



Effect of Exogenous Boron Addition on Root Restoration Efficiency of *Helianthus tuberosus* L. under Soil Aluminum Pollution

Fangyu Lyu, Xiu Wu, Mengchi Li

School of Life Sciences, Zhejiang Normal University, Jinhua, China
Email: 18157503632@163.com

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Abstract

As an important cash crop in China, Jerusalem artichoke is widely used in ecological protection, vegetable development, industrial and animal husbandry production and other directions, and has important production value. However, with the rapid development of industry and agriculture in China, a large number of acid pollution gas emissions, the excessive application of agricultural fertilizers and the unreasonable farming activities of human beings, the problem of soil acidification becomes increasingly severe, which affects the growth and development of plants and seriously restricts the cultivation and application of Jerusalem artichoke. At present, there are still shortcomings such as soil reacidification and difficult to be applied in practice on a large scale. As an essential nutrient element for plants, boron is also an important factor for plants to resist external adverse stress, and it plays a role in alleviating heavy metal stress in plants. The paper aims to provide support for the development of the industries.

Subject Areas

Plant Physiology

Keywords

Helianthus tuberosus L., Aluminum Stress, Boron-Aluminum Interaction

1. Introduction

In recent years, China's farmland soil acidification is serious, the degree of heavy metal pollution is deepening, the ecological environment and agricultural production are greatly threatened [1]. Influenced by the unnatural factors such as the

excessive application of physiological and acidic chemical fertilizers in recent decades, the emission of large amounts of acid pollution gases, and the disturbance of human planting activities, the soil alkaline ions are constantly lost, and the acidification problem is becoming increasingly serious. At present, soil acidification almost throughout the whole south, the acidification area reached 2.18 million km², accounting for about 22.7% of the national land area. This also leads to the change of aluminum from Al(OH)₃ or other insoluble form which is not toxic to plants to ionic form, forming the toxic stress effect of aluminum and affecting crop production. Aluminum stress can inhibit the normal growth of plants by various mechanisms such as destroying hormone balance, affecting stomatal conductance and reducing DNA synthesis [2], resulting in the decrease of plant photosynthesis rate, water and nutrient imbalance, and causing great harm to the stability of the ecosystem and human health [3].

Jerusalem artichoke (*Helianthus tuberosus* L.), the family Asteraceae (Asteraceae), the genus sunflower (*Helianthus* L.), is a perennial herb, origin located in the Great Lakes region of North America, adapted to a variety of climatic conditions. It has the dual effect of both medicine and food, and also plays an important role in the preparation of chemicals and microbial fermentation, and also has the energy value of biomass, so it is widely used in human life. As one of the planting areas of Jerusalem artichoke in Zhejiang Province, as it is also an area greatly affected by aluminum toxicity, it is urgent to study the anti-aluminum toxin mechanism of Jerusalem artichoke and find the methods to alleviate the stress. It accounts for approximately 21% of the national Jerusalem artichoke planting area. However, there are still the disadvantages of plant treatment technology, such as soil reacidification and difficult to be applied in practice on a large scale. At present, it is found that boron (B) can alleviate the adverse effects of aluminum stress on plants by participating in external aluminum exclusion and internal aluminum resistance. However, there is no report on the physiological response of root and DNA damage in boron aluminum interaction. Therefore, it is of great theoretical and practical significance to explore the optimal concentration of boron aluminum interaction and the relieving effect of exogenous boron addition on the physiological damage of Jerusalem artichoke aluminum stress, to improve the production quality of Jerusalem artichoke and expand its planting range. This paper summarizes the value and biological characteristics of Jerusalem artichoke, the current situation of plant aluminum stress, the physiological regulation of boron under stress and the regulation mechanism of boron-aluminum interaction, explores the mitigation effect of boron and the comprehensive utilization prospect, to provide theoretical guidance and technical support to improve the normal growth of chrysanthemum taro under aluminum stress, and also to reduce the damage of soil acidification and aluminum toxicity to other plants.

