Cultivos Tropicales, Vol. 43, No. 3, July-September 2022, e-ISSN: 1819-4087, p-ISSN: 0258-5936, https://ediciones.inca.edu.cu

Cu-ID: https://cu-id.com/2050/v43n3e13

Bibliographic review

Water deficit in crops and the action of microorganisms

El déficit hídrico en los cultivos y la acción de los microorganismos

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ABSTRACT: One third of the planet's surface is considered arid or semi-arid, while most of the remaining surface is subject to temporary periods of water deficit. Drought is considered to be one of the world's major natural disasters, the most frequent and persistent, the one with the greatest negative effect on agricultural production and also the one that causes real adverse impacts on the environment. Water is the main limiting factor for plant growth on earth, acting as a first degree selective force for the evolution and distribution of plant species. Soil microorganisms are known to contribute a wide range of essential services to the sustainability of all ecosystems. They act as the main drivers of nutrient cycling; they regulate soil organic matter dynamics, carbon sequestration and greenhouse gas emissions; they modify soil physical structure and water regime. Inoculation of some microorganisms improves the efficiency of nutrient uptake, promotes plant growth and yield, thus attenuating the adverse effects of stress. The present work was aimed to deepen the knowledge of water deficit effects on crops and the role of some microorganisms in the mitigation of this stress on plants.

Key words: water, stress, inoculation, sustainability.

RESUMEN: Una tercera parte de la superficie del planeta se considera como árida o semiárida, mientras que la mayoría de la superficie restante está sujeta a períodos temporales de déficit hídrico. La sequía es considerada como uno de los mayores desastres naturales del mundo, el más frecuente y persistente, el de mayor efecto negativo para la producción agrícola y también como la causante de impactos adversos reales en el medio ambiente. El agua constituye el principal factor limitante del crecimiento de las plantas en la tierra, actuando como una fuerza selectiva de primer grado para la evolución y distribución de las especies vegetales. Se conoce, que los microorganismos del suelo contribuyen con un amplio rango de servicios esenciales a la sostenibilidad de todos los ecosistemas. Ellos actúan como los principales agentes impulsores del ciclo de nutrientes; regulan la dinámica de la materia orgánica del suelo, el secuestro de carbono y la emisión de gases de efecto invernadero; modifican la estructura física del suelo y el régimen de agua. La inoculación de algunos microorganismos mejora la eficiencia de la toma de nutrientes, promueve el crecimiento y rendimiento de las plantas, atenuando de esta forma los efectos adversos del estrés. El presente trabajo estuvo encaminado a profundizar en el conocimiento de los efectos del déficit hídrico en los cultivos y el papel de algunos microorganismos en la mitigación de este estrés sobre las plantas.

Palabras clave: agua, estrés, inoculación, sostenibilidad.

INTRODUCTION

Water is the essential component of life; in plants, it constitutes approximately 85 to 90 % of their mass and is present in all the vital processes that take place within them (1). Agriculture consumes, annually, 70 % of the total water used for all uses (2) and during crop establishment, its success will depend largely on the access to water available (3). It is a widely known fact that each stage of crop development is individually sensitive to environmental factors and, in particular, to the lack of soil moisture that can cause water stress (4). For these reasons, mankind is facing a new challenge, that of producing more food with less water.

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Received: 15/12/2020

Accepted: 27/09/2021

The functions of microorganisms in the soil and the possibility of plants to associate with many of them are dissimilar, which provide them with the capacity to adapt to the environmental conditions where they develop; they act directly and indirectly on the growth of plants and their capacity to tolerate adverse conditions of biotic and abiotic stress, their functions differ, from biofertilizers, phytostimulators, biocontrollers, bioprotectors, to the combination of several of them (5). Hence, their use is of great importance in the search for new alternatives to mitigate the consequences caused by water scarcity.

The present work aims to deepen the knowledge of water deficit effects on crops and the role of some microorganisms in the mitigation of this stress on plants.

