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REVIEW PAPER **OPEN ACCESS**

Groundnut (*Arachis hypogaea* L.) presents many similar responses to drought and salinity, two water stress factors

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ABSTRACT

The current trend of climate change revived researchers' interest in the study of exacerbated abiotic constraints that hamper crop production, such as drought and salinity. Although they are distinct stress factors, both drought and salinity result in water stress for plants. Water stress is an environmental constraint that threatens crop production in many regions of the planet. Counterintuitively, drought or lack of sufficient water in the plant root environment is not the sole cause of water stress, which also results from the difficulty for the plant to take-up water due to salinity. However, it is not clear whether plants respond likewise to drought-induced and salinity-induced water stress. Therefore, comparing these two sources of water stress was necessary to understand how groundnuts respond and what tolerance mechanisms are deployed to cope with them. To this end, we have drawn on scientific publications from journals indexed in Scopus, DOAJ, AGRIS, Web of Science, etc., to gather relevant information about the effects of drought and salinity on the physiological, biochemical and molecular responses of groundnut. The present review thus examined (a) the responses of groundnut to drought, (b) the responses of groundnut to salinity, and (c) the synthesis highlighting the similarities and differences between these two responses.

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INTRODUCTION

Drought is a recurrent phenomenon in West Africa, particularly in the Sahel, exacerbated by climate change and causing considerable damage to crops (Imran *et al.*, 2021). This hostile climatic condition imposes water stress on plants, which occurs when the amount of water transpired exceeds that absorbed (Yang *et al.*, 2021). This seriously affects crop growth and productivity (Imane and Fatima Zahra, 2022). Water stress can also result from salinity, due to an excess of salts in the soil (Singh, 2022). Salinity is a growing scourge that affects more than a billion hectares (Tian *et al.*, 2020) and nearly 25% of the world's arable land (Hammam and Mohamed, 2020). Drought and salinity are therefore major constraints for agriculture, which need to be studied further to develop ways of continuing to produce in these austere conditions. These stresses reduce the capacity of plants to absorb water and minerals, thus hindering their development and productivity (Imran *et al.*, 2021; Imane and Fatima Zahra, 2022).

The purpose of this study is to understand the responses of crops undergoing water stress due to drought and salinity, as well as the plant's adaptation mechanisms to these stressful conditions. Using groundnut as an example, understanding the response of the species will better facilitate the planning of varietal improvement and selection for both salinity and drought tolerance, in order to improve its productivity in affected regions.

Groundnut (*Arachis hypogaea* L.) is a legume of worldwide importance. It is grown for human and animal consumption and is a major source of income for producers. However, its production faces many biotic and abiotic constraints (Sarkar *et al.*, 2016), exacerbated by its cultivation in tropical semi-arid or arid regions where climatic conditions are often extreme or unsteady (Banavath *et al.*, 2018).

It is known that plant resistance to water stress involves a complex mechanism in the plant, inducing morphological, physiological, biochemical and molecular changes (L'taief *et al.*, 2009). However, although drought and salinity both impose water stress on plant cells, it is not clear whether plants respond to these two sources of water stress in the same way.

This review article first presents an overview of two major abiotic stresses in groundnut production: salinity and drought. It then reviews the morphological, phenotypic, biochemical and molecular responses of groundnut to these stresses. Finally, research issues are explored in order to contribute to the development of cultivars tolerant to water stress coming either from salinity or drought.

RESULTS AND DISCUSSION

Drought-induced water stress in groundnut

Drought is one of the most important environmental stresses, creating water stress in the plant and affecting agricultural productivity (Diakalia *et al.*, 2011). The concept of water stress can be defined as the ratio between the quantity of water required for plant growth and the quantity of water available in its environment (Douib, 2013; Yang *et al.*, 2021). In other words, water stress occurs when the demand for water exceeds the quantity available over a certain period, or when its poor quality limits its use (Rao *et al.*, 2006). In fact, if the water is calcium chloride or sodium chloride, it is characterised as saline, and therefore reduces plant productivity. Water stress also occurs when the plant's transpiration rate exceeds its water uptake rate; in other words, when the plant's water needs cannot be met by the soil's water reserves (Tellah, 2016). Water stress causes physiological, biochemical and molecular disorders in plants depending on its degree (Josephine *et al.*, 2020) (Table 1).