2. Biological Properties and Value of Jerusalem Artichoke

Jerusalem artichoke for chrysanthemum family (Asteraceae) sunflower (*Helian-*

thus L.) perennial root herbs, also known as artiker, devil ginger, its rich in inulin, can be used as a biological fermentation, ethanol production and a good source of oil, with heat cool blood and water dehumidification effect, is an important economic crops in China, has a broad application prospect of [4]. Jerusalem artichoke has high ecological adaptability, drought tolerance, cold tolerance and salt and alkali tolerance, and strong regeneration ability. The seeds fall on the ground and can reproduce everywhere, and its underground tuber can also reproduce asexually. It is a kind of cultivated plant with low requirements for living environment and diverse functions. Jerusalem artichoke has strong adaptability to soil, can grow in $EC_e < 30$ d/m, it also has certain resistance under metal stress, metal stress, and low concentration of single acid, single aluminum stress makes its superoxide dismutase (Superoxide Dismutase, SOD) activity increased, antioxidant enzyme activity coordinated, make it has strong stress resistance. In recent years, the research on Jerusalem artichoke mainly focuses on germplasm resources, kinship and salinity stress, while there are few studies on acid and aluminum resistance of Jerusalem artichoke.

3. The Dynamic Study of Aluminum Pollution

3.1. Soil Aluminum Pollution and Its Current Situation

Heavy metal pollution in soil has attracted wide attention due to its characteristics of toxicity, accumulation and easy access to the food chain. When the soil acidity reaches a certain degree, aluminum toxicity becomes the most important factor affecting crop growth. When the soil pH value is lower than 5.5 [5]. In the soluble form is dissolved by Al^{3+} , $Al(OH)^{2+}$ can be absorbed by the plant root, and the enrichment of a large amount of Al^{3+} usually leads to the symptoms of aluminum poisoning, which affects the development and normal growth of the plant body.

Acid rain area accounted for about 30% of the land area, central China, south China, southwest and northeast parts is still acid rain pollution area, in recent years, due to the acid deposition and ammonium nitrogen excessive application, farmland soil present accelerated acidification trend, aluminum poison become acid soil limit one of the main obstacles to crop growth. With the expansion and intensity of soil acidification, Al^{3+} activity in soil is also increasing in, while aluminum forming ionic state will have toxic effects on the environment and crops, and then pose a great threat to human health problems [6]. Al^{3+} has toxic effects on both aboveground and underground parts of plants, which will force the decrease of chlorophyll content, stomatal conductivity, respiratory resistance, concentration of reactive oxygen species, antioxidant enzyme activity, osmotic destruction, and root vitality, thus disturbing the secondary metabolic effect [7]. If plants absorb active aluminium for a long time and in excessive amounts, their root systems' ability to absorb nutrients and water will be inhibited, and they may even die. Through the enrichment effect in the food chain, it will pose a threat to the health of animals and humans.

3.2. Physiological Response of Plants to Aluminum Stress

3.2.1. Inhibition of Plant Photosynthesis by Aluminum

Under Al^{3+} stress, the chloroplast membrane was destroyed, ATP enzyme, glyceraldehyde-3-phosphate dehydrogenase, 1,5-bisphosphol and 5-phosphol glucokinase were inhibited, and the fixed amount of CO_2 reduced [8], resulting in a significant decrease in chlorophyll and carotenoid mass fraction of [9]. It affects the absorption and utilization of light energy by the chloroplast, hinders the photosynthetic electron transport, reduces the photosynthetic rate, and reduces the final plant dry matter and yield.

Al^{3+} may make the cell structure of plant leaves changes, including the stomatal defend cells produced certain harm, indirectly lead to plant leaf stomatal resistance increases, reducing stomatal conductivity, defend CO_2 between cells, the concentration, leaves for photosynthesis CO_2 also reduced, photosynthesis by inhibiting [10]. The study showed that under aluminum stress, the net leaf photosynthesis rate (P_n) decreased, CO_2 saturation point decreased, and CO_2 compensation point increased [11].

