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Chapter

Toxic Aluminum and Water Deficit Interaction in Plants: Physiological Aspects and Chemical Soil Management to Improve Root Environment in the Context of Global Climate Change

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Abstract

Human activity has contributed to the intensification of climate change. These climate changes cause a reduction in plant growth and agricultural production due to increasingly frequent periods of water restriction. This effect can be more severe in tropical regions where the acid pH of the soil and the toxic levels of aluminum have a natural origin due to the weathering of the soils. In this context, water deficiency and aluminum toxicity alone or together promote biochemical and physiological changes in plants. This suggests the need to adopt soil management strategies that minimize the joint impact of these two abiotic stresses. Thus, liming and gypsum contribute to improving the edaphic environment, because they reduce the availability of toxic aluminum but increase the soil pH. In this chapter, we propose a systematic review of the isolated and combined effects of water deficiency and aluminum toxicity in plants based on physiological, biochemical, and nutritional variables. Thus, the understanding of these responses will improve the understanding of the mechanisms of tolerance to the two abiotic stresses, indicating the need to use soil correctives to minimize the effects of water deficiency and toxic aluminum in the soil on plant growth.

Keywords: toxic metal, soil pH, global warming, plant growth, gas exchange

1. Introduction

Drought is a factor that leads to environmental degradation and has adverse effects on rural populations dependent on natural resources such as water and soil. Drought can eventually lead to the loss of livelihoods, promote migration in affected areas [1], and have a significant impact on the economy, society, and environment [2]. According to the IPCC, the global population exposed to extreme or exceptional total scarcity of stored water will be 3–8%. In this context, risks of drought are predicted...
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throughout the 21st century in many regions, increasing the probability of an economic crisis [3]. This prediction is worrying because the world population reached 8 billion inhabitants in 2022 [4], a fact that increases the demand for food. However, global climate changes can negatively affect agricultural production by altering the rainfall regime, inducing water deficiency and, consequently, reducing agricultural production [5, 6].

In tropical regions, high precipitation over time promotes the leaching of exchangeable bases and increases the levels of toxic aluminum. These two edaphic aspects result from the intense weathering of the soil. However, in tropical regions the occurrence of periods of water deficiency is normal. Thus, the sum of the factors of water deficiency and toxic aluminum potentiate the reduction of plant growth and agricultural production, because they cause disorders in gas exchange, nitrogen metabolism, and antioxidant in plants [7–10].

The chemical management of weathered tropical soils with toxic levels of aluminum can contribute to minimizing the effect of water deficit because liming reduces the toxic aluminum content and increases the surface pH and the calcium and magnesium content of the soil. In addition, gypsum contributes to the reduction of subsurface aluminum content and the increase of sulfur content in the soil.

Together, liming and plastering can minimize the effects of water deficiency, because they create an edaphic environment that improves root growth in volume and depth and, consequently, increases the absorption of nutrients and water. Therefore, the use of these two agricultural inputs can mitigate the effects of water deficiency on plants in acid soils.

This chapter will address the problem of water deficiency and aluminum toxicity in plants in the context of global climate change, emphasizing plant responses to aluminum toxicity and water deficiency, and liming and gypsum management as mitigating agents of soil chemical stress.

2. Physiological mechanism of plants under water deficit

With the advancement of global climate change, the occurrence of longer periods of water deficiency becomes more frequent, causing climatic risks to plant growth and, consequently, to agricultural activity. In the environmental context, prolonged periods without precipitation cause a reduction in soil water content and a decrease in vegetation growth, except in plants adapted to conditions of water scarcity, a fact quite common in arid and semi-arid regions. In the semi-arid region of northeastern Brazil, the occurrence of prolonged periods of water scarcity is common, with a drastic reduction in the availability of water in the soil, with the permanence of only species adapted to the semi-arid climate (Figure 1).

Physiologically, plants under water stress manifest a set of responses that culminate in reduced plant growth. Thus, the decrease in water availability induces stomatal closure due to greater synthesis and physiological action of abscisic acid on stomata. These close as a physiological strategy to reduce water loss through perspiration. This physiological phenomenon induces stomatal limitation to photosynthesis due to the reduction in the intercellular concentration of carbon dioxide [11].

