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Regulatory Effects of Exogenous Boron on Physiological Metabolism of *Helianthus tuberosus* under Aluminum Stress

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Abstract

With the acceleration of industrialization, soil pollution caused by acid deposition has gradually evolved into a major global ecological and environmental problem, among which aluminum acid stress has become one of the main environmental factors restricting plant growth and agricultural production in China. Jerusalem artilum is not only a cash crop with high utilization value in many fields, such as food and medicine, but also has ecological effects, such as environmental restoration. It has an obvious regulation effect on aluminum ions in soil, which can effectively reduce the harm of soil aluminum pollution and promote the growth of plants. Studies have shown that boron plays an important role in alleviating metal stress in plants and can effectively enhance the adaptability of plants to stress. Based on the current situation of soil aluminum pollution, this paper briefly discusses the biological characteristics of Jerusalem artichoke and its application value in the field of soil aluminum pollution control, comprehensively analyzes the mitigation effect of boron on plant stress and aims to lay a foundation for the research on the physiological response of Jerusalem artichoke in aluminum-polluted soil and the mitigation effect of exogenous boron. It provides a guarantee for the full utilization of the absorption capacity of aluminum ions, promotes the treatment process of soil aluminum pollution and improves the exploitation and utilization value of aluminate soil.

Subject Areas

Biomedical & Life Sciences

Keywords

Aluminum Stress, Exogenous Boron, Phytoremediation of Soil, Mitigative

Effect, Regulation of Physiology

1. Introduction

Aluminum toxicity is a major limiting factor affecting the growth of herbaceous plants in acidic soil areas. In recent years, due to unreasonable agricultural fertilization and irrigation and acid rain precipitation [1], the global soil acidification problem has become increasingly serious, resulting in the chemical form changes of insoluble silicate compounds and oxides of aluminum, which are gradually transformed into exchangeable aluminum ions and remain in the soil. Thus, aggravating the harm of aluminum pollution [2]. Al^{3+} not only has a serious toxic effect on the growth of plants, but also is difficult to degrade in the natural environment, and is enriched into organisms through migration, transformation and other processes, enriched through the food chain, and ultimately causing harm to human health, and even destroying the entire ecosystem. At present, for the serious problem of soil aluminum pollution, the mainstream methods include physical, chemical, and biological remediation, but the former two have defects such as large engineering, high investment, causing secondary pollution, and so on. As one of the biological remediation methods, phytoremediation technology is more economical, green, efficient, and has a wider range of use which is more conducive to the sustainable development of ecological environment

Helianthus tuberosus L., as a crop widely planted in our country, not only has edible and medicinal values, but also has the effect of absorbing metal ions in the soil. Studies have shown that it has a certain absorption and transport capacity for aluminum ions [3]. At present, soil aluminum toxicity has posed a certain threat to agricultural production and other fields, but the application of some exogenous substances, such as Ca^{2+} and organic acids, can effectively enhance the resistance of Jerusalem artichoke to aluminum pollution. In addition, exogenous boron can chelate with aluminum to mitigate aluminum toxicity [4], thus greatly improving the repair ability of Jerusalem artichoke to aluminum-contaminated soil. At present, there have been some studies on the physiological and biochemical aspects of aluminum toxicity in *Helianthus tuberosus*, but the studies on molecular biology, mitigation measures and mechanisms need to be further expanded and in-depth. At present, the mitigation measures of aluminum toxicity mainly focus on mixed planting and the mitigation effects of calcium, phosphorus and hormones, while the research on boron and aluminum toxicity of Jerusalem artijac is still lacking. This study reviewed the effects of aluminum pollution on crop growth, and explored the sustainable regulation of exogenous boron on plant physiological changes and DNA damage repair effect. This study laid a foundation for exploring the response mechanism of Jerusalem arum to exogenous boron and its cgrowth andapplication under aluminum pollution, in order to effectively alleviate the problem of aluminum pollution in soil, and provide theoretical guidance and technical support for the further development and utilization of aluminum acid soil.

2. Aluminum Pollution in Soil and Aluminum Acid Stress to Plant

2.1. Present Situation and Control Methods of Aluminum Poisoning in Soil

Aluminum is one of the most common metallic elements in the Earth's crust, usually in the form of aluminosilicate or $Al(OH)_3$, the hydroxide of aluminum. Aluminum has no toxic effect on plants, the environment and humans [5]. However, with the advancement of industrialization, acid rain frequently penetrates into the soil, dissolving solid aluminum into the soil solution, thereby increasing the content of active aluminum in the soil [6]. When soil is significantly acidified, solid aluminum is released in toxic forms such as Al^{3+} and $Al(OH)^{2+}$, which greatly reduces crop productivity. In China, the total area of acid soil is about 20.3 million hectares, accounting for 21% of the total cultivated land area in the country, covering an important area for cash crops and grain production in the south of the Yangtze River [7]. The aggravation of aluminum sulfate toxicity in soil can reduce the yield and quality of crops, which has a negative impact on the green and sustainable development of the region.