Morphological and physiological responses of groundnut to drought

Groundnut has several physiological responses to drought, which are crucial for its survival and yields in arid environments. As with most plant species, water stress leads to changes in both plant morphology and physiology in order to adapt to the water deficit.

Table 1. Summary of groundnut responses to drought and salinity stress

Nature of response	Common responses to drought and salinity	Specific responses		Bibliographical references
		Salinity	Drought	
Physiological	1. Reduction in leaf area 2. Leaf senescence 3. Closure of stomata 4. Reduction in the number and weight of pods and seeds 5. Reduction in the number of nodules 6. Reduction in chlorophyll content	1. Reduction in the rate at which leaves appear 2. Modification of leaf histology 3. Compartmentalisation of toxic ions within the vacuole 4. Exclusion of toxic ions from the cell	1. Loss of turgidity 2. Reduction in above-ground and below-ground biomass 3. Drop in water potential 4. Development of the root system	(Alejandro *et al.*, 2017) (Ben Ahmed *et al.*, 2010) (Chaib *et al.*, 2015) (Chen *et al.*, 2019) (Lamri *et al.*, 2020) (Farooq *et al.*, 2015) (Furlan *et al.*, 2017) (Zaidi *et al.*, 2020)
Biochemical	1. Accumulation of osmotic substances (polyols, soluble sugars, proline) 2. Synthesis and regulation of antioxidant enzymes (superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD)).	1. Increase in cell wall rigidity; 2. Decrease in plasma membrane fluid conductance 3. Decreased assimilation of CO_2. 4. Generation and accumulation of reactive oxygen species (ROS).	1. Reduction in leghaemoglobin in nodules, 2. Decrease in nodule-specific activity 3. Reduction in nitrate reductase activity 4. Decrease in NO3 flux 5. Modification of cellular homeostasis 6. Accumulation of oxygen radicals	(Ankita *et al.*, 2020) (Banavath *et al.*, 2018) (Jallouli, 2019) (Li *et al.*, 2020) (Prévost *et al.*, 2024) (Rojas-Tapias *et al.*, 2012)
Molecular	1. Increase in abscisic acid 2. Activation, in the nucleus, of transcription factors associated with the expression of stress response genes 3. Expression of stress genes encoding proteins that manage the stress situation 4. Modification of the structure of the plasma membrane.	1. Activation of ion transporters, chaperone proteins and salt-specific transcription factors 2. Increase in the rate of methylation of genomic DNA 3. Modification of molecular signalling pathways	1. Change in phospholipid composition 2. Activation of phospholipase 3. Stimulus perception 4. Transduction of stress signal from cytoplasm to cell nucleus 5. Accumulation of Ca2+ ions 6. Activation of protein kinases	(Amouri, 2016) (Foncéka, 2010) (Gaufichon *et al.*, 2010) (Li *et al.*, 2021) (Long *et al.*, 2019) (Wan and Li, 2006) (Zhang *et al.*, 2023)

Slower plant growth and development

One of the most harmful consequences of sensitivity to drought is the marked reduction in leaf area, which slows down plant growth, especially during the early stages of development (Zaidi *et al.*, 2020). Thus, the impact of water deficit caused by drought is often reported in terms of plant height, number of branches and leaf area index (Rima and Aymen, 2022). In fact, when the plant is subjected to insufficient water supply, the cells lose water and the volume of the vacuole decreases (Morot-Gaudry and Prat, 2009). This loss of turgidity can lead to leaf senescence (Deng *et al.*, 2012), and a decrease in organic compounds in the reserve organs (Alleidi *et al.*, 2016), resulting in a reduction in the aerial biomass of the groundnut (Ben Ahmed *et al.*, 2010).

The groundnut plant can adapt its morphology in response to water stress caused by drought, for example by reducing the active leaf area to reduce water loss through transpiration and conserve moisture in the tissues (Alleidi *et al.*, 2016). This reduction in above-ground biomass makes it possible to minimise water use by the plant, as reported in various crops, such as broad bean (Mwanamwenge *et al.*, 1999), chickpea (Slim *et al.*, 2008) and cowpea (Hamidou *et al.*, 2005).