Chlorophyll fluorescence, emitted from the plant body, with rich photosynthesis information, can be applied to the study of plant stress degree [12]. Chlorophyll fluorescence analysis technology is a kind of fast, efficient, accurate and no damage determination of plant leaf fluorescence parameters to reflect the plant photosynthesis process dynamic change technology, in the determination of leaf photosynthesis in light system of light energy absorption, transmission, dissipation, distribution has a unique role, reflects the characteristics of “internality” [13]. With the increase of Al^{3+} concentration, the initial fluorescence (F_0), maximum fluorescence (F_m) and variable fluorescence (F_v) all showed a trend of decrease and then increase, and all lower than CK, indicating that the photosynthetic capacity of the leaves under aluminum stress was inhibited.

3.2.2. Effect of Aluminum Stress on Plant Antioxidant Enzyme Activity

ROS is an important signaling molecule in plant stress response, and ROS over-accumulates in plants under aluminum stress. The plant antioxidant enzyme system is mainly composed of superoxide dismutase (SOD), peroxidase (Peroxidase, POD) and catalase (Catalases, CAT), which can clear ROS and protect the structural stability of the cell membrane. Among them, SOD cleared $\cdot\text{O}^{2-}$, and POD and CAT remove H_2O_2 [14]. Under stress conditions, the cell homeostasis in plants is broken, and the production and removal of ROS are unbalanced, which makes the cell antioxidant system overload, producing oxidative stress, leading to enzyme inactivation and other phenomena [15]. However, plants can cooperate with SOD, POD and CAT to maintain the reactive oxygen species at a low level, slowing down or defending against aluminum stress to a certain extent. Studies have pointed out that aluminum stress can lead to the increase of antioxidant enzyme activity in plants, and can remove excess ROS in a short period of time. However, with the extension of aluminum stress time and the deepening of the stress degree, this protective function gradually decreases or even collapses [16].

3.2.3. Effects of Aluminum Stress on Plant Metabolism and Nutrient Transport

Aluminum stress has profound effects on plant metabolism and nutrient transport. As the most abundant metal element in the earth's crust, aluminum increases its solubility in acidic soil and produces ionic Al^{3+} , which is toxic to plants. These ions can inhibit the growth of plant roots, interfere with the absorption and metabolic process of nutrients and water, resulting in changes in a variety of metabolic substances in plants. Aluminum stress significantly affects plant photosynthesis and respiration, resulting in decreased chlorophyll content and decreased photosynthesis rate, which then affects the accumulation of plant biomass. At the same time, aluminum can also interfere with the activity of cell wall-modifying enzymes, affecting the malleability and plasticity of the cell wall, thereby inhibiting cell growth. In terms of plant hormone regulation, aluminum stress can affect the synthesis and signaling of hormones such as auxin, ethylene, and cytokinin, and then affect plant growth and development. Organic acids not only exist in plant cells, but also can be excreted through metabolic process. A large number of studies have confirmed that the exudation of organic acid anions is one of the effective ways to overcome the growth inhibition caused by aluminum toxicity [17]. Plants secrete organic acid anions such as citrate, malate and oxalic acid through the root tip, and chelate with toxic aluminum to form a stable non-phytotoxic complex, thus achieving the purpose of alleviating plant aluminum toxicity. Organic acids can not only chelate Al^{3+} in the outside, but also seal Al^{3+} into the vacuole inside the cell, thus improving the aluminum-resistance of plants [18].

3.2.4. Effect of Aluminum Stress on Plant DNA Damage

DNA is a carrier of genetic information and plays an essential role in the development and normal operation of living organisms. Both exogenous factors with genotoxic effects or endogenous factors formed during natural cell metabolism can cause DNA damage, and aluminum has high affinity for DNA. Through molecular sieve chromatography analysis of chrysanthemum plant, we concluded that the preferential binding of Al^{3+} to DNA in nucleic acids would improve its double helix stability and reduce the speed of DNA synthesis [19]. Metal ions induce reactive oxygen species produced by plant cells, which can damage DNA by breaking nucleic acid chains and modifying bases. In the experiments under aluminum stress, tail length, tail DNA content and tail distance were significantly increased, and DNA damage was significantly [20]. When the pH value is lower than 5.0, acid aluminum can inhibit the root DNA synthesis of citrus (*Citrus reticulata* Blanco) seedlings. In addition, exogenous aluminum stress leads to nucleotide loss or increase in primer binding sites, which ultimately affects gene mapping changes, thus exacerbating the damage caused by aluminum on plants [21].