In view of the serious problem of aluminum pollution in soil, physical, chemical, biological remediation and other methods are generally adopted for treatment. Physical remediation are mainly used to change soil conditions through physical operations, including soil exchange and deep soil tillage. Chemical remediation methods mainly use chemicals to modify the soil environment to reduce the toxicity of aluminum in soil. Common methods include leaching and application of amendments. Although these methods can reduce soil aluminum pollution to a certain extent, they cannot achieve a radical effect, and may damage soil structure, bring secondary pollution and other risks, which have adverse effects on sustainable development of land. In recent years, domestic and foreign researchers have focused on bioremediation methods, which use biological absorption, degradation and transformation of pollutants in soil to reduce the concentration of aluminum to low levels through biological activity. Bioremediation is environmentally friendly and sustainable, which can eradicate aluminum toxicity in soil to a certain extent. Nowadays, phytoremediation technology, as one of the bioremediation methods, has gradually developed and matured. Studies have shown that *Rudbeckia hirta* L. has remediation effects on oiling soil in the Loess Plateau. Yang Binjuan found that *Helianthus annuus* L. can repair soil Cd pollution, and *Hippochaete ramosissimum* L. can reduce soil copper content. Compared with traditional methods, phytoremediation technology has stronger economic applicability, less secondary pollution, is more suitable for large-scale promotion, and has broad application and development prospects.

2.2. Physiological Changes of Plants Under Aluminum Acid Stress

2.2.1. Physiological Responses of Plants to Aluminum Acid Stress

Aluminum toxicity is one of the main factors affecting agricultural production in acid soils [8], among which Al^{3+} is the main form of stress, which seriously harms the growth of crops. Changes in the content, proportion and structure of plant root tip cell wall components induced by aluminum stress lead to decreased rigidity of cell wall, thus inhibiting cell elongation, and the abscission or even disappearance of lateral roots and root hairs [9], leading to poor root development and atrophy. The main manifestations of aluminum poisoning in plant shoots are that young leaves become smaller and yellow, and photosynthesis is weakened. Experiments have shown that the increase of aluminum concentration can significantly inhibit the relative expansion of the primary root of *Brassica napus* L. By competing for the binding sites of cations, aluminum binds to the membrane surface of root tip cells and the core of the cell wall [10], inhibiting their growth and division, continuously affecting the absorption of water, nutrients, minerals and other substances in the root system, and destroying plant homeostasis. In addition, activated aluminum can reduce the metabolic activity of enzyme reactions, stomatal conductance, etc., and reduce the programmed cell death. A large amount of enriched aluminum also induces the generation of reactive oxygen species (ROS), which leads to membrane lipid peroxidation and the reduction of peroxidase activity, and further inhibits the ion movement. This can cause oxidative loads of lipids, proteins, etc., and lead to the destruction of cell membranes, thereby weakening the resistance of plants to stress [11].

2.2.2. Stress Effects of Aluminum on Jerusalem Artichoke

In recent years, with the acidification of soil, the content of Al^{3+} with phytotoxicity has increased rapidly. The growth and development of *Helianthus tuberosus L.* in soil with high aluminum ion content [12], especially the elongation of root system, is significantly inhibited, which is mainly manifested as the destruction of cell structure, the enhancement of cell membrane lipid peroxidation, and the production of a large number of reactive oxygen species and the reduction of root hair due to the significant reduction of superoxide dismutase (SOD) and peroxidase (POD) content. Root and cap abscission. Excessive reactive aluminum can lead to self-toxic effect. When Jerusalem arum is exposed to excessive reactive aluminum, chlorophyll content and chlorophyll fluorescence characteristics will decrease, stomatal conductance will decrease, and CO_2 assimilation ability will weaken, which will affect the generation of photosynthetic intermediates and lead to the decline of photosynthesis. In addition, respiration, osmoregulation and soluble sugar content of Jerusalem arum will be affected [13], mineral nutrient metabolism will be inhibited [11], and the damage degree of leaf cell structure will be aggravated, thus affecting plant growth and development.