However, this adaptation is accompanied by a drop in photosynthesis, resulting in a slowdown in the development of the plant and reproductive organs, and a significant drop in yields (Lazali, 2009). Water stress causes a decrease in the development and elongation of groundnut pods, which can affect seed size and quality by up to 30% (Prakash *et al.*, 2023) and reduce the number and weight of pods and seeds (Kabore *et al.*, 2019). Drought is therefore a major constraint on groundnut productivity.

Stomatal regulation and photosynthesis

Stomata are orifices located on the leaf surface that allow the plant to transpire and assimilate atmospheric CO_2 necessary for growth (Nguyen, 2012). During water stress, these stomata close, modulated by two so-called guard cells (Kollist *et al.*, 2014). This reduces transpiration, thereby preserving water while maintaining photosynthetic activity.

Early stomatal closure has been observed in some varieties, contributing to better tolerance of water stress caused by drought (Clavel *et al.*, 2005). However, complete closure would slow down the plant's metabolism (Xiao-li and BAO, 2012). This is why, under water stress, stomatal function is a compromise between the need to preserve the plant's water status and the need to maintain minimal metabolism in order for the plant to survive (Chahbar and Belkhodja, 2016).

Similarly, the drop in the plant's leaf water potential following water stress (Benjelloun *et al.*, 2013) results in a drop in photosynthesis and a halt in the transfer of assimilates from the leaves to the other plant organs (Ben Naceur *et al.*, 1999). The depressive effect on photosynthesis results from an alteration in the photosynthetic apparatus and a reduction in the leaf's internal CO_2 concentration following the closure of the stomata in response to water stress (Ben Naceur *et al.*, 1999). At the same time, the photosynthetic apparatus becomes disorganised, affecting the integrity of chloroplast membranes and disrupting photochemical reactions (Lawlor and Cornic, 2002). With the reduction in the efficiency of the electron transport chain in photosystem II, the quantum yield of photosynthesis is greatly reduced. Therefore, the ability to maintain sustained photosynthetic activity despite water stress is a desirable varietal trait, facilitating improved water use efficiency (WU (Tshiabukole, 2018). The challenge here will be to find germplasm with genetic diversity for traits related to photosynthetic activity to develop water stress tolerant cultivars.

Osmotic adjustment

Cell growth is very important for plant development but is one of the processes most sensitive to drought (Tshiabukole, 2018). When the plant is under water stress, the cells accumulate inorganic ions and synthesise osmolytes (proteins, prolins, mannitol, sorbitol, etc.) in order to minimise water loss from the cells by osmosis. These osmolytes play a very important role, firstly in the osmotic balance to conserve water in the cells, and secondly by providing carbohydrates that can be mobilised as sources of energy for growth once the water stress is lifted. Osmotic adjustment therefore appears to be a key mechanism in the adaptation of plants to water stress (Poormohammad Kiani, 2007). It maintains cell turgidity by accumulating solutes. In certain extreme cases, hydroxyl groups can replace water to a certain extent, by establishing hydrogen bridges, thus playing a crucial role in protecting enzyme and membrane activity (Chaib *et al.*, 2015). The identification of genotypes with the facility to accumulate osmolytes is then desirable to develop drought-tolerant groundnut varieties.

Root development

Roots play a major role in the response of plants to drought (Smith and Smet, 2012). They adjust their hydraulic conductance via aquifer proteins called aquaporins in response to numerous stimuli, including drought stress. This is why, under water stress, groundnut roots can be seen to elongate, sinking deeper into the soil (El Fakhri *et al.*, 2010). A study conducted on groundnut varieties showed that water stress positively affects root volume, with a variable response depending on the genotype (El Fakhri *et al.*, 2010). A similar conclusion was made by Furlan *et al.* (2017) who showed a positive correlation between root biomass and water stress tolerance level. Indeed, they found that a groundnut cultivar produced 25% more root dry weight under drought than under optimal irrigation conditions.

