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Abbreviations:

SOD: Superoxide Dismutase; POX: Peroxidases; APOX: Ascorbate Peroxidase; DHAR: DeHydroAscorbate Reductase; GR: Glutathione Reductase; CAT: Catalase; NPQ: Non-Photochemical Quenching; HSP: Heat Shock Proteins; SPS: Sucrose Phosphate Synthetase; AI: Acid Invertase

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Mini-Review

Plant Responses and Their Adaptation to Water Deficit

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Mini-Review

The world population has been increasing enormously, especially in the third world's poorest and most vulnerable countries, where food production is not enough to maintain this growing population because they are marginal areas for agriculture, with water and nutrient deficiency [1]. Drought is a circumstance in which plants suffer reduced growth and productivity, due to insufficient water supply or a significant deficit of air moisture, even with an adequate water supply from the soil, which leads to an initial destabilization of the functions of the plant, followed by normalization and induction of the physiological processes of adaptation [2]. Water availability is considered the climatic factor with the most significant effect on agricultural productivity, and it is a factor that governs the distribution of species in the different climatic zones of the globe [2]. Under predicted climate change, drought frequency will increase, and the plant yield will be reduced in the marginal areas for agriculture, especially in the tropics [1,3]. Low precipitation rates are much higher in the tropical zone than in the other zones. However, there are dry regions in these others too. More than 60% of the cultivation of sensitive plants, such as the common bean or tomatoes (Table 1), in the tropics suffer a significant reduction in production due to the lack of water because the plant's water requirement, during its cycle, is not satisfied [4].

Table 1: Approximate values of lethal leaf water potential ($\Psi_{a,l}$) for some species.

Specie	Lethal $\Psi_{a,l}$
Sensitive plants	
Lycopersicum esculentum	-1.4*
Phaseolus vulgaris	-1.5
Vitis vinifera	-1.5*
Citrus spp	-2.0
Zea mays	-2.0
Plants moderately tolerant to water deficit	
Helianthus annuus	-2.2*
Vigna unguiculata	-2.5
Glycine Max	-2.5*
Hordeum vulgare	-3.0*
Triticum aestivum	-3.0*
Plants tolerant to water deficit	
Pennisetum glaucum	-3.0
Arachys hypogea	-3.5*
Cajanus cajans	-3.5
Sorghum bicolor	-3.5*
Gossypium hirsutum	-3.5
Prosopis juliflora	-4.5*
Beta vulgaris	-5.0*
Atriplex nummularia	-6.0
Atriplex halimus	-6.0
Acácia harpophylla	-6.0*

* Data from Boyer (1978).

There is enormous variability in the degree of tolerance to lack of water between species (which can be seen by the value of the lethal leaf water potential $\Psi_{a,l}$ for plants, without recovery, shown in Table 1) and, even within a species, between genotypes [4]. Environmental adaptation is independent of the photosynthetic pathway, such as C_3 or C_4 plants. Only CAM plants can adapt to drought and high temperatures [5]. In addition, the stage of plant development, where stress occurs, is also critical for agricultural productivity. In the corn crop, for example, the two weeks preceding and following the formation of the reproductive organs are the period where water supplementation for the crop has the most significant effect on its yield. Water deficiency, for example, reducing the corn $\Psi_{a,l}$ to -2.0 MPa (Table 1) when there is a stoppage of its photosynthetic activity, causes a 25% decrease in production when applied before flowering, 50% when flowering, and 21% in grain filling. The pollination stage is the most sensitive to environmental stresses, such as water deficit [2]. Water stress effects in the field occur gradually in three stages (Figure 1), while the effects are more quickly imposed in pots, and sometimes the plants do not have time to induce metabolic defense reactions to reduce negative responses to drought.