Water deficit

Water deficit is the abiotic stress with the greatest impact on plant growth (6). From an ecophysiological point of view, it occurs when there is not enough water in plant root zone to meet their needs at a given time and place, i.e., when the water transpired exceeds the water absorbed (7). From a physiological point of view, the word stress refers to some kind of suffering, i.e., an alteration of normal functioning with consequences on plant growth or development (8).

The lack of water availability that causes stress may be due to an edaphic water deficit, to an excessive atmospheric evaporative demand, or to the interaction of both factors (9). This type of hydroedaphic or agricultural drought stress, as it is known, is considered a transitory episode for plants (10).

There are two criteria, based on authors who affirm, taking into account thermodynamic theoretical considerations, that water stress is caused by a decrease in soil water potential (Ψs); and those who affirm, based on empirical evidence, that it is caused by a decrease in edaphic moisture content, referred to in terms of the fraction of transpirable edaphic water (FTSW) (11). It is reasonable to think that both positions may have some reason, since insufficient water availability could be due to a decrease in Ψs as the soil dries out, but also, to a decrease in the soil's capacity to supply water, the latter aspect that could depend on its FTSW. Not only does water deficit occur when there is little water in the environment (12), it can also be the result of low rainfall, excessive salinity, and extreme temperatures, hot or cold (13).

Effects of water deficit on plants

Water deficit has important consequences for plant physiology and morphology. It causes, in the short and medium term, a decrease in water potential, relative water content and stomatal conductivity (14). This effect results in negative impacts on plant growth and production, causing anatomical changes due to modifications in cell size, senescence, and even death in many species (15). The magnitude of the damage caused depends mainly on its duration, intensity and the time in which it occurs within the crop cycle (16).

When at the beginning of a productive crop cycle of the first stage of seed germination is compromised, with moisture deficiencies present in the soil during sowing, imbibition is affected and, consequently, the activation of metabolic processes, such as rehydration, repair mechanisms (membranes, proteins and DNA), cell elongation and the appearance of the radicle (11). In a research carried out in wheat (*Triticum aestivum* L.), simulating drought with polyethylene glycol, it was determined that as drought increases, seedling germination decreases by 50 % (17).

Some investigations in several crops make reference to the fact that the physiological process of photosynthesis is also affected by the different levels of drought (18). Other manifestations are a decrease in protein synthesis and photorespiration, photosynthate translocation and growth regulators are affected (19) and gas exchange is reduced, limiting biomass production (20). These events result in a reduction of plant organ growth (21) which, if maintained for prolonged periods, leads to a modification of the specific leaf area (22), resulting in less leaf area exposed to solar radiation (23). An example of this is a study carried out on cotton plants (*Gossypium hirsutum* L.), indicating that in environments of hydric deficit there is a strong decrease in leaf expansion (24). In rice (*Oryza sativa* L.), less leaf growth was also found in plants subjected to drought in the vegetative phase, due to a reduction in the expansion rate of the aerial part and the development of the leaf area, caused by a decrease in the turgor pressure of the leaves (25).

Regarding plant reproduction, a phase negatively influenced by water shortage is flowering. It seems to be the most sensitive in most crops where the final product is grain or fruit (4). As water stress becomes more severe, the reduction in photosynthetic activity causes a decrease in the rate of cell division and, consequently, the initiation of new leaf primordia is halted (26). The balance between productions of assimilates and the demand for the development of reproductive organs is severely affected by the reduction of the photosynthetically active leaf area (27). In this regard, in plants of sweet orange [*Citrus sinensis* (L.) Osbeck] cv. 'Valencia late', an increase in floral abortion was observed in plants that received less water, and moderate stress increased flower and fruit abscission (28).