2.3. Corresponding Countermeasures of Plant Resistance to Aluminum Stress

At present, acid soils are widely distributed in the world, and their treatment is difficult and costly. Therefore, the use of plants to absorb Al^{3+} in soil is the preferred way to effectively reduce aluminum toxicity. This approach, known as the plant Al tolerance mechanism, can be reduced in the soil by selecting plant species that are able to tolerate Al Toxic effects of reactive aluminum on plants, thereby improving plant growth and increasing yield. This method can improve the texture of acidic soil, and is relatively economical and sustainable. In terms of this method, it is the key to enhancing the aluminum tolerance of plants, among which the accumulation and secretion of organic acids in roots is one of the important mechanisms of aluminum tolerance in plants. In addition, some exogenous substances can also be applied to enhance the resistance, such as phosphorus, which can promote the differentiation and growth of plant cells and reduce the total aluminum content and monocytic aluminum content in roots. Exogenous salicylic acid and exogenous nitrogen oxide (NO) can enhance the resistance of Jerusalem artijac to aluminum toxicity by improving the activity of antioxidant enzymes and photosynthetic efficiency. In recent years, the mitigation effect of boron, which is similar to calcium, on Al toxicity in plants has been widely concerned.

3. Boron-Aluminum Interaction

The symptoms of boron deficiency in plants mainly occur in areas with heavy rainfall and acidic soil ($pH \leq 5$), so areas with severe aluminum poisoning are generally accompanied by boron deficiency. Therefore, Blevins [14] pointed out that both inhibit plant growth. In addition, there is evidence that there is a certain interaction between aluminum and boron in plants [15]. In soil, boron is mainly absorbed by plant roots in the form of boric acid, while Al is absorbed by plants in the form of aluminate $Al(OH)_3$. The structure of $Al(OH)_3$ aluminate is similar to boric acid ($B(OH)_3$) [14]. Both boron and aluminum are involved in the structure of plant cell wall [16], and both act at the root tip. The symptoms of boron deficiency are similar to those of aluminum toxicity, and boron content and plant species can also affect the toxicity of aluminum to plants [14]. It has been reported that boron alleviates Al toxicity by changing the absorption pattern of Al and other nutrients, thus reducing the toxicity of Al to plant growth [17]. In view of the various relationships between B and Al, it is particularly important to explore the mitigation mechanism of B on Al toxicity. The study of Yang [18] in soybean showed that under low Al (2 mM) stress, boron could significantly improve the growth characteristics including root length, but under 5 mM Al stress, the inhibition of root length was not alleviated by the presence of boron, indicating that boron not only acted on plants, but had some interaction with aluminum.

4. Exploration of the Regulation of Boron on Plant Physiology

4.1. Effects of Boron on Plant Physiology and Biochemistry

Boron is a non-plant structural element, which is not easy to move in plants, and its absorption is mainly affected by transpiration. The effects of boron on plant physiology and biochemistry can be divided into four categories: one is the effect of boron on carbohydrate transport and nitrogen metabolism. Boron can promote the synthesis and efflux of sucrose and regulate the metabolism of glucose. B is directly or indirectly involved in the processes of pollen germination, pollen tube elongation and plant insemination, which is ultimately manifested as the high or low fruit set rate. The third is related to the accumulation of phenols and the metabolism of some hormones. Boron can reduce the oxidation of phenols in plants and inhibit IAA oxidase system. In the state of boron deficiency, the oxidation system is disordered, the glycolysis pathway of glucose is inhibited, and the pentose phosphate pathway is entered, and phenolic compounds are accumulated. IAA, ethylene and other growth hormones in vascular bundle cells of green plants, which promote fruit ripening, increase and fruit abscision. The fourth is the effect of boron on the content of mineral nutrients in plants.

Boron does not directly participate in enzyme synthesis or chelate with other organic compounds, but plays an irreplaceable role in plant cell wall. Studies have shown that boron is easy to complexate in plant cell wall and forms a stable complex (BPC) with pectin polysaccharide rhamnogalturonic acid II, which enhances the mechanical strength and elasticity of plant cell wall. Plants require the greatest amount of boron during the vegetative and reproductive growth phases. Boron deficiency in plants is generally manifested as underdeveloped roots with short and thick root morphology [19], swollen stems, shedding of apical young parts, fading of young leaves, and damage of old leaves [20], and short and slow growth of plants. Boron deficiency during the breeding period usually leads to a decrease in crop quality and crop yield [21]. Plant root tips are very sensitive to changes in boron concentration, which will generally lead to deformation and damage of internal organelles [22] [23], manifested as green loss, scorching-off and shedding of old leaves, and gradually new leaves also show the same symptoms. In the parts of the plant with vigorous metabolism, it is easy to cause the necrosis of the meristematic tissue, the enrichment of boron in other simple tissues, and the failure of fruiting [21] [24].