This parameter reflects an extension of the root system to colonise a greater volume of soil, enabling the plant to explore more sources of water for its survival under conditions of water stress (Smith and Smet, 2012). This not only increases water and nutrient uptake capacity, but also the exclusion of excess salt from root cells to maintain a favourable osmotic balance (Vadez *et al.*, 2007). The ability to produce root biomass is an important trait for drought tolerance.

Symbiotic response

Drought also affects the ability of groundnut to fix nitrogen through nodules. Studies have shown that water stress due to drought reduced nodulation in groundnut by around 30% compared to well-watered controls (Furlan *et al.*, 2017). This is explained by a decrease in nodule formation, specific activity and size (Streeter, 2003). This decreases results from the drop in nodule cortical permeability, limiting oxygen availability for bacteria, thus reducing their respiration and their contribution to symbiotic nitrogen fixation (Hungria and Vargas, 2000). There is also a negative impact on nodular leghaemoglobin, which is important for oxygen availability to bacteria, and on the number and dry weight of nodules (Marino *et al.*, 2006).

However, interactions between groundnut and certain rhizobium strains also play a positive role in tolerance to water stress (Badreddine, 2021). Strains reported by Amari *et al.* (2022) have shown improved adaptation to drought conditions, favouring both atmospheric nitrogen fixation and plant growth.

Biochemical and molecular responses of peanuts to drought

Drought imposes complex biochemical and molecular responses in groundnut, involving an interplay between gene expression, accumulation of compatible solutes, modification of membrane lipids and antioxidant response (Tellah, 2016). These mechanisms allow groundnut not only to survive but also to optimise its yield under drought conditions (Ouali, 2011). Clearly, the phenotypic responses discussed above are underpinned by biochemical and molecular alterations.

Accumulation of compatible solutes

The aim of solute accumulation is to maintain cellular integrity and water potential in the event of water stress. These compounds, known as osmoprotectants, help to stabilise proteins and cell membranes, enabling cells to resist dehydration (Ruan *et al.*, 2010). These are essentially osmotic substances such as polyols and soluble sugars (glycerol, glucose, sucrose, etc.) as well as non-essential amino acids (proline, glycine, betaine, etc.) (Ouali, 2011). Soluble sugars are produced during photosynthesis and are exported from chloroplasts as triose phosphates, which are then converted to sucrose in the cytosol (Yokota *et al.*, 2006).

Proline is the compound most accumulated during water stress (Johari, 2010). It is synthesised from glutamate by the action of two enzymes: 5-carboxylic acid Δ1 pyroline synthetase (P5CS) and pyroline 5-carboxylic reductase²w (P5CR). Proline stabilises membranes, proteins and nucleic acids, and regulates cytoplasmic pH. In fact, proline is a source of energy, nitrogen and carbon (Yokota *et al.*, 2006). A genuine mediator in osmotic adjustment, proline accumulation is a marker of tolerance to water stress in peanuts (Ashraf and Foolad, 2007).

Drought-induced solutes accumulate in the cell cytoplasm, increase osmotic pressure, restore turgidity and protect macromolecule structures from denaturation (Kim *et al.*, 2004). The plant's ability to synthesise solutes under water stress is a desirable trait for the development of drought-tolerant cultivars.

Modification of membrane lipids

Water stress due to drought causes changes in the lipid composition of cell membranes (Prévost *et al.*, 2024). Cellular membranes are made up of phospholipids, glycolipids and sterols, which play a role in maintaining cellular integrity, signalling and membrane transport (Wafaa, 2019). Acylhydrolases play a key role in this process by regulating lipid degradation (Amouri, 2016). Water stress also leads to a reduction in phospholipid content and a change in the fatty acid profile, favouring saturated fatty acids. This leads to a rigidification of membranes, making cells more vulnerable (Li *et al.*, 2020). To remedy this cellular vulnerability, peanuts reorganise their membrane lipids by increasing the proportion of unsaturated lipids. This helps to maintain membrane fluidity and consequently essential functions such as ion transport and signalling (Upchurch, 2008). There is also a reduction in lipid peroxidation induced by ROS (Reactive Oxygen Species) under accumulation of compatible lipids (phosphatidylcholines, phosphatidylglycerols) which helps stabilise membranes against damage caused by water stress (Farooq *et al.*, 2009).