In relation to the production stage of a crop, photosynthesis plays an important role (29), since grain yield is potentially influenced by the duration of the rate of carbohydrate accumulation (30). Water deficit can affect the use of carbohydrates, basically by changing the efficiency with which photoassimilates are converted into the development of new plant parts (31). The yields to be obtained in a crop will depend on production, the latter being another factor vulnerable to drought. It has been proven in grape plants (*Vitis vinifera* L.) that the lowest yields are obtained when the plants do not receive irrigation, in the stage between reproductive sprouting and greening (22). Similarly, in pomegranate (*Punica granatum* L.) plants grown under severe stress, yield and fruit quality were found to be affected (32).

Plant response to water deficit

Throughout evolution, plants have developed several strategies facing water deficit that allow them to alleviate, tolerate and adapt to such circumstances (33). Stress conditions produce two types of response in organisms: those that tend to avoid or prevent stress (avoidance mechanisms) and those that allow them to resist it (tolerance mechanisms) (34). Another type of mechanism, not considered by many authors as a true resistance to water deficit, is the elusive or drought escape mechanism (35). Within this strategy, some annual plants complete their life cycle before water stress (in spring), and therefore produce seeds that can withstand the unfavorable period for a prolonged period of time (36). However, this escape strategy may include species that enter partial vegetative dormancy during drought (35).

In avoidance mechanisms, plants minimize the penetration of stress into their tissues. Species following this strategy maximize water uptake, for example, through deep root systems, or minimize water losses through rapid and sensitive stomatal closure to slight decreases in tissue water content or water potential, the formation of small leaves, low transpiration rates, and changes in xylem hydraulic properties (37). Therefore, within this strategy there are two avoidance mechanisms: one, by water wastage, which allows maintaining the tissues hydrated in full drought, as long as the access to soil water and its internal distribution through the xylem is not limiting, and the other, by water saving. Both maintain the plants in the turgor state, and when water deficit conditions are accentuated, the wasters cannot maintain the high transpiration rates, so they become water savers or the individual dies (38).

Regarding tolerance mechanisms, they are very specific to the deformation that occurs. Different modes of resistance are triggered, and even plastic deformations are tolerated. These species have mechanisms that minimize or eliminate the deformation they may suffer as a consequence of stress, reaching a thermodynamic equilibrium with the stress without suffering damage. An important aspect of this strategy is the stress repair mechanisms, which the plant has to activate when the stress has ceased to act (12). The mechanisms that confer tolerance to drought are based on structural stabilization by preferential hydration, whereas the mechanisms that confer tolerance to desiccation are based on the replacement of water by molecules that form hydrogen bonds (39).

At the cellular and molecular level, one of the main responses of plants to adapt to the environment in the face of this limitation is the modification of specific genes. This action depends on the nature, duration, and severity of the stress (37). Genes induced by water deficit are categorized into three groups: 1) genes encoding proteins with known structural or enzymatic functions; 2) proteins with as yet unknown functions; and 3) regulatory proteins (40). But the function of these genes is not only to protect plant cells from dehydration, but they also act in the regulation of other genes that translate into signals in response to water stress (41). In situations of water deficiency, certain enzymes and proteins are affected and lose their biological activity. Therefore, the maintenance of proteins in their functional form and the prevention of protein aggregation is particularly important for the life of the cell under stress conditions (39).

It has been detected that when some plants develop under water deficiency, they accumulate higher amounts of ABA, proline and some soluble sugars. Following this process, chemical signals are sent from the roots to the leaves by increasing the concentration in the cytoplasm of ABA, pH, ethylene precursor and malate, in immediate response to water stress, which causes stomatal closure (42). Studies have also demonstrated the importance of this acid in root growth in drought environments by regulating the negative effect of ethylene on root development (43).

Other biochemical responses generated, due to the decrease of the osmotic potential through accumulations of inorganic (K^+, $Ca_2{}^+$, $Mg_2{}^+$) and organic (proline, aspartic acid, proteins and sugars) solutes (44), K^+ and $Ca_2{}^+$ outflows in the leaf mesophyll, regulate the response to drought (45). The stomatal response allows an increase in transpiration efficiency 46), which is why, when there is a significant decrease in leaf water potential, there is an increase in resistance to water loss (47), coupled with a decrease in net CO_2 fixation (48).