3.3. Corresponding Countermeasures to Alleviate Plant Aluminum Toxicity

Recently, the effects of plant growth regulators under aluminum stress have been

increasingly explored, and they play an important role in maintaining plant morphology, stomatal closure, flowering and growth. Application of exogenous plant growth regulators can inhibit the production of ROS, H₂O₂ and MDA, and improve the activity of plant antioxidant enzymes, proline content, etc. However, the study of boron-aluminum interaction to alleviate the aluminum toxicity of plants has not been reported [22]. Boron is an essential trace element for higher plants and can enhance plant tolerance in stress environments. It was found that exogenous boron could alleviate the aluminum-induced oxidative damage in citrus (*Citrus reticulata* Blanco), rape (*Brassica napus* L.) and rice (*Oryza sativa* L.) by enhancing the rhizosphere pH, and crosslinking the plum galacturonate glycan II (RG-II) to stabilize the cell wall and reduce the aluminum accumulation of pea (*Pisum sativum* L.) [23].

4. Regulation of Plant Resistance by Boron Addition

4.1. Biological Characteristics and Physiological Functions of Boron

Boron is an essential trace element for plant growth, which plays an irreplaceable role in promoting the formation of cell wall, sugar synthesis and transport, protein synthesis and gene expression. It can effectively promote plant metabolism and improve plant stress resistance, thus promoting its growth and development [24]. Leafar boron application can improve the root surface of pea seedlings pH to weaken the degree of aluminum toxicity. Boron can also remove the accumulated reactive oxygen species in the plant by regulating the antioxidant enzyme system and antioxidant system to improve the aluminum resistance.

Boron can reduce the accumulation of Al³⁺ and promote the transfer of aluminum to the ground, thus alleviating the inhibitory effect of aluminum on auxin polar transport, regulating root surface pH, promoting root elongation, and reducing the accumulation of root tips in aluminum pea [25]. The expression pattern of plant genes is also altered under boro-aluminum interaction.

4.2. Relief Effect of Boron on Aluminum Toxicity

4.2.1. Boron Alleviates Aluminum Toxicity by Regulating the External Rejection Mechanism

Chelation of aluminum and organic acids is recognized as an important mitigation mechanism of plant aluminum toxicity. The aluminum resistance of plants is closely related to the organic acid content and exocrine ability in plants. The secretion of organic acids is localized to the root tip, and the complex of aluminum and organic acids in the rhizosphere environment cannot be taken up by the roots or transported across the membrane. Boron chelates Al³⁺ by regulating the external rejection mechanism and promoting the secretion of organic acids by the root cells, thus relieving aluminum toxicity. The exudation of organic acids such as citric acid, malate acid and oxalic acid will repel Al³⁺ outside the apical cells and prevent them from entering the root tip, thus reducing the binding of aluminum

and cell wall sites and reducing aluminum toxicity. Tang Ning [26] pointed out that under aluminum stress, the content of citrate in the roots increased significantly under 10 and 25 $\mu\text{mol/L}$ boron treatment, while the content of malic acid in the root showed a negative correlation with the boron concentration. Boron can also reduce the damage of aluminum to the plant by changing the absorption mode of aluminum and other nutrients on the biological membrane, reducing the fluidity of the membrane and changing its permeability. At the same time, in the study of citrus stock, add boron can increase aluminum stress plasma membrane H^+ -ATPase activity, promote H^+ efflux, reduce plasma pH and further reduce the pectin methylesterase (Power Management Event, PME) activity, increase the pectin methyl esterification, thus inhibit pectin hydrolysis of more carboxyl group, thus reduce aluminum content, eventually alleviate the toxicity of aluminum on the plant [27]. Li [28] found that boron enhanced the activity of PME enzymes to promote the demethylation process of pectin. This increases the proportion of uronic acid residues in the long chain of alkali-soluble pectin relative to the chelate soluble pectin, thus promoting the dissociation of the aluminum ions that were originally bound to the chelate soluble pectin and rebound to the alkali-soluble pectin. Finally, through the cross-linking of boron and RG-II (a special pectin structure), the aluminum ions are firmly fixed in the alkali-soluble pectin, thus effectively preventing the further invasion of the aluminum ions into the cytoplasm.