Antioxidant response

Like osmoprotectants, drought increases the production of antioxidant compounds in peanuts to minimise oxidative stress caused by dehydration (Tellah, 2016). This includes increased levels of antioxidant enzymes such as ascorbate peroxidase, which protects cells from oxidative damage (Clavel, 2002). This is an antioxidant defence mechanism present in plant cells and their organelles such as chloroplasts, mitochondria and peroxisomes (Havaux *et al.*, 2005). This antioxidant system is a very important defence mechanism against water stress, and detoxifies ROS molecules such as hydrogen peroxide, superoxide and oxygen in order to maintain an adequate cellular redox balance (Banavath *et al.*, 2018).

Protein catabolism

The effect of water stress is also felt on protein metabolism in the plant. There is a slowdown in protein metabolism, accompanied by an increase in the catabolism of cellular proteins (Clavel *et al.*, 2005). This can lead to increased degradation of essential proteins such as cell membranes, thus affecting photosynthesis and respiration (Khaled and Amdjed, 2023), causing a delay in plant growth under stress and a drop in yield.

Genetic expression

Groundnut varieties react differently depending on the physiological and biochemical mechanisms used to maintain water balance. These drought-induced mechanisms are correlated with alterations in the expression of water-stress-responsive genes in groundnut.

Certain genes, such as those encoding phospholipases and proteases, are differentially expressed depending on the water stress sensitivity of the varieties (Clavel *et al.*, 2005). The phospholipase D (PLD) gene encodes the enzyme associated with lipid degradation, which is associated with drought sensitivity in groundnut (Zhang *et al.*, 2023). Studies have shown an increase in PLD accumulation in drought-sensitive groundnut cultivars (Dramé *et al.*, 2007).

However, tolerance is associated with the dehydration response protein gene LEA (Late Embryogenis Abundant), which is more activated in resistant cultivars (Amouri, 2016). Its accumulation has been observed in drought-tolerant cultivars (Guo *et al.*, 2006).

The expression of all LEA-type genes is transcriptionally regulated under the control of abscisic acid (ABA) (Wang *et al.*, 2003). Transcriptome analysis confirmed the existence of ABA signalling pathways under water stress (Li *et al.*, 2014). Studies have shown up-regulation of the expression of genes such as AhNCED1, AhZEP and AhBG24 linked to ABA production. There are also genes such as AhABCG22.1, which is linked to ABA transport under drought conditions (Long *et al.*, 2019). Similarly, membrane proteins such as aquaporins (arPIP1;3 and arPIP2;7) are differentially regulated in response to water stress (Gaufichon *et al.*, 2010).

In general, gene expression in response to water deficit involves two steps: perception of the stimulus, which involves amplification (Bouassaba and Chougui) and integration of the signal, which regulates gene expression by capturing variations in the external environment (Amouri, 2016). It should also be noted that several gene families are activated under water stress. Transcription factors such as DREB (Dehydration Responsive Element Binding) enable the expression of genes involved in hosmopotection and the stabilisation of cell structures.

In addition, genomics has made it possible to identify QTLs (Quantitative Trait Loci) associated with drought tolerance in peanuts (Foncéka, 2010). This has encouraged the development of genetic improvement strategies based on marker-assisted selection (MAS). These advances will make it possible to create or identify varieties that are more resilient to water stress, which is important for coping with climate change.

Salt stress

Salinity is one of the most formidable abiotic factors limiting the productivity of agricultural crops, particularly in arid and semi-arid regions (Muchate *et al.*, 2016). It impacts the growth and development of groundnuts. Soil salinity is due to a process of accumulation of several soluble mineral salts in the soil, mainly in the form of NaCl and Na_2SO_4 (Beghin and Lutts, 2019). It is either natural (alteration of parent rock, evaporation from former salt seas or lakes or external natural inputs) or anthropogenic, due to inappropriate agricultural practices, in particular irrigation with salt-laden water (Barbouchi *et al.*, 2013). Salinity has a negative impact on seed germination, plant growth and development, dry matter production and the quality yield of groundnuts (Salwa *et al.*, 2010).