On the other hand, it has been observed that complete recovery of photosynthesis is slow as the plant approaches the point of permanent wilting, varying with plant species, soil type, and method of irrigation water application (49).

Many of these adaptations that plants have developed are related to a greater capacity to absorb water, or to a more efficient use of this resource (50). This is the case of leaf senescence, which constitutes the major regulator in the endogenous activity of the associated processes and contributes to reduce water loss and induces plant dormancy for survival (36). It has been demonstrated that, in the presence of soil water deficit, leaf expansion accelerates senescence (51). The increase of this process in the vegetative phase becomes a potential limitation for crop productivity (52). However, when water tension in the stomata increases, CO_2 assimilation is reduced and the plant prioritizes the synthesis of primary metabolites and, therefore, fruit growth (53).

Role of some microorganisms against water deficit in plants

Most plants adapted to diverse ecological niches are associated with soil microorganisms, which play a key role in the protection against environmental stress to which they may be subjected (54).

Among the PGPR (Plant Growth Promoting Rhizobacteria) genera most commonly used in crops of economic importance in the face of water deficit are: *Bacillus*, *Rhizobium*, *Azospirillum*, *Azotobacter*, *Pseudomonas* (55), *Herbaspirillum* (56), *Bradyrhizobium*

(57), *Enterobacter* (58), *Achromobacter*, *Serratia* (59), *Klebsiella* and *Beijerinckia* (60). Among the positive effects associated with these microorganisms are biological nitrogen fixation, production of plant growth regulating substances such as auxins, cytokinins and gibberellins, increased root growth and pathogen control (61). These characteristics, added to their tolerance to osmotic stress, the endophytic capacity that in some cases provide morphophysiological changes, such as accumulation of osmolytes, stomatal regulation and decrease in membrane potential, contribute to the mitigation of water stress in host plants (62).

Several mechanisms by which rhizobacteria induce tolerance to water deficit stress have been proposed, including the production of phytohormones such as abscisic acid, gibberellic acid, cytokinins, and indolacetic acid; the synthesis of ACC (1-aminocyclopropane-1-carboxylate) deaminase, which reduces the level of ethylene in roots; the induction of induced systemic tolerance; and the presence of exopolysaccharides (Figura 1) (63).

Some of these bacteria form resistance structures to favor their survival in circumstances of drought stress (60). The production of ACC deaminase can be incorporated into the ethylene production pathway, capturing the amino acid ACC (ethylene precursor) and decreasing the levels of this hormone. This action promotes greater plant tolerance to water stress (64).

Eighty percent of dinitrogen (N_2) fixing bacteria produce IAA (3-indolacetic acid) (65). This growth regulator leads to an increase in total phenols, calcium content and the activity of the polyphenol oxidase enzyme that protects the crop against pathogens. It also improves plant growth by eliminating reactive oxygen species, which are formed in the plant as a result of water stress (66). It has been observed that bacterial production of IAA has high sensitivity in plant roots inoculated with this hormone. For example, root length and height in guinea grass (*Megathyrsus maximus*) were favored by inoculation with *Bacillus* sp. strains in two trials conducted in the presence of water stress (67).

Plants inoculated with this type of rhizobacteria that promote growth under abiotic stress due to drought, improve the water status of the leaves, since they tend to have higher values of water use efficiency, that is, the ratio between dry mass gain and water consumed (68). In this sense, it is likely that rhizobia produce antioxidant enzymes (catalase), exopolysaccharides and other substances to be able to survive in extreme environments, especially in drought (69).