The drop in the intercellular concentration of carbon dioxide can decrease the consumption of ATP and the NADPH₂ reducing power by the Calvin cycle, allowing electrons from the electron transport chain to interact with free molecular oxygen forming superoxide radicals, since NADPH₂ is chemically reduced (Figure 2).
This set of events culminates in oxidative stress that causes lipid peroxidation and important cellular damage in plants under water deficit [12]. However, although water deficiency reduces the carboxylation activity of the enzyme RUBISCO (ribulose
1,5-bisphosphate carboxylase-oxygenase), its oxygenase function is increased, which allows temporary consumption of NADPH and ATP, reducing the production of reactive oxygen species (ROSs). However, photorespiration allows the recycling of phosphoglycolate (a toxic compound) to phosphoglycerate during carbon fixation [13, 14].

Despite the cellular damage caused by ROS, they have a dual role in cells because they participate in cell signaling, but they are also toxic products of aerobic metabolism in plants [15, 16]. The main free radicals produced in plants under water deficit are the superoxide radical (O$_2^-$), peroxide radical (H$_2$O$_2$), and hydroxyl radical (OH$^-$). The O$_2^-$ radical is synthesized in the apoplast, chloroplast, mitochondria, peroxisomes, and electron transport chain. The H$_2$O$_2$ radical, in turn, can be synthesized in peroxisomes, chloroplasts, mitochondria, cytosol, apoplast, and cytosol. The OH$^-$ radical is synthesized from the H$_2$O$_2$ radical according to Fenton’s reaction [16]. The oxidative stress resulting from water deficiency, in addition to increasing lipid peroxidation, reduces photosynthetic activity due to the harmful action of ROS on the photosynthetic machinery causing photoinhibition [17].

The mineral metabolism of plants is considerably affected by water deficiency, especially by nutrients that are absorbed through mass flow such as nitrogen [18]. The key enzyme present in plants that allows the entry of nitrogen into plants is nitrate reductase (RN, EC 1.6.6.1) which converts nitrate (NO$_3^-$) to nitrite (NO$_2^-$). One of the environmental factors that modulate the activity of the RN enzyme is the availability of nitrate, which is absorbed by the root system via transpiration [19]. Thus, water deficiency is a factor that indirectly decreases NR activity, because it limits the absorption of nitrate by the roots [20].

Water deficiency imposes limitations on plants regarding the acquisition of water in the environment in which they live since with the advancement of water restriction, the water potential of the soil tends to become more negative. In this sense, plants must maximize water use to avoid excessive loss through transpiration and maintain their water status favorable to their physiological activities. A biochemical strategy aimed at tolerating water deficiency is the synthesis of compatible osmolytes, which reduce the cellular osmotic potential for water influx into cells. Furthermore, compatible osmolytes preserve the conformational structure and maintain the biological activity of biomolecules [21, 22]. Amino acids (proline, glycine betaine, gamma-aminobutyric acid) and carbohydrates (sorbitol, sucrose, trehalose, manitol, and raffinose) are compatible osmolytes used by plants during water deficit for osmotic adjustment and improvement of water status [21, 23]. Proline and glycine betaine are two important compatible osmolytes involved in modulating the response of plants to water stress [24, 25].

It should be emphasized that there is a negative correlation between the water content and the concentration of compatible osmolytes in plants under water deficit. However, increases in the concentration of compatible osmolytes do not necessarily imply an increase or stability in the plant growth rate in the face of water restriction experienced by the plants [7].

3. Physiological mechanisms of aluminum toxicity in plants

Metal toxicity is one of the world’s biggest problems for agricultural production. Some metals are not essential to plants but are very toxic when present in certain forms in soil. Among metals, aluminum (Al) is one of the most toxic because it reduces the growth and production of many crops in acidic soils [26]. Around 50%
of arable land in the world is acidic [27] and around 60% of acidic soils are found in tropical and subtropical regions because in these regions the soil acidification process is natural [28].