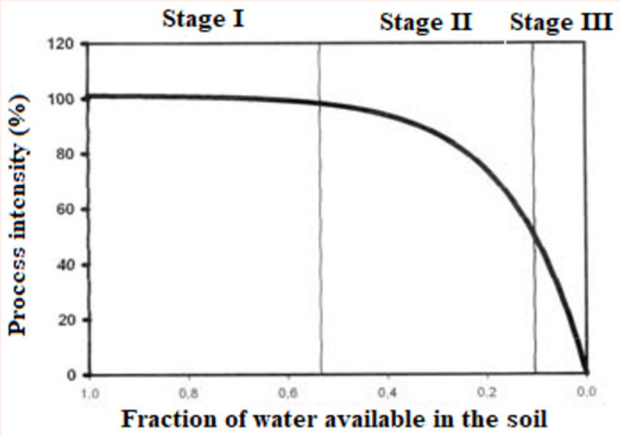

Figure 1: The three stages of dehydration, according to Sinclair & Ludlow (1986).

It is essential to highlight that in some cases, the mechanism for the defense against water deficit in pots is different than when imposed in the field [5]. The gradual imposition of water deficit is essential for the plant's activation of drought tolerance mechanisms, allowing better discrimination of genotypic tolerance to drought. In the work of [6], identifying the three stages of dehydration (Figure 1), the plants were grown in plastic bags, 0.13 m in diameter and 2.3 m high, covered with plastic, to avoid direct water evaporation from the soil to the atmosphere. In this case, cowpea and pigeon pea, which are water deficit tolerant species (Table 1), took 31 and 43 days, respectively, to reach the lethal $\Psi_{a,l}$ as in (Figure 1), thus having a gradual imposition of the stress, as would occur with the plants in the field [6]. For some time, a single test was sought to indicate drought tolerance to discriminate genotypes of the same species as for leaf proline content [5]. Today, it is known that this is impossible due to the diversity of physiological events in different plant organs, which confer the adaptation to the lack of water, which is, thus, considered a multigenic characteristic [2,5,6]. Among the many different responses of plants to water deficiency (Table 2), there are some harmful to plants (such as a metabolic imbalance in the plant with increased production of reactive oxygen species [ROS], which can lead to plant death. However, other responses are favorable (such as increased synthesis of antioxidant compounds [ascorbic acid, glutathione, carotenes, etc...], for the adaptation of the plant to these conditions [5]. Studying the favorable responses for the specie in the analysis is essential for increasing agricultural production, even in areas of maximum productivity, but especially in areas marginal to agriculture [5]. The global anthropogenic climate changes will also cause increased air temperatures and more frequent droughts reducing crop yield, especially in the marginal regions for agriculture, where population growth is higher [1].

Table 2: Classification of plant responses to water deficit, according to Sinclair & Ludlow (1986).

Slight water deficit (Stage I, with no reduction in transpiration, which can occur, even in irrigated plants, when the air vapor pressure deficit is high:
Change in phytohormone content (↑* ABA, ↓* cytokinin, and auxin); ↓ foliar growth; ↓ turgescence potential; ↓ protein biosynthesis; ↑ photoinhibition (ROS production: singlet oxygen, hydrogen peroxide, and hydroxyl).
Moderate water déficit (Stage II, with reduction in transpiration):
↓ Stomatal conductance (g_s); ↑ Root conductivity (Lp), with the increase in aquaporins activity and apoplastic flow ↓ Photosynthesis and transpiration rates (due to the reduction in g_s); ↓ nitrate reductase activity, Sucrose Phosphate Synthetase (SPS) and Acid Invertase (AI); ↑ soluble carbohydrate and amino acids contents, (passive concentration or osmotic adjustment); ↓ Ascorbate (Vit. C), tocopherol (Vit. E), xanthophylls and other carotenes, ATP, $NADPH_2$, and RuBP; ↓ Photosynthesis, due to enzymatic activity (regeneration of RuBP and RubisCO activity) and photosystems activity (ATPase activity).
Severe water deficiency (Stage III, minimal transpiration, via cuticle):
↓ Root Lp; ↓ carbohydrates flow to the drain to be harvested; ↑ activity of hydrolytic enzymes, such as α-amylase, proteases, and lipases, and degradation of membrane galactolipids; ↓ peroxidase activity (superoxide dismutase, ascorbate peroxidase, glutathione reductase, and catalase); ↓ starch, soluble proteins and, lastly, chlorophylls contents; ↑ ROS production; e ↑ electrolyte leakage.
lethal water deficiency:
↑ Damage to cellular organelles (loss of membrane integrity, especially chloroplasts, and mitochondria).