4.2. Boron Alleviates Al Toxicity by Regulating the External Repulsion Mechanism

4.2.1. Boron Stimulates the Secretion of Organic Acid Chelated Al^{3+} in Root Cells

Groundbreaking physiological studies on plants have shown that there is a clear relationship between aluminum toxicity resistance and the level of aluminum-dependent organic acid release. In particular, the amount of exogenous boron, malic acid, and oxalic acid exudation in roots determines aluminum tolerance in plants resistance. The effect of boron on the change of organic acid content under Al stress has long been studied. Tang Ning found that under aluminum stress, the exogenous boron content in roots increased significantly under 10 and 25 μmol/L boron treatment. Yang [25] also confirmed that although abundant enzymes in roots were involved in organic acid metabolism under high boron treatment, organic acid metabolism was not the main mechanism of boron induced reduction of aluminum toxicity.

4.2.2. Boron Stimulates the Secretion of Organic Acid Chelated Al^{3+} in Root Cells

The change of pH value in the rhizosphere or nutrient solution has an important impact on the availability or solubility of nutrients [26], and rhizosphere pH largely affects the presence and solubility of aluminum in soil and other media. Maintaining a higher rhizosphere pH can reduce the solubility of aluminum and alleviate its toxicity. Therefore, the change of pH in the rhizosphere can be used as an important indicator to evaluate the aluminum tolerance of plants [27]. In the study of aluminum-resistant Arabidopsis mutants, it was found that the application of exogenous boron caused the extracellular H^+ to enter the cells, which increased the pH around the root cap and reduced the solubility of Al^{3+}, thereby reducing the Al^{3+} activity around the root tip and improving the aluminum tolerance of the plant [28]. Intracellular changes in root surface, intracellular and cytoplasmic pH may reduce Al absorption by roots or attenuate Al toxicity in plants, thereby reducing Al induced ROS accumulation in roots. Boron and aluminum have different regulation effects on the pH of different root zones in the root tip. Boron application can reduce the damage of aluminum on plants by increasing the pH of root surface in the root transition zone.

4.2.3. Boron Stimulates the Secretion of Organic Acid Chelated Al^{3+} in Root Cells

Pectin in the root cell wall acts as the main binding site for Al^{3+} [29], which can cause toxicity to the plant. At present, Riaz [30] showed that the higher the pectin content and methyl esterification in the apical cell wall, the higher the aluminum binding. Yan [31] found that boron could reduce the uronic acid content of pectin in the cell wall and increase the methyl esterification degree of alkali-soluble pectin, improve the binding of boron to cell wall RG-II, and reduce the content of carboxyl group in pectin and the binding site of Al^{3+} in the cell wall, so as to reduce the accumulation of aluminum in the cell wall and alleviate its toxicity to citrus seedlings. Under the condition of boron addition, the cellulose content in the root cell wall decreases and the crystallinity increases, thereby improving the rigidity and extensibility of the cell wall and maintaining the normal growth of the root system [31]. In addition, the addition of boron in the case of aluminum toxicity can reduce the disordered distribution of homo-galacturonic acid (HG, a cell wall structural component), thereby enhancing the aluminum tolerance of citrus [32].

4.3. Boron Alleviates Al Toxicity by Regulating Internal Tolerance Mechanisms

4.3.1. Boron Regulates Antioxidant Enzyme System and Antioxidant System to Alleviate Al Toxicity

Under aluminum stress, a large number of reactive oxygen species (ROS) will be produced in plants, which will cause strong toxic effects on plant cell development. Boron can regulate the antioxidant enzyme system and antioxidant system in plants to remove the accumulated reactive oxygen species and improve the tolerance of plants to aluminum. For example, boron can regulate the activities of superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) to eliminate the accumulation of reactive oxygen species in roots induced by aluminum stress [33] [34]. In addition, boron addition under aluminum stress can reduce the content of raw materials in the synthesis pathway of ascorbic acid (AsA) in roots, thereby reducing the content of AsA [35]. At the same time, boron addition also increased glutathione (GSH) content and regulated enzyme activities related to AsA-GSH cycle [35], which reduced the aluminum-induced oxidative stress in plant roots.