The absorption of Al via symplast or apoplast can cause injuries to biomolecules in the cell wall, membrane, cytoplasm, and nucleus, affecting the structure of root cells and, consequently, the ability of root cells to absorb water and mineral salts from the soil [28]. Al bound to root cells appears to be localized to the apoplast cell wall and plasma membrane surface [29]. Therefore, the toxic effect of Al results from its external connection with root cells [27]. Thus, the initial site of Al toxicity occurs in the roots, which present physiological and biochemical changes that result in reduced root growth (Figure 3).

The physiological activity of the root system is affected by Al as it is the initial site of toxicity for this toxic metal. Thus, the ability to absorb water and mineral nutrients is compromised by toxic levels of Al. Therefore, toxic Al affects water relations in plants, reducing transpiration, water use efficiency, and intrinsic water use efficiency [30]. In addition, transpiration, root hydraulic conductivity, and leaf water potential are negatively affected by Al and these disorders in plant water relations coincide with increased levels of ABA in plants treated with toxic Al, indicating that this metal has a broad spectrum of action. Physiology in plants [31].

The mineral metabolism of plants is affected by the toxic action of Al, because this toxic metal inhibits the activity of the nitrate reductase enzyme and, consequently, the conversion of nitrate to nitrite in plants. In addition, Al reduces the levels of macronutrients (calcium, magnesium, phosphorus, and potassium) inducing nutritional disorders in plants that result in reduced plant growth [32, 33].

Although there is a greater accumulation of Al in the root system than in the aerial part of the plants, the physiological activity of the leaves is considerably affected by Al. This metal reduces the concentration of chlorophylls and, consequently, the

Figure 3. Toxic aluminum primarily targets the root system. Aluminum concentrations above 4 mmol L⁻¹ severely reduce root and shoot growth of Cajanus cajan seedlings. Source: Author.
Aluminum toxicity induces the production of $\text{O}_2^-$, $\text{H}_2\text{O}_2$, and OH- both in shoots and roots, causing lipid peroxidation and electrolyte leakage in plants [34, 38-40]. Although Al triggers oxidative stress in plants [34], the mechanism itself is indirect because Al activates NADPH oxidase (Figure 4) one of the main sources of ROS generation in plants under Al stress [39].

Respiratory burst oxidase homolog proteins (RBOHS) are integral plasma membrane proteins. They are formed by six transmembrane domains that support two heme groups, C-terminal FAD and NADPH hydrophilic domains, and two N-terminal calcium-binding domains (EF-hand). NADPH oxidase acts as a cytosolic electron donor to the extracellular $\text{O}_2$ electron acceptor, which is reduced to $\text{O}_2^-$ via FAD and two independent hemes [41].

4. Interaction between stress: water deficiency and aluminum toxicity

In tropical countries, the occurrence of periods of water scarcity is common in regions where the soil is weathered and with high levels of toxic Al. However, with global climate changes, the occurrence of water deficiency has become more frequent.
Thus, the interaction between toxic Al and water deficiency potentiates the reduction of plant growth and production.

Under non-stressful conditions (absence of water deficiency and Al toxicity), cell growth can be explained by cell expansion resulting from the action of the enzyme xyloglucan endotransglycosylase—XET (EC 2.4.1.207). This enzyme promotes the cleavage and reformation of bonds between the xyloglucan chains (Figure 5) allowing cell expansion to occur due to the entry of water into the cell and an increase in cell pressure potential [41].

However, the interaction between water deficiency and toxic aluminum results in lower water influx into the cell and inhibition of XET activity. This set of events implies less cellular expansion of the root system with negative repercussions on plant growth and production (Figure 5). Therefore, toxic aluminum has as its primary target the root system whose elongation rate is considerably reduced when there is an interaction between toxic aluminum and water deficiency [8, 42].

The interaction between toxic Al levels and reduced water availability induces an increase in leaf contents of important compatible osmolytes such as glycine betaine, proline, and trehalose. However, a greater accumulation of compatible osmolytes does not prevent the decrease in plant growth [7, 43] represented by the dry mass of roots and shoots, and leaf area [43, 44].