4.2.2. Boron Alleviates Aluminum Toxicity by Regulating the Internal Tolerance Mechanism

When subjected to stress, their own defense system regulates the content of antioxidants by increasing the activity of antioxidant enzymes to improve their aluminum tolerance. Boron can induce the association between oxidative stress, antioxidant system, and polyamine metabolism, improve the growth capacity, relative water content, green pigment, photosynthetic activity, and membrane stability index, and further enhance the activity of antioxidant enzymes, osmoregulatory substances, leaf polyamine concentration, and hydrogen [29]. When rapeseed is poisoned by aluminum, the SOD, POD and CAT enzyme activities in rapeseed are improved to remove the reactive oxygen species accumulated in the body and improve the aluminum resistance of plants [30]. Ascorbic acid and glutathione as a common antioxidant, in the rice after aluminum treatment ascorbic acid and glutathione content have increased significantly, in exogenous AsA by regulating antioxidant enzyme activity, improve the osmoregulatory material content and antioxidant content to reduce the accumulation of H_2O_2 , thus alleviate the aluminum stress rice plasma membrane oxidation, enhance the aluminum resistance of rice [31]. Boron is related to the accumulation of phenolic substances and the metabolism of some hormones, which can reduce the oxidation amount of phenolic substances in plants and inhibit the IAA oxidase system, which plays an important role in the oxidative system. In addition, boron can also change the components of the cell wall and reduce the polysaccharide content in the cell wall to reduce the

accumulation of aluminum in the cell wall. Aluminum toxicity leads to the epitope change of galacturonic acid (HG) in the cell wall of trefoil orange root. Boron treatment can effectively reduce the disordered distribution of HG to protect the cell wall structure. The DNA damage response mechanism of *Arabidopsis thaliana* was activated under aluminum stress, and MAC complex and 26S proteasome were involved in DNA damage repair. The supply of boron can regulate the activity of these complexes and proteasomes, promote the repair of DNA damage, and maintain the normal growth and development of *Arabidopsis*.

5. Summary and Outlook

In recent years, climate change, excessive fertilization, unreasonable irrigation and other reasons make soil acidification more and more serious, and the effective form of aluminum increases, thus forming aluminum poison harm plants. Under aluminum stress, plant metabolism is disturbed, which changes physiological traits such as biomass and leaf area, weakens enzyme vitality, and decreases the ability to absorb and utilize nutrients in the soil, leading to a serious decline in the quality and yield of grain, vegetables and fruits. As an important edible crop, Jerusalem artichoke has excellent production and economic value, but in the acidic environment, the aluminum-sensitive biological characteristics make it suffer from the serious threat of aluminum toxicity in the process of growth and development. As an essential trace element in plants, researchers have proved that boron can alleviate the adverse effects of aluminum stress on plants and enhance the stress resistance of plants by participating in the external aluminum resistance and internal aluminum resistance.

Based on the above background and content, it is speculated that boron addition significantly improves the root repair efficiency of Jerusalem artichoke under aluminum pollution of farmland soil. This project plans to select aluminum resistant Shijiazhuang Jerusalem artichoke and aluminum sensitive Heze Jerusalem artichoke as experimental materials, Reasonable establishment of the aluminum concentration gradient, Different concentration gradient of boron was applied to the seedlings, By analyzing the dynamic changes of plant height, root length, MDA content, antioxidant enzyme activity, chlorophyll content, superoxide anion and DNA damage, root vitality, root tip aluminum ion content, organic acid and other indicators to comprehensively assess the degree of Jerusalem artichoke stress from four perspectives: morphology, physiology, molecule and photosynthesis, Lay the foundation for exploring the mitigation effect and determining the optimal boron application concentration, In order to improve the yield and quality of Jerusalem artichoke, Promoting the better development of agriculture, To achieve farmers' income generation and provide horizontal thinking for other crops to resist aluminum stress adversity, It is of far-reaching significance to promoting sustainable ecological and economic development, To further ensure the sustainable development of grain agriculture in China, It is of great significance to give full play to the role of Jerusalem artichoke in the national agricultural development.

Conflicts of Interest

The authors declare no conflicts of interest.

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