Peanut responses to salt stress and physiological responses of groundnut to salt stress

On growth and development

The first phenotypic effects of salt stress observable in groundnut is the reduction in the rate of leaf appearance and leaf area (Ben Nja, 2014). Reducing the number of leaves and leaf area minimises water use and the photosynthetic balance under salinity conditions (Duarte *et al.*, 2013, Abdenour, 2019). This results in a reduction in plant height (Chen *et al.*, 2019), due to inhibition of cell elongation (Alejandro *et al.*, 2017) and a decrease in carbohydrate synthesis (Abdenour, 2019). Salinity can also modify the histology of growing leaves and has an impact on mesophyll conductance (Roy *et al.*, 2014). The effect of salt stress on vegetative development varies according to species and variety (Ullah *et al.*, 2009), developmental stage, as well as soil salt level and time of exposure (Forni *et al.*, 2017).

Water and nutrient uptake

Salt stress is manifested in groundnut by a difficulty in water absorption by the roots (Boughaba and Mefathi, 2018). The accumulation of excess Na+ and Cl- ions under salinity increases osmotic pressure in the soil, creating conditions similar to those of water stress, even in the presence of water (Munns and Tester, 2008). This is why salinity is often presented as water stress. However, salinity can also cause toxicity due to the accumulation of salts in the plant (Rai, 2017) or hinder the uptake of certain essential ions such as Ca2+ and K+, which are essential for the stability of the phospholipids in the membrane bilayer (Souana, 2021). Salt stress attacks the plant's metabolism, causing cellular damage that can lead to plant death (Farooq *et al.*, 2015). As a result, the peanut deploys mechanisms to adapt to the difficult living conditions, such as the compartmentalisation of toxic ions in the vacuole, then their gradual exclusion from the cell (Apse and Blumwald, 2007). This vacuolar compartmentalisation allows excess Na+ ions to be repelled from the cytoplasm into the vacuole in order to avoid their toxic and inhibitory effect on enzymatic processes (Hanana *et al.*, 2011).

Stomatal activity and photosynthesis under salt stress

As previously mentioned, salinity leads to water stress (Zineb *et al.*, 2023), and as such causes the stomata to close in order not only to minimise the plant's water losses but also to improve its water-use efficiency (Acosta-Motos *et al.*, 2017). Excess salt, which is toxic, activates root signals through the superproduction of abscisic acid (ABA) and its translocation to the stomata (Chaves *et al.*, 2003). These signals cause the stomata to close, limiting transpiration and the plants' ability to fix CO_2 and engage in photosynthetic activity (Qin *et al.*, 2011).

Salinity therefore has a significant influence on the activity of stomata, the true seats of photosynthesis (Mao *et al.*, 2007), causing a significant reduction in the chlorophyll content of groundnuts (Chen *et al.*, 2019). A reduction in chlorophyll contents (a) and (b) is observed under the effect of salinity, systematically leading to a reduction in photosynthetic activity (Bouassaba and Chougui, 2018). Similarly, $K+$ deficiency following the accumulation of $Na+$ ions under salinity conditions leads to inhibition of photosynthetic enzymes (Rejeb, 2015). The plant's need to survive in salty soil conditions requires it to limit its photosynthetic balance by modifying pigment content, reducing the number of leaves and reducing leaf area (Duarte *et al.*, 2013).

Symbiotic reaction

In general, symbiotic interactions in plants are strongly influenced by the nature of the soil, its pH and its chemical composition (Benzahra *et al.*, 2022). For example, soil salinity is a determining factor in the composition of the soil microflora, particularly its intra- and interspecific diversity (Halima and Racha, 2022). This can have a considerable impact on symbiotic interactions.

Indeed, nodulation is sensitive to salt. This could be due to an effect on the symbiotic interaction between the bacteria (particularly of the Bradyrhizobium genus, which is involved in root nodule formation and biological nitrogen fixation) and its host (Berstein and Ogata, 1966). Salt causes a drop in rhizobium colonisation and reduces the number and weight of nodules, which negatively affects nitrogen fixation (Lamri *et al.*, 2020).