*↑: increase; ↓: decrease.

Therefore, future crop breeding programs must search for yield under drought and high temperature stresses to produce more food for the fast-growing population in marginal areas for agriculture [5]. The process of natural selection in marginal regions for agriculture, subject to lack of water and nutrients and high temperatures, has made the genetic materials native to these areas more adapted to the stresses of this environment, such as pigeon peas, peanuts, wheat, oats, barley, pearl millet, and sorghum, when compared with genotypes originating from wetter regions, under lower temperatures, and high natural fertility, like common beans, tomatoes and corn [5]. It is crucial to study the local varieties of these marginal areas to select more adapted genotypes [1]. As a further complication, plants are exposed to various environmental stresses in the field, such as high temperatures, lack of water, high light radiation, and nutrient deficiency, causing multiple stress on the plant [4]. Among these different stresses, the lack of nutrients is also frequent in regions subject to water shortage [1], and both stress significantly affects agricultural productivity. The deficiency of water will affect the absorption and assimilation of nutrients. The lack of nutrients will affect photosynthesis (N deficiency decreases the synthesis of proteins and, consequently, of Rubisco, a key enzyme in the assimilation of CO_2, which corresponds to more than 50% of the soluble leaf proteins, according to [3]), and the response of the vegetable to water deficit. Nitrogen deficiency decreases hydraulic conductivity (Lp) and water absorption, as well as the production of ABA (which induces stomatal closure in the shoot) by the roots [1]. Another example of the interaction is that phosphorus deficiency affects the balance between ABA and cytokinins and the stomatal opening. A vegetable with a high supply of nutrients keeps the stomata more open to maintain photosynthesis under lower soil water potential values than poorly supplied plants [2].

In any process that requires several independent aspects acting simultaneously, such as photosynthesis and consequent accumulation of dry mass, the speed of the process will be governed by the factor at a lower intensity or slower, a concept that is known as Blackman's law (19thcentury researcher) [2]. This concept applies very well to agricultural productivity and the effect of drought on it since practically all aspects of plant growth are affected by the lack of water (from the microscopic to the macroscopic level), especially the accumulation of dry matter (Table 2), which will account for plant production [4]. The plant's response to drought is characterized by fundamental changes in the cell's relationship with water, in its physiological processes, in the structure of membranes and cellular organelles, in addition to the morphological and phenological changes of the plant (Table 1), altering the relationship of its canopy with the environment [2]. At the plant level, ann usual response to stress in stage I (Figure 1), even before there is variation in leaf water content, is a decrease in shoot growth and protein synthesis associated with changes in carbon and nitrogen metabolism and stomatal closure due to leaf ABA accumulation and reduction of Lp [5]. With the imposition of dehydration, there is a decrease in starch content in the cell, especially in stage II of dehydration, with a reduction in photosynthesis and an increase in soluble sugars due to the paralyzation of cell growth and sucrose synthesis for export. In stage III, with a severe imposition of stress and a severe reduction of CO_2 assimilation due to lower photosystem activity, the reserve starch begins to be hydrolyzed to supply the maintenance of respiration [2]. Thus, there will be a more significant accumulation of soluble carbohydrates, amino acids (due to the stop of protein synthesis in stage I and the increase in proteolysis in stage II), and organic acids [2].