4.3.2. Boron Attenuates Al Toxicity by Compartmental Intracellular Al^{3+} in Plants

Al^{3+} entering cells can stored in vacuoles, which is an effective way to alleviate aluminum toxicity in plants [36]. Zhu [37] found in the study of rice roots that under Al stress, boron addition could reduce the expression of OsNRAT I gene (responsible for the transport from the outside of the cell to the cytoplasm) induced by Al, that is, inhibit the absorption of Al by root tip cells. At the same time, the expression of OsALS I gene in the root system is increased, so that the Al^{3+} in the cytoplasm is isolated in the vacuole and the level of aluminum toxicity is reduced [37].

4.3.3. Boron Improves Al Tolerance by Regulating Plant Hormones (Auxin)

As signaling molecules, plant hormones play an important role in responding to aluminum stress. Several studies have reported that the effect of boron on auxin metabolism in plants varies according to plant species and organs [38] [39]. The study on root tip of pea found that under aluminum stress, boron can promote the polar transport of auxin and increase the content of auxin in the transition zone. More importantly, boron can also promote the absorption and sensing of auxin by cells under aluminum stress, alleviate the toxicity of aluminum to the plant, and thus maintain the elongation of root tip.

5. Effects of Other Exogenous Substances on Plants under Al Stress

5.1. Salicylic Acid

The results showed that exogenous SA could effectively alleviate aluminum stress and enhance photosynthesis of Jerusalem artijac plants. Exogenous SA could significantly improve the activity of antioxidant enzyme system, reduce the production rate of MDA and O^{2-}, and alleviate the damage caused by aluminum poisoning. Exogenous SA could promote proline accumulation in Jerusalem artichoke seedlings under dislocation stress. These results suggested that exogenous SA could alleviate Al stress and improve Al tolerance of Jerusalem artijac.

5.2. Citric Acid

The results showed that exogenous SA could effectively alleviate aluminum stress and CA can activate a series of physiological reactions in plants, effectively stimulate antioxidant enzymes, remove excess reactive oxygen species, and improve the antioxidant capacity of Jerusalem potato, so that it can better adapt to the aluminum toxic environment. The application of exogenous CA could improve Gs and Tr to a certain extent, thus alleviating the adverse effects of aluminum poisoning on photosynthesis of Jerusalem artichoke. Exogenous CA can maintain the genetic stability of cells in vivo under aluminum stress. The application of CA could alleviate Al toxicity by chelating cations and regulating the transport of nutrients in Jerusalem artichoke, so as to achieve the homeostasis of nutrients in the plant. These results indicate that exogenous CA can alleviate Al stress and improve the Al tolerance of Jerusalem artichots.

6. Prospect

Aluminum toxicity has become one of the key factors limiting plant growth and crop production in acidic soil areas. How to solve a series of ecological problems caused by aluminum and acid pollution has gradually become a research hotspot. As an important cash crop in China, *Helianthus tuberosus* has great value in the field of drug research and food development. As a typical bioremediation plant, it has a strong ability to repair contaminated soil, which can greatly alleviate the problem of aluminum pollution in soil. However, boron can alleviate plant aluminum toxicity by inducing the secretion of organic acids in roots, reducing the binding of aluminum to carboxyl groups in the cell wall, regulating the pH of root surface and cells, changing the absorption and transport of aluminum ions, and regulating plant antioxidant enzymes and antioxidant systems. Improving plant aluminum tolerance is of great significance for improving crop growth, soil health, and sustainable agricultural development, which provides a solid theoretical basis for the development of this experiment.

However, there are few studies on the effects of exogenous boron on plant physiology under stress conditions, and the results are diverse. Moreover, there are few reports on the application of exogenous boron in the resistance of Jerusalem artijac to aluminum stress. Therefore, this paper reviewed the status of aluminum pollution in soil, the basic research of plant resistance to aluminum stress, and the role of exogenous boron in alleviating aluminum stress in plants. Through systematic exploration and improvement, a series of exogenous boron content gradients were applied to the soil with different degrees of aluminum poisoning, and the effects of exogenous boron on the growth of *Helianthus tuberosus* L. under aluminum stress could be discussed and analyzed, as well as the internal physiological effects of exogenous boron on *Helianthus tuberosus* L.; this paper elucidates the damage degree of *Helianthus tuberosus* under aluminum stress and the ability of exogenous boron to enhance its resistance to aluminum from the morphological, physiological and molecular levels, and further explores the damage mechanism of aluminum on *Helianthus tuberosus* and the mitigation mechanism of exogenous boron. The aim is to find new, green, and efficient measures to enhance the aluminum tolerance of Jerusalem artichoke, apply them in practical production, achieve both ecological and economic benefits, and promote the healthy development of related industries and environmental protection efforts.

Conflicts of Interest

The authors declare no conflicts of interest.

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