As a result of salt stress, there is also a disruption in electron transport, which disrupts the uptake of nitrogen by nodules (Jajoo, 2012). In addition, there is a decrease in nodular respiration due to a drop in O_2 levels or a drop in the production of leghemoghobin by nodules (Bargaz *et al.*, 2011).

Biochemical and molecular responses to salt stress in peanuts

Like any stress, salinity affects numerous biochemical and molecular processes in peanuts, even leading to dysfunction of the entire cellular metabolism (Munns and Tester, 2008). The plant under salinity conditions undergoes various stresses including water stress, ion toxicity, nutritional disorders, oxidative stress, altered metabolic processes and reduced cell division (Boukerma, 2017).

Accumulation of compatible solutes

Under the effect of salt stress, groundnuts accumulate osmo-protectants such as soluble sugars, proline, salicylic acid, total proteins, flavonoids etc. The ability of plants to tolerate salinity is complex and involves biochemical mechanisms (Stefanov *et al.*, 2016). To tolerate salt stress, peanuts accumulate compatible compounds in the cytoplasm and organelles, which are mainly amino compounds and sugars. These compounds are involved in maintaining osmotic balance (Silva-Ortega *et al.*, 2008), detoxifying active forms of oxygen (Kocsy *et al.*, 2005) and stabilising proteins (Majumder *et al.*, 2010). These compounds also protect cellular structures from dehydration (Chen and Jiang, 2010).

Modification of membrane lipids

It has been reported that salt stress can affect protein synthesis and lipid metabolism (Rojas-Tapias *et al.*, 2012). During salt stress, the membrane is disorganised and its permeability is increased following the disruption of its lipid and protein composition by salt stress (Lutts *et al.*, 2004). This stress increases the rigidity of the cell wall and reduces the water conductance of the plasma membrane (Liu *et al.*, 2016), which alters its permeability by increasing the inflow of external ions and the outflow of solutes from the cytosol.

To cope with the salt stress, membrane lipids are remodelled. In fact, there is an alteration in the composition and fluidity of membrane lipids, which can lead to a loss of permeability and an alteration in membrane functions. This was demonstrated by (Rahma, 2020) in the context of his study on *Phaseolus vulgaris* L. A study currently underway will make it possible to verify whether peanuts are capable of synthesising specific lipids, and precisely which ones, that confer increased fluidity and improved membrane stability. We also have salt exclusion, which is one of the mechanisms put in place by peanuts to survive under salt stress. Sodium ions are excluded from the cytoplasm towards the outside of the cell (Hanana *et al.*, 2011).

Production of toxic substances

Salt stress induces the closure of stomata, which reduces CO_2 uptake. This limitation alters the carboxylation of Rubisco and causes changes in leaf photochemistry and carbon metabolism (Jallouli, 2019). Indeed, the reduction of CO_2 in the chloroplast leads to an excess of photochemical energy at the membrane level following the accumulation of reducing power, thus allocating electrons to dioxygen (Jallouli, 2019). This activates photorespiration to the detriment of photosynthesis and leads to the generation and accumulation of reactive oxygen species (ROS). This accumulation of ROS can cause damage to photosystem II (PSII) and DNA and lead to the degradation of lipids and proteins (Blokhina *et al.*, 2003). There is also a production of free radicals which form toxic substances such as lipid peroxides which lead to peroxidation of cell membranes and cell death (Apel and Hirt, 2004).

Hormonal responses

Plant's hormonal balance is disrupted with salt stress, leading to changes in molecular signalling in groundnuts, including the regulation of phytohormones such as abscisic acid (ABA) and gibberellins (Gimeno-Gilles and Christine, 2009). They are produced in the roots in response to a decrease in soil water potential due to salt stress and transported to the leaves, where they bind to receptors on the plasma membrane of stomatal guard cells (Babu *et al.*, 2012). They spread the signal emitted by the stressed cell to neighbouring cells and the rest of the plant (Yaiche, 2017).