In addition to these organic compounds, inorganic ions (K^+, NO_3^-, Cl^-, etc...) can be actively accumulated, promoting, along with the organic ions mentioned above, osmotic adjustment, in plants that present this response, as sorghum, wheat, oats, barley, and others grasses, and among grain legumes, only pigeon pea and peanuts make osmotic adjustment [5]. In addition, with the imposition of water deficiency in stage II, the concentration of antioxidant compounds such as ascorbate, glutathione, tocopherol, and other carotenoids (including xanthophylls) decreases, which further increases the concentration of free ROS in the cell, which will cause peroxidation of membrane lipids, proteins, and other compounds, as DNA and RNA [5]. In addition, the central enzymatic systems of detoxification of these ROS, which involve the action of Superoxide Dismutase (SOD), Peroxidases (POX), and reductases, removing electrons from the ROS, with consumption of reducing power, are altered. With the lack of water, the activity of these enzymes is decreased, such as SOD, POX, and especially Ascorbate Peroxidase (APOX), but also DeHydroAscorbate Reductase (DHAR) and Glutathione Reductase (GR) and Catalase (CAT). In addition, the lipid composition of cell membranes and the ability of their de novo synthesis (membrane restoration) with rehydration directly affects the survival capacity of the cell [2,5]. Under a severe water deficit in stage III, there is a change in the composition of membrane lipids, with a reduction in the content of polar and polyunsaturated lipids, first of the glycolipids and, with the severity of stress, of the galactolipids, with a lower percentage of linolenic acid, associated with an increase in the content of linoleic acid [2]. This decrease in lipid content in the membranes of stressed plants is due to the reduction of lipid biosynthesis and the rise in degradation processes by the higher activity of lipases [5].

In stage III, there is an intense decrease in the water content in the cell, and distortions of the cell wall occur, causing rupture and lysis of the plasmalemma, chloroplasts, mitochondria, and other organelles (which can lead to the collapse of the intercellular spaces and lysis of the cell). This effect reduces the activity of the reactions associated with the membranes, such as the biochemical activity of photosynthesis. Chloroplasts and mitochondria are very sensitive organelles to drought, suffering rupture and lysis of their membranes (Table 2) and losing their integrity [2]. Despite the many studies to understand the causes of the numerous physicochemical changes that occur in the cell under dehydration, the cellular conditions, which cause changes in metabolism, are still poorly understood [5]. In the study of the plant's responses to the water deficit, there are still many doubts about the advantages or disadvantages of these responses because they are complex, covering the levels of the cell, the plant, and the canopy in the field and, thus, reflect the integration of the effects of stress and the responses of the plant, under all levels of the organization, in space and time. Therefore, adaptation to drought is considered a multigenic characteristic, with numerous characteristics, which are variable between species, and consequently difficult to determine [2] (Table 3), presents some physiological mechanisms of drought adaptation, but a specie cannot have all of them, and some of the mechanisms shown can be addictive. Also, the characteristics of the root system, regarding the ability to obtain water, should be one of the first pieces of information to be sought for the study of the capacity of a plant to tolerate the lack of water. Some plants, such as pearl millet, originating in semi-arid regions of West Africa, in the Sahel, and considered one of the most drought-tolerant plants [4,5], can extract water from the deep layers of the soil without presenting other well-developed tolerance characteristics. Another subject to increase the research for higher yield is the interaction of the genotypes with the so-called Plant-Growth-Promoting Rhizobacteria (PGPR), especially under environmental stresses [4,5].

Table 3: Physiological mechanisms of drought adaptation, which can be addictive.

Escape mechanisms (The ability of the plant to complete the cycle before severe water shortages occur):
Rapid phenological development (during the short rainy season) and developmental plasticity (shortening or extending the cycle when water shortages occur).
Tolerance mechanisms under high water content (The ability of the plant to maintain high hydration):
Stomatal closure (1st line of defense); leaves rolling; change in leaf angle; increased root Lp (aquaporin activity and apoplastic flow); rapid and deep root; leaf area maintenance of the source leaves, in the pre and post-flowering, with senescence of the older leaves; tillering and flowering of secondary tillers; remobilization of reserves of stalks and branches for grain; reduction in the number and sterility of grains per panicle; reduction of the interval between male and female flowering [in corn]; xeromorphic characteristics (multiple and sclerotic epidermises, thick cuticle, trichomes, waxiness, exodermal sclerosis (when existing), etc...); increased Non-Photochemical Quenching of fluorescence (NPQ) and CAM metabolism.
Tolerance mechanisms under low water content (The ability of the plant to be submitted to intense dehydration):
Smaller leaf area; accumulation of carbohydrates in roots; cell wall and, or osmotic adjustment; ability to recover in rehydration (inactivation of enzyme systems without its degradation); increased soluble sugars and amino acids accumulation in the leaves [maintaining macromolecules structure]; water transport in the root via aquaporins, with reduction of root Lp; protoplasmic tolerance (maintenance of membrane integrity and other macromolecules, due to: composition in membrane phospholipids, lower lipase and protease activity, higher peroxidase activity, and synthesis of protective compounds, such as xanthophylls, polyols, ascorbate, tocopherol, small Heat Shock Proteins (HSP), polyamines, dehydrins, jasmonic acid, brassinosteroids, and salicylic acid; tolerance to desiccation (anhydrobiosis) (< 23% water) of seeds, spores, pollen and lichens (cytoplasm vitrification: soluble sugars replace the water in the structure of macromolecules