The photosynthetic machinery is greatly affected by the interaction between aluminum toxicity and water deficiency because the concentration of photosynthetic pigments is considerably reduced [8] due to the production of free radicals that lead to lipid peroxidation, degradation of chlorophyll, and carotenoids [9, 45]. The degradation of chloroplast pigments may originate from lower root absorption and reduced

![Figure 5](image_url)

**Figure 5.** Cell expansion in the presence (left) and absence (right) of water and aluminium. The symplastic and apoplastic influx of H\(_2\)O into cells increases the activity of the cell wall enzyme xyloglucan endotransglycosylase (XET) and the pressure potential on the cell wall. XET improves cell wall extensibility which is favored by intracellular water influx. These biochemical and physical phenomena imply cell expansion (left). Toxic aluminium reduces water influx into the cell and decreases XET activity. This implies less cell expansion (right). Source: Figure adapted from Yang et al. [42].
accumulation of magnesium in plant leaves due to toxic Al since magnesium is an integral part of the chlorophyll molecule [46].

Despite the large production of ROS such as $\text{O}_2^-$, $\text{H}_2\text{O}_2$, and $\text{OH}^-$ due to the interaction between toxic Al and water deficiency, plants activate detoxification enzymatic mechanisms. In this context, the enzymes superoxide dismutase and guaiacol peroxidase have their activities increased to reduce the production of ROS and lipid peroxidation [9].

The mineral metabolism of plants is affected by the interaction between Al toxicity and water deficiency because the joint action of these two limiting factors reduces the calcium, magnesium, and phosphorus content in the leaves and roots of plants [47]. Essential macronutrients absorbed mainly by mass flow such as calcium and magnesium can be found in lower levels in plants due to the lower flow of water in the soil-plant-atmosphere system under conditions of water deficit.

This negative effect of water deficiency can be potentiated by Al toxicity. For example, in acid soil with an Al content of 12 mmol L$^{-1}$ (soil depth of 0–20 cm) and with 50% of its pores filled with water, the contents of nitrogen, phosphorus, potassium, calcium, magnesium, zinc, and manganese were reduced in maize plants under the interaction of stresses [48]. Similarly, in soybean plants, the contents of nitrogen, phosphorus, potassium, calcium, magnesium, sulfur, copper, and manganese are reduced under the interaction of stresses. Furthermore, root density and biomass production of soybean and corn is strongly reduced by the interaction between toxic aluminum and water stress [48].

5. Liming and gypsum: Chemical soil management aimed at mitigating toxic aluminum and improving the water status of plants

Agricultural production can be limited by physical and chemical factors in the soil, which reduce root growth and restrict the uptake of mineral nutrients and water. In this context, toxic Al plays an important role in tropical regions where soil pH is not corrected because growth, development, and, consequently, agricultural production are negatively affected. This effect on plants is aggravated when there are dry spells or periods of water deficiency, an increasingly recurrent phenomenon in the context of global climate change.

The water conduction mechanisms in the soil-plant system represented by hydraulic conductivity and stomatal conductance are affected by the increase in the cellular concentration of abscisic acid induced by Al toxicity [31]. In addition, cellular and structural damage to the root system caused by toxic Al reduces cell turgor [49] and decreases plant root growth [31]. The negative effects of toxic Al on plants are potentiated by the action of water deficiency which, together, reduce plant growth [7].

A soil chemical management strategy aimed at neutralizing toxic Al consists of the adoption of liming based on soil chemical analysis. Liming raises the pH and reduces Al availability in the layers where limestone is applied [50], increases the availability of calcium and magnesium in the soil, and the assimilation of nutrients such as nitrogen, phosphorus, potassium, and sulfur by plants [51]. The increase in pH occurs through the exchange of $\text{H}^+$ for $\text{Ca}^{2+}$ in the soil colloids and its neutralization (Figure 6).

Similarly, the $\text{Al}^{3+}$ is exchanged for $\text{Ca}^{2+}$ in the soil colloids forming a little toxic compound (AlOH$_3$) that rushes into the soil (Figure 7).