Molecules such as salicylic acid, jasmonic acid, abscisic acid and ethylene are involved in plant tolerance to salinity (López *et al.*, 2008). They mitigate the inhibitory effect of NaCl on photosynthesis and assimilate translocation (Farissi *et al.*, 2014). They also regulate cell division and differentiation (Shahba *et al.*, 2014).

Antioxidant enzyme activity

Antioxidant enzymes are synthesised and regulated during salt stress in peanuts. There is also an increase in the production of reactive oxygen species (ROS) in peanut cells, such as hydrogen peroxide, the superoxide radical and the hydroxyl radical (Ankita *et al.*, 2020).

These ROS cause oxidative damage to proteins and DNA, which affects plant growth (Gill and Tuteja, 2010). To neutralise these ROS, peanuts synthesise and regulate antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) (Foyer and Noctor, 2011). These enzymes help to detoxify ROS and minimise oxidative damage (Ankita *et al.*, 2020). Enzymes such as ascorbate peroxidase and glutathione reductase also play a role in adaptive regulation to maintain the NADPH/NADP+ ratio and support redox balance. Similarly, to protect itself, the plant synthesises the LEA protein and osmolytes, which improve tolerance to salt stress (Gimeno-Gilles and Christine, 2009).

Regulation of gene expression

Salt stress affects the expression of genes that respond to excess salt in groundnut. Certain salt tolerance genes, such as ion transporters, chaperone proteins and salt-specific transcription factors, are activated to help the plant manage salt stress (Amouri, 2016). In addition, specific transcription factors are activated to bind to specific DNA sequences and regulate the expression of salt tolerance genes. These transcription factors can act as molecular switches to control the adaptive responses of peanut to salt stress (Tam, 2012).

Thus, salinity can modulate the expression of specific genes to protect peanut cells from the adverse effects of salt. For example, this is the case for the expression of the AhNCED1 gene in peanuts, whose transcripts accumulate mainly in peanut leaves and stems (Wan and Li, 2006). Overexpression of this gene leads to an increase in the level of endogenous ABA and therefore promotes stomatal closure, resulting in a reduction in the rate of leaf transpiration and an improvement in the plant's tolerance to water stress (Iuchi *et al.*, 2001).

Regulation of the expression of genes involved in peanut response to salinity requires various epigenetic pathways including DNA methylation, histone modifications and regulation by microRNAs (miRNAs) and interfering RNAs (RNAi) (Petitpas, 2023). A study on barley subjected to salt stress showed that salt massively induced methylation changes in its genomic DNA (Konate *et al.*, 2018). The sites of these changes were close to genes involved in the response of barley to stress in general. In addition, some genes whose expression is altered by salinity are involved in non-essential growth and development processes, allowing energy and resources to be saved to better cope with stress (Hanana *et al.*, 2011). Histone modifications following salinity affect chromatin structure and conformation, as well as the accessibility of transcription factors to the promoter regions of salt response or tolerance genes (Li *et al.*, 2021). Similarly, the involvement of miRNAs in the response to salt has been reported, influencing the expression of genes linked to the accumulation of osmoprotectants such as proline, which is an important molecule in adaptation to osmotic stress caused by salinity (Zhang *et al.*, 2022).

CONCLUSION

The challenges to groundnut production are diverse and entangled. This review highlighted the phenotypic, biochemical and molecular responses of groundnut to these two major water stress factors. It appeared clearly that drought and salinity induce many similar responses in groundnut, despite the existence of some specific responses. Therefore, it is important to highlight that drought is not the only cause of water stress. Salinity is an important water stress factor, which results in the inability of the affected plant to up-take the water present, due to unfavourable osmotic pressure. So, while drought causes water stress through lack of water, soil salinity causes osmotic water stress.

Since drought and salinity all appeared to be water stress factors for groundnut, it is expected that they activate various similar signalling and response pathways in the plant. However, there are still gaps in current knowledge, particularly with regard to some specific molecular mechanisms and the complex biochemical responses in both types of stress. Furthermore, it was not yet clear whether there is a correlation between salinity tolerance and drought tolerance. We shall further investigate this pivotal question in our future studies, to harness the possibility of developing groundnut cultivars that tolerate both stresses simultaneously.

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