Other soil microorganisms that establish symbiotic relationships and increase nutrient assimilation and tolerance to various types of biotic and abiotic stresses in plants are arbuscular mycorrhizal fungi (AMF) (70). These fungi promote resistance to water deficiencies in the host plant, which is a consequence of different mechanisms, ranging from a physical response to a biochemical response (71). The mitigation of the negative effect of water stress by mycorrhization is the result of modifications of the water balance (transpiration and efficient use of water) and nutritional balance, specifically for P (phosphorus), N (nitrogen) and K (potassium) (72). The development of extraradical mycelium allows the roots to have greater access to soil water and thus increase their hydration (73).

The mycorrhizal association alters water relations, independently of the plant stage, which favors plant establishment, vigor, productivity and survival in an

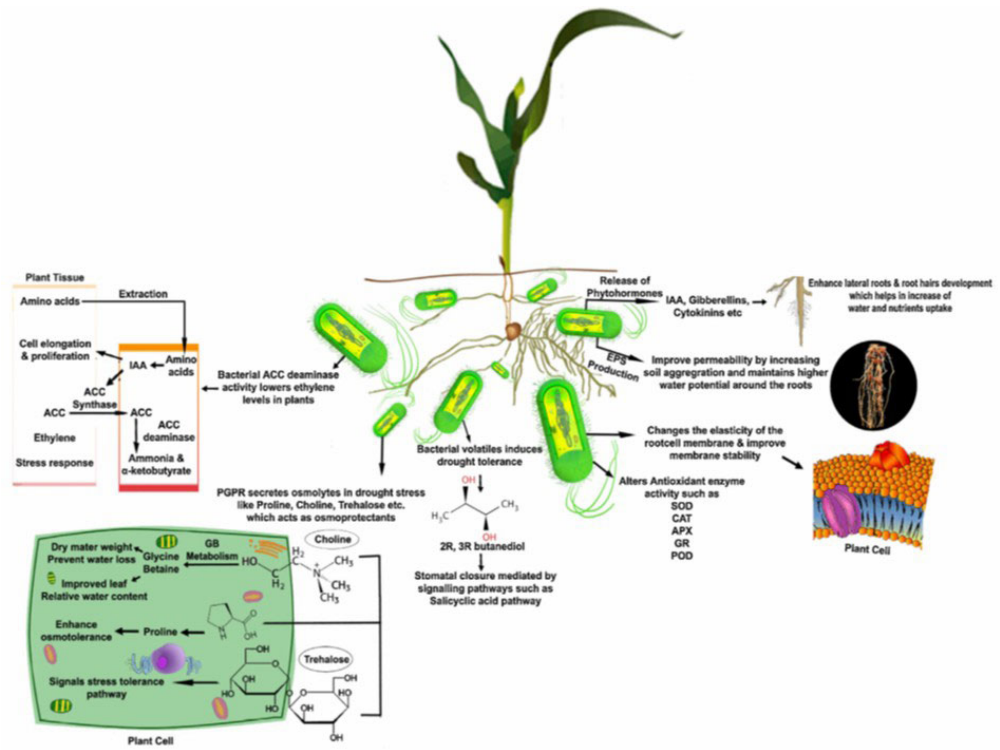

Figure 1. Water deficit tolerance mechanisms induced by plant growth-promoting rhizobacteria

environment with limited water conditions (71). It has been demonstrated that mycorrhizal plants subjected to water deficit conditions recover faster and resist drought conditions longer (74). A study carried out on corn shows that when the crop is subjected to drought and is mycorrhized by *Glomus intraradices* and *Glomus mosseae*, it recovers faster and presents higher values of leaf water potential and CO_2 assimilation rate (75).

CONCLUSIONS

In recent years, considerable progress has been made in the knowledge of the responses induced in plants by water stress. Likewise, in the beneficial effect that microorganisms exert on crops, by promoting the growth of the aerial and root part in times of drought stress. The understanding of the different biochemical and physiological mechanisms involved in stress tolerance allows us to have a better vision of the development obtained by many plants and their interaction with microorganisms throughout their evolutionary process, due to climate change and other environmental events occurring worldwide.

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