Another strategy, to neutralize toxic Al, but in subsurface soil layers, is plastering. Gypsum renders Al insoluble causing it to be leached into deep soil layers. In addition,
gypsum improves the physical and chemical quality of the soil, creating better conditions for root development and growth. These changes promoted by gypsum nullify the effects of Al toxicity, increase root growth and attenuate the effects of water deficiency in plants [52]. These effects of gypsum indicate that the practice of gypsum can mitigate the effects of global climate change on water deficiency because there is greater root growth of plants in depth in the soil. Agricultural gypsum provides calcium and sulfur that improve soil fertility. In addition, the gypsum insolubilizes toxic aluminium, allowing its leaching to the subsurface layers of the soil (Figure 8).
The benefit of gypsum is related to the greater root growth of plants. For example, the mean percentage distribution of the root system of sugarcane plants in the 0–20 cm, 20–40 cm, and 40–60 cm layers after gypsum soil application was 51.80, 29.72, and 18.64%, respectively. Furthermore, gypsum shows a positive effect on the root density of sugarcane plants [53]. Gypsum also increases the percentage of water absorbed by the root system at depths greater than 40 cm (Figure 9) because gypsum improves the physical and chemical attributes of the soil, allowing greater root growth in depth [53]. Gypsum improves the physical properties of the soil because it has a flocculating action on soil particles. This favors the aggregation of clay, reducing its dispersion. Thus, there is greater soil porosity, increased permeability, and water retention capacity in the soil. These changes promoted by gypsum create a favorable environment for the root growth of crops.

The interaction between limestone and gypsum in the soil shows a positive effect on root growth and agricultural production. For example, the application of gypsum and limestone in the soil shows positive effects on root growth because it improves the relative root distribution in depth [53], in addition to increasing the production of soybeans by 11.4% in conditions of water deficit [54]. Under conditions of water deficit, gypsum is shown to be efficient in increasing grain production in grasses such as maize and wheat [55].

In an oat cultivation area, liming and plastering increase grain production under water deficit [50]. These positive effects of gypsum, together or not with liming, result in a better edaphic environment that favors greater root growth with a positive impact on the absorption of water and mineral nutrients, two essential factors for plant production. Thus, the mechanism of action of gypsum and limestone in the soil suggests that these two agricultural inputs can be used to mitigate the effects of global warming on plant growth.

Figure 8. Gypsum action on subsurface toxic aluminium. Gypsum supplies calcium and sulfur to the soil. Ca" from gypsum displaces Al". This will form with sulfate ions a poorly soluble compound, Al(SO₄), which is leached to deeper layers of the soil. Source: Author.
climate change, particularly in tropical regions where the natural acidity of the soil is a limiting factor for plant growth and agricultural production [52].

6. Conclusion

In the context of global climate change, water deficiency is an increasingly frequent phenomenon in many regions of the world, directly impacting plant and animal production, which have water as a vital input. In tropical regions in particular, water deficiency is particularly serious because in these regions many soils are acidic and with high Aluminum saturation. This metal compromises plant growth and production because its target is the root system, the organ responsible for absorbing nutrients and water from the soil. Thus, water deficiency and Al toxicity together potentiate the reduction of plant growth and production, with considerable social and economic impacts. The increasingly frequent periods of water deficiency restrict soil water availability, inducing less water absorption and cellular water influx. These events culminate in the loss of cell turgor, lower cell expansion, and, consequently, lower plant growth with a negative impact on gas exchange, and mineral and antioxidant metabolism. These effects of water deficiency are potentiated by the action of toxic Al present in the soil because the primary site of Al action is the root system. Al reduces the fluidity of cell membranes, affecting their capacities related to the absorption of mineral nutrients and water, inducing nutritional and water deficiency in plants. Although the genetic improvement of plants aimed at tolerance to Al toxicity is an important tool to increase agricultural productivity in Al-affected soils, it occurs slowly and in few areas. A strategy that can be adopted to overcome the problem of acidity and toxic Al is the use of gypsum and agricultural limestone as soil amendments. Together, the use of gypsum and limestone reduces toxic Al in depth.
and surface, increases soil pH, and thus creates an edaphic environment favorable to
greater root growth in volume and depth. Thus, crops will be more tolerant to periods
of water deficit in soils treated with gypsum and limestone. However, the physiologi-
cal and biochemical mechanisms of plant responses to liming and soil gypsum need
further studies, since these two agricultural inputs, when applied to the soil, improve
the absorption mechanisms of mineral nutrients and water, gas exchange, and the
production of cultures.

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