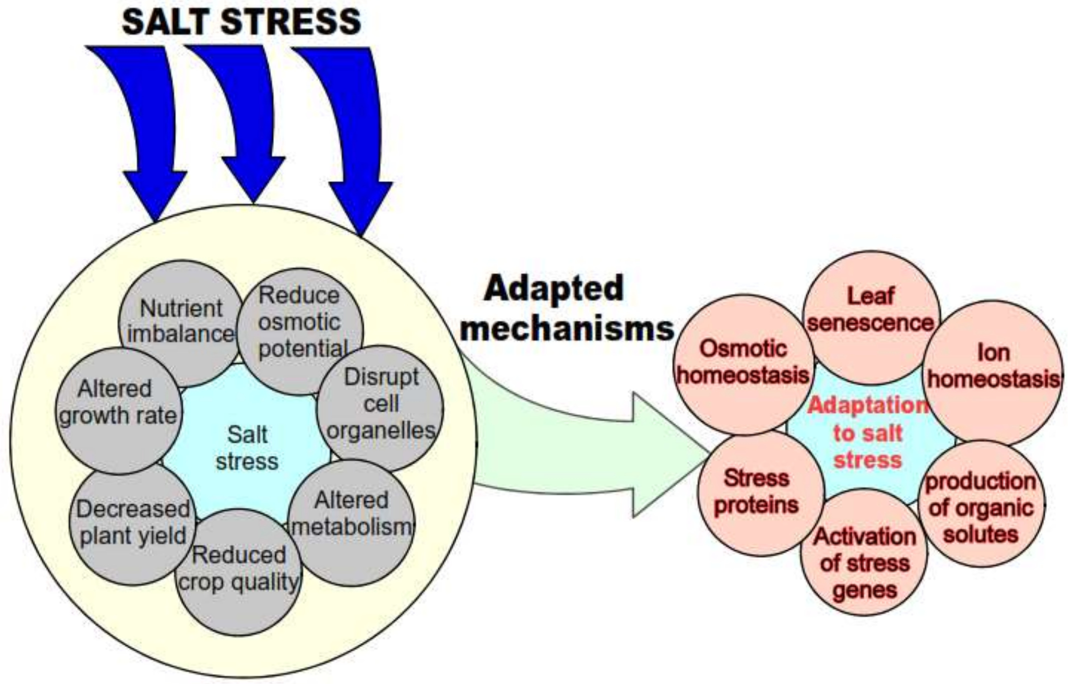

FIGURE 2 Influence of salt stress on growth and physiology of date palm.

Salt stress reduces the water relations and increases the production of reactive oxygen species (ROS) which in turn limits different enzymes and genes involved in carbohydrate metabolism. Salinity increases the uptake of Na$^+$ and its accumulation $^+$ in plant tissue.All these cause a decrease in leaf growth, and induce early leaf abscission. Salt stress induces stomatal closure, and a decrease in CO$_2$ influx. Reduction in CO$_2$ intake reduces the carboxylation rate. Under severe salt stress, the activities of carboxylation enzymes are also reduced. High salt stress causes the disruption of physiological and metabolic mechanisms reducing translocation of assimilates to the fruiting sites with a reproductive failure and a reduced fruit and bunch yield.

FIGURE 3 Mechanism of drought escape in plants.

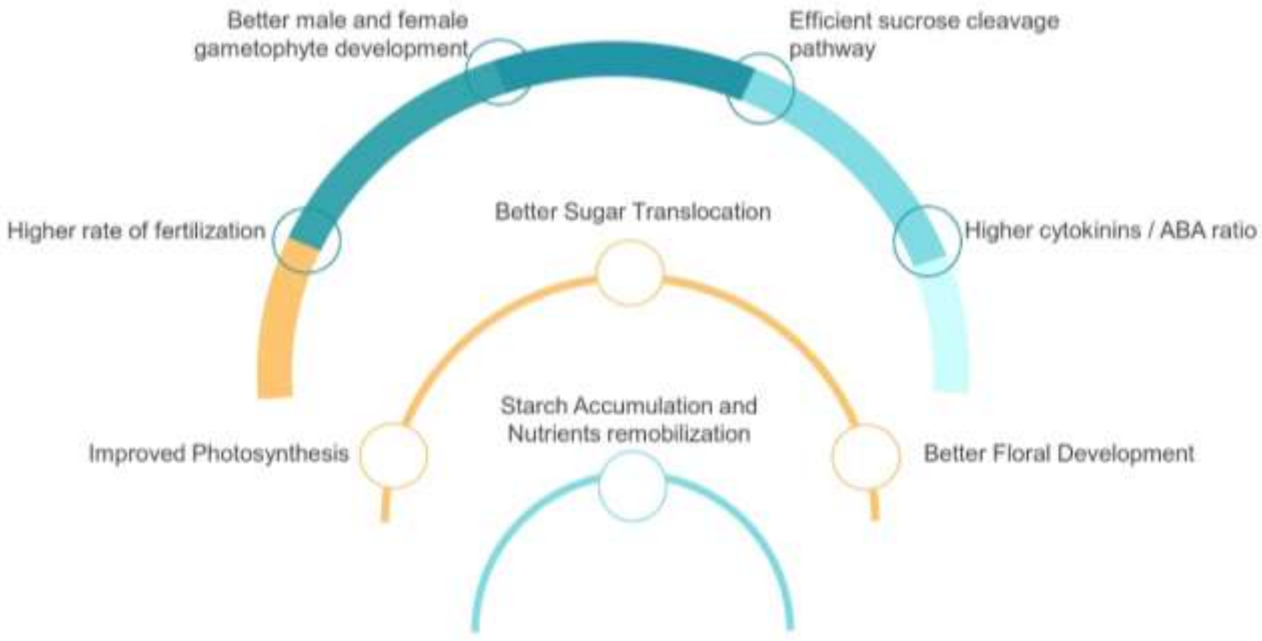

FIGURE 4 Positive effects of stay green (retain green leaves and maintain photosynthetic activity even under adverse conditions) in date palm.