Some characteristics allow the plant to avoid the dry period, shortening the cycle, for example; other characteristics will maximize the absorption of water through a high capacity of the root system to absorb it or are associated with the optimization of the use of absorbed moisture for the production of dry matter. Yet, a third type of characteristic is related to the ability of plant tissue to tolerate a low water content while maintaining its metabolic activity. Therefore, three types of adaptive responses of plants under stress due to water deficiency (contemplating the abovementioned characteristics) were proposed in the literature (Table 3), escape mechanisms, tolerance mechanisms under high water content, and tolerance mechanisms under low water content. Following the classification proposed (Table 3), the primary adaptive responses of escape to drought are rapid phenological development and the plasticity of development. Species with rapid phenological growth complete their reproductive cycle during the short rainy season of arid and semi-arid regions. For example, in the African Sahel, 300 to 600 mm of annual precipitation occurs in 75 to 119 days, the season for agricultural cultivation. The seeds produced during these rainy seasons stay in the soil until the next rainy season when they will germinate quickly for the installation of the plant in the next year [4]. Regarding the tolerance mechanisms under high water content (Table 3), stomatal control is considered a mechanism of the aerial part, which tends to favor the vegetable, when the water deficit has a short duration (summers).

However, if the stress is long-lasting, stomatal closure can cause a significant reduction in CO_2 absorption and, consequently, drastically reduce yield. Stomatal closure is considered the first line of defense of the vegetable to avoid desiccation. As for the mechanisms of drought tolerance, under low water content, the small size of plants, with small leaf area, leaves with xeromorphic characteristics, and a deep and dense root system are morphological characteristics of adaptation to these conditions, which have been widely studied [2]. In addition, the higher efficiency of converting photoassimilates into dry mass, with a more significant accumulation of starch (carbohydrate reserve), is considered a desirable characteristic for adaptation to dehydration under low water content. This accumulation of starch can be done in roots, as occurs in cassava, for example, and has already been successfully used as a characteristic for selecting genotypes of oil palm and cotton more tolerant to drought [4]. Another drought tolerance mechanism under low water content is the active accumulation of osmotically active solutes in the cell, called an osmotic adjustment. It allows the maintenance of turgidity, growth, and photosynthesis under low water content. However, the osmotic adjustment alone does not allow cell growth because the turgescence generated with it is not the only factor controlling it. Growth depends on cell turgescence, but it also depends on the elasticity of the cell wall and, consequently, on its elasticity coefficient [4]. The osmotic adjustment will promote the turgor necessary for growth. Still, if there is no adjustment of the elasticity of the cell wall, increasing its capacity for extension, there will be no. cell growth [2,4]. In addition to the accumulated carbohydrates, amino acids, and organic acids, many other compounds have a protective effect on the cell under dehydration, such as those cited for mild dehydration in stages I and II, but also have a protective effect on plants in stage III of dehydration.

As an example, one can cite the accumulation of ascorbate, glutathione, tocopherol, and xanthophylls, detoxifying the cell of the ROS, also dehydrins, and polyamines [2, 4], which stabilize macromolecules, allowing cell growth, in roots under drought, and other protective compounds, such as polyols, small Heat Shock Proteins (HSP), and LEA proteins, which activate membrane damage repair systems, as well as phytohormone candidates, jasmonic acid, brassinosteroids, and salicylic acid, which protect membrane, DNA and RNA integrity [4]. In a study of water deficit effects on a different species, it is crucial to search in the literature what kind of response and drought adaptation mechanism the specie shows